USDA

United States
Department of
Agriculture

Forest Service

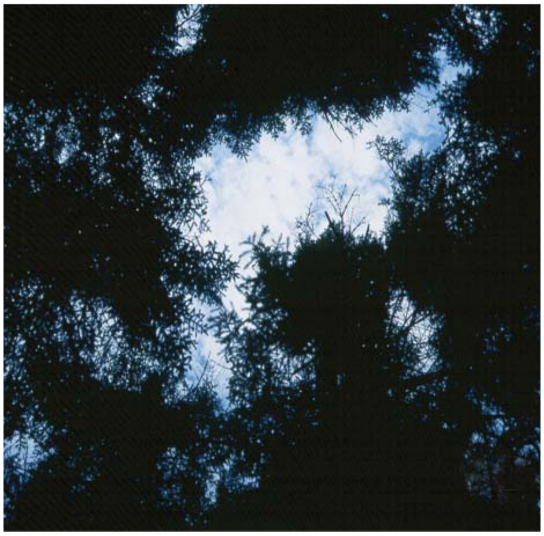
**Northern
Research Station**

General Technical
Report NRS-80

Assessment of Nitrogen Deposition Effects and Empirical Critical Loads of Nitrogen for Ecoregions of the United States

L.H. Pardo, M.J. Robin-Abbott, C.T. Driscoll, editors






Abstract

Human activity in the last century has led to a substantial increase in nitrogen (N) emissions and deposition. This N deposition has reached a level that has caused or is likely to cause alterations to the structure and function of many ecosystems across the United States. One approach for quantifying the level of pollution that would be harmful to ecosystems is the critical loads approach. The critical load is defined as the level of a pollutant below which no detrimental ecological effect occurs over the long term according to present knowledge.

The objective of this project was to synthesize current research relating atmospheric N deposition to effects on terrestrial and aquatic ecosystems in the United States and to identify empirical critical loads for atmospheric N deposition. The receptors that we evaluated included freshwater diatoms, mycorrhizal fungi and other soil microbes, lichens, herbaceous plants, shrubs, and trees. The main responses reported fell into two categories: (1) biogeochemical, and (2) individual species, population, and community responses.

The range of critical loads for nutrient N reported for U.S. ecoregions, inland surface waters, and freshwater wetlands is 1 to 39 kg N ha^{-1} y^{-1}. This broad range spans the range of N deposition observed over most of the country. The empirical critical loads for N tend to increase in the following sequence for different life forms: diatoms, lichens and bryophytes, mycorrhizal fungi, herbaceous plants and shrubs, trees.

The critical loads approach is an ecosystem assessment tool with great potential to simplify complex scientific information and effectively communicate with the policy community and the public. This synthesis represents the first comprehensive assessment of empirical critical loads of N for ecoregions across the United States.

Cover Photos

Front, left to right, top: elevated nitrogen inputs to a prairie grassland in Minnesota (control) resulted in a decrease in species richness and an increase in invasive grasses (N addition). Photos by David Tilman, University of Minnesota, used with permission.

Front, left to right, bottom: elevated nitrogen inputs to a high elevation spruce fir forest (control) in Vermont resulted in decreased growth and increased mortality (high treatment). Photos by Linda Pardo, U.S. Forest Service.

Back top: The endangered checkerspot butterfly (*Euphydryas editha bayensis*). Photo by Stuart Weiss, used with permission.

Back bottom: The threatened purple pitcher plant (*Sarracenia purpurea* L.). Photo by Lingli Liu, used with permission.

Manuscript received for publication 25 February 2010

Published by:

U.S. FOREST SERVICE
11 CAMPUS BLVD SUITE 200
NEWTOWN SQUARE PA 19073

May 2011

For additional copies:

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Acknowledgments

This project was funded, in part, by the U.S. Environmental Protection Agency's Clean Air Markets Division. Initial work on this project was funded by the U.S. Forest Service Air Resource Management program. Funding was provided by the UCR Center for Conservation Biology and NSF grant DEB 04-21530. We appreciate the reviews of Suraj Ahuja, Allison Aldous, Mary Arthur, Jayne Belnap, John Blair, Tamara Blett, Matthew Brooks, Andrew Burton, William Currie, Daniela Cusack, Robert Edmonds, Heather Erickson, Ilka Feller, Benjamín Sánchez Gimeno, Rick Graw, Rick Haeuber, Cindy Huber, Randy Kolka, Steven Lindberg, Kathleen Lohse, Michelle Mack, Bill McDowell, Steve McNulty, Anne Mebane, Tom Meixner, John Melack, Kristi Morris, Bengt Nihlgård, Annika Nordin, Rock Ouimet, Michael Pace, Gareth Phoenix, Cindy Prescott, James Sickman, Jack Triepke, David Wedin, Trent Wickman, and Mark Williams. We would also like to thank Scott Collins, Robin Dennis, Amanda Elliot Lindsey, Ray Gomez, Robert Johnson, Duan Lei, and Bethany Zinni.

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1 INTRODUCTION

L.H. Pardo, C.T. Driscoll, C.L. Goodale

1.1 Objectives

This publication provides a scientific synthesis of the current state of research and knowledge about the response of terrestrial and aquatic ecosystems to nitrogen (N) inputs (N deposition or N additions), and, where possible, identifies critical loads for atmospheric N deposition. It also targets policy makers and resource managers who are seeking a scientific basis for making decisions about the potential broad ecological impacts of air pollution, as well as the impact of specific pollution sources on particular ecosystems.

1.2 Background

1.2.1 Historical N Deposition

Human activity in the past century has led to an exponential increase in N emissions (Galloway et al. 2003). Primary sources of anthropogenic N emissions are high temperature combustion of fossil fuels (i.e., electric power plants, motor vehicles), and the production and use of fertilizers and animal manure (Galloway et al. 2003). Deposition of N has paralleled emissions (Butler et al. 2003; US EPA 2009a, 2009b) so that, in most areas, current rates of N deposition are an order of magnitude higher than pre-industrial levels (Dentener et al. 2006, Holland et al. 1999). Pre-industrial atmospheric N deposition is thought to have been 0.4 to 0.7 kg ha^{-1} y^{-1} (Holland et al. 1999). Contemporary N deposition levels in the United States are on average one-fifth of those observed in Europe (Holland et al. 2005). Wet N deposition reported by the National Atmospheric Deposition Program (NADP) ranges from <1 to >7 kg ha^{-1} y^{-1} for 2008 (NADP 2008), and dry deposition can supply large quantities of additional N, but is far more difficult to quantify (e.g., Dentener et al. 2006). Regional maximum values can be substantially higher than the wet deposition reported by NADP. In the Northeast, maximum N deposition of 30 kg ha^{-1} y^{-1} has been reported for high elevation sites (Miller 2000); in the Southeast, deposition was modeled as high as 31 kg N ha^{-1} y^{-1} (Weathers et al. 2006); and in the Pacific Southwest, where dry deposition and fog events can represent the bulk of N deposition, mean annual N deposition of 71 kg ha^{-1} y^{-1} was reported (Fenn et al. 2008). Nitrogen deposition has increased significantly in the last decade in some regions of the United States and is projected to increase further in certain regions of the country (Lehmann et al. 2005, Nilles and Conley 2001). Estimates of N deposition are discussed in more detail in Chapter 3.

1.2.2 Effects of N deposition

The increases in atmospheric N deposition after the middle of the 20th century initially raised few concerns about detrimental ecosystem impacts. Many terrestrial ecosystems are N limited. Hence, additional N inputs could have a fertilizing effect, which was perceived as beneficial for some ecosystems. Increased tree growth due to N deposition has been demonstrated in northeastern U.S. forests (Thomas et al. 2010). However, substantial debate continues over the existence and magnitude of deposition-induced growth enhancement in forests globally (DeVries et al. 2008, Magnani et al. 2007, Nadelhoffer et al. 1999, Sutton et al. 2008). Furthermore, elevated N inputs can lead to detrimental effects on ecosystems (Nihlgård 1985), including soil and surface water acidification, plant nutrient imbalances, declines in plant health, changes in species composition, increases in invasive species, increased susceptibility to secondary stresses such as freezing, drought, and insect outbreaks, as well as eutrophication of fresh and coastal waters (Galloway et al. 2003). High concentrations of ammonia (NH_3) can be directly toxic to plants (Krupa 2003).

Nitrogen saturation can be defined as the condition when available N exceeds plant and microbial demand. Aber et al. (1989, 1998) described four stages of N saturation in forest ecosystems (Fig. 1.1): background conditions (stage 0), an initial fertilization response (stage 1), flattened response of N mineralization but increased net nitrification (stage 2), and detrimental effects on plant health and growth and general decrease

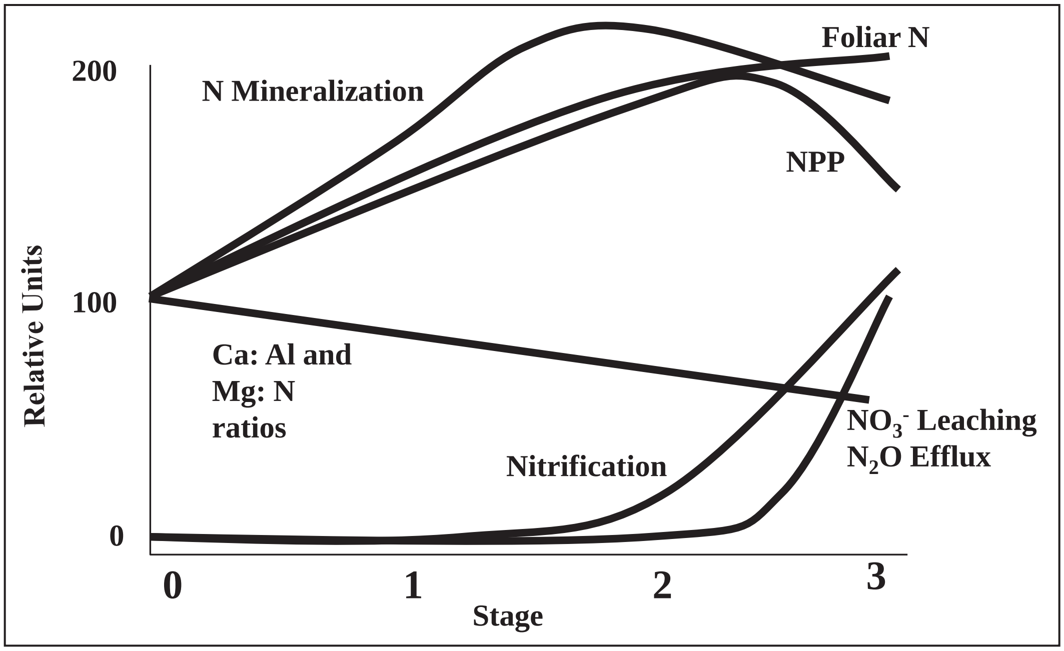

Figure 1.1—Stages of N saturation for forest ecosystems (reprinted with permission in modified format from Aber et al. 1998).

in N retention (stage 3). When vegetation is no longer N limited, but before damage is incurred, nitrate (NO_3^-) immobilization will be reduced and NO_3^- export is likely to increase gradually. The increase in NO_3^- export may occur earlier in this progression of N saturation than initially thought (Emmett 2007). Adverse consequences on plant health and growth occur in the last stage of N saturation, resulting from some combination of insufficient allocation of plant carbon to roots and mycorrhizae and soil acidification induced by NO_3^- leaching. Nutrient imbalances (e.g., elevated N:Ca or N:Mg) may also affect plant health. In addition, alterations in an ecosystem's N status may lead to increased susceptibility to secondary stresses, including freezing injury (Schaberg et al. 2002), pest outbreak, and drought (Bailey et al. 2004).

At the catchment level, N saturation is indicated by increased NO_3^- leaching, especially during the growing season (Aber et al. 2003, Stoddard 1994). Stoddard (1994) described the stages of surface water response to N saturation (Fig. 1.2).

At Stage 1, seasonal losses of NO_3^- occur during periods of hydrologic flushing (e.g., snowmelt); in stage 2, episodic NO_3^- losses remain high, and growing season losses increase as biotic demand for N is depressed; in stage 3, the base flow NO_3^- concentration becomes elevated to such an extent that seasonal patterns are no longer significant (Stoddard 1994).

Among the most significant indicators of N saturation are changes in species composition or community structure in terrestrial and aquatic ecosystems. Alterations in species composition may result from shifts in dominance of species present, for epiphytic lichens, for example (Geiser and Neitlich 2007, Jovan 2008, McCune and Geiser 2009), or increased dominance of invasive species, and may lead to significant changes in vegetation. Nitrogen deposition may affect species richness and has been implicated in dramatic declines in species richness, for example, in coastal sage scrub[1], grasslands (Stevens et al. 2004).

1.2.3 Critical Loads of N Deposition

A critical load is the level of input of a pollutant below which no harmful ecological effect occurs over the long

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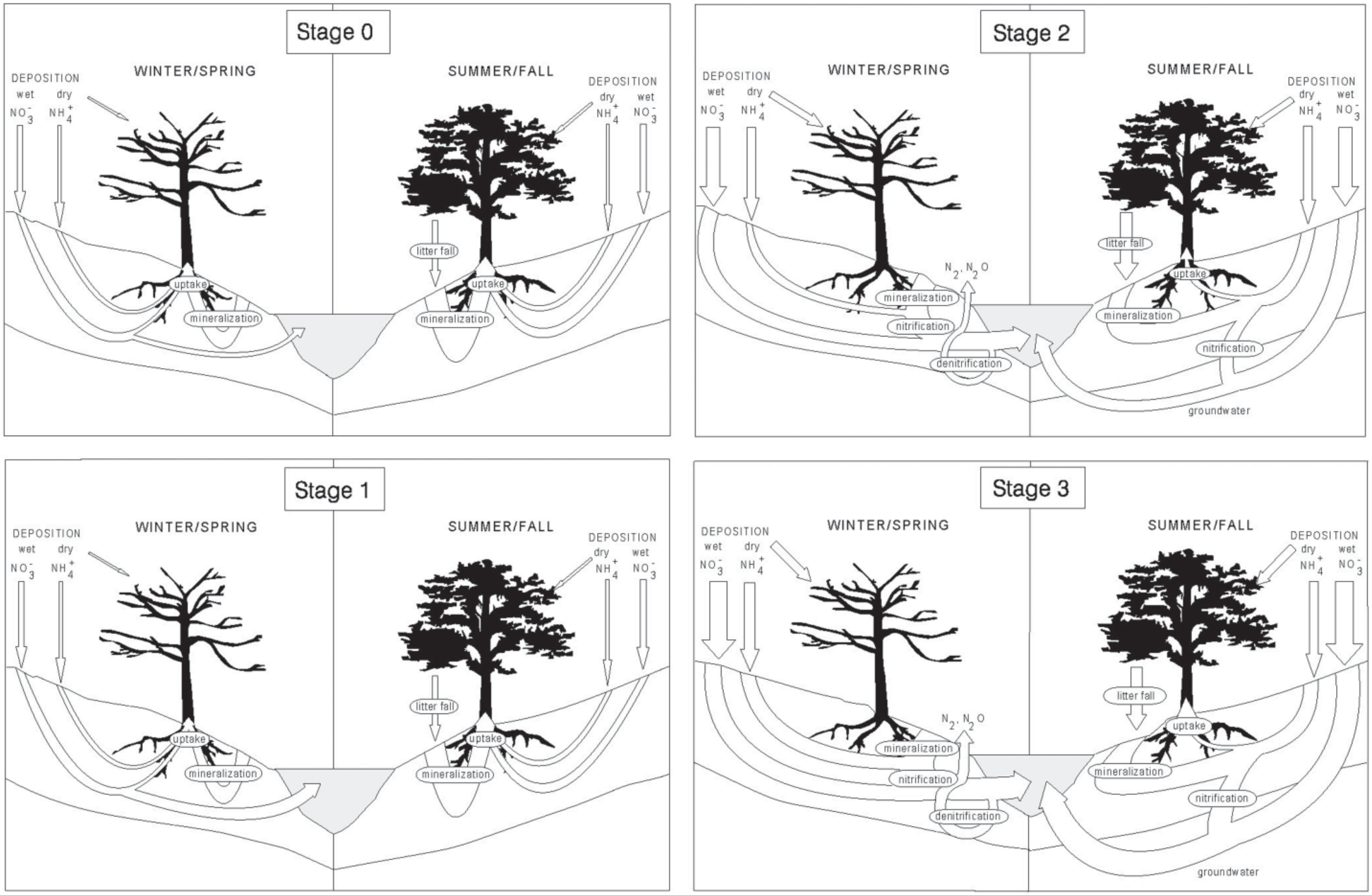

Figure 1.2—Stages of N saturation for surface water (reprinted with permission in modified format from Stoddard 1994, as published by the American Chemical Society).

term (UBA 2004). Critical loads have been defined for Europe (Posch et al. 1995, Posch et al. 2001) and have been used as a tool in the process of negotiating air pollution emission reductions in Europe. In the United States, critical loads have been calculated for specific regions (Dupont et al. 2005, Fenn et al. 2008, NEG ECP 2003, Williams and Tonnessen 2000), and are of interest to policy makers for assessing emission reduction programs and to resource managers as a tool to evaluate the potential impact of new pollution sources (Burns et al. 2008, Porter et al. 2005).

There are three main approaches for calculating critical loads: empirical, simple mass balance, and dynamic modeling approaches (Pardo 2010). Empirical approaches are based on observations of the response of an ecosystem or ecosystem component (e.g., foliage, lichens, soil) to a given, observed deposition level. Empirical critical loads are calculated using data obtained from a single site or multiple sites; generally, they are applied to similar sites where such data are not available.

Simple mass balance approaches are based on estimating the net loss or accumulation of N based on inputs and outputs. Simple mass balance methods are steady-state models that calculate the critical load of deposition to an ecosystem over the long term (i.e., one rotation in land managed for timber, 100+ years in wilderness). They are based on defining acceptable values for fluxes into and out of the ecosystem (soil N accumulation, N leaching, or acceptable/critical NO_3^- concentration in leachate).

Dynamic models use a mass balance approach expanded by incorporating internal feedbacks, such as accumulation of N in the system. Dynamic models can predict the amount of time it takes for N deposition to damage an ecosystem, as well as the amount of time necessary for recovery. Dynamic models that capture the complexity of the N cycle are currently unavailable for broad-scale use across multiple ecosystems in the United States. This review focuses on the data available to identify empirical critical loads for ecoregions of the United States.

1.3 Report Organization

This document is organized by ecoregion. The ecoregions are described in detail in Chapter 2. Issues and challenges in estimating total N deposition are described in Chapter 3. The methods are described in Chapter 4 for mycorrhizal fungi, lichens, herbaceous plants and shrubs, and forest ecosystems. For other receptors or ecosystem types, the methods are described in the individual chapters. Explanation of the response parameters and details of how the critical load was set are given in each ecoregion chapter. For each ecoregion, the ranges of responses reported are presented, and estimates for critical loads are made, where possible; the critical load values are compared to values presented for similar ecosystems types outside the United States (when possible); and the steps necessary to identify or improve critical loads estimates are described.

LITERATURE CITED

Aber, J.D.; Goodale, C.L.; Ollinger, S.V.; Smith, M.-L., Magill, A.H.; Martin, M.E.; Hallett, R.A.; Stoddard, J.L. 2003. **Is nitrogen deposition altering the nitrogen status of northeastern forests?** BioScience. 53(4): 375-389.

Aber, J.; McDowell, W.; Nadelhoffer, K.; Magill, A.; Berntson, G.; Kamakea, M.; McNulty, S.; Currie, W.; Rustad, L.; Fernandez, I. 1998. **Nitrogen saturation in temperate forest ecosystems.** BioScience. 48: 921-934.

Aber, J.D.; Nadelhoffer, K.J.; Steudler, P.; Melillo, J.M. 1989. **Nitrogen saturation in northern forest ecosystems.** BioScience. 39: 378-386.

Bailey, S.W.; Horsley, S.B.; Long, R.P.; Hallett, R.A. 2004. **Influence of edaphic factors on sugar maple nutrition and health on the Allegheny Plateau.** Soil Science Society of American Journal. 68: 243-252.

Burns, D.A.; Blett, T.; Haeuber, R.; Pardo, L.H. 2008. **Critical loads as a policy tool for protecting ecosystems from the effects of air pollutants.** Frontiers in Ecology and the Environment. 6(3): 156-159.

Butler, T.J.; Likens, G.E.; Vermeylen, F.M.; Stunder, B.J.B. 2003. **The relation between NOx emissions and precipitation NO_3- in the eastern USA. Atmospheric Environment.** 37: 2093-2104.

Dentener, F.; Drevet, J.; Stevenson, D.S.; Ellingsen, K.; Van Noije, T.; Schultz, M.g.; Atherton, C.; Bell, N.; Butler, T.; Eickhout, B.; Fiore, A.; Galloway, J.N.; Galy-Lacaux, C.; Kulshestha, U.C.; Lamarque, J.F.; Montanaro, V.; Muller, J.-F.; Rodriguez, J.; Sanderson, M.; Savage, N.; Szopa, S.; Sudo, K.; Wild, O.; Zeng, G. 2006. **Nitrogen and sulphur deposition on regional and global scales: a multi-model evaluation.** Global Biogeochemistry Cycles. 20: GB4003.

DeVries, W.; Solberg, S.; Dobbertin, M.; Sterba, H.; Laubhahn, D.; Reinds, G.J.; Nabuurs, G.-J.; Gundersen, P.; Sutton, M. 2008. **Ecologically implausible carbon response?** Nature. 451: E26-E28.

Dupont, J.; Clair, T.A.; Gagnon, C.; Jeffries, D.S.; Kahl, J.S.; Nelson, S.; Peckenham, J. 2005. **Estimation of critical loads of acidity for lakes in northeastern United States and eastern Canada.** Environmental Monitoring Assessment. 109: 275-292.

Emmett, B.A. 2007. **Nitrogen saturation of terrestrial ecosystems: some recent findings and their implications for our conceptual framework.** Water, Air, and Soil Pollution: Focus. 7: 99-109.

Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W.; Neitlich, P. 2003. **Ecological effects of nitrogen deposition in the western United States.** BioScience. 53(4): 404-420.

Fenn, M.E.; Jovan, S.; Yuan, F.; Geiser, L.; Meixner, T.; Gimeno, B.S. 2008. **Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests.** Environmental Pollution. 155: 492-511.

Galloway, J.N.; Aber, J.D.; Erisman, J.W.; Seitzinger, S.P.; Howarth, R.W.; Cowling, E.B.; Cosby, B.J. 2003. **The nitrogen cascade.** BioScience. 53: 341-356.

Geiser, L.H.; Neitlich, P.N. 2007. **Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens.** Environmental Pollution. 145: 203-218.

Holland, E.A.; Braswell, B.H.; Sulzman, J.M.; Lamarque, J.-F. 2005. **Nitrogen deposition onto the United States and Western Europe: synthesis of observation and models.** Ecological Applications. 15: 38-57.

Holland, E.A.; Dentener, F.J.; Braswell, B.H.; Sulzman, J.M. 1999. **Contemporary and pre-industrial global reactive nitrogen budgets.** Biogeochemistry. 46: 7-43.

Jovan, S. 2008. **Lichen bioindication of biodiversity, air quality, and climate: baseline results from monitoring in Washington, Oregon, and California.** Gen.Tech. Rep. PNW- 737. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 115 p.

Krupa, S.V. 2003. **Effects of atmospheric ammonia (NH_3) on terrestrial vegetation: a review.** Environmental Pollution. 124: 179-221.

Lehmann, C.M.B.; Bowersox, V.C. ; Larson, S.M. 2005. **Spatial and temporal trends of precipitation chemistry in the United States, 1985-2002.** Environmental Pollution. 135: 347-361.

Magnani, F.; Mencuccini, M.; Borghetti, M.; Berbigier, P.; Berninger, F.; Delzon, S.; Grelle, A.; Hari, P.; Jarvis, P.G.; Kolari, P.; Kowalski, A.S.; Lankreijer, H.; Law, B.E.; Lindroth, A.; Loustau, D.; Manca, G.; Moncrieff, J.B.; Rayment, M.; Tedeschi, V.; Valentini, R.; Grace, J. 2007. **The human footprint in the carbon cycle of temperate and boreal forests.** Nature. 447: 848-850.

McCune, B.M.; Geiser, L.H. 2009. **Macrolichens of the Pacific Northwest.** 2nd Edition. Corvallis, OR: Oregon State University Press. 448 p.

Miller, E.K. 2000. **Atmospheric Deposition to Complex Landscapes: HRDM – a strategy for coupling deposition models to a high-resolution GIS.** In: Arts, R., ed. NADP 2000: Ten years after the Clean Air Act amendments: Adirondacks in the balance. Proceedings of the NADP technical meeting; 2000 October 17-20. Champaign, IL: Illinois State Water Survey: 74.

Nadelhoffer, K.J.; Emmett, B.A.; Gundersen, P.; Kjønaas, O.J.; Koopmans, C.J.; Schleppi, P.; Tietema, A.; Wright, R. 1999. **Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests.** Nature. 398: 145-148.

NADP (National Atmospheric Deposition Program). 2008. **National Atmospheric Deposition Program.** Available at http://nadp.sws.uiuc.edu/ (Accessed May 12, 2010.)

NEG ECP (New England Governors and Eastern Canadian Premiers). 2003. **Assessment of forest sensitivity to nitrogen and sulfur deposition in New England and Eastern Canada - pilot phase report.** Boston: Conference of the New England Governors and Eastern Canadian Premiers.16 p. Available at http://www.ecosystems-research.com/fmi/reports.htm (Accessed May 12, 2010).

Nihlgård, B. 1985. **The ammonium hypothesis - an additional explanation to the forest dieback in Europe.** Ambio. 14(1): 2-8.

Nilles, M.A.; Conley, B.E. 2001. **Changes in the chemistry of precipitation in the United States, 1981-1998.** Water, Air and Soil Pollution. 130: 409-414.

Pardo, L. H. 2010. **Approaches for estimating Critical Loads of N and S Deposition for Forest Ecosystems on U.S. Federal Lands.** Gen. Tech. Rep. NRS-71. Newtown Square, PA: U.S. Department of Agriculture Forest Service, Northern Research Station. 25 p.

Porter, E.; Blett, T.; Potter, D.; Huber, C. 2005. **Protecting resources on federal lands: Implications of critical loads for atmospheric deposition of nitrogen and sulfur.** BioScience. 55: 603-612.

Posch, M.; de Smet, P.A.M.; Hettelingh, J.-P.; Downing, R.J., eds. 1995. **Calculation and mapping of critical thresholds in Europe. Status Report 1995.** RIVM Rep. No. 259101004. Bilthoven, Netherlands: Coordination Center for Effects, National Institute for Public Health and the Environment. Available at http://www.rivm.nl/bibliotheek/digitaaldepot/PBL_CCE_SR95.pdf (Accessed May 12, 2010).

Posch, M.; de Smet, P.A.M.; Hettelingh, J.-P.; Downing, R.J., eds. 2001. **Modelling and mapping of critical thresholds in Europe. Status report 2001.** RIVM Rep. No. 259101010. Bilthoven, The Netherlands: Coordination Center for Effects, National Institute for Public Health and the Environment. Available at http://www.rivm.nl/bibliotheek/digitaaldepot/PBL_CCE_SR01.pdf. (Accessed May 12, 2010).

Schaberg, P.G.; DeHayes, D.H.; Hawley, G.J.; Murakami, P.F.; Strimbeck, G.R.; McNulty, S.G. 2002. **Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon storage in montane red spruce.** Canadian Journal of Forest Research. 32:1351-1359.

Stevens, C.J.; Dise, N.B.; Mountford, J.O.; Gowing, D.J. 2004. **Impact of nitrogen deposition on the species richness of grasslands.** Science. 303: 1876-1879.

Stoddard, J. 1994. **Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences.** In: Baker, L.A., ed. Environmental chemistry of lakes and reservoirs. Washington, DC: American Chemical Society: 223-284.

Sutton, M.A.; Simpson, D.; Levy, P.E.; Smith, R.I.; Reis, S.; van Oijen, M.; deVries, W. 2008. **Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration.** Global Change Biology. 14: 1-7.

Thomas, R.Q.; Canham, C.D.; Weathers, K.C.; Goodale, C.L. 2010. **Increased tree carbon storage in response to nitrogen deposition in the US.** Nature Geoscience. 3: 13-17.

UBA (UmweltBundesAmt). 2004. **Manual on methodologies and criteria for modeling and mapping critical loads and levels and air pollution effects, risks, and trends.** Berlin: Federal Environmental Agency (UmweltBundesAmt). Available at http://icpmapping.org/cms/zeigeBereich/11/manual-english.html (Accessed May 12, 2010).

US EPA (U.S. Environmental Protection Agency). 2009a. **Clean air markets - data and maps.** Washington, DC: U.S. Environmental Protection Agency. Available at http://camddataandmaps.epa.gov/gdm (Accessed May 12, 2010).

US EPA (U.S. Environmental Protection Agency). 2009b. **Clean air markets - progress reports.** Washington, DC: U.S. Environmental Protection Agency. Available at http://www.epa.gov/airmarkets/progress/progress-reports.html (Accessed May 12, 2010).

Weathers, K.C.; Simkin, S.M.; Lovett, G.M.; Lindberg, S.E. 2006. **Empirical modeling of atmospheric deposition in mountainous landscapes.** Ecological Applications. 16(4): 1590-1607

Williams, M.W.; Tonnessen, K.A. 2000. **Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA.** Ecological Applications. 10(6): 1648-1665.

2 ECOSYSTEM CLASSIFICATION

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The ecosystem classification in this report is based on the ecoregions developed through the Commission for Environmental Cooperation (CEC) for North America (CEC 1997). Only ecosystems that occur in the United States are included. CEC ecoregions are described, with slight modifications, below (CEC 1997) and shown in Figures 2.1 and 2.2. We chose this ecosystem classification system because it is easily accessible, hierarchical, and based on biological, rather than purely climatic characteristics. An ecoregion is a geographically defined area that contains distinct physical features and biological communities. The descriptions include the whole ecoregion as it occurs in North America. Descriptions in the individual chapters reflect the ecoregion as represented in the United States.

Within the ecoregions, where data are available, we present the results by subcategory (e.g., for forest, chaparral and coastal sage scrub ecosystems within the Mediterranean California ecoregion). Certain life forms that occur across many ecosystem types, such as lichens and mycorrhizal fungi, are presented within each ecosystem for which data are available, and also, in some detail, in Chapter 19. Common names for species are used throughout this report; scientific names are given at first mention in each chapter, and are also provided in Appendix 1. Wetlands and inland surface waters occur across most ecoregions in the United States and are addressed extensively in Chapters 17 and 18. Ecoregion chapters include a cursory discussion of wetlands and surface water where data are available.

2.1 Ecosystem Descriptions

Tundra

This ecoregion is a mosaic of alpine meadows, foothills, mesas, low-lying coastal plains, river corridors, and deltas. A key feature is that soils are frozen in permafrost and contain large stores of organic carbon. Vegetation is characterized by dwarf shrubs that decrease in size moving north, with very low and flattened plants being most characteristic of the northern and central locales. Major river valleys support scattered clumps of stunted spruce trees. Typical shrubs include dwarf birch (*Betula nana*), willows (*Salix* spp.), and heath species commonly mixed with various herbs and lichens. Wetlands are common in the low-lying areas, mainly supporting sedge and moss covers.

Taiga

The Taiga ecoregion contains elements of both Tundra and Northern Forests ecoregions. It is characterized by innumerable lakes, bogs, other wetlands, and northern boreal forests, interwoven with open shrublands and sedge meadows more typical of the tundra. From south to north, forests become open and form woodlands with a characteristic groundcover of lichens, which merge into areas of tundra. Along the northern edge of this ecological region the latitudinal limits of tree growth are reached and dwarf birch, Labrador tea (*Ledum* spp.), willow, bearberry (*Arctostaphylos alpina*), mosses, and sedges are dominant. Further south, the region contains open stands of stunted black spruce (*Picea mariana)* and jack pine (*Pinus banksiana)* accompanied by alder (*Alnus* spp.), willow, and tamarack (*Larix larcinia)* in the fens and bogs. Mixed wood associations of white (*Picea glauca)* and black spruce, lodgepole pine (*Pinus contorta)*, quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera)*, and white birch (*Betula papyrifera*) are found on well drained and warm upland sites, as well as along rivers and streams. Along the nutrient-rich alluvial flats of the larger rivers, white spruce and balsam poplar grow to sizes comparable to the largest in the boreal forests to the south.

Northern Forests

Over 80 percent forested, the ecoregion is dominated by conifers, largely white and black spruce, jack pine, balsam fir (*Abies balsamea*), and tamarack. Toward the south and the Canadian Maritimes provinces, there is a wider distribution of white birch, quaking aspen, balsam poplar, eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), sugar maple (*Acer saccharum*),

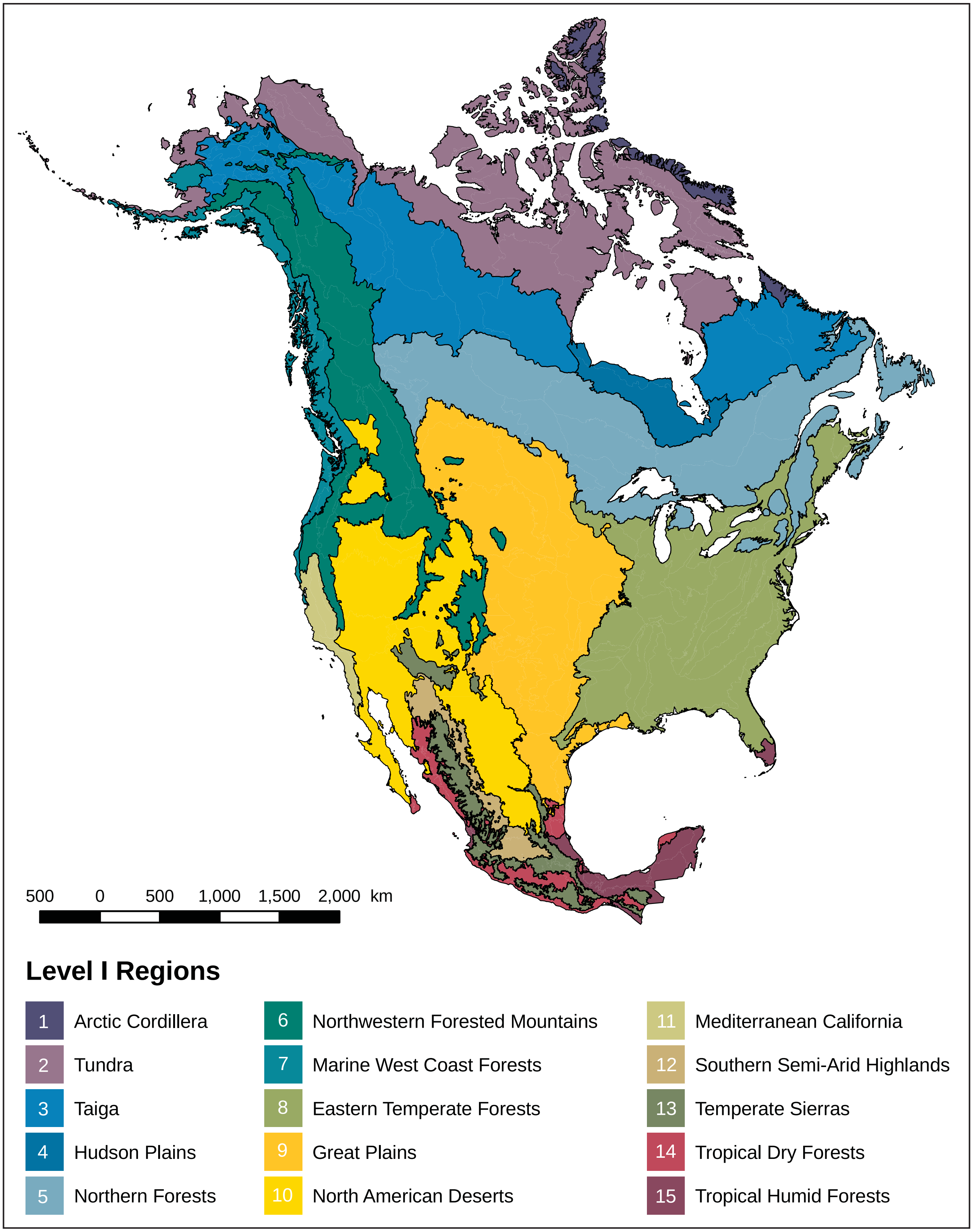

Figure 2.1—Ecological Regions of North America, Level I. From the Commission for Environmental Cooperation (1997).

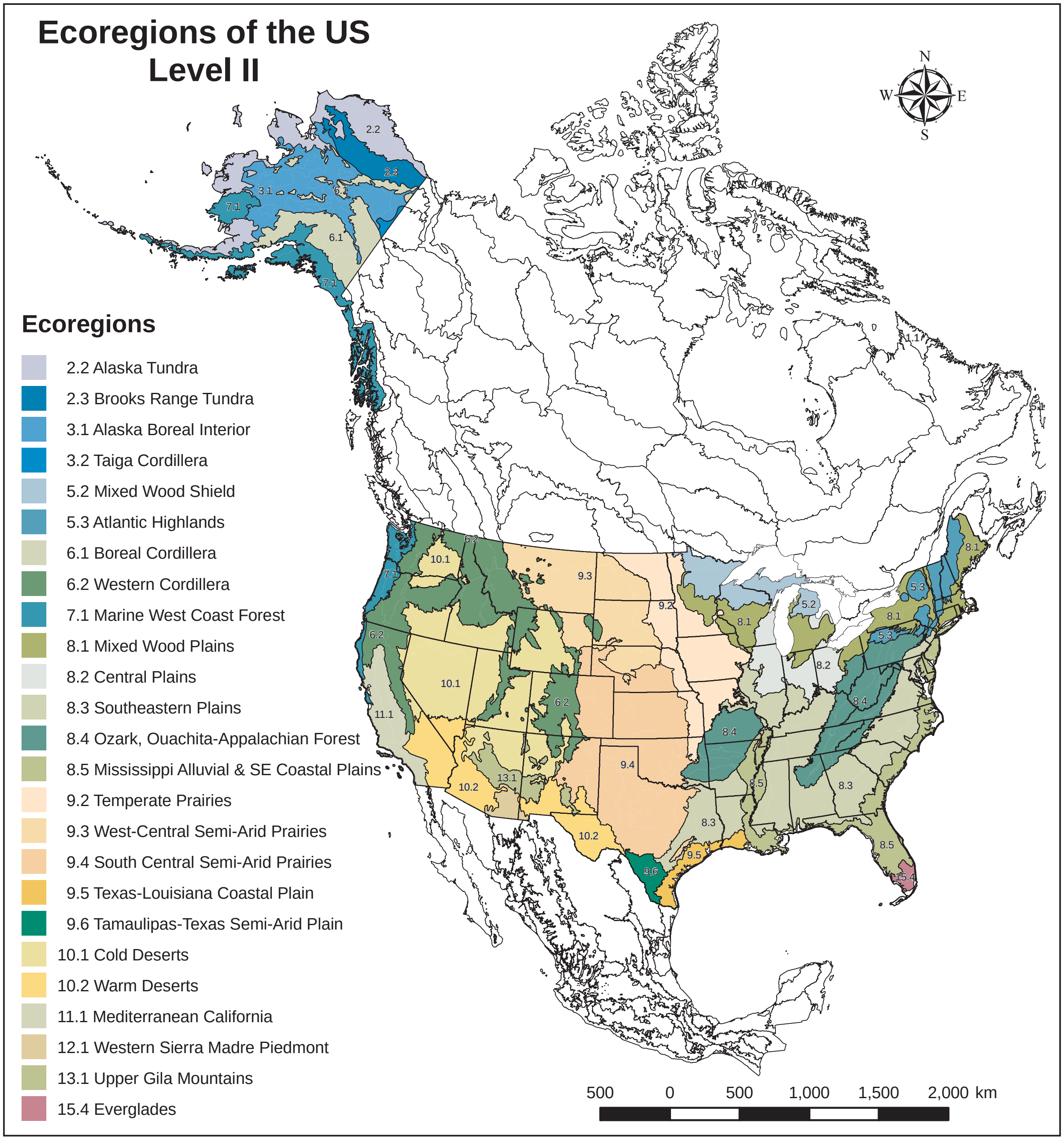

Figure 2.2—Ecological Regions of North America, Level II. From the Commission for Environmental Cooperation (1997).

beech (*Fagus* spp.), red spruce (*Picea rubens*), and various species of oak (*Quercus* spp.). Areas of shallow soils and exposed bedrock are common and tend to be covered with a range of plant communities, dominated by lichens, shrubs and forbs. It is underlain by ancient Canadian Shield bedrock interspersed with glacial moraine deposits, creating a hilly terrain dotted with numerous lakes. Soils derived from the bedrock are generally coarse textured and nutrient-poor. Peatlands are extensive in northern Minnesota. The climate is characterized by long, cold winters (means of -20.5 °C in the west to -1 °C in the east) and short, warm summers (means of 11 to 18 °C). Annual precipitation ranges from 400 to 1,000 mm.

Northwestern Forested Mountains

Vegetative cover is extremely diverse, with distinct elevational bands: alpine environments contain various herb, lichen, and shrub associations; whereas the subalpine forest has species such as lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) in interior assemblages; and Pacific silver fir (*Abies amabilis*), grand fir (*Abies grandis*), lodgepole pine, and Engelmann spruce in the west. Mid-elevation forests are characterized by ponderosa pine (*Pinus ponderosa*), Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), lodgepole pine, and quaking aspen in much of the southeast and central portions; and western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*) and western white pine (*Pinus monticola*) in the west and southwest. White and black spruce dominate the plateaus of the north. Shrub vegetation found in the dry southern interior includes big sagebrush (*Artemisia tridentata*), rabbit brush (*Chrysothamnus* spp.), and antelope bitterbrush (*Purshia tridentata*). Most of the natural grasslands that existed in the dry south have been replaced by agriculture.

Marine West Coast Forests

Variations in altitude create widely contrasting ecological zones within the region. They range from mild, humid coastal rain forest to cool boreal forests and alpine conditions at higher elevations. The maritime influence of the Pacific Ocean causes high precipitation (600 to 5000 mm), a long growing season, and moderate mean annual temperatures (5 to 9 °C). The temperate coastal forests are composed of mixtures of western red cedar, Nootka Cypress (Alaska yellow cedar; *Callitropsis nootkatensis*), western hemlock, Douglas-fir, Pacific silver fir, white spruce, Sitka spruce (*Picea sitchensis*), California redwood (*Sequoia sempervirens*), and red alder (*Alnus rubra*). Many of these trees reach very large dimensions and live to great age, forming ancient or old growth. In the drier rain-shadow areas, Oregon white oak (Garry oak; *Quercus garryana*) and Pacific madrone (*Arbutus menziesii*) occur with Douglas-fir. Sub-alpine forests are characterized by mountain hemlock (*Tsuga mertensiana*) and Pacific silver fir. Alpine tundra conditions are too severe for growth of most woody plants except in dwarf form. This zone is dominated by shrubs, herbs, mosses, and lichens.

Eastern Temperate Forests

The Eastern Temperate Forests form a dense forest canopy consisting mostly of tall, broadleaf, deciduous trees and needle-leaf conifers. Beech-maple (*Fagus-Acer*) and maple-basswood (*Acer-Tilia*) forest types occur widely, especially in the eastern reaches of this region; mixed oak-hickory (*Quercus-Carya*) associations are common in the Upper Midwest, changing into oak-hickory-pine (*Quercus-Carya-Pinus*) mixed forests in the south and the Appalachians. These forests have a diversity of tree, shrub, vine, and herb layers. While various species of oaks, hickories (*Carya* spp.), maples (*Acer* spp.), and pines (*Pinus* spp.) are common, other wide-ranging tree species include ashes (*Fraxinus* spp.), elms (*Ulmus* spp.), black cherry (*Prunus serotina*), yellow-poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), basswood (*Tila* spp.), hackberry (*Celtis occidentalis)*, persimmon (*Diospyros virginiana*), eastern red cedar (*Juniperus virginiana*), and flowering dogwood (*Cornus florida*). A key tree species, the American chestnut (*Castanea dentata*), was virtually eliminated from the Eastern Temperate Forests in the first half of the 20th century by an introduced fungus.

Great Plains

The Great Plains ecoregion was once covered with natural grasslands that supported rich and highly specialized plant and animal communities. The interaction of climate, fire, and grazing influenced the development and maintenance of the Great Plains. Rainfall increases from west to east, defining different types of native prairies. Short-grass prairie occurs in the west, in the rain shadow of the Rocky Mountains, with mixed-grass prairie in the central Great Plains and tall-grass prairie in the wetter eastern region. Because of the suitability of the Great Plains for agricultural production, many native prairie vegetation types have been radically altered. The short-, mixed-, and tallgrass prairies now correspond to the western rangelands, the wheat belt, and the corn/soybean regions, respectively. Drier sites are home to prickly pear (*Opuntia* spp.), with sagebrush (*Artemisia* spp.) also abundant.

The Aspen Parkland, the northern transition zone to the boreal forest, has expanded south into former grasslands since settlement effectively stopped prairie fires. In the United States, native prairie vegetation ranges from grama grass (*Bouteloua* spp.), wheatgrass (*Agropyron* spp.), and bluestem (*Andropogon* spp.) prairie in the north to different shrub and grassland combinations (e.g., mesquite-acacia (*Prosopis-Acacia*) savanna and mesquite-Texas live oak (*Prosopis-Quercus fusiformis*) savanna) and grassland and forest combinations (e.g., juniper-oak [*Juniperus-Quercus*] savanna and mesquite-buffalo grass [*Prosopis-Buchloe dactyloides*]) in the south. There are also patches of blackland prairie, bluestem-sacahuista (*Andropogon-Nolina*) and southern cordgrass (*Spartina*) prairie in the southern United States. The eastern border of the region, stretching from central Iowa to Texas, shows patterns of grassland and forest combinations mixed with oak-hickory forest. Throughout the remainder of the Great Plains there are few native deciduous trees that occur, except in the eastern regions or in very sheltered locations along waterways or at upper elevations.

North American Deserts

In this ecological region of altitudinal, latitudinal, and landform diversity, there are a variety of vegetation types, but low-growing shrubs and grasses predominate. In the northern Palouse and Snake River Basin areas, grasslands and sagebrush steppes were once common. However, most of these northern grasslands have been converted to agriculture, and in some areas, the sagebrush steppe is being invaded by western juniper (*Juniperus occidentalis*) and cheatgrass (*Bromus tectorum*). The Great Basin and greater Colorado Plateau are characterized by sagebrush (*Artemisia* spp.), with saltbush (*Atriplex* spp.) and greasewood (*Sarcobatus* spp.) on more alkaline soils.

In the warmer southern deserts, creosote bush (*Larrea tridentata)* is common; the Mojave Desert also contains areas of the distinctive Joshua tree (*Yucca brevifolia*). The Sonoran Desert has greater structural diversity in its vegetation than the other North American deserts. Its paloverde (*Parkinsonia* spp.), cactus, and shrub vegetation includes various types of succulents, such as saguaro (*Cereus gigantea*), cholla (*Cylindropuntia* spp.), and agave (*Agave* spp.). The Chihuahuan Desert is characterized by smaller leaved, shorter statured vegetation such as American tarwort (*Flourensia cernua*), creosote bush, and intermixed grasses.

Mediterranean California

The Mediterranean California region is characterized by a mostly evergreen shrub vegetation called chaparral, plus patches of oak woodland, grassland, and coniferous forest on upper mountain slopes. The chaparral has thickened, hardened foliage resistant to water loss, and forms a cover of closely spaced shrubs 1 to 4 m tall. Common shrubs include chamise (*Adenostoma fasciculatum*), buckbrush (*Ceanothus cuneatus*), and manzanita (*Arctostaphylos* spp.). Coastal sagebrush (*Artemisia californica)*, summer-deciduous plants that tolerate more xeric, or dry, conditions than the evergreen chaparral, are found at lower elevations. About 80 percent of the presettlement coastal sage scrub in southern California has been displaced, primarily by residential development and agriculture. Several dozen threatened and endangered species occur in the coastal sage scrub community. To the north, the chaparral is less continuous, occurring in a mosaic with grassland, as well as broadleaf and coniferous forests. A blue oak-California foothills pine (*Quercus douglasii –Pinus sabiniana*) woodland community forms a ring around the Central Valley, which itself once had extensive grasslands and riparian forests. The southern oak woodland extends into the transverse and peninsular ranges and includes California walnut (*Juglans californica*) and Engelmann oak (*Quercus englemannii*). The high elevation mixed pine forests are dominated by Jeffrey pine (*Pinus jeffreyi*) and ponderosa pine, with incense cedar (*Calocedrus decurrrens*), black oak (*Quercus velutina*), white fir (*Abies concolor*), and others.

Southern Semi-Arid Highlands

The characteristic natural vegetation, which presently is very diminished or altered, consists of grasslands and combinations of grasslands with scrublands, and woodlands and forests in the higher elevations. Certain species of grasses are dominant, particularly bluestem, threeawn (*Aristida* spp.), galleta (*Hilaria jamesii*), and muhly (*Muhlenbergia* spp.) grasses. Among the shortgrasses, blue grama (*Bouteloua gracilis*) is important in Arizona, New Mexico, and in the northern Mexican states at the foot of the Western Sierra Madre. On deep clay soils, mesquite groves are the most conspicuous plant community, and mesquite occurs with acacia in some sites, especially in Mexico. Oak and western juniper are common at the foot of the Sierras. Where the climate is warmer in Mexico, one finds subtropical scrublands with a diversity of shrub species.

Temperate Sierras

Vegetation can be evergreen or deciduous, composed primarily of conifers and oaks. They grow from 10 to 30 m, sometimes reaching 50 m. This vegetative cover may comprise from one to three tree layers, one or two shrub layers, and an herbaceous stratum. This forest community is characterized by about 3,000 vascular plant species, 30 percent of which are endemic to Mexico. Overall most of this vegetation type occurs in Mexico, where there is a high diversity of oaks, pine and other species, and includes mountain cloud forests that do not occur in the United States.

Tropical and Subtropical Humid Forests

This ecoregion includes tropical humid forests at the southern tip of the Florida Peninsula in the United States, as well as subtropical humid forests in coastal, low-elevation, and lower montane regions on the Hawaiian Islands and in Puerto Rico. The region spans from sea level to approximately 1,800 m of altitude. For subtropical and tropical humid forests, including those in the lower montane regions, average annual precipitation typically exceeds 1,000 mm and year round temperatures average between 16 °C and 26 °C. Evergreen and semi-deciduous forests are the most characteristic plant communities of this region, which is one of the most biodiverse zones in the world. Forest stands are typically of mixed ages with a great abundance of air plants (epiphytes), including bromeliads, ferns, and orchids. The mature tree layer may attain heights up to 30 m or more. In the tropical humid forest of the Florida peninsula, flooded marshes and swamps (both saltwater and freshwater) are widespread, with characteristic mangrove vegetation and tropical tree islands. Native subtropical humid forests in Hawaii include the common dominant trees Ohi'a lehua (*Metrosideros polymorpha)* and Koa (*Acacia koa*), as well as tree ferns and a diverse understory of epiphytes and shrubs. Puerto Rican forests on volcanic soils include Tabonuco, Colorado, and dwarf cloud forests; sclerophyllous, evergreen vegetation is found on serpentine and limestone derived soils.

LITERATURE CITED

CEC (Commission for Environmental Cooperation). 1997. Ecological regions of North America. **Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

3 DEPOSITION

K.C. Weathers and J.A. Lynch

3.1 OVERVIEW

To determine the effects of air pollution on ecological systems using the critical load approach, accurate estimates of total nitrogen (N) deposition are essential. Empirical critical loads are set by relating observed ecosystem responses to N deposition (measured, experimentally manipulated, or modeled). Because many manipulation studies are done under natural conditions where the total N deposition is not known, the empirical critical load is often crudely estimated. However, making accurate measurements or models of N deposition is difficult, and such estimates are not available at the fine spatial resolution required for determining empirical critical loads.

The purposes of this chapter are threefold. First, it presents an overview of atmospheric deposition to ecosystems and provides a brief summary of the processes and challenges of measuring and estimating total (wet, dry, cloud, or fog) atmospheric deposition. Second, we present a map (Fig. 3.1) of wet plus dry deposition for the more than 3200 U.S. locations for which we report ecological responses to N deposition in subsequent chapters. Third, we compare two methods of estimating deposition at the national scale (Weathers and Lynch 2008).

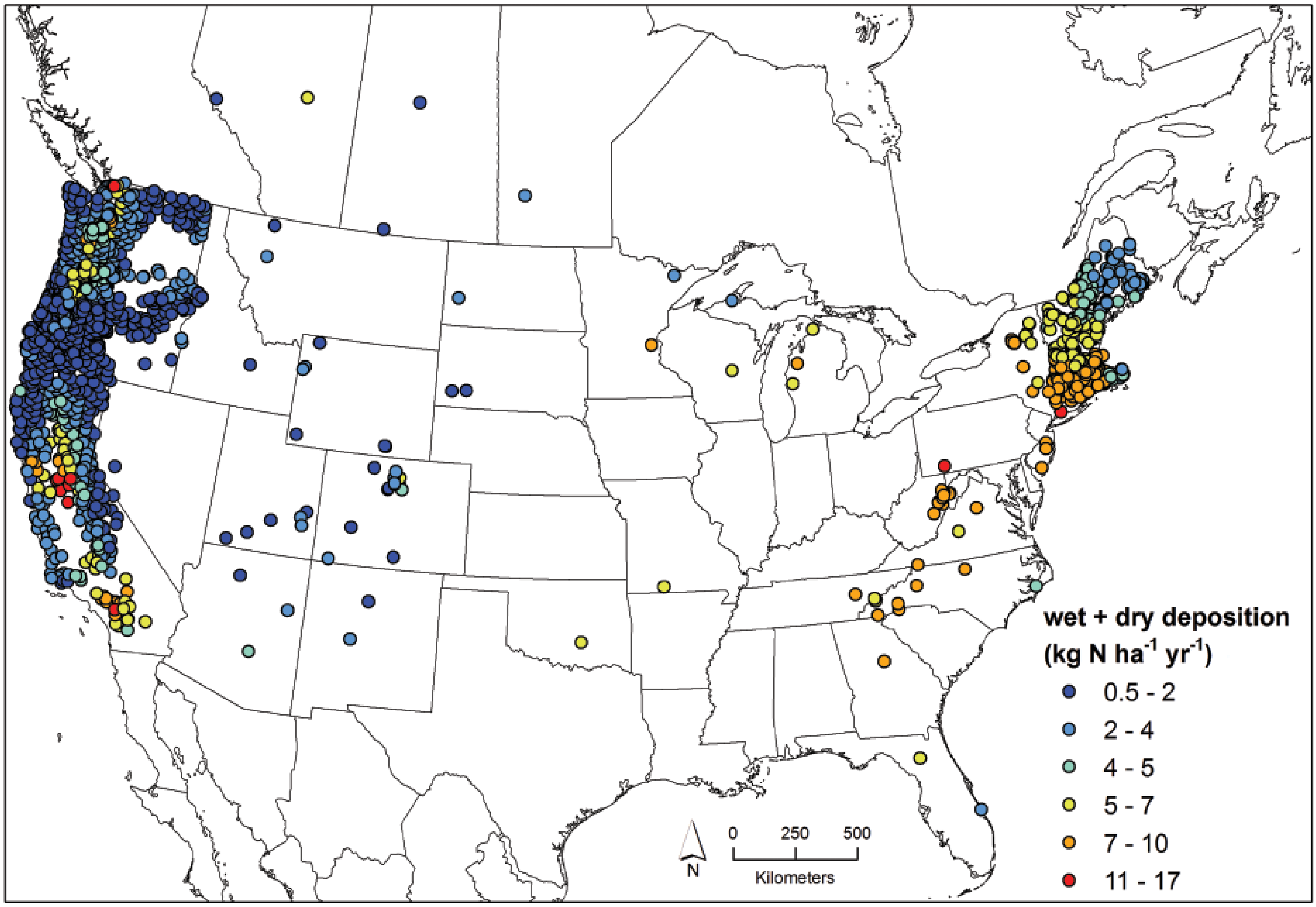

Figure 3.1—Estimates of wet plus dry N deposition (including, as N, wet ammonium (NH$_4^+$) and nitrate (NO$_3^-$), and dry nitric acid (HNO$_3$), ammonia (NH$_3$), NH$_4^+$, and NO$_3^-$) generated by the CMAQ 2001 model for more than 3200 locations across the United States for which we report ecological responses to N deposition in subsequent chapters.

3.2 Background on total N deposition

The primary forms of inorganic N deposition that have been measured routinely are secondary products of nitrogen oxide (NO_x) emissions—nitrate (NO_3^-; particulate and aqueous) and nitric acid vapor (HNO_3) —and ammonium (NH_4^+; particulate and aqueous). The primary anthropogenic source of NO_x is fossil fuel combustion. Transportation accounted for more than 50 percent of the total NO_x emissions in 2002 (Driscoll et al. 2003, Weathers et al. 2007), while the primary sources of ammonia (NH_3) and NH_4^+ are agricultural activities (Driscoll et al. 2003, Weathers et al. 2007). (Chemical formulas and common names for elements and compounds are provided in Appendix 2.)

Nitrogen is deposited from the atmosphere to the Earth's surface in the form of wet (rain and snow), dry (gases and particles), and cloud and/or fog deposition (Fenn et al. 2009; Lovett 1994; Weathers et al. 1988, 2000a, 2000b, 2006). Wet N deposition can be measured directly, but often only some of the components are measured. Dry deposition cannot be measured directly. Moreover, the estimates that exist are either site specific, or are modeled (e.g., dry deposition) assuming flat, homogeneous terrain, e.g. Clean Air Status and Trends (CASTNET) sites (US EPA 2010). For this reason, a combination of monitoring data, deposition models (e.g., the Multi-Layer Model [MLM] for estimating dry deposition), empirical measures of atmospheric deposition (e.g., throughfall), and emissions-based modeling outputs, are often necessary to estimate total N deposition. In the ecoregion chapters that follow, we consider total deposition to include wet (rain and snow) plus dry and, in some cases, cloud/fog.

There are several factors that reduce the accuracy of total N deposition estimates:

- Not all forms (wet, dry, and cloud) of atmospheric deposition are measured or modeled routinely. Thus, estimates that are based on wet deposition only, for example, result in an underestimation of the total N delivered to an ecosystem (Lovett 1994, Weathers et al. 2007). Dry and cloud N deposition can contribute from 50 to 80 percent of total N deposition (Johnson and Lindberg 1993); these forms of deposition are not often estimated.
- Not all of the chemical species of N that are deposited to ecosystems (e.g., NH_3 and organic N) are currently measured and/or modeled, which also leads to an underestimate of N deposition.
- Estimates of dry and cloud deposition depend upon measured air chemistry and modeled deposition. These estimates are therefore likely to be imprecise. For example, the influences of local meteorology, complex terrain (elevation and slope), as well as canopy architecture all affect rates of dry deposition, yet these characteristics of landscapes and canopies are extremely difficult to represent in models, and thus represent serious limitations to accurate estimates of dry N deposition (Lovett 1994; Weathers et al. 1992, 1995, 2000a, 2000b, 2006). Total deposition is therefore often underestimated for high elevation regions and/or for complex terrain (Anderson et al. 1999; Johnson and Lindberg 1993; Weathers et al. 1992, 2000a, 2000b, 2006).
- Estimates of deposition are also highly uncertain for regions with high snowfall, such as the montane west, and regions with a high proportion of dry deposition, such as the arid south and west (see Fenn et al. 2009 for a complete description of issues and potential solutions for these regions).
- Finally, inadequate number and spatial extent of monitoring stations is a crucial issue that adversely impacts deposition estimates across space, particularly in complex terrain. This is a significant problem in the western United States (Fenn et al. 2009), where few monitoring stations exist.

Inorganic species of N most commonly measured or modeled in the field (Fig. 3.2) include: NO_3^-, NH_4^+, and nitric acid (HNO_3). In recent years, dissolved organic nitrogen (DON) has also been shown to be prevalent in precipitation (e.g., Neff et al. 2002) and in clouds

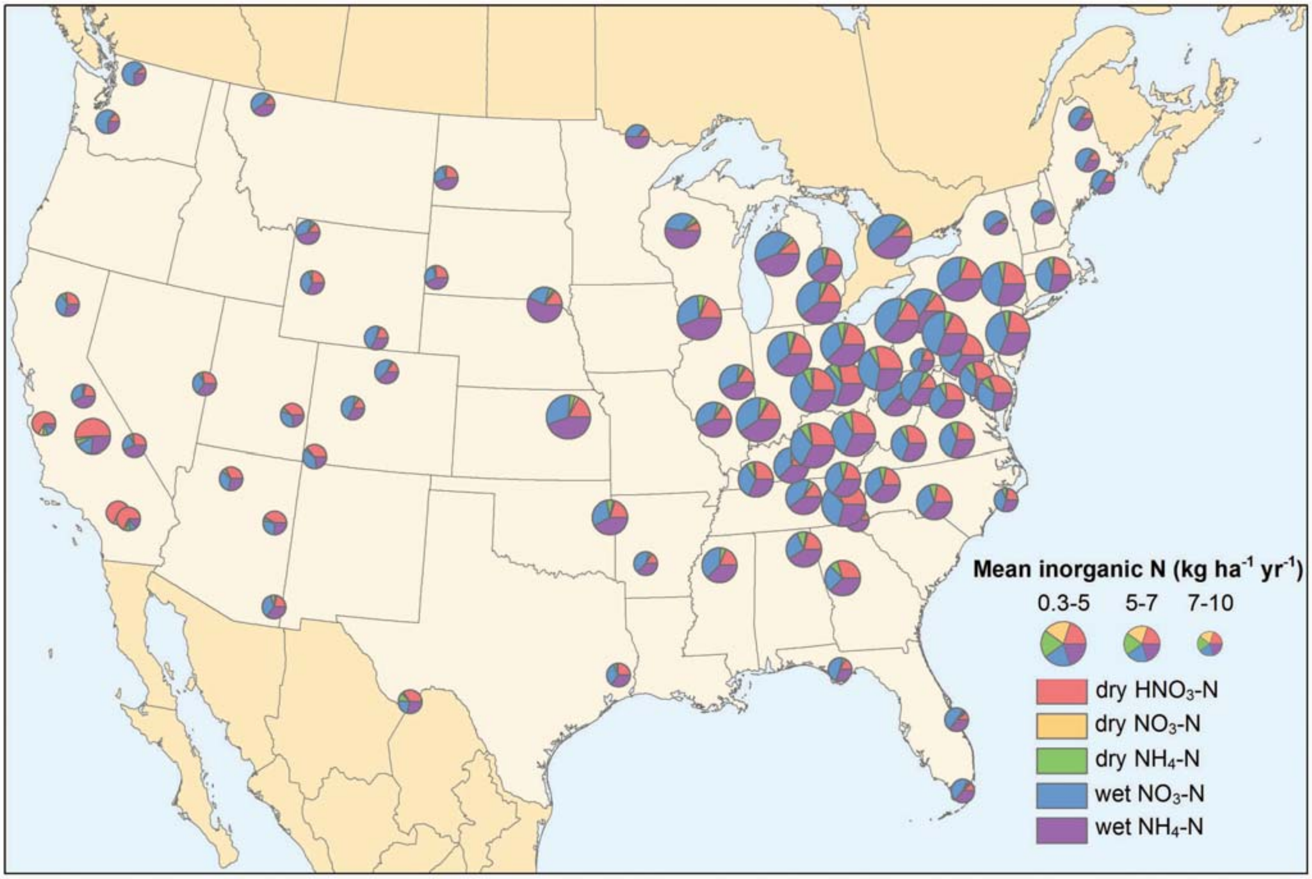

Figure 3.2—Total (wet plus dry, including wet NH_4^+ and NO_3^-, dry HNO_3, particulate NO_3^-, and NH_4^+) mean N deposition for 85 CASTNET site locations for 2004 to 2008. Size of circle indicates relative total deposition. Proportion of wet and dry species for each are shown within circle. Note that HNO_3-N is the largest proportion of dry deposition.

(Weathers et al. 2000a). Other potentially important N species not addressed here, primarily because they are not measured at National Atmospheric Deposition Program (NADP) or CASTNET monitoring stations (see descriptions, Chapter 4), are wet and dry NH_3, NO, NO_2, N_2O_5, peroxyacetal nitrate (PAN) (US EPA 2001). We note that fluxes of these species are estimated by the Community Multiscale Air Quality (CMAQ) model, however (see description, Chapter 4). One of the most important species that is not measured at CASTNET and NADP monitoring stations is NH_3. This form of N is currently increasing in the atmosphere and will be critically important to measure in both the short and long term (Driscoll et al. 2001, 2003).

In sum, estimates of total N deposition are still highly uncertain for several reasons, including the facts that (1) deposition models cannot accommodate complex terrain; (2) important N species are not often measured; (3) snow, dry, fog, or cloud deposition are not often considered, yet represent potentially important vectors for N deposition in some locations; and (4) there is inadequate monitoring (e.g., Driscoll et al. 2001, Lovett 1994, Weathers et al. 2000b, 2006).

3.3 Measurements and Estimates of N Deposition

3.3.1 Wet Inorganic N Deposition

Wet deposition is measured at approximately 250 monitoring stations across the United States as part of the NADP network. Wet deposition is the sum of NO_3^--N and NH_4^+-N delivered via rain and snow. Wet deposition is also estimated at various resolutions (e.g., 36 km x 36 km; 12 km x 12 km) via versions of the CMAQ model (Byun and Ching 1999, Byun and Schere 2006, US EPA 2009; Fig 3.1). The CMAQ model derives estimates of deposition from emissions, atmospheric chemistry, meteorology, and deposition velocities as influenced by land cover (US EPA 2009).

The chemical species we consider here from the CMAQ model are wet NH_4^+ and NO_3^-.

3.3.2 Cloud Deposition Monitoring

There exists only one cloud deposition monitoring network, the Mountain Atmospheric Deposition Program (MADPro), where cloud water samples are collected and measured for chemistry (NO_3^- and NH_4^+). These data are subsequently used to model cloud deposition for a few sites in the eastern United States (Anderson et al. 2006, Baumgartner et al. 2003). Cloud deposition estimates are not routinely extrapolated beyond the mountain tops where they are measured, such as Clingman's Dome, North Carolina, Whitetop Mountain, Virginia, and Whiteface Mountain, New York. Obtaining accurate estimates of cloud/fog deposition across the landscape is a significant problem (Fenn et al. 2009; Johnson and Lindberg 1993; Lovett 1994; Weathers et al. 1988, 2000a, 2000b, 2006). Where it is frequent, cloud/fog deposition can represent up to 80 percent of total N deposition (Anderson et al. 1999, Fenn et al. 2009, Johnson and Lindberg 1993).

3.3.3 Dry Deposition

Dry deposition is estimated at approximately 80 monitoring locations across the United States (US EPA 2010; Fig 3.2). For the ground-based CASTNET and AIRMoN (Atmospheric Integrated Research Monitoring Network) programs, air N chemistry is measured (HNO_3, particulate NO_3^-, and particulate NH_4^+), and dry deposition is modeled based on meteorologic conditions and multiple resistances of the receptor surfaces (CASTNET and AIRMoN; NADP 2009, US EPA 2010). Because protocols differ between the CASTNET and AIRMoN programs and there are fewer than 10 AIRMoN sites, we restrict our analysis to CASTNET data. Researchers have used CASTNET air concentration data to estimate deposition across the landscape (e.g., Fenn et al. 2009, Ollinger et al. 1993, NEG/ECP 2003, Weathers and Lynch 2008). The Environmental Protection Agency's CMAQ model also estimates dry deposition based on emissions, combined with air chemistry, meteorology and land cover-based deposition velocities. The chemical species we consider here from the CMAQ model are NH_4^+-N, NO_3^--N, and HNO_3-N.

3.3.4 Total Deposition

Total (wet plus dry plus cloud) inorganic N deposition has rarely been estimated across the U.S. landscape. In cases in which it has, indices of deposition or estimated air chemistry and meteorologic conditions have been used in combination with statistical and spatial tools (e.g., geographic information systems; NEG/ECP 2003; Weathers et al. 2000b, 2006). Wet plus dry (not cloud) deposition has been estimated across the country via the CMAQ modeling effort (Fig 3.1) as well as through statistical techniques (Ollinger et al. 1993), and for CASTNET locations using CASTNET and NADP data (Fig 3.2). Total flux to the forest floor (including cloud; throughfall) has been measured directly in many locations using bulk precipitation samplers (e.g. Simkin et al. 2004, Fenn et al. 2004). By comparing throughfall to wet-only deposition, estimates of dry (plus cloud, where relevant) deposition can be made (e.g., Ewing et al. 2009, Lovett 1994). However, often it is difficult to interpret these data vis-à-vis atmospheric deposition since canopy processing (uptake, leaching, and transformation) of N is common (Lovett 1994, Weathers et al. 2006).

As noted above, organic N has been identified as an important component of total N deposition for some ecosystems (Neff et al. 2002, Weathers et al. 2000a). However, few data are available to assess its temporal or spatial extent or importance in contributing to total deposition across the United States. Thus, throughout this document, unless otherwise noted, we will refer to total inorganic N deposition (or total N deposition) as the sum of NO_3^--N, NH_4^+-N, and HNO_3-N for dry deposition, deposited via wet and dry deposition (cloud deposition only when noted).

3.3.5 Temporal Trends in Wet plus Dry N Deposition Across the United States

Figure 3.3 shows wet plus dry N concentration and deposition across the United States for the 18-year period from 1990 through 2007, based on data from 34 CASTNET and NADP locations (US EPA 2007). While no trend lines are reported for these data, a 17 percent decrease in total inorganic N deposition over the period was reported. The proportion of wet to dry

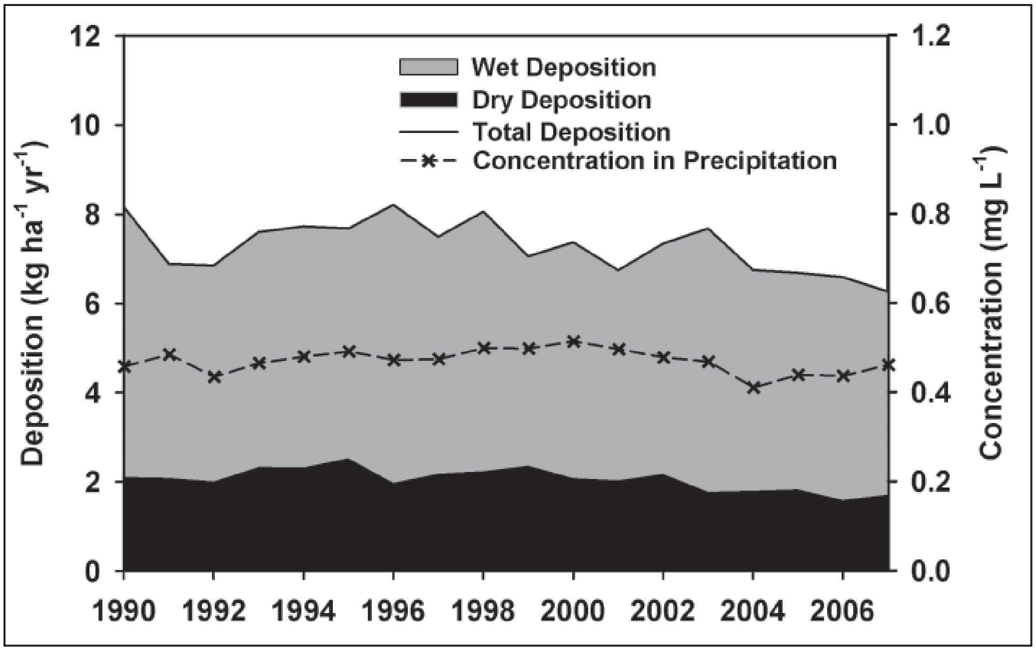

Figure 3.3—Total (solid black line), wet (gray area), dry (black area) deposition (kg N ha^{-1} yr^{-1}) and wet concentration (dotted line in mg L^{-1}) for 34 sites from 1990 to 2007 as estimated and measured by the NADP and CASTNET programs. Figure from US EPA 2007.

deposition also varies commensurate with changes in annual precipitation; when there is more precipitation, wet:dry ratios are greater (US EPA 2007).

3.4 Atmospheric N Deposition Across the Landscape

In this report, we have used the EPA's 2001 CMAQ model v. 4.3 (which use 2001 reported data and is hereafter referred to as CMAQ 2001 model) to provide comparative estimates of wet plus dry deposition to the more than 3200 locations included in this assessment of critical loads. We chose to use the CMAQ 2001 model (using the 36 km x 36 km resolution version) so that we could make comparisons across the country using the same method. For some regions, a 12 km x 12 km resolution version of CMAQ is available, but since it is not available for the whole country, we have not used it here. It is not possible to extrapolate either CASTNET or AIRMoN estimates of dry deposition beyond a 1 km x 1 km region surrounding the stations because the parameters required for the model are site-specific (US EPA 2010). It is also well known that estimates of total deposition that do not sufficiently consider landscape heterogeneity are likely to underestimate total deposition (Driscoll et al. 2001; Fenn and Bytnerowicz 1997; Fenn et al. 1998, 2000, 2009; Holland et al. 2005; Ito et al. 2002; Lovett 1994; Miller et al. 1993; Nanus et al. 2003; Ollinger et al. 1993; Weathers et al. 1992, 1995, 2000a, 2006). These issues notwithstanding, the CMAQ 2001 model represents a current state-of-the-art model to create cross-site deposition comparisons.

3.5 CMAQ Deposition Across Critical Loads Sites/Comparison Between CMAQ and Monitoring Stations

Average annual deposition across the more than 3200 critical load sites varied more than 30-fold, from 0.5 to 17 kg N ha^{-1} yr^{-1} (Fig 3.1). Total N deposition estimates based on the CMAQ 2001 model for CASTNET site locations compared well to those generated using CASTNET dry plus NADP wet data (Fig. 3.4, R^2=0.75). Note that in order to compare these two estimates, total N deposition included wet NO_3^- and NH_4^+ and dry HNO_3 and NH_4^+ as N, only since NH_3 data were not available for CASTNET sites.) However, air concentrations of HNO_3-N, the largest proportion of dry deposition, show a consistent difference (CMAQ < CASTNET), with a positive linear relationship (Fig 3.5; R^2=0.68). This is in contrast to estimates of dry deposition of HNO_3-N, which are also positively correlated (Fig 3.6; R^2=0.45), but with

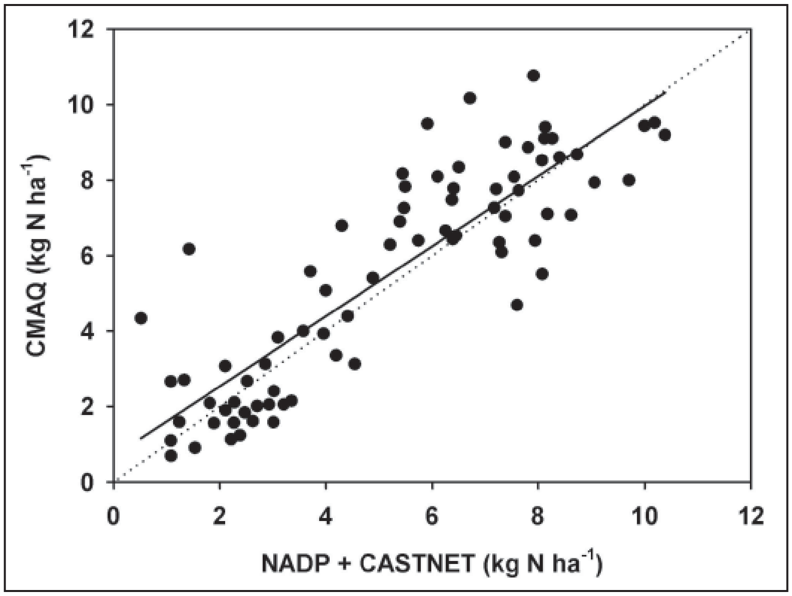

Figure 3.4—Comparison between wet plus dry deposition estimates for 2001 (includes wet NH_4^+ and NO_3^-, dry HNO_3, particulate NO_3^- and NH_4^+) from CASTNET and NADP (NADP site nearest to CASTNET locations) and CMAQ 2001 model for 77 CASTNET site locations. y = 0.9281x + 0.6818, R^2 = 0.75. 1:1 line is shown (from Weathers and Lynch 2008).

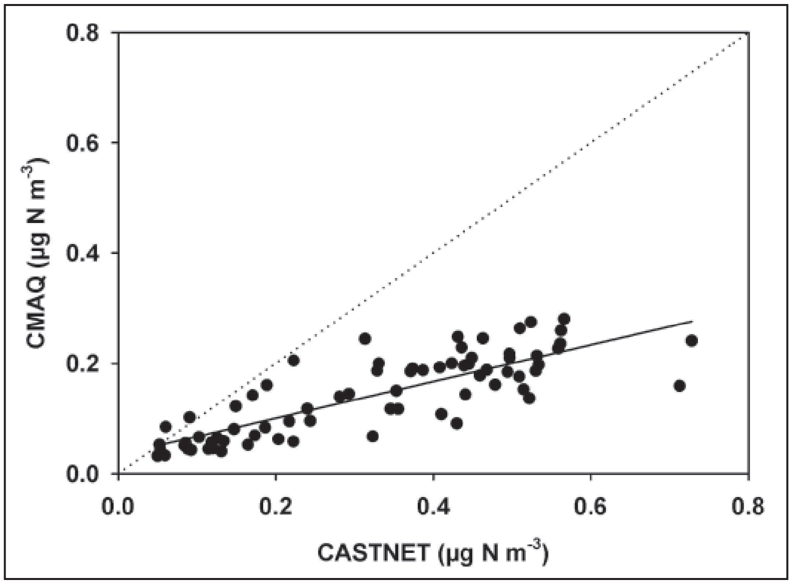

Figure 3.5—Mean air concentration (µg m^{-3}) of HNO_3-N during 2001 measured at 77 CASTNET sites vs. the mean air concentrations generated by the CMAQ 2001 model for those sites during 2001. y = 0.3324x + 0.034, R^2 = 0.6832. The 1:1 line is shown (from Weathers and Lynch 2008).

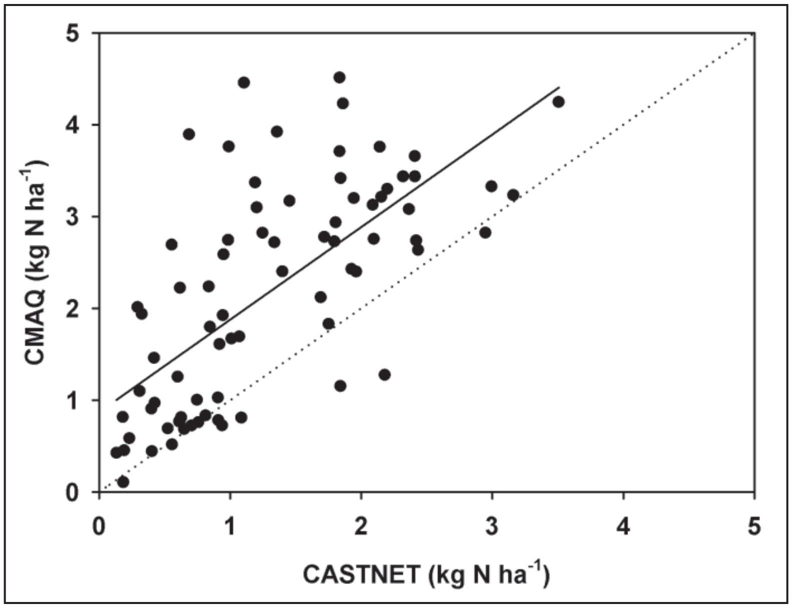

Figure 3.6—N dry deposition (kg N ha^{-1} yr^{-1}) during 2001 modeled at 77 CASTNET sites vs. the N dry deposition generated by the CMAQ 2001 model for those sites during 2001. y = 1.008x + 0.869, R^2 = 0.45. The 1:1 line is shown (from Weathers and Lynch 2008).

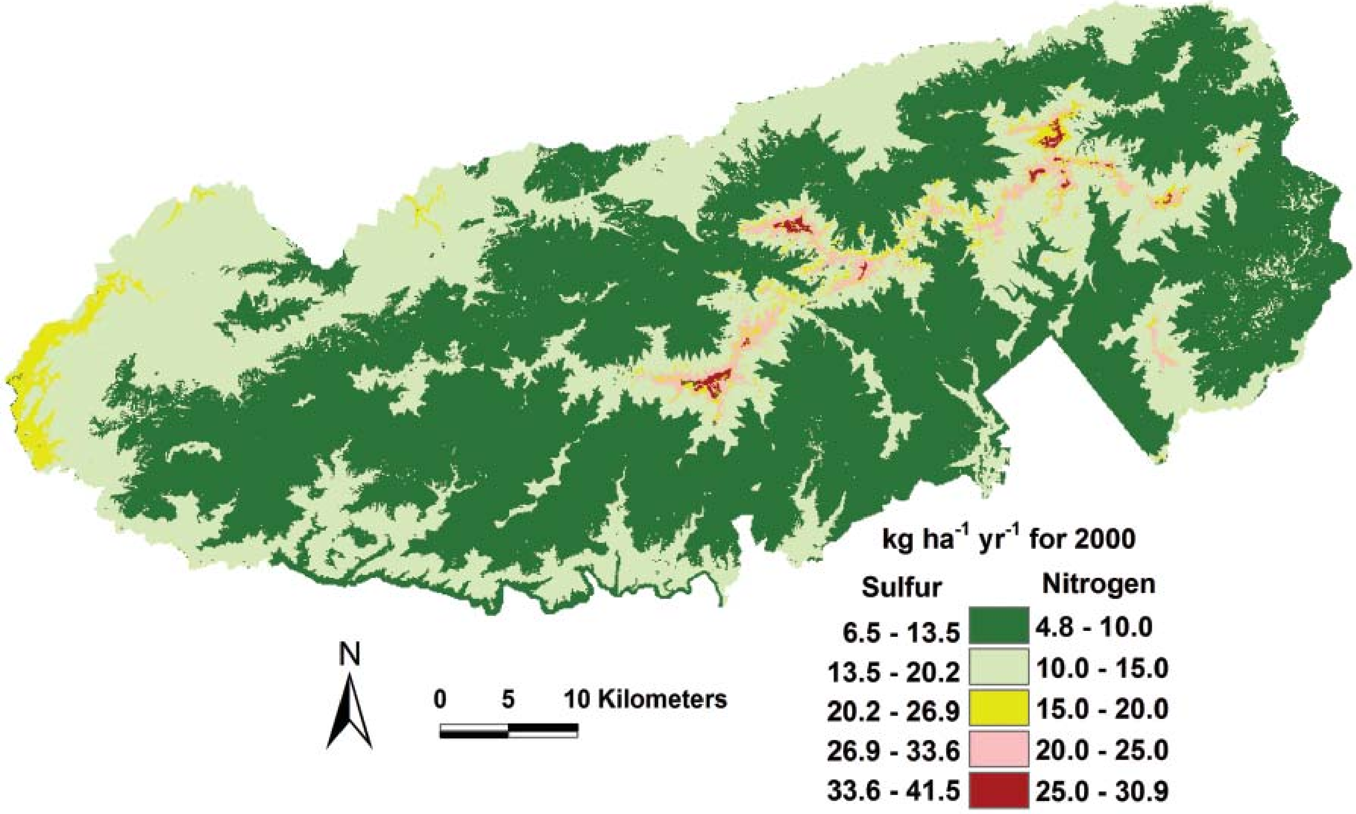

Figure 3.7—Total (wet, dry, and cloud) inorganic N (and S) deposition estimated for Great Smoky Mountain National Park for the year 2000 (from Weathers et al. 2006).

CMAQ estimates greater than CASTNET estimates, suggesting that dry deposition velocities applied to air concentration data for the two different methods vary (these analyses based on Weathers and Lynch 2008).

We note, however, that the CMAQ 2001 model that was available to us at the time of this analysis could not resolve deposition levels below 36 km x 36 km grids compared to deposition that has been measured in the field. For example, Fenn et al. (2000, 2008) have measured 71 kg N ha^{-1} yr^{-1} deposition in the San Bernardino Mountains, an area that, according to the CMAQ 2001 model, would receive only 3 to 5 kg N ha^{-1} yr^{-1}. Similarly, Weathers et al. (2006) have estimated N deposition to be as high as 31 kg N ha^{-1} yr^{-1} at Clingman's Dome, North Carolina (Fig. 3.7), whereas both CMAQ and NADP plus CASTNET deposition for that same location and year would be less than 10 kg N ha^{-1}yr^{-1}. In these cases, the CMAQ estimates are several times lower than on-site measures of deposition that include wet plus dry plus cloud deposition.

In summary, the comparison of N deposition estimates from the CMAQ model to CASTNET plus NADP suggest that either method could be used to generate a comparative estimate of wet plus dry deposition to flat, homogenous terrain (Fig. 3.4). The differences between CMAQ and other estimates of N deposition (Fenn et al. 2003, Weathers et al. 2006) are not surprising, given the inadequacy of dry deposition models in handling complex terrain and the lack of cloud deposition estimates (Weathers et al. 2006), as well as the coarse scale (36 km x 36 km) over which the CMAQ model predicts deposition (Weathers and Lynch 2008).

3.6 Future Research Directions and Gaps in Data

Despite decades of research, accurate estimates of total N deposition are lacking. While various methods for estimating deposition (see above) exist, almost all methods estimate only portions of total N inputs to ecosystems. Not all chemical species of N are measured or monitored, nor are all forms of deposition estimated. Priorities for future deposition research include: expanding monitoring station spatial coverage (especially in high elevation and arid sites and in the West); measuring more chemical species of N; generating better estimates of dry (and, where it is an important component of atmospheric deposition, cloud/fog) inputs; creation of models and maps of deposition across heterogeneous landscapes that incorporate or reference existing modeling and/or monitoring data (e.g., Ollinger et al. 1993, Holland et al. 2005, Weathers et al. 2006); expanding the use of passive sampling devices for chemical species such as NH_3 (e.g., Fenn et al. 2009); coupling empirical measurements (such as throughfall) with monitoring data (e.g., Weathers et al. 2006); and comparing estimates of deposition using different methods.

LITERATURE CITED

Anderson, J.B.; Baumgardner, R.E.; Grenville, S.E. 2006. **Trends in cloud water sulfate and nitrate as measured at two mountain sites in the Eastern United States: Regional contributions and temporal changes compared with changes in emissions, 1986-1999.** Atmospheric Environment. 40(23): 4423-4427.

Anderson, J.B.; Baumgardner, R.E.; Mohnen, V.A.; Bowser, J.J. 1999. **Cloud chemistry in the eastern United States, as sampled from three high-elevation sites along the Appalachian Mountains.** Atmospheric Environment. 33(30): 5105-5114.

Baumgardner, R.E.; Isil, S.S.; Lavery, T.F.; Rogers, C.M.; Mohnen, V.A. 2003. **Estimates of cloud water deposition at mountain acid deposition program sites in the Appalachian Mountains.** Journal of the Air and Waste Management Association. 53(3): 291-308.

Byun, D.W.; Ching, J.K.S., eds. 1999. **Science algorithms of the EPA models-3 Community Multiscale Air Quality model (CMAQ) modeling system.** EPA/600/R-99/030. Washington, DC: U.S. Environmental Protection Agency. Available at http://www.epa.gov/asmdnerl/CMAQ/CMAQscienceDoc.html. (Accessed May 12, 2010).

Byun, D.; Schere, K.L. 2006. **Review of the governing equations, computational algorithms, and other components of the Models-3 Community Multiscale Air Quality (CMAQ) modeling system.** Applied Mechanics Reviews. 59: 51-77.

Driscoll, C.T.; Lawrence, G.; Bulger, A.; Butler, T.; Cronan, C.; Eagar, C.; Lambert, K.; Likens, G.; Stoddard, J.; Weathers; K. 2001. **Acidic deposition in the northeastern US: Sources, inputs, ecosystem effects, and management strategies.** BioScience. 51(3): 180-198.

Driscoll, C.T.; Whitall, D.; Aber, J.; Boyer, E.; Castro, M.; Cronan, C.; Goodale, C.; Groffman, P.; Lambert, K.; Lawrence, G.; Ollinger, S. 2003. **Nitrogen pollution in the northeastern United States: Sources, effects, and management options.** BioScience. 53(4): 357-374.

Ewing, H.A.; Weathers, K.C.; Templer, P.H.; Dawson, T.E.; Firestone, M.K.; Elliott, A.; Boukili, V. 2009. **Fog water and ecosystem function: Heterogeneity in a California redwood forest.** Ecosystems.12: 417-433.

Fenn, M.E.; Bytnerowicz, A. 1997. **Summer throughfall and winter deposition in the San Bernardino Mountains in southern California.** Atmospheric Environment. 31(5): 673-683.

Fenn, M.E.; Poth, M.A. 2004. **Monitoring nitrogen deposition in throughfall using ion exchange resin columns: A field test in the San Bernardino**

Mountains. Journal of Environmental Quality. 33: 2007-2014.

Fenn, M.E.; Haeuber, R.; Tonnesen, G.S.; Baron, J.S.; Grossman-Clarke, S.; Hope, D.; Jaffe, D.A.; Copeland, S.; Geiser, L.; Rueth, H.M.; Sickman, J.O. 2003. **Nitrogen emissions, deposition, and monitoring in the western United States.** BioScience. 53(4): 391-403.

Fenn, M.E.; Jovan, S.; Yuan, F.; Geiser, L.; Meixner, T.; Gimeno, B.S. 2008. **Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests.** Environmental Pollution. 155(3): 492-511.

Fenn, M.E.; Poth, M.A.; Aber, J.D.; Baron, J.S.; Bormann, B.T.; Johnson, D.W.; Lemly, A.D.; McNulty, S.G.; Ryan, D.E.; Stottlemyer, R. 1998. **Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies.** Ecological Applications. 8(3): 706-733.

Fenn, M.E.; Poth, M.A.; Schilling, S.L.; Grainger, D.B. 2000. **Throughfall and fog deposition of nitrogen and sulfur at an N-limited and N-saturated site in the San Bernardino Mountains, southern California.** Canadian Journal of Forest Research. 30(9): 1476-1488.

Fenn, M.E.; Sickman, J.O.; Bytnerowicz, A.; Clow, D.W.; Polotch, N.P.; Pleim, J.E.; Tonnesen, G.S.; Weathers, K.C.; Padgett, P.E.; Campbell, D.H. 2009. **Methods for measuring atmospheric nitrogen deposition inputs in arid and montane ecosystems of western North America.** In: Legge, A.H., ed. Developments in environmental science, Volume 9. Amsterdam, The Netherlands: Elsevier: 177-227.

Holland, E.A.; Braswell, B.H.; Selzman, J.; Lamarque, J-F. 2005. **Nitrogen deposition onto the United States and western Europe: Synthesis of observations and models.** Ecological Applications. 15(1): 38-57.

Ito, M.; Mitchell, M.J.; Driscoll, C.T. 2002. **Spatial patterns of precipitation quantity and chemistry and air temperature in the Adirondack region of New York.** Atmospheric Environment. 36(6): 1051-1062.

Johnson, D.W.; Lindberg, S.E., eds. 1993. **Atmospheric deposition and forest nutrient cycling: A synthesis of the integrated forest study.** New York, NY: Springer Verlag. 707p.

Lovett, G.M. 1994. **Atmospheric deposition of nutrients and pollutants in North America: an ecological perspective.** Ecological Applications. 4(4): 629-650.

Miller, E.K.; Friedland, A.J.; Arons, E.A.; Mohnen, V.A.; Battles, J.J.; Panek, J.A.; Kadlecek, J.; Johnson, A.H. 1993. **Atmospheric deposition to forests along an elevational gradient at Whiteface Mountain, NY, USA.** Atmospheric Environment Part A-General Topics. 27(14): 2121-2136.

NADP (National Atmospheric Deposition Program). 2009. **Atmospheric integrated research monitoring network.** Available at http://nadp.sws.uiuc.edu/airmon/. (Accessed May 17, 2010).

Nanus, L.; Campbell, D.H.; Ingersoll, G.P.; Clow, D.W.; Mast, M.A. 2003. **Atmospheric nitrogen deposition maps for the Rocky Mountains.** Atmospheric Environment. 37(35): 4881-4892.

NEG/ECP (New England Governors and Eastern Canadian Premiers). Forest Mapping Group. 2003. **Assessment of forest sensitivity to nitrogen and sulfur deposition in New England and eastern Canada.** Conference of New England Governors'/Eastern Canadian Premiers' Forest Mapping Group pilot phase report. http://www.ecosystems-research.com/fmi/VT-NF-Forest-Sensitivity-Report-Executive-Summary.pdf (Accessed April 12, 2011).

Neff, J.C.; Holland, E.A.; Dentener, F.J.; McDowell, W.H.; Russel, K.M. 2002. **The origin, composition and rates of organic nitrogen deposition: A missing**

piece of the nitrogen cycle? Biogeochemistry. 57(1): 99-136.

Ollinger, S.V.; Aber, J.D.; Lovett, G.M.; Millham, S.E.; Lathrop, R.G.; Ellis, J.M. 1993. **A spatial model of atmospheric deposition for the northeastern U.S. Ecological Applications.** 3(3): 459-472.

Simkin, S.M.; Lewis, D.N.; Weathers, K.C.; Lovett, G.M.; Schwarz, K. 2004. **Determination of sulfate, nitrate and chloride in throughfall using ion-exchange resins.** Water, Air and Soil Pollution. 153: 343-354.

US EPA (U.S. Environmental Protection Agency). 2001. **CMAQ Model performance evaluation.** Research Triangle Park, NC: U.S. Environmental Protection Agency.

US EPA (U.S. Environmental Protection Agency). 2007. **CASTNET 2007 Annual Report.** Available at http://epa.gov/castnet/javaweb/docs/annual_report_2007.pdf (Accessed March 18, 2011).

US EPA (U.S. Environmental Protection Agency). 2009. **Community multiscale air quality.** Washington, DC: U.S. Environmental Protection Agency. Available at http://www.epa.gov/amad/CMAQ/index.html. (Accessed May 17, 2010).

US EPA (U.S. Environmental Protection Agency). 2010. **Clean air status and trends.** Washington, DC: U.S. EPA. Available at http://www.epa.gov/castnet. (Accessed May 17, 2010).

Weathers, K.C.; Likens, G.E.; Bormann, F.H.; Bicknell, S.H.; Bormann, B.T.; Daube, B.C. Jr.; Eaton, J.S.; Galloway, J.N.; Keene, W.C.; Kimball, K.D.; McDowell, W.H.; Siccama, T.G.; Smiley, D.; Tarrant, R. 1988. **Cloud water chemistry from ten sites in North America.** Environmental Science and Technology. 22(9): 1018-1026.

Weathers, K.C.; Likens, G.E.; Butler, T.J. 2007. **Acid rain.** In: Rom, W.N., ed. Environmental and occupational medicine. Philadelphia, PA: Lippincott Williams & Wilkins: 1507-1520.

Weathers, K.C.; Lovett, G.M.; Likens, G.E. 1992. **The influence of a forest edge on cloud deposition.** In: Schwartz, S.E.; Slinn, W.G.N., eds. Proceedings of the fifth international conference on precipitation scavenging and resuspension. Washington, DC: Hemisphere Publishing Corp: 1415-1423.

Weathers, K.C.; Lovett, G.M.; Likens, G.E. 1995. **Cloud deposition to a spruce forest edge.** Atmospheric Environment. 29(6): 665-672.

Weathers, K.C.; Lovett, G.M.; Likens, G.E.; Caraco, N.F.M. 2000a. **Cloudwater inputs of nitrogen to forest ecosystems in southern Chile: Forms, fluxes and sources.** Ecosystems. 3: 590-595.

Weathers, K.C.; Lovett, G.M.; Likens, G.E.; Lathrop, R. 2000b. **The effect of landscape features on deposition to Hunter Mountain, Catskill Mountains, New York.** Ecological Applications. 10(2): 528-540

Weathers, K.C.; Lynch, J.A. 2008. **How much atmospheric deposition across the US: Comparison of N and S deposition estimates.** Eos, Transactions, American Geophysical Union. 89(53) Supplement, abstract B42A-01.

Weathers, K.C.; Simkin, S.M.; Lovett, G.M.; Lindberg, S.E. 2006. **Empirical modeling of atmospheric deposition in mountainous landscapes.** Ecological Applications. 16(4): 1590-1607.

4 METHODS

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4.1 Approach

We present an up-to-date review of current knowledge relating nitrogen (N) inputs to ecological effects, from published literature, reports, and some recent unpublished studies. Our goal is to summarize research on ecosystems across the United States. We include N gradient, long-term, and fertilizer studies; for fertilizer studies, we focus on those with low N additions (i.e., close to ambient deposition). We include both publications that report a response and those that report the lack of response.

Empirical critical loads are determined by recording the deposition level at which detrimental ecological effects have occurred in the field. The lowest deposition level at which a detrimental response occurs is considered the critical load. In cases where there is a variation in the level of N input that causes a given response, a range for the critical load is often reported (e.g., Bobbink et al. 2003). Empirical critical loads are useful because they can be used to determine the critical load based on the best available information for an ecosystem type when data are not available at a given site. Under the best circumstances, empirical critical loads link observed ecosystem response to deposition.

Disadvantages of empirical critical loads stem from their reliance on observed cause-and-effect responses rather than an understanding of a process or mechanism. Because the observed responses to a given deposition level are based on past deposition scenarios, they may not be indicative of the response that might occur in the future. For example, if a response is observed to a given rate of deposition (or fertilization) after a certain number of years, it is possible that a lower deposition over a longer time period would cause the same detrimental effect. For critical loads derived from gradient studies, generally, the assumption is that the N deposition rate is the major factor contributing to changes in a particular response (e.g., foliar N concentrations, species richness) along the gradient, even though soil, climate, and biogeochemical factors may also influence the response. For lichens (see section 4.3), these factors were taken into account. For critical loads derived from fertilization studies, the effects of added N are isolated through controlled experimentation; however, the scale of these experiments is often fairly small and their numbers are limited, making extrapolation to the ecoregion level difficult. Another pitfall of the empirical approach is that the observed response may be unique to the site at which it was measured (because of location-specific disturbance history or site characteristics such as soil thickness) and may not be truly representative of the ecosystem type. Observations used to determine or estimate empirical critical loads are generally made over a relatively short term. In contrast, the residence time of N within major ecosystem compartments (e.g., soil, sediment, forest biomass) is generally on the order of decades to centuries. As a result, empirical critical loads provide a limited understanding of true ecosystem response to sustained elevated N inputs or their response to changes in these inputs. Critical loads dynamic modeling addresses some of the disadvantages of the empirical critical loads approach. However, current modeling capabilities do not enable large scale mechanistic modeling of critical loads for ecoregions across the United States. Thus we utilize multiple sources of current empirical information (multiple gradient and fertilization studies) to determine critical loads. To address these uncertainties, we present the ranges of responses observed. Where we have estimated an empirical critical load for N, we have made some assessment of the reliability of that estimate. We used the same categories for reliability as those used in European assessments (Bobbink et al. 2003, UBA 2004):

- reliable ##: when a number of published papers of various studies show comparable results
- fairly reliable #: when the results of some studies are comparable
- expert judgment (#): when very few or no empirical data are available for this type of ecosystem. The N critical load is then based

upon expert judgment and knowledge of ecosystems, which are likely to be more or less comparable with this ecosystem.

In all cases, accurate estimates of N deposition are essential for developing useful empirical critical loads of N.

In presenting the ecosystem responses and critical loads, we identify the response parameter and the threshold. Within an ecosystem, there could be very different types of response parameters; hence the critical load or input which induces each response may vary considerably. This poses a challenge in setting a critical load for the ecosystem. In some cases, it may be appropriate simply to choose the lowest critical load value, while in other cases, there may be some responses more characteristic or of greater concern which should be considered the primary indicator for that ecosystem. Furthermore, comparing critical loads that were set using different critical responses presents a challenge.

Several criteria should be determined before assigning empirical critical loads to an ecosystem type. There are four key criteria to consider: what response variables are relevant, what types of studies are acceptable, how to choose the value for the critical load, and if and when we can extrapolate conclusions beyond the study area.

Approaches for setting empirical critical loads for N for specific ecosystem components are discussed below. Approaches for setting critical loads for aquatic ecosystem components are presented in Chapters 17 and 18.

4.2 Mycorrhizal Fungi

4.2.1 Response Variables

The impacts of N deposition on arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF) have been determined primarily by examining the changes in percent root colonization, soil spore density (AMF) or sporocarp production (EMF), spore or sporocarp species composition, DNA or immunologic assays of species composition and structure on root tips or of hyphae in soils, and functional analysis of fungal communities. Data from naturally occurring, anthropogenic N deposition gradients have been particularly useful in determining critical loads because of the ability to fit response curves. In deciding if N inputs are affecting mycorrhizal fungi, we focused mostly on community response (species richness and community structure changes) and functional responses. However, where these are lacking, we considered biomass responses, giving them less weight than the other factors.

4.2.2 Acceptable Studies

For information sources, we put more weight on results of long-term (>10 yr) fertilizations and gradient studies rather than short-term fertilizations, as the latter are unlikely to represent a steady-state response to N. Gradients have the advantage over typical two-level experiments in that response curves and threshold responses can be derived. However, even a two-level study with only a control and treatment can put an upper bound on critical loads if there is a response and lower bound if there is no response. Therefore we have included some data from experimental sources, recognizing their limitations.

4.2.3 How the Critical Load Value was Chosen

For our purposes, any detectable deviation in mycorrhizal community structure or composition from the baseline state is considered to have crossed a critical load threshold. For example, if the best-fit response curve in an N deposition gradient indicates a linear response starting from the baseline, then any addition above the baseline would exceed the critical load. If, in contrast, the data suggest a nonlinear response with a threshold below which no directional community change can be detected, then the critical load is set at this threshold. The criterion of any detectable directional change is a very strict criterion that could be open to debate, but it has the merit of being relatively easy to define.

One justification for using the community change criterion is that there appear to be functional consequences for host plants arising from N-driven community change. This has been determined by growing plants using inoculum that has been subject to elevated N. Nitrogen-affected inoculum not only has lower spore density, but also has lower diversity and shifts in species composition (Egerton-Warburton and Allen 2000, Egerton-Warburton et al. 2007, Sigüenza et al. 2006). Growth response studies showed that native late successional plants had reduced biomass with N-affected inoculum, while early successional plants were unaffected or sometimes had increased biomass. This indicates that long-term trends in losses of late seral (successional) vegetation and replacement by early seral or invasive species were in part promoted by shifts in mycorrhizal fungal species composition due to elevated N deposition (Corkidi et al. 2002, Sigüenza et al. 2006).

4.2.4 Extrapolation

For ecological regions for which there are no data, we have cautiously extrapolated our critical load values to regions that have similar biota, climate, and soils. For example, we have suggested that ectomycorrhizal community response to N in an Engelmann spruce forest in the Rockies (Northwestern Forested Mountains ecoregion), for which there are no data of which we are aware, would be similar to that of communities in Alaskan white spruce (Marine West Coast Forest ecoregion) and northeastern red spruce-balsam fir (Northern Forest ecoregion) forests, for which we do have data. Thus we have used, with qualification, the critical loads for the latter two as the basis for a provisional estimate for the critical load for the former.

4.3 Lichens and Bryophytes

Lichens and bryophytes are among the most sensitive bioindicators of N in terrestrial ecosystems (Blett et al. 2003, Bobbink et al. 2003, Fenn et al. 2003, Vitt et al. 2003). Consequently, the implementation of critical loads protective of the most sensitive lichens and bryophytes is likely to prevent undesired impacts to the broader terrestrial ecosystem by also protecting less N-sensitive vegetation. Protecting the integrity of lichen and bryophyte communities, moreover, ensures preservation of their contribution to biological diversity and their varied ecological roles in nutrient cycling, hydrological flux, and supply of wildlife forage and nesting materials (McCune et al. 2007).

Lichens, especially forest epiphytes, have been systematically surveyed for air quality monitoring purposes by the U.S. Forest Service Forest Inventory Analysis (FIA) program and other U.S. Forest Service and National Park Service efforts, and many of these data are available electronically: the NPLichen database (Bennett and Wetmore 2005a, 2005b; U.S. Geologic Survey 2010), the NPElement database (U.S. Geologic Survey 2009), the U.S. Forest Service Forestry Inventory and Analysis Program (U.S. Forest Service 2005, 2007), and the U.S. Forest Service National Lichens and Air Quality Database (U.S. Forest Service n.d.). No equivalent efforts exist for bryophytes in the United States. Therefore, apart from the Tundra and Taiga chapters (Chapters 5 and 6) (which extrapolate some critical loads from European and Canadian studies) and the Desert chapter (Chapter 12) (in which bryophytes are integral components of cryptogamic crusts), we primarily reference lichen studies.

4.3.1 Terminology

Lichens are adapted to different levels of N availability and most species can be sorted into one of three N indicator groups: *oligotrophs* are more or less restricted to nutrient-poor environments; *mesotrophs* have an intermediate nutrient requirement; and *eutrophs* thrive in nutrient-enhanced environments. A few lichens have broad ecological amplitudes and tolerate a large range of N availability. As anthropogenic N is added to background N levels, the excess N favors the small, cosmopolitan eutrophs at the expense of native oligotrophic and mesotrophic forage and N_2-fixing lichens (McCune and Geiser 2009).

To avoid possible confusion from variable terminology in the literature, we consistently used the broad terms 'oligotroph', 'mesotroph' and 'eutroph' in lieu of the more classic lichenological terms, 'acidophyte', 'neutrophyte', and 'nitrophyte or nitrophile', respectively. This is necessary because most North American studies of N deposition effects have not considered substrate pH, deposition pH, or N source when classifying lichens to N indicator groups. Because low-fertility environments are frequently dominated by acidic conifer substrates, and moderate- to high-fertility environments generally include more hardwoods with more neutral bark and more nutrient-enriched canopy drip, the classic and broad terms usually correspond to similar lichen lists (Jovan 2008, Geiser et al. 2010)

Common names for lichens follow the Natural Resources Conservation Service PLANTS database (NRCS 2011). Because many lichen common names in PLANTS are not unique, the scientific name and authority are specified when a common name is used for the first time within a chapter. Scientific nomenclature follows Esslinger (2010).

4.3.2 Response Variables

To identify critical loads for the Marine West Coast Forests, Northwest Forested Mountains, and Mediterranean California ecoregions, we used two epiphytic lichen responses that are closely linked to ecological impact: N concentration in lichen thalli, and composition of lichen communities. Changes in thallus N concentrations and physiology usually precede measurable changes in lichen community composition. Local N deposition is correlated with N concentrations of lichen thalli, which passively accumulate N in excess of nutritional requirements (Bruteig 1993, Søchting 1995). This response is typically linear at low N deposition levels (Glavich and Geiser 2008). The upper limit of thallus N concentrations among clean sites is typically used as the response threshold. Increasing N deposition, likewise, causes changes in lichen community composition—such as a decrease in the number of oligotrophic species and an increase in the number of eutrophic species.

For the Taiga, Tundra, and North American Desert ecoregions, we included physiological and morphological measures of lichen status, such as changes in photosynthetic capacity (e.g., chlorophyll pigment ratios, carbon dioxide (CO_2) uptake), membrane integrity, amounts of characteristic protective chemicals (e.g., usnic acid), apportionment of resources to algal vs. fungal partners, ultrastructural integrity, or growth rates.

4.3.3 Acceptable Studies

As with the mycorrhizal fungi, we primarily relied on gradient studies as information sources rather than short-term fertilizations. In addition, studies of epiphytes are considered superior to studies of ground-dwelling species due to epiphytes' greater independence from soil nutrients. For the Rocky Mountain, Marine West Coast Forests, and Mediterranean California ecoregions, we were fortunate to obtain community data from regional, systematic surveys of epiphytic lichens, primarily conducted by the FIA program. Most of the physiological studies were N-addition studies. Since they were short-term additions or added N to already elevated background deposition levels, we feel they do not adequately predict long-term effects. However, they do prescribe upper limits for critical loads.

4.3.4 How the Critical Load Value was Chosen

We determined the critical load by identifying the level of N deposition which led to specific ecological impacts (changes in community composition and increased thallus N concentration) using the datasets described above. The ecological impact at any N deposition level was quantified by doing a regression on N deposition against proportions of oligotrophic, mesotrophic, and eutrophic species, or an index called the "air score" (Geiser and Neitlich 2007, Jovan 2008). The value of N deposition at the ecological threshold is the critical load. The ecological thresholds were community shift toward a higher proportion of eutrophic species and elevated thallus N concentration. The exact value for the threshold thallus N concentration was typically set based on the 97.5 percent quantile for clean sites. The 97.5 percent quantile is the thallus N concentration below which 97.5 percent of clean site thallus N concentrations fall. The exact threshold for species composition varied because the baseline (species composition at an unpolluted site) varied in different ecosystems (see Table 4.1 and section 4.3.5). Because all the lichen response measures were linear with respect to deposition, we favor response thresholds high enough to allow for natural variability across clean sites, but low enough to protect communities from a shift in dominance of indicator groups. We used the 95 percent confidence interval as the range for the critical load.

Forest Inventory and Analysis (FIA) Program lichen-community based "air scores" are a measure of air quality generated from lichen community data and

Table 4.1—The input variables, assumptions, and rationale behind the calculation of lichen critical loads for U.S. ecoregions, derived from the Marine West Coast Forest model: Critical load *kg N* ha^{-1} yr^{-1}= (0.0918 + 0.0024 [mean annual precipitation] + threshold air score)/0.1493. Precipitation is estimated from PRISM 1961-1990 annual average precipitation maps; lichen response thresholds are based on expert opinion (Geiser et al. 2010).

Ecoregion	Mean ann. precip. (cm) Min	Mean ann. precip. (cm) Max	Air score	Biological response threshold Minimum % oligotrophs	Biological response threshold Maximum % eutrophs	Rationale/Assumptions
Taiga (US)	20	80	0.02-0.21	41	27	Acidic coniferous substrates, cold temperatures favor oligotrophs. Therefore, community response threshold set with comparatively high oligotroph and low eutroph composition.
Northern Forests (US)	100	240	0.21	30-41	27-34	Climate and forest type similar to Marine West Coast Forest. Therefore, use same threshold. Synergistic or confounding effects of acid deposition of S and N, which is much greater here than Marine West Coast Forest, is not considered in this analysis.
Northwestern Forested Mountains: Alaska	30	80	0.02-0.21	41	27	Lower thresholds needed for Alaska because of cooler temperatures (see Taiga rationale).
Marine West Coast Forests	44	451	0.21	30-41	27-34	Model was developed for this region by Geiser et al. (2010)
Northwestern Forested Mountains: non-Alaska	30	203	0.21-0.49	25-40	27-47	Lower and upper thresholds calculated by Fenn et al. 2008. Low humidity and high temperatures favorable to eutrophs and unfavorable to oligotrophs except in high elevation fog zones.
Eastern Temperate Forest: eastern hardwoods	71	305	0.33	25-30	34-47	Humid climate favors oligotrophs but hardwood dominance favors mesotrophs and eutrophs, so response threshold allows comparatively more eutrophs. Synergistic or confounding effects of acid deposition of S and N are not considered in this analysis.
Eastern Temperate Forest: southeast Coastal Plain	102	178	0.21-0.33	30	34	Humid climate and acidic conifer substrates favor oligotrophs. Warm summer temperatures limiting to oligotrophs? Synergistic or confounding effects of acid deposition of S and N are not considered in this analysis.
Mediterranean CA: mixed Conifer Forest	41	127	0.33-0.49	25	47	Climate and forest type closest to Northwestern Forested Mountains--used Fenn et al. 2008 upper threshold to account for comparatively warmer, drier conditions compared to the Sierras.
Mediterranean CA: Chaparral and Central Valley	17	156	0.33-0.49	25	47	Threshold (50% eutrophs) selected from overlay of CMAQ data on Jovan and McCune 2006 analysis of this ecoregion. Hot dry summers, hardwood dominance favors mesotrophs and eutrophs.
Temperate Sierras	30	178	0.49	21-25	47-57	Natural contribution of eutrophs to lichen community composition presumed relatively high due to dry, hot climate.

region-specific interpretive models separating air pollution effects on community composition from climate, elevation and other site effects (Jovan 2008). Models are typically developed from a calibration subset of regional FIA lichen community data using nonmetric multidimensional scaling and Sorenson's distance measure (McCune and Mefford 1999) to ordinate sites in N-dimensional space. With the aid of overlays, regression, scatter plots and other tools, at least two strong gradients can usually be extracted from the ordination: one relating to air quality and a second relating to macroclimate. Air quality and climate are then scored as the distance of the community (site) along the respective gradient. Repeat or additional surveys can be fitted and scored at any time to assess spatial and temporal trends. Finished models are available for the southeastern United States (McCune et al. 1997), California's greater Sacramento Valley (Jovan and McCune 2005) and Sierra Nevada (Jovan and McCune 2006), and western Oregon and Washington (Geiser and Neitlich 2007). In the western United States, nutrient N deposition is considered the dominant air pollutant affecting lichen communities (Jovan 2008, Geiser et al. 2010); in the southeastern United States, N- and S-containing acidifying and fertilizing compounds are considered most influential (McCune et al. 1997).

Lichen community and thallus N concentration appear to correlate better with N concentration (mg L^{-1}) in deposition as opposed to N load (kg ha^{-1} yr^{-1}) (Geiser et al. 2010). Because lichen thalli accumulate and leach N in dynamic equilibrium with concentrations of pollutants in precipitation, precipitation can have a diluting effect on the concentrations of pollutants to which lichens are exposed. Thus, the same load of N deposited in a higher volume of precipitation will have a smaller impact. Therefore, we accounted for precipitation volume when developing lichen critical loads based on measurements of bulk (NADP-style) or modeled N deposition.

In the Marine West Coast Forests, Northwest Forested Mountains, and Mediterranean California ecoregions, lichen-based critical loads were derived by correlating lichen responses (described above) to Interagency Monitoring of Protected Visual Environments (IMPROVE[2]; fine particulate ammonium nitrates (NH_4NO_3) and sulfates ($(NH_4)_2SO_4$) in air) and NADP[3] monitoring networks (wet deposition of inorganic N), 10 year total annual average deposition of 16 N-species modeled by CMAQ[4], or *in-situ* deposition measurements of ammonium (NH_4^+) and nitrate (NO_3^-) in bulk and canopy throughfall.

4.3.5 Extrapolation

To make initial estimates of lichen-based critical loads for N in forested ecological regions where existing analyses were lacking, (i.e., Taiga, Northern Forests, Eastern Forests, and the Temperate Sierras), and to encompass more of the Northwest Forested Mountains ecoregion, we applied a model that was developed in western Oregon and Washington for the Marine West Coast Forests ecoregion (Geiser et al. 2010). This model has been shown to replicate previously published critical loads for wet oak woods of Scotland,

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[2] IMPROVE (Interagency Monitoring of Protected Visual Environments) monitors include an aerosol sampler that measures total fine particulate (<2.5 µm diameter) NO_3^- and sulfate (SO_4^-) concentrations over 24 hours every third day. These anions are presumed balanced by NH_4^+ and best correlations between fine particulate N and lichen-based air scores were observed when mean annual averages included N from both sources (IMPROVE 2010; University of California, Davis 1995).

[3] NADP (National Atmospheric Deposition Program); weekly samples of precipitation captured in buckets designed to open during rain and snow events are analyzed for concentrations (mg L^{-1}) and total wet deposition (kg ha^{-1} y^{-1}) of NH_4^+ and NO_3^- and total inorganic N (from NH_4^+ and NO_3^-). Data that meet quality control criteria can be downloaded from the website (NADP 2009).

[4] CMAQ (Community Multiscale Air Quality model). The CMAQ model forecasts wet and dry deposition of 16 primary and secondary N-containing air pollutants: HNO_3, NH_3, NO_2, PAN, NO, RNO_3, PAN2, N_2O_5, HONO, ANH_4I, MA-PAN, ANO_3I, PBZN, ANO_3J, and ANH_4J. Model output accounts for complex interactions among many variables (e.g., landscape, vegetation density, atmospheric chemistry, and climate). Mean annual deposition, based on 1990-1999 emissions data, was calculated on a 36 km grid as described in Porter (2007). For model details, see the online CMAQ science documentation (US EPA 2009). Lichen response was related to the total sum of wet and dry deposition of all 16 air pollutants.

mesic conifer forests of the California Sierras, and dry mixed hardwood-conifer forests of California's Greater Sacramento Valley (Geiser et al. 2010). Input variables required are minimum and maximum mean annual precipitation and a lichen community response threshold (e.g., maximum acceptable percent eutrophs). Mean annual minimum and maximum precipitation within each ecoregion was estimated from Parameter-elevation Regressions on Independent Slopes Model (PRISM) national map of 1971-2000 normals (Daly et al. 2002, PRISM 2010). Expert judgment was used to choose reasonable community response thresholds (Table 4.1). The thresholds are a minimum allowable oligotroph or maximum allowable eutroph percentage of the community composition. Input variables and response threshold justifications are presented in Table 4.1. Basically, forests with hardwood components were assigned a higher response threshold than western Oregon and Washington coniferous forests because the more alkaline bark and richer canopy exudates of hardwoods favor eutrophs. Colder forests were assigned lower response thresholds than warmer forests because native epiphytes are typically oligotrophs adapted to cold- and low-nutrient environments—eutrophs are better adapted to nutrient-concentrated, heat and drought-stressed environments typical of warmer climates. The most problematic areas were the Eastern Forest ecoregion, for which systematically sampled lichen community data exist but are confounded by current or historic levels of N and sulfur (S) deposition and atmospheric concentrations of sulfur dioxide. Because the synergistic effects of multiple pollutants on epiphytic lichens are not well understood, our critical load estimate for eastern forests, based on a western model that accounts for nutrient N deposition alone, are clearly provisional.

4.4 Herbaceous species and shrubs

4.4.1 Response Variables

Responses of herbaceous species to N deposition included changes in species abundances and composition, particularly increases in nitrophilic and invasive species, increases in productivity, and changes in foliar chemistry. In some herbaceous-dominated communities, changes in N cycling and inorganic N leaching below the rooting zone were also used. Typically, the critical loads for these variables were about 10 kg ha^{-1} yr^{-1} above the value estimated from changes in plant composition.

In more impacted ecoregions such as the forested areas of the eastern United States using herbaceous species for critical loads may be problematic, because, as previously stated, N deposition (in combination with S deposition) over the last half century has probably already significantly altered community composition. The critical loads obtained using herbaceous species in these more impacted regions will therefore potentially overestimate the level associated with the initial changes in plant diversity.

4.4.2 Acceptable Studies

We included studies across N deposition gradients and low level N fertilization experiments to evaluate herbaceous species and shrub responses to N deposition. We excluded fertilization studies when single input rates of more than double the current ambient level were used. As noted above, an implicit assumption was made that the primary factor influencing variation in herbaceous species composition in gradient studies was N deposition. We considered studies that included a range of N experimental inputs to be more reliable (##) than those which used single fertilization values or gradient studies.

4.4.3 How the Critical Load Value was Chosen

The critical load value was estimated as the range between the input level at which no response was observed and the lowest level at which an alteration in species abundance or changes in N cycling occurred. In some cases, the input level where a response occurred could be quantitatively assessed by fitting the response data to simple mathematical functions (Bowman et al. 2006). Quantitative changes in species composition for both gradient and N fertilization studies are best determined using point-intercept or frequency estimates. Subtle changes may be missed or misinterpreted using more subjective estimates (e.g., visual estimates of cover). An increase in nitrophilic species cover was used to determine critical loads in tallgrass prairies, Mediterranean shrublands and deserts, and alpine tundra. Changes in community structure, using ordination analysis, was also used in alpine vegetation. In fire-prone western ecosystems, the increased productivity of invasive grasses has promoted increased fire risk, and the productivity threshold under N deposition that promotes fire has been set as the critical load (Rao et al. 2010). Decreases in the diversity of understory herbaceous species were used in eastern forests, again indicating that the initial increase in nitrophilic species has already occurred in these more impacted ecosystems.

Gradient studies were used for only a few ecoregions (e.g., coastal sage scrub). Critical loads were estimated as a range below the deposition rate where significant increases in nitrophilic species occurred. In general, this approach has not been widely used for herbaceous species composition due in large part to the multitude of factors, other than N deposition, that influence herbaceous species composition and chemistry.

Critical loads based on changes in N cycling in an alpine ecosystem were estimated as below the N inputs where significant changes in net N mineralization, nitrification, and inorganic N leaching below the rooting zone were observed

4.5 Forests

4.5.1 Response Variables

The variables considered for forests include changes in percent N in trees and soils, alterations in soil N cycling, which lead to elevated NO_3^- losses, increased susceptibility to secondary stressors (freezing, drought, pests), declines in tree health, changes in tree growth, and increased mortality. We elected to include increases in tree growth as a response, because it is an indication of alteration by N inputs. In Europe, in contrast, growth responses were not considered in setting empirical critical loads for forest ecosystems (Bobbink et al. 2003). In setting the critical load, we only included declines in growth and survivorship and increases in mortality. There is considerable variation in N concentration in tissue by species and site and over time. Thus, setting a threshold value for tissue N concentration as was done for lichens is difficult. Because repeated surveys at the same site are not often available, establishing a value for acceptable percentage increase typically is not feasible.

Changes in species composition, such as those reported for communities of shorter-lived organisms, are infrequently observed for trees. We included some studies that reported decreased tree health and growth and increased mortality, which is observed only rarely. Therefore, even more for trees than other organisms, it is important to understand the mechanisms leading to catastrophic changes to be able to identify early indicators of change.

4.5.2 Acceptable Studies

We included N gradient, fertilization, and long-term studies. Results from long-term, low-level fertilization and gradient studies are considered the most reliable. The additions of N in most forest fertilization studies are much greater than ambient deposition. While we note these high N fertilization studies in our discussion of biomass responses to N deposition, they are typically not relevant for calculating the critical load. Gradient studies have the advantage of demonstrating changes in real time. When a single gradient study was used, the results could not be considered more than fairly reliable, #. When many gradient studies were included (e.g., Aber et al. 2003), the results could be considered reliable, ##.

4.5.3 How the Critical Load Value was Chosen

In some cases (Eastern Temperate and Northern Forest ecoregions) with extensive datasets, we were able to identify an inflection point on the response curve, the point at which the response begins, and thereby identify the critical load with high certainty. We used this approach for NO_3^- losses from forest ecosystems which have been shown to increase above a threshold N deposition (Aber et al. 2003, Wright et al. 2001). In regions with sparser NO_3^- loss data (Northwestern Forested Mountains ecoregion), we were able to identify only the range within which the critical load is most likely to lie. For gradient studies without a clear inflection point, for example, the tree growth and mortality studies in eastern and northern forests, we set the critical load to be greater than the low end of the range of deposition over which the response was observed. For fertilization studies, we identified the critical load as lying in the range between the highest N input for which we observed no response and the lowest N input for which we observed a response.

4.5.4 Extrapolation

For the Tropical and Subtropical Humid Forests ecoregion for which there are no data, we have cautiously extrapolated our critical load values from regions that have similar biota, climate, and soils. Thus we have used, with qualification, the critical loads for the Southeastern Coastal Plain forests as the basis for a provisional estimate for the critical load for the Tropical and Subtropical Humid Forests. We did not extrapolate critical loads for forests to other ecoregions.

4.6 Other Ecosystems

Methods for the Great Plains, North American Deserts, Tropical and Subtropical Humid Forests, Wetlands and Inland surface waters are described in those chapters.

LITERATURE CITED

Aber, J.D.; Goodale, C.L.; Ollinger, S.V.; Smith, M.L.; Magill, A.H.; Martin, M.E.; Hallett, R.A.; Stoddard, J.L. 2003. **Is nitrogen deposition altering the nitrogen status of northeastern forests?** BioScience. 53: 375-389.

Bennett, J.P.; Wetmore, C.M. 2005a. **Lichens of the U.S. National Parks.** The Bryologist. 108(4): 544-553.

Bennett, J.P.; Wetmore, C.M. 2005b. **NPLichen: A database of lichens in the US National Parks. 2005 Final Report.** Available at http://www.nbii.gov/files/nplichen/npl_report.pdf (Accessed May 12, 2010).

Blett, T.; Geiser, L.; Porter, E. 2003. **Air pollution-related lichen monitoring in national parks, forests, and refuges; guidelines for studies intended for regulatory and management purposes.** Tech. Rep. NPS-D2292. Denver, CO: U.S. Department of the Interior, National Park Service, Air Resources Division and U.S. Fish and Wildlife Service, Air Quality Branch; Portland, OR: U.S. Department of Agriculture, Forest Service. 26 p.

Bobbink, R.; Ashmore, M.; Braun, S.; Flückinger, W.; van den Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbick, R., eds. Empirical critical loads for nitrogen. Environmental Documentation No. 164. Berne, Switzerland: Swiss Agency for the Environment, Forests, and Landscape: 43-170.

Bowman, W.D.; Larson, J.R.; Holland, K.; Wiedermann, M.; Nieves, J. 2006. **Nitrogen critical loads for alpine vegetations and ecosystem response- are we there yet?** Ecological Applications. 16(3): 1183-1193.

Bruteig, I.E. 1993. **The epiphytic lichen *Hypogymnia physodes* as a biomonitor of atmospheric nitrogen and sulphur deposition in Norway.** Environmental Monitoring and Assessment. 26: 27-47.

Corkidi, L.; Rowland, D.L.; Johnson, N.C.; Allen, E.B. 2002. **Nitrogen fertilization alters the functioning of arbuscular mycorrhizas at two semiarid grasslands.** Plant and Soil. 240: 299-310.

Daly, C.; Gibson, W.P.; Taylor, G.H.; Johnson, G.L.; Pasteris, P. 2002. **A knowledge-based approach to the statistical mapping of climate.** Climate Research. 22: 99-113.

Egerton-Warburton, L.M.; Allen, E.B. 2000. **Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient.** Ecological Applications. 10: 484-496.

Egerton-Warburton, L.M.; Johnson, N.C.; Allen, E.B. 2007. **Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands.** Ecological Monographs. 77: 527-544.

Esslinger, T.L. 2010. **A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada.** Fargo, ND: North Dakota State University. Available at http://www.ndsu.edu/pubweb/~esslinge/chcklst/chcklst7.htm. (Accessed June 18, 2010).

Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W.; Neitlich, P. 2003. **Ecological effects of nitrogen deposition in the western United States.** BioScience. 53: 404-420.

Fenn, M.E.; Jovan, S.; Yuan, F.; Geiser, L.; Meixner, T.; Gimeno, B.S. 2008. **Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests.** Environmental Pollution. 155: 492-511.

Glavich, D.A.; Geiser, L.H. 2008. **Potential approaches to developing lichen-based critical loads and levels for nitrogen, sulfur and metal-containing atmospheric pollutants in North America.** The Bryologist. 111: 638–649.

Geiser, L.H.; Jovan, S.E.; Glavich, D.A.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in western Oregon and Washington Forests, USA.** Environmental Pollution. 158: 2412-2421.

Geiser, L.H.; Neitlich, P.N. 2007. **Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens.** Environmental Pollution. 145: 203-218.

Jovan, S. 2008. **Lichen bioindication of biodiversity, air quality, and climate: baseline results from monitoring in Washington, Oregon, and California.** Gen. Tech. Rep. PNW -737. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 115 p.

Jovan, S.; McCune, B. 2005. **Air-quality bioindication in the greater Central Valley of California, with epiphytic macrolichen communities.** Ecological Applications 15: 1712-1726.

Jovan, S.; McCune, B. 2006. **Using epiphytic macrolichen communities for biomonitoring ammonia in forests of the greater Sierra Nevada, California.** Water, Air and Soil Pollution. 170: 69-93.

IMPROVE (Interagency Monitoring of Protected Visual Environments). N.d. **Data resources.** Available at http://vista.cira.colostate.edu/Improve/Data/IMPROVE/improve_data.htm. (Accessed May 5, 2010).

McCune, B.; Dey, J.; Peck, J.; Heiman, K.; Will-Wolf, S. 1997. **Regional gradients in lichen communities of the southeast United States.** The Bryologist. 100: 145-158.

McCune, B.M.; Geiser, L.H. 2009. **Macrolichens of the Pacific Northwest.** 2nd Edition. Corvallis, OR: Oregon State University Press. 448 p.

McCune, B.; Grenon, J.; Mutch, L.S.; Martin, E.P. 2007. **Lichens in relation to management issues in the Sierra Nevada national parks.** Pacific Northwest Fungi. 2: 1-39.

McCune, B; Mefford, M.J. 1999. **PC-ORD. Multivariate analysis of ecological communities, Version 4.24.** MJM Software: Gleneden Beach, OR.

NADP (National Atmospheric Deposition Program). 2009. **NADP maps and data.** Available at http://nadp.sws.uiuc.edu/data/. (Accessed May 5, 2010).

NRCS (Natural Resources Conservation Service). 2011. **The PLANTS database.** Baton Rouge, LA: U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Center. Available at http://plants.usda.gov. (Accessed Feb. 9, 2011).

Porter, M.K. 2007. **Regional modeling of nitrogen, sulfur, and mercury atmospheric deposition in the Pacific Northwest.** Pullman, WA: Washington State University. 127 p. M.S. thesis.

PRISM (Parameter-elevation Regressions on Independent Slopes Model). 2010. **PRISM climate group.** Available at http://www.prism.oregonstate.edu/. (Accessed December 3, 2010)

Rao, L.E.; Allen, E.B.; Meixner, T. 2010. **Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts.** Ecological Applications. 20: 1320-1335.

Sigüenza, C.; Crowley, D.E.; Allen, E.B. 2006. **Soil microorganisms and fatty acid methyl ester profiles along a N deposition gradient.** Applied Soil Ecology. 32: 13-26.

Söchting, U. 1995. **Lichens as monitors of nitrogen deposition.** Cryptogamic Botany. 5 (3): 264-269.

University of California Davis. 1995. **IMROVE data guide.** Available at http://vista.cira.colostate.edu/Improve/Publications/OtherDocs/IMPROVEDataGuide/IMPROVEDataGuide.htm (Accessed May 5, 2010).

UBA (UmweltBundesAmt). 2004. **Manual on methodologies and criteria for modeling and mapping critical loads and levels and air pollution effects, risks, and trends.** Berlin: Federal Environmental Agency (UmweltBundesAmt). Available at http://icpmapping.org/cms/zeigeBereich/11/manual-english.html. (Accessed May 12, 2010).

US EPA (U.S. Environmental Protection Agency). 2009. **CMAQ science documentation.** Available at http://www.epa.gov/asmdnerl/CMAQ/CMAQscienceDoc.html. (Accessed May 5, 2010).

U.S. Forest Service. N.d. **National lichens and air quality database and clearinghouse.** Available at http://gis.nacse.org/lichenair/. (Accessed May 5, 2010).

U.S. Forest Service. 2005. **Forest Inventory and Analysis National Program.** Lichen communities. Monitoring air quality and biodiversity. Available at http://fia.fs.fed.us/lichen (Accessed May 5, 2010).

U.S. Forest Service. 2007. **Forest Inventory and Analysis Program.** Phase 3 Field Guide - Section 10. Lichen Communities, Version 4.0. Available at http://fia.fs.fed.us/library/field-guides-methods-proc/docs/2007/p3_4-0_sec10_10_2007.pdf. (Accessed May 5, 2010).

U.S. Geologic Survey. 2009. **NPElement, a database of lichen elemental concentrations in the U. S. National Parks.** Version 1.0. Available at http://www.nwhc.usgs.gov/our_research/np_element.jsp (Accessed May 5, 2010).

U.S. Geologic Survey. 2010. **NPLichen, a database of lichens in the U. S. National Parks.** 2010. Version 4.5. Available at http://www.nbii.gov/nplichen. (Accessed May 5, 2010).

Vitt, D.H.; Wider, K.; Halsey, L.A.; Turetsky, M. 2003. **Response of *Sphagnum fuscum* to nitrogen deposition: A case study of ombrogenous peatlands in Alberta, Canada.** The Bryologist. 106(2): 235-245.

Wright, R.F.; Alewell, C.; Cullen, J.M.; Evans, C.D.; Marchetto, A.; Moldan, F.; Prechtel, A.; Rogora, M. 2001. **Trends in nitrogen deposition and leaching in acid-sensitive streams in Europe.** Hydrology and Earth System Sciences. 5: 299-310.

5 TUNDRA

K. Nadelhoffer and L.H. Geiser

5.1 Ecoregion Description

The North American Arctic, comprising the Tundra and Arctic Cordillera ecoregions (CEC 1997, Chapter 2), covers more than 3 million km^2 (300 million ha), and accounts for nearly 14 percent of the North American land mass. The North American Arctic also constitutes about 20 percent of the much larger circumpolar Arctic shared by Canada, the United States, and six European and Asian countries. The ecoregion description is adapted from CEC (1997). The Tundra ecoregion (CEC 1997, Figure 2.2) is a mosaic of alpine meadows, foothills, mesas, low-lying coastal plains, river corridors, and deltas encompassing northern and western Alaska, the arctic islands of Canada, northern portions of the Yukon and Northwest Territories, and far northern Quebec. Coastal plains are typically wet with high densities of shallow lakes which are covered by ice for 9 months or more. Uplands have fewer, deeper lakes, most of which are connected to river networks draining into the Arctic Ocean or Bering Sea. A key feature is that soils are frozen in spatially contiguous permafrost and often contain large stores of organic carbon (or "peat"). Soil surface layers thaw in summers, usually to a depth of <1 m. The climate is characterized by long, dark, cold winters and short, cool summers with up to several months of daylight. Annual precipitation varies from 10 to 50 cm; snow may fall any month and snow pack usually persists for at least 9 months. Snowfall and its redistribution by winds both influence and are partly determined by plant community structure. The vegetation is characterized by combinations of sedges, grasses, shrubs, bryophytes, lichens, and forbs. Shrubs include dwarf birch (*Betula nana*), willows (*Salix spp.*), and heath species. Moving from south to north, shrub densities typically decrease, and sedges, mosses, and lichens increasingly dominate. River valleys are often lined with tall birch or willow shrubs, and occasionally with small balsam poplar (*Populus balsamifera*) or stunted white and black spruce (*Picea glauca* and *P. mariana*) trees. Wetlands are common in low-lying areas and support sedges and bryophytes.

5.2 Ecosystem Responses to N Deposition

A growing body of literature shows that plant growth, litter and soil organic matter decomposition, primary productivity, ecosystem carbon (C) storage, and plant community composition in arctic tundra ecosystems are at least partly controlled by nitrogen (N) availability and N deposition rates. This is because low N availability limits both microbial decomposition and plant growth in arctic tundra (Robinson and Wookey 1997, Shaver et al. 1992). For example, high rates of N addition can lead to large losses of organic C from tundra peat as well as to increases in vascular plant growth (Mack et al. 2004). Experimental N additions typically increase plant growth in tundra and responses are moderated by environmental factors. Graminoids and shrubs become dominant in dry heath tundra in well drained uplands, shrubs become dominant in moist tundra on gentle slopes, graminoid biomass increases in low-lying wet tundra, and bryophyte (mosses, hornworts, and liverworts) and lichen biomass increases with increasing moisture availability (Shaver et al. 1998, van Wijk et al. 2004). Even though N deposition may increase plant growth and net primary production, increases in peat and soil organic matter decomposition resulting from N deposition could be large enough to offset C accumulation by vegetation, resulting in net C losses from tundra ecosystems (Nowinski et al. 2008).

Bryophytes and lichens (referred to collectively as cryptogams) are of particular concern in the arctic because they regulate tundra water balances and energy balances. Cryptogams, especially sphagnum mosses, can dominate the top layer of tundra; the accumulated necrotic biomass can be a major component of peat, which is highly hygroscopic. In addition, acids and phenolic compounds in cryptogams inhibit decay. The growth and abundances of bryophytes and lichens can be diminished by the direct effects of moderate to high N inputs. In addition, increased growth of competing graminoid and shrub species in response to N inputs can result in shading of low-lying bryophytes and lichens, thereby decreasing cryptogam biomass indirectly, even when cryptogam growth is N limited (Berendse et al. 2001, Bubier et al. 2007, van der Wal et al. 2005). Shifts in cryptogam cover, biomass, morphology, and chemistry; changes in the composition of vegetative communities; and shifts in vegetation growth forms to greater dominance by vascular plants (graminoids and shrubs in particular) are indicators of tundra ecosystem responses to N deposition, as well as to other climate change drivers. Also, changes in cryptogam communities and bryophyte-lichen layer thickness, whether derived from N toxicity, shading from vascular plants, or other factors, can alter tundra soil moisture balances, temperature, and nutrient cycling rates (Gornall et al. 2007).

Aquatic ecosystems are often "first responders" to changes in environmental conditions, as their structure and functionality can be altered by changes in exports of nutrients and organic materials from terrestrial ecosystems within drainage basins. This sensitivity is particularly true in arctic tundra, where shallow depth of soil thaw and short residence times of soil solutions can lead to rapid changes in drainage water chemistry in response to biogeochemical changes in terrestrial ecosystems (Hobbie et al. 1999a, Keller et al. 2007), such as could result from elevated N deposition. Arctic streams are sensitive to N inputs, whether from increased N deposition or from increased decomposition in drainage basins due to warming and deeper soil thaw (Benstead et al. 2005). Evidence is emerging from Canada that diatom communities, nutrient cycling, and sediment formation in arctic lakes are being altered by elevated N deposition (Wolfe et al. 2006). Such studies indicate that N deposition may be altering the functioning of terrestrial as well as aquatic ecosystems in arctic tundra regions over broad scales, even when the effects of N deposition on individual terrestrial communities and ecosystems are undetectable.

5.3 Range of Responses Observed

Similarities among Northern Hemisphere arctic ecosystems in climate, soils, marine influences, hydrology, and vegetation justify the application of Eurasian research to assessments of the North American tundra response to N deposition. The definition of tundra employed by Bobbink et al. (2003) and the UNECE (2007) for Europe is based on the European University Information Systems (EUNIS) system of classification (Davies et al. 2004). 'Tundra' ecosystems share similarities with 'arctic, alpine and subalpine scrub habitats' ecosystems in that the growing season is short, temperatures are low, winds are frequent and strong, and the distribution of plant communities depends on the distribution of snow during winter and spring. Both ecosystem types are influenced by frost activity or solifluction, slow rates of organic matter decomposition and nutrient cycling, and limitation of primary production due to low nutrient availability (Robinson and Wookey 1997). As with North American tundra, the key feature that distinguishes tundra from other ecological regions in both the CEC and EUNIS systems is the presence of permafrost, which restricts deep root penetration and often keeps the overlying thawed soil layer waterlogged in summer. Responses to N deposition are summarized in Table 5.1.

5.3.1 Community Level Responses of Tundra Vegetation

Long-term N addition experiments typically add N at high rates, e.g., 10 to100 kg ha^{-1} yr^{-1}. These rates are one to two orders of magnitude greater than background N deposition rates and well in excess of tundra plant N uptake requirements. Such experiments provide insights into mechanisms of vascular plant responses to atmospheric N deposition but are of limited use in quantifying ecosystem response levels. Growth rates of vascular plant species typically increase in response to experimental N additions in dry, moist, and wet tundra ecosystems in both low and high latitude arctic regions. Because vascular plant species differ in sensitivity to N deposition and N availability, plant community composition typically shifts after several years or decades of experimental N additions. For example, primary productivity increased dramatically in dry heath tundra near Toolik Lake, Alaska, after 8 years of fertilization at 100 kg N ha^{-1} yr^{-1} (Gough et al. 2002). Species richness decreased in this study as dwarf birch, a low-lying shrub, became dominant and various graminoids, shrubs, forbs, and cryptogams declined. Species shifts and primary productivity may increase with N additions in high arctic systems as well. For example, Madan et al. (2007) reported increases in growth and biomass of shrubs (willows and purple mountain saxifrage (*Saxifraga oppositofolia*)) as well as increases in cryptogam cover in Greenland polar deserts (ambient deposition 1 kg N ha^{-1} yr^{-1}) in response to relatively low levels (5 kg N ha^{-1} yr^{-1}) of experimental N addition.

A recent 3-year study in northwest Greenland (Arens et al. 2008) suggests that N addition rates as low as 1 to 5 kg ha^{-1} yr^{-1} (ambient deposition of 0.1 to 5 kg N ha^{-1} yr^{-1}) can dramatically increase photosynthesis and growth of grass species, and significantly alter the structure and function of high arctic systems, particularly with increases in phosphorus (P) availability. The target high arctic ecosystem encompassed dwarf shrubs, graminoids, forbs, bryophytes, and lichens. Measuring carbon dioxide (CO_2) fluxes in a portable field chamber, the authors demonstrated a near doubling of gross ecosystem photosynthesis at plots with 0.5 and 1 kg added N ha^{-1} yr^{-1} after both 1 and 2 years of treatment. The photosynthesis response saturated between 1 and 5 kg added N ha^{-1} yr^{-1}, presumably because P became limiting. Total plant cover followed the same pattern, increasing up to the addition of 1.0 kg N ha^{-1} yr^{-1}, then decreasing or not changing through 5 kg added N ha^{-1} yr^{-1}; grasses invaded much of the bare ground. Cover of deciduous shrubs increased 41 percent in the 0.5 kg N ha^{-1} yr^{-1} treatment, graminoids cover increased 97 percent with the 1 kg N ha^{-1} yr^{-1} treatment, and forb cover increased 296 percent and 740 percent with 1 and 5 kg N ha^{-1} yr^{-1} treatments. Bryophyte and lichen cover appeared to increase to 1 kg N ha^{-1} yr^{-1} and then decrease, but significance was not noted. The N+P treatment (5 kg N ha^{-1} yr^{-1} plus 2.5 kg P ha^{-1} yr^{-1})—produced the greatest responses, including significant increases in cover of alpine fescue (*Festuca brachyphylla*) grass (from 1.3 percent to 43.8 percent), arctic willow (*Salix arctica*) (4.5 percent to 13.8 percent), bryophytes (3 percent to 10.7 percent), alpine chickweed (*Cerastium alpinum*) (0.2 percent to 4.8 percent), the establishment of arctic bluegrass (*Poa arctica*) (from 0 percent to 6.5 percent), significant decreases in total lichen cover (from 8.2 percent to 2.3 percent), and the eradication of purple mountain saxifrage (from 0.8 to 0 percent). Among the three dominant plants (curly sedge [*Carex rupestris*], entireleaf mountain-avens [*Dryas integrifolia*], and arctic willow), foliar N increased linearly through 5 kg ha^{-1} yr^{-1} of added N. These results provide striking evidence of ecologically important increases in ecosystem productivity, vegetative cover, and altered community composition after just 1 to 2 years of very low N additions.

A meta-analysis by van Wijk et al. (2004) showed that vascular plant growth, primary productivity, and biomass of wet and moist tundra ecosystems in mid-arctic regions of Alaska and Scandinavia increased dramatically in experimental nutrient addition plots (N alone and in combination with P and other nutrients). However, increases in shrub growth in moist tundra were greater in Alaska than in Europe and were greater in moist than in wet tundra. Shrub and graminoid growth increased in both regions, but at the expense of forbs and cryptogams. Also, recent work in mid-arctic Alaska suggests that N deposition on non-acidic tundra (with base-rich soils), unlike the more extensive acidic tundra, may not lead to shrub dominance (Gough and Hobbie 2003). In non-acidic tundra types, enhanced graminoid growth will likely diminish the importance of forbs and cryptogam species.

Bryophytes, particularly mosses, can have positive growth responses to atmospheric N deposition because they lack roots and assimilate N and other nutrients almost exclusively via foliar uptake (Salemaa et al. 2008, Solga and Frahm 2006). Thus, where graminoid and shrub species do not overtop mosses and other bryophytes, N deposition could increase plant growth, primary productivity, and moss mat thickness. However, N deposition can also increase tissue turnover and mortality in some arctic mosses (Koranda et al. 2007), and thereby diminish moss cover in some tundra ecosystems. Also, competition by more erect vascular plants can lead to competitive suppression of moss growth and decreases in moss cover even when moss growth is N limited (Klanderud 2008). Positive growth responses of vascular plants to increased N availability can lead to declines in lichen biomass in low- and mid-arctic regions (van Wijk et al. 2004), but probably not in the high arctic (Cornelissen et al. 2001, Madan et al. 2007), where plant cover is typically less than 100 percent of soil surface area.

A seminal, long-term experiment in the high arctic of the Svalbard Islands, Norway, by Gordon et al. (2001) has been used to identify plant responses observed at different N input levels. The experiment involved three common tundra communities dominated by dwarf shrubs (mountain-avens, mountain heather (*Cassiope)*, and willow species) and also characterized by lichens and bryophytes. Background deposition was very low (<1 kg N ha^{-1} yr^{-1}) with N treatments of 0, 10 and 50 kg ha^{-1} yr^{-1} as ammonium nitrate (NH_4NO_3) solution and 0 and 5 kg P ha^{-1} yr^{-1} as potassium dihydrogen phosphate (KH_2PO_4) in five applications per growing season over 8 years. They reported the following:

- Responses were rapid and persistent. Both N and P concentrations in a dicranum moss (*Dicranum scoparium*) and the juniper polytrichum moss (*Polytrichum juniperinum)* increased with each level of nutrient application. Nitrate (NO_3^-) reductase activity decreased in juniper polytrichum at the low N treatment, suggesting N saturation and the potential for nitrate to pass through the bryophyte layer to become available to microbes and higher plants. Composition of the vegetation communities shifted significantly with a notable decrease in lichen cover. Bryophyte productivity increased and persisted 5 years after N additions ceased, suggesting that N (mainly NH_4^+) was strictly conserved in the bryophyte layer and that any reversal of the effect would be slow.
- The P treatment provided unequivocal evidence of partial limitation by P in this ecosystem, with greater response to N when P was applied. Therefore, in tundra systems, critical loads are expected to be lower in ecosystems that are not P-limited. This is especially notable because global warming is expected to increase both N and P availability (currently wet tundra sites are more likely to be P-limited than moist sites with a thinner peat layer, while dry tundra sites are primarily N-limited [Shaver et al. 1998]).

A circumpolar comparison of effects of N deposition and temperature-warming treatments on lichen cover by Cornelissen et al. (2001) included three studies from North America: Chapin et al. (1995), Hik (as reported in Cornelissen et al. 2001), and Hobbie et al. (1999b), and 11 studies from Sweden and Norway. The Cornelissen meta-analysis demonstrated consistent marked decreases in lichen cover with increased N availability and increasing temperature; all N application rates were relatively high, between 40 and 100 kg ha^{-1} yr^{-1} for a minimum of 3 years. In the low arctic and subarctic, this response was attributed to increased shading of lichens by shrubs, which generally reached a taller stature and were more responsive to N fertilization at lower latitudes compared to the high arctic. Although lichens can achieve a net positive photosynthesis rate very rapidly after hydration, they are often light-limited in the Arctic due to low incident radiation (Hahn et al. 1993). Shading, whether from shrubs or fog and cloud cover, significantly reduces lichen growth rates. Lichen cover responses in the high arctic were more ambiguous, with some studies showing slight increases and others small decreases. Cornelissen (2001) concluded that tundra lichens in climatically milder arctic ecosystems may decline with global climate change because higher temperatures are associated with greater availability of N and P, all of which favor vascular plants.

In addition to the above three North American studies, a study was conducted by Weiss et al. (2005) at the Toolik Lake Tundra LTER site (Alaska), in the northern foothills of the Brooks Range. They documented an essential absence of lichens after 10+ years of fertilization at 100 kg N ha^{-1} yr^{-1}. Phosphorus fertilization at 50 and 100 kg ha^{-1} yr^{-1} improved N_2 fixation rates of the felt lichens, *Peltigera apthosa* and *P. polydactylon*, but the effect was unimportant compared to the reduction in lichen cover.

Since the Bobbink et al. (2003) assessment, a number of studies have provided further insight regarding the effects of N and P availability on tundra vegetation. During a 10-year experiment, Fremstad et al. (2005) tested species cover in low alpine and middle alpine vegetation communities in the Dover Mountains of south-central Norway. Nitrogen was added at 7, 35, and

70 kg ha^{-1} yr^{-1}; background N deposition was 2 to 4 kg ha^{-1} yr^{-1}. The most sensitive species at the warmer, low-alpine site were a witch's hair lichen (*Alectoria nigricans*) and a cetraria lichen (*Cetraria ericetorum*). These species exhibited significant decreases in cover at the lowest N application rate of 7 kg ha^{-1} yr^{-1}. Cover of other witch's hair *(Alectoria ochroleuca*), cetraria (*Flavocetraria cucullata, F. nivalis*), and reindeer (*Cladonia mitis, C. rangiferina, C. stellaris*) lichens decreased at the application rate of 35 kg N ha^{-1} yr^{-1}. The only lichen unaffected by any level of N application was the N_2-fixing snow lichen, *Stereocaulon paschale*. In contrast, fertilization had no significant effect on the bryophytes or vascular plants (dwarf shrubs and graminoids) except for sheep fescue (*Festuca ovina)*, a grass, which increased slightly. At the colder, mid-alpine site, a cetraria lichen (*Cetrariella delisei*), was the only species in which cover changed over 10 years due to N application, and then only at the addition rate of 70 kg ha^{-1} yr^{-1}, implying a slower response time in colder climates.

5.3.2 Physiological and Chemical Responses of Vegetation

The adaptation of arctic vegetation, especially lichens and bryophytes, to N-limited ecosystems through extreme conservation has been well illustrated recently by two studies employing ^{15}N as a tracer. Tye et al. (2005) conducted one-time additions of 1 or 5 kg ^{15}N ha^{-1}, using separate applications of ^{15}N-labeled sodium nitrate ($NaNO_3$) and ammonium chloride (NH_4Cl) at both levels of N addition, in addition to the background deposition rate of 1 kg N ha^{-1} yr^{-1} at two sites in the high arctic tundra of Svalbard, Norway. They observed a highly conservative retention by soil, litter, and vegetation of ~60 percent of both N ions of the initial application across all 3 years. On a unit weight basis, the lichens and graminoids were especially good scavengers of ^{15}N and exhibited a high capacity to immobilize additional N released compared to other sinks (microbes, vascular plants, mosses, willows, litter, humus, mineral soils), although the bulk of ^{15}N was stored in humic and mineral fractions of the soil and in bryophytes. Kytöviita and Crittenden (2007), in a study of lichen mats dominated by reindeer and snow lichens (*Cladonia* and *Stereocaulon*) in a dry boreal forest of Finland, demonstrated that a significant portion of ^{15}N fed to the lower parts of lichens is translocated towards growing apices. They concluded that internal recycling of N improves N use efficiency in lichens and is likely ecologically important in N-limited environments typical of the undisturbed arctic. These and other studies have repeatedly shown a direct correlation between N application or N availability and concentrations of N in lichen thalli (Hahn et al. 1993; Hyvärinen and Crittenden 1998a, 1998b; Hyvarinen et al. 2003; Walker et al. 2003; Weiss et al. 2005).

In addition to decreases in lichen cover with increasing N availability, mostly at relatively high application rates, new evidence points to clear but more subtle effects of low rates of N application (3 to 10 kg ha^{-1} yr^{-1}) on lichen physiology. Makkonen et al. (2007) showed the vulnerability of normally N- and P-limited lichens to nutrient enrichment. Lichen cushions of the star reindeer lichen (*Cladonia stellaris*) were treated with 3 and 10 kg N ha^{-1} yr^{-1} and 10 kg P ha^{-1} yr^{-1}, alone and in combination, over 14 weeks. Nitrogen, P, and N:P ratios influenced the proportion of the medullary layer volume occupied by the algal cells, the thallus volume occupied by the internal lumen, and the algal cell-wall area covered by fungal hyphae, indicating that ecologically realistic changes in the availability of key macronutrients can alter the growth of symbionts. Hyvärinen et al. (2003) showed that a moderate N treatment (3 kg ha^{-1} against a background of 0.5 kg ha^{-1} wet deposition in 3 months) lowered usnic acid ($C_{18}H_{16}O_7$) concentrations in the star reindeer lichen with and without P application; P alone increased usnic acid, and higher N (10 kg ha^{-1}) had no effect on usnic acid. None of the treatments increased growth rate. Usnic acid in lichens has well established anti-microbial and UV-β protection properties (Rikkinen 1995) relating to lichen fitness. By inhibiting catalysis of urea to carbon dioxide (CO_2) and ammonia (NH_3), usnic acid likely moderates metabolic imbalances in lichens created by excess C and insufficient N (Rikkinen 1995).

Sundberg et al. (2001), in an elegant study of lichen transplants, demonstrated the highly regulated, species-specific balance of C and N for coordinated development of lichen thalli. Nitrogen availability to transplants of the arctic kidney lichen (*Nephroma* *arcticum*) and a felt lichen (*Peltigera aphthosa*) was manipulated during 4 summer months by removing cyanobacterial N_2-fixing structures to cause N starvation, or by weekly irrigation with NH_4NO_3 at a rate of 9 kg N ha^{-1} yr^{-1} plus background deposition of 5 kg ha^{-1} yr^{-1}. N-starved lichens continued to gain weight, but did not increase in cover, demonstrating that C-fixation can proceed under N-limited conditions, although N is required for hyphal growth. Cover of lichens with added N increased more slowly than nonfertilized controls. For all treatments, weight gain was dependent on the proportion of N invested in algal photosynthetic tissue and there was a positive correlation between light use efficiency and thallus N. Intra-specific ratios of chlorophyll *a*:chitin (an N-containing polysaccharide in cell walls) and chlorophyll *a*:ergosterol (an N-containing component of cell membranes in fungi and algae) were relatively constant across a two- to threefold variation in thallus N, suggesting that lichens regulate N distribution within the thallus.

5.4 Critical Loads Estimate

We have few experiments assessing the effects of N additions at our proposed critical load for the North American Tundra ecoregion. There is only one published study specific to the North American Tundra ecoregion (Arens et al. 2008) that has used ecologically realistic N input rates to suggest vascular plant, bryophyte, or lichen-based critical loads (see Table 5.1). Critical loads are summarized in Table 5.2.

In 2003, the empirically derived critical load for tundra ecosystems in Europe proposed by Bobbink et al. (2003) and adopted by the UNECE (2007) was 5 to 10 kg N ha^{-1} yr^{-1}. This range was considered reliable, even though it is based primarily on one long-term experiment in the high arctic of the Svalbard Islands, Norway, by Gordon et al. (2001). This study is compelling because it included the critical load range, involved controlled additions of N, and looked at responses over an 8-year period (Table 5.1). Data from Fremstad et al. (2005) and Madan et al. (2007), which demonstrated vegetation community responses at 9 to 11 and 6 kg N ha^{-1} yr^{-1}, respectively, corroborate the research by Gordon et al. (2001) and point to the important mediating role of other environmental and genetic factors in cryptogam and vascular plant responses to N deposition. In particular, harsher climates and intrinsic properties of individual species may slow the rate of, or override, responses.

European analyses suggest critical loads not exceed 5 to 10 kg N ha^{-1} yr^{-1}, but the long-term effects of deposition rates lower than 5 kg N ha^{-1} yr^{-1} on tundra ecosystems have not yet been adequately assessed. Recent work, however, suggests arctic systems may respond to rates of N deposition between 1 and 5 kg ha^{-1} yr^{-1} with altered gross photosynthetic productivity, structure, and function of plant communities (Arens et al. 2008). Background N deposition rates in European tundra are higher than N deposition in relatively less polluted regions of the North American Arctic. For example, precipitation chemistry measurements at the Toolik Lake Arctic Tundra LTER site in northern Alaska (Hobara et al. 2006, Shaver[5]) and at NADP sites elsewhere in Alaska (See Chapter 6, and data from Ambler, Alaska, at http://nadp.sws.uiuc.edu/ads/2004/AK99.pdf) show that inorganic N inputs from the atmosphere are <0.5 kg N ha^{-1} yr^{-1}.

Given the multiple lines of evidence from Arens et al. (2008) that deposition as low as 1 kg N ha^{-1} yr^{-1} can impact tundra ecosystems, setting critical loads at 10 to 20 times current N deposition rates measured at relatively pristine tundra sites would be unwise. Aquatic systems in arctic drainages (Wolfe et al. 2006) and indicator species among the shrubs, grasses, lichens, and mosses appear to be responding to N deposition at low levels of ambient atmospheric or experimental N inputs. Cellular ultrastructure and pigment production are sensitive to deposition loading of ≤3 kg N ha^{-1} yr^{-1} (Hyvärinen et al. 2003, Makkonen et al. 2007). Moreover, vegetation in tundra ecosystems is highly efficient with respect to N cycling (Chapin et al. 1980), with plant N uptake from soil ranging between 1 to 6 kg ha^{-1} yr^{-1}, or 20 to 25 percent of the 5 to 20 kg N used to supply annual primary productivity (Shaver et al. 1991,

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[5] Shaver, G.R. Unpublished data. Senior scientist of Marine Biological Laboratory, Ecosystems Center, Woods Hole, MA 02543.

Table 5.1—Responses to N deposition for the Tundra ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	N input *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
NW Greenland	1-5	##	Increased net CO_2 uptake by combined vegetation saturating at 1.5 kg N ha^{-1} yr^{-1}; changes in shrub, graminoid, forb, bryophyte, and lichen diversity and cover; increased grass cover, increased foliar N	Response is greater if P availability increases	Arens et al. 2008
Hailuota Island, northern Finland, 65° N	<3	(#)	Decreased usnic acid concentrations in lichens at 3 kg; no effect at 10 kg (concave response)	3 kg ha^{-1} on background of 0.5 kg ha^{-1} for 3 months. P increased usnic acid	Hyvärinen et al. 2003
Hailuota Island, northern Finland, 65° N	3 to 10	(#)	Increase in lichen N concentrations, reduction in medullary volume, increase in internal lumen volume	14 week addition of 3 and 10 Kg N (total) and 10 kg P to lichen cushion transplants; P moderated N response	Makkonen et al. 2007
Greenland polar deserts	6	##	Increases in shrub and cryptogam growth and biomass	N addition of 5 kg ha^{-1} yr^{-1}, plus 1 kg ha^{-1} yr^{-1} deposition	Madan et al. 2007
Dover Mtns, south-central Norway 60 ° N	<9-11	##	Decreased lichen cover and increased grass cover at warmer but not colder site	10 yr experimental addition of N at 7, 35 and 70 kg ha^{-1} yr^{-1} to low and mid alpine vegetation, plus 2 to 4 kg N ha^{-1} yr^{-1} deposition	Fremstad et al. 2005
Svalbard Islands, Norway 78 ° N	<10	##	Increased N and P concentrations in cryptogams, reduced nitrate reductase activity in bryophytes, N saturation of cryptogam layer, decrease in lichen cover, and increase in bryophyte cover	8 yr addition of 0, 10 and 50 kg N ha^{-1} yr^{-1}; 0 and 5 kg P ha^{-1} yr^{-1} to three high arctic vegetation types. Adding P exacerbated adverse N effects. Wet tundra (P limited) may have higher critical loads than dry tundra (N limited)	Gordon et al. 2001
Västerbotten, Sweden 66.2° N (collected); Ulterviken, Sweden 63.5° N (transplanted)	<14	#	Increased lichen N concentrations; slightly slowed growth in cover area; increase in chlorophyll a, ergosterol, and chitin	Comparison of N starved (cephalodia removed), control and 10 kg ha^{-1} yr^{-1} N to N_2-fixing lichens. After 4 months fertilization appeared to mostly benefit lichens, which were N-limited	Sundberg et al. 2001
Circumpolar arctic	<40	#	Increased growth of shrubs, decrease in lichen cover (attributed to shading by shrubs)	Meta-analysis of 14 arctic studies. Responses diminish with latitude due to colder temps and poorer N and P mobilization	Cornelissen et al. 2001
Toolik Lake tundra LTER, Brooks Range, Alaska 66° N	<50	##	Decreased cover and species diversity of lichens	Lichens disappeared after 10 years fertilization at 100 kg ha^{-1} yr^{-1}	Weiss et al. 2005

Table 5.2—Empirical critical loads of nutrient N for the Tundra ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical Load for N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Tundra: herbs	1-3	##	Changes in CO_2 exchange, cover, foliar N, and community composition of vascular plants	N addition study, Greenland high arctic, P enhanced N effects	Arens et al. 2008
Tundra: cryptogams	1-3	(#)	Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover	N addition studies, high and low arctic, P enhanced or moderated N effects	Arens et al. 2008, Hyvärinen et al. 2003, Makkonen et al. 2007

Shaver and Chapin 1991). Nitrogen deposition rates equal to or in excess of annual plant N uptake would likely alter competitive interactions among plant species, dominant growth forms, biogeochemical exports, and energy balances of tundra ecosystems. Given the high degree of N limitation of plant growth in the North American Tundra ecoregion, low background levels of N deposition in historic and geological time, low levels of N cycling between tundra plants and soils, and the apparent sensitivity of freshwater ecosystems in the Arctic to changes in landscape biogeochemistry, the North American Tundra ecoregion critical load for N deposition should considerably lower than the European tundra critical load. We recommend that the critical load for the North American Tundra ecoregion be 1 to 3 kg N ha^{-1} yr^{-1}; the lower value is two times estimates for inorganic N deposition in Alaskan tundra monitoring sites. We consider this critical load to be reliable, but note that it is primarily supported by work in a single high arctic location in North America (Arens 2008).

5.5 Future Research Directions and Gaps in Data

A more extensive network of atmospheric deposition monitoring stations is clearly needed in the North American Tundra ecoregion. These monitoring stations should focus on acquiring high quality, year-round measurements of inorganic, particulate, and organic N forms as well as other biologically active elements including S, mercury (Hg), calcium (Ca), magnesium (Mg), and potassium (K). Further research is needed, specifically in North American tundra locations outside of Greenland, in both high and low arctic environments. This research should compare ecologically realistic applied, measured, or modeled N deposition with biogeochemical responses to N deposition, with physiological/morphological/distribution data for various indicator vascular plant, bryophyte and lichen species, and with foliar or thallus N concentrations. Until then, critical loads based on responses from Nordic countries will remain our best estimates.

LITERATURE CITED

Arens, S.J.T.; Sullivan, P.F.; Welker, J.M. 2008. **Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a high arctic ecosystem.** Journal of Geophysical Research-Biogeosciences. 113: G03509.

Benstead, J.P.; Deegan, L.A.; Peterson, B.J.; Huryn, A.D.; Bowden, W.B.; Suberkropp, K.; Buzby, K.M.; Green, A.C.; Vacca, J.A. 2005. **Responses of a beaded arctic stream to short-term N and P fertilisation.** Freshwater Biology. 50: 277-290.

Berendse, F.; Van Breemen, N.; Rydin, H.; Buttler, A.; Heijmans, M.; Hoosbeek, M.R.; Lee, J.A.; Mitchell, E.; Saarinen, T.; Vasander, H.; Wallen, B. 2001. **Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs.** Global Change Biology. 7: 591-598.

Bobbink, R.; Ashmore, M.R.; Braun, S.; Fluckiger, W.; van der Wyngaert, I.J.J. 2003. **Empirical**

nitrogen critical loads for natural and semi-natural ecosystems: 2002 update. In: Achermann, B.; Bobbink, R., eds. Empirical critical loads for nitrogen. Environmental Documentation 164. Berne, Switzerland: Swiss Agency for the Environment, Forests and Landscape: 143-170.

Bubier, J.L.; Moore, T.R.; Bledzki, L.A. 2007. **Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog.** Global Change Biology. 13: 1168-1186.

CEC (Commission for Environmental Cooperation). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf. (Accessed May 24, 2010).

Chapin, F.S., III; Miller, P.C.; Billings, W.D.; Coyne, P.I. 1980. **Carbon and nutrient budgets and their control in coastal tundra.** In: Brown, J.; Miller, P.C.; Tieszen, L.L.; Bunnell, F.L., eds. An arctic ecosystem: The coastal tundra at Barrow, Alaska. Stroudsburg, PA: Dowden, Hutchinson, and Ross: 458-483.

Chapin, F.S.; Shaver, G.R.; Giblin, A.E.; Nadelhoffer, K.J.; Laundre, J.A. 1995. **Responses of arctic tundra to experimental and observed changes in climate.** Ecology. 76: 694-711.

Cornelissen, J.H.C.; Callaghan, T.V.; Alatalo, J.M.; Michelsen, A.; Graglia, E.; Hartley, A.E.; Hik, D.S.; Hobbie, S.E.; Press, M.C.; Robinson, C.H.; Henry, G.H.R.; Shaver, G.R.; Phoenix, G.K.; Jones, D.G.; Jonasson, S.; Chapin, F.S.; Molau, U.; Neill, C.; Lee, J.A.; Melillo, J.M.; Sveinbjornsson, B.; Aerts, R. 2001. **Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass?** Journal of Ecology. 89: 984-994.

Davies, C.E.; Moss, D.; Hill, M.O. 2004. **EUNIS habitat classification revised 2004.** Copenhagen, Denmark: European Environment Agency, and Paris, France: European Topic Centre of Nature Protection and Biodiversity. 310 p. Available at http://eunis.eea.europa.eu/upload/EUNIS_2004_report.pdf (Accessed May 24, 2010).

Fremstad, E.; Paal, J; Mols, T. 2005. **Impacts of increased nitrogen supply on Norwegian lichen-rich alpine communities: a 10-year experiment.** Journal of Ecology. 93: 471-481.

Gordon, C.; Wynn, J.M.; Woodin, S.J. 2001. **Impacts of increased nitrogen supply on high Arctic heath: the importance of bryophytes and phosphorus availability.** New Phytologist. 149: 461-471.

Gornall, J.L.; Jonsdottir, I.S.; Woodin, S.J.; Van der Wal, R. 2007. **Arctic mosses govern below-ground environment and ecosystem processes.** Oecologia. 153: 931-941.

Gough, L.; Hobbie, S.E. 2003. **Responses of moist non-acidic arctic tundra to altered environment: productivity, biomass, and species richness.** Oikos. 103: 204-216.

Gough, L.; Wookey, P.A.; Shaver, G.R. 2002. **Dry heath arctic tundra responses to long-term nutrient and light manipulation.** Arctic Antarctic and Alpine Research. 34: 211-218.

Hahn, S.C.; Tenhunen, J.D.; Popp, P.W.; Meyer, A.; Lange, O.L. 1993. **Upland tundra in the foothills of the Brooks Range, Alaska - diurnal CO_2 exchange patterns of characteristic lichen species.** Flora. 188: 125-143.

Hobara, S.; McCalley, C.; Koba, K.; Giblin, A.E.; Weiss, M.S.; Gettel, G.M.; Shaver, G.S. 2006. **Nitrogen fixation in surface soils and vegetation in an arctic tundra watershed: A key source of atmospheric nitrogen.** Arctic, Antarctic, and Alpine Research. 38: 363-372.

Hobbie, J.E.; Peterson, B.J.; Bettez, N.; Deegan, L.; O'Brien, W.J.; Kling, G.W.; Kipphut, G.W.; Bowden, W.B.; Hershey, A.E. 1999a. **Impact of**

global change on the biogeochemistry and ecology of an Arctic freshwater system. Polar Research. 18: 207-214.

Hobbie, S.E.; Shevtsova, A.; Chapin; F.S. 1999b. **Plant responses to species removal and experimental warming in Alaskan tussock tundra.** Oikos. 84: 417-434.

Hyvärinen, M.; Crittenden, P.D. 1998a. **Growth of the cushion-forming lichen, *Cladonia portentosa*, at nitrogen-polluted and unpolluted heathland sites.** Environmental and Experimental Botany. 40: 67-76.

Hyvärinen, M.; Crittenden, P.D. 1998b. **Relationships between atmospheric nitrogen inputs and the vertical nitrogen and phosphorus concentration gradients in the lichen *Cladonia portentosa*.** New Phytologist. 140: 519-530.

Hyvärinen, M.; Walter, B.; Koopmann, R. 2003. **Impact of fertilisation on phenol content and growth rate of Cladina stellaris: a test of the carbon-nutrient balance hypothesis.** Oecologia. 134:176-181.

Keller, K.; Blum, J.D.; Kling, G.W. 2007. **Geochemistry of soils and streams on surfaces of varying ages in arctic Alaska.** Arctic Antarctic and Alpine Research. 39: 84-98.

Klanderud, K. 2008. **Species-specific responses of an alpine plant community under simulated environmental change.** Journal of Vegetation Science. 19: 363-U109.

Koranda, M.; Kerschbaum, S.; Wanek, W.; Zechmeister, H.; Richter, A. 2007. **Physiological responses of bryophytes *Thuidium tamariscinum* and *Hylocomium splendens* to increased nitrogen deposition.** Annals of Botany. 99: 161-169.

Kytöviita, M.M.; Crittenden, P.D. 2007. **Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*.** Annals of Botany. 100: 1537-1545.

Mack, M.C.; Schuur, E.A.G.; Bret-Harte, M.S.; Shaver, G.R.; Chapin, F.S. 2004. **Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization.** Nature. 431: 440-443.

Madan, N.J.; Deacon, L.J.; Robinson, C.H. 2007. **Greater nitrogen and/or phosphorus availability increase plant species' cover and diversity at a High Arctic polar semidesert.** Polar Biology. 30: 559-570.

Makkonen, S.; Hurri, R.S.K.; Hyvärinen,M. 2007. **Differential responses of lichen symbionts to enhanced nitrogen and phosphorus availability: An experiment with Cladina stellaris.** Annals of Botany. 99: 877-884.

Nowinski, N.S.; Trumbore, S.E.; Schuur, E.A.G.; Mack, M.C.; Shaver, G.R. 2008. **Nutrient addition prompts rapid destabilization of organic matter in an arctic tundra ecosystem.** Ecosystems. 11: 16-25.

Rikkinen, J. 1995. **What's behind the pretty colours? A study on the photobiology of lichens.** Bryobrothera. 4: 1-239.

Robinson, C.H.; Wookey, P.A. 1997. **Microbial ecology, decomposition and nutrient cycling in arctic environments.** In: Woodin, S.J.; Marquiss, M., eds. The ecology of arctic environments. 13th special symposium of the British Ecological Society. Cambridge, UK: Cambridge University Press: 41-68.

Salemaa, M.; Makipaa, R.; Oksanen, J. 2008. **Differences in the growth response of three bryophyte species to nitrogen.** Environmental Pollution. 152: 82-91.

Shaver, G.R., Billings, W.D.; Chapin, F.S.; Giblin, A.E.; Nadelhoffer, K.J.; Oechel, W.C.; Rastetter, E.B. 1992. **Global change and the carbon balance of arctic ecosystems.** BioScience. 42:433-441.

Shaver, G.R.; Chapin, F.S., III. 1991. **Production:biomass relationships and element**

cycling in contrasting arctic vegetation types. Ecological Monographs. 61: 1-31.

Shaver, G.R.; Johnson, L.C.; Cades, D.H.; Murray, G.; Laundre, J.A.; Rastetter, E.B.; Nadelhoffer, K.J.; Giblin, A.E. 1998. **Biomass and CO_2 flux in wet sedge tundras: Responses to nutrients, temperature, and light.** Ecological Monographs. 68: 75-97.

Shaver, G.R.; Nadelhoffer, K.J.; Giblin, A.E. 1991. **Biogeochemical diversity and element transport in a heterogeneous landscape, the North Slope of Alaska.** In: Turner, M.; Gardner, R., eds. Quantitative methods in landscape ecology. New York NY: Springer-Verlag: 105-125.

Solga, A.; Frahm, J.P. 2006. **Nitrogen accumulation by six pleurocarpous moss species and their suitability for monitoring nitrogen deposition.** Journal of Bryology. 28: 46-52.

Sundberg, B.; Nasholm, T.; Palmqvist, K. 2001. **The effect of nitrogen on growth and key thallus components in the two tripartite lichens, *Nephroma arcticum* and *Peltigera aphthosa*.** Plant, Cell and Environment. 24: 517-527.

Tye, A.M.; Young, S.D.; Crout, N.M.J.; West, H.M.; Stapleton, L.M.; Poulton, P.R.; Laybourn-Parry, J. 2005. **The fate of N-15 added to high Arctic tundra to mimic increased inputs of atmospheric nitrogen released from a melting snowpack.** Global Change Biology. 11: 1640-1654.

UNECE (United Nations Economic Commission for Europe). 2007. **1979 Convention on long-range transboundary air pollution.** Geneva, Switzerland: United Nations Economic Commission for Europe. Available at http://www.unece.org/env/lrtap/ (Accessed May 24, 2010).

van der Wal, R.; Pearce, I.S.K.; Brooker, R.W. 2005. **Mosses and the struggle for light in a nitrogen-polluted world.** Ecophysiology. 142: 159-168.

van Wijk, M.T.; Clemmensen, K.E.; Shaver, G.R.; Williams, M.; Callaghan, T.V.; Chapin, F.S.; Cornelissen, J.H.C.; Gough, L.; Hobbie, S.E.; Jonasson, S.; Lee, J.A.; Michelsen, A.; Press, M.C.; Richardson, S.J.; Rueth, H. 2004. **Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change.** Global Change Biology. 10: 105-123.

Walker, T. R.; Crittenden, P.D.; Young, S.D. 2003. **Regional variation in the chemical composition of winter snow pack and terricolous lichens in relation to sources of acid emissions in the Usa river basin, northeast European Russia.** Environmental Pollution. 125: 401-412.

Weiss, M.; Hobbie, S.E.; Gettel, G.M. 2005. **Contrasting responses of nitrogen-fixation in arctic lichens to experimental and ambient nitrogen and phosphorus availability.** Arctic, Antarctic, and Alpine Research. 37: 396-401.

Wolfe, A.P.; Cooke, C.A.; Hobbs, W.O. 2006. **Are current rates of atmospheric nitrogen deposition influencing lakes in the Eastern Canadian Arctic?** Arctic Antarctic and Alpine Research. 38: 465-476.

6 TAIGA

L.H. Geiser and K. Nadelhoffer

6.1 Ecoregion Description

The Taiga ecoregion (CEC 1997; Figure 2.1) includes most of interior Alaska and much of Canada's northern boreal forest. The ecoregion description is adapted from CEC (1997). The Alaskan portion is underlain by horizontal limestone, shale, and sandstones, creating a flat to gently rolling plain covered with organic deposits, hummocky moraines, and lacustrine deposits; the eastern portion is underlain by the Canadian Shield. Lowlands are mostly peatlands and permafrost is widespread. Nutrient-poor soils dominate southern portions and permafrost soils occur in the north. The climate is subarctic: the short summers have long daylight and cool temperatures; winters are long and very cold. Snow and freshwater ice persist for 6 to 8 months annually. Mean annual temperatures are -10 to 0 °C; mean annual precipitation is 200 to 500 mm. Innumerable lakes, bogs, other wetlands, and forests are interspersed with tundra-like shrublands and sedge meadows. In the north, forests transition to woodlands with a lichen groundcover and finally merge into tundra at the climatic limits of tree growth. Mid-zone, dwarf birch (*Betula nana*), Labrador tea (*Ledum* spp.), willow (*Salix* spp.), bearberry (*Arctostaphylos alpina*), mosses, and sedges dominate. In the south, open stands of stunted black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) are accompanied by alder (*Alnus* spp.), willow, and tamarack (*Larix larcinia*) in fens and bogs. White spruce (*Picea glauca),*black spruce, lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*), balsam polar (*Populus balsamifera*), and paper birch (*Betula papyrifera*) grow on well drained, warm upland sites, rivers, and streams. Mat-forming lichens can constitute in excess of 60 percent of the winter food intake of caribou and reindeer (Longton 1997). The abundant wetlands attract hundreds of thousands of birds (e.g., ducks, geese, loons, and swans) which come to nest, or rest and feed on their way to arctic breeding grounds.

6.2 Ecosystem Responses

Responses to increased nitrogen (N) deposition in boreal regions (which include Taiga and Northern Forests ecoregions) include increased productivity, foliar N concentration, and N leaching from soils, plant community changes (including vascular plants, bryophytes, lichens, and algae), and physiological changes. In boreal ecosystems and other largely oligotrophic environments, N is growth-limiting, and most plant species are adapted to low available N. As N availability increases, faster growing, but less N-use efficient species (more N taken up per unit growth) typically outcompete slower growing species (Aerts and Chapin 2000). Increasing N deposition alters plant community structure, often leading to a short-term "positive" response of increased productivity and vigor, followed by long-term changes in species composition and richness (Gough et al. 2000). Such community-level responses occur at low deposition rates and have been used to mark the low end of ecosystem N response (Bobbink et al. 2003, de Vries et al. 2007). In boreal forests, overall ground flora species number may not be affected by N enrichment, despite a drastic change in species composition, due to reciprocal increases in nitrophilous species with declines in typical species (Bobbink 2004). However, in peatland bogs, where high water levels and low pH prevent nitrophyte invasions (Allen 2004), decline in species richness is a more characteristic response.

Increased N supply is often accompanied by increased foliar N concentration, which in turn may increase susceptibility of vegetation to frost or diseases. This effect is documented for boreal forest trees (e.g., Aronsson 1980, Balsberg-Påhlsson 1992, Kallio et al. 1985, Schaberg et al. 2002), for their common understory ericaceous species (e.g., Strengbom et al. 2002, 2003), and for bogs (e.g., Wiedermann et al. 2007). At higher deposition levels, as N is no longer completely taken up by vegetation or immobilized in soils, N saturation and leaching may occur (Lamontagne 1998; Lamontagne and Schiff 1999, 2000; Tamm et al. 1999).

The severity of N deposition impacts depends on: duration and amount of N deposition, the form(s) of atmospheric N, the sensitivity of the ecosystem components; other environmental conditions; and management history (Bobbink et al. 2003). As a result, ecosystem response to N loading varies temporally, spatially, and by habitat type. Change or loss of habitats can have direct implications on the animals using these habitats.

6.3 Range of Responses Observed

Like the Tundra ecoregion, the paucity of North American studies and the many similarities in climate, topography, and vegetation communities across the circumboreal environment support consideration of European findings to predict ecosystem N responses for North America. Therefore, we include European data in this discussion of the range of observed responses. European analyses considered Taiga and Northern Forest ecoregions (CEC 1997) as a single boreal biogeographic region under the European University Information System (EUNIS) classification system; hence the frequent use of the term 'boreal' in the following sections. Responses to N inputs are summarized in Table 6.1.

6.3.1 Deposition

Our knowledge of current N deposition and deposition effects in the North American taiga is limited. Wet deposition of inorganic N at the National Atmospheric Deposition Program (NADP) monitors at Denali National Park and Preserve and Fairbanks, Alaska, has been low and stable, averaging 0.23 kg ha^{-1} yr^{-1} (std. dev. = 0.129) from 1981 to 2007 (NADP 2008). Total nitrate (NO_3^-) deposition in snow at two interior Alaska sites north of Fairbanks in 1988 was consistent with this range and averaged 0.32 kg N ha^{-1} (Jaffe and Zukowski 1993). Recent measurements of N from ammonium (NH_4^+) and NO_3^- ions in throughfall deposition at remote sites in northeastern Alberta, Canada (Berryman and Straker 2008) ranged from 0.6 to 2.0 kg N ha^{-1} yr^{-1}.

6.3.2 Forests and Woodlands

Plant community composition changes. A large number of studies, summarized by Bobbink et al. (2003), have demonstrated increases in abundance of nitrophilous species with increased N deposition over time and along N gradients. In Swedish boreal forests, changes in ground vegetation, e.g., decreasing whortleberry (*Vaccinium myrtillus*), occurred at deposition rates ≥ 6 kg N ha^{-1} yr^{-1} (Nordin et al. 2005, Strengbom et al. 2003) and increased growth of wavy hairgrass (*Deschampsia flexuosa*) at ≥ 5 kg N ha^{-1} yr^{-1} (Kellner and Redbo-Torstensson 1995, Nordin et al. 2005).

In an N fertilization experiment with 0, 12.5, and 50 kg N ha^{-1} yr^{-1} (background atmospheric deposition 2 to 3 kg N ha^{-1} yr^{-1}), the abundance of wavy hairgrass increased significantly after 3 years with 12.5 kg N ha^{-1} yr^{-1} while the abundance of whortleberry decreased (Strengbom et al. 2002). Bryophyte species are also responsive; the biomass of Schreber's big red stem moss (*Pleurozium schreberi*) and a dicranum moss (*Dicranum polysetum*) fertilized with 25 and 30 kg N ha^{-1} yr^{-1} was reduced by 60 percent and 78 percent, respectively, after 4 years (Mäkipää 1998).

Pest and disease resistance. In a large-scale field study of 557 coniferous stands in Sweden, the occurrences of whortleberry, lingonberry (V*accinium vitis-idaea)* and wavy hairgrass, were investigated (Strengbom et al. 2003). Where N deposition was ≥ 6 kg ha^{-1} yr^{-1}, whortleberry was less frequent and more susceptible to the fungal leaf pathogen *Valdensia heterodoxa*. Frequency of lingonberry was also strongly negatively correlated with increasing N deposition (Strengbom et al. 2003).

Whortleberry showed increased parasite burdens at N fertilization ≥ 12.5 kg ha^{-1} yr^{-1} (Nordin et al. 1998, 2005; Strengbom et al. 2002). Disease incidence by the fungus *Valdensia heterodoxa* was more than twice as high in plots receiving 12.5 kg N ha^{-1} yr^{-1} and more than three times as high in plots receiving 50 kg N ha^{-1} yr^{-1} compared to controls. The abundance of the fungus *V. heterodoxa* on whortleberry was increased tenfold by 25 kg N ha^{-1} yr^{-1} compared to 0.5 kg N ha^{-1} yr^{-1}. As a consequence, whortleberry density decreased, and wavy hairgrass cover increased (Strengbom et al. 2002). In addition, shoots of whortleberry were significantly more damaged by moth larvae such as the rusty tussock moth (*Orgyia antique*) after addition of 12.5 kg N ha^{-1} yr^{-1} in the first year of treatment (Nordin et al. 1998). Cover of wavy hairgrass continued to increase over 5 years of N additions between 8 and 12 kg ha^{-1} yr^{-1}, induced by increased light penetration resulting from disease damage to whortleberry (Nordin et al. 2005).

Cold tolerance. Frost hardiness and plant tissue cold hardiness can be reduced by N additions. For example, after 12 years of fertilization with ammonium chloride (NH_4Cl) at 15 kg N ha^{-1} yr^{-1}, first-year foliage in red spruce (*Picea rubens*) at a high elevation forest in New England (with ambient wet + dry deposition of ~10 kg N ha^{-1} yr^{-1}) showed diminished cold tolerance, greater electrolyte leakage, and increased susceptibility to frost damage (Schaberg et al. 2002). Nutrient imbalances created by N and sulfur (S) fertilization and low potassium (K), phosphorus (P), and magnesium (Mg) status in southern Sweden and Denmark have been shown to increase the risk for development of cold temperature-related bark lesions in beech (*Fagus* spp.); advance bud burst of needles, putting young needles at risk for frost damage by a temperature backlash; and increase the frost-sensitivity of the inner bark and needles of Norway spruce (*Picea abies*) (Jönsson et al. 2000, 2001, 2004a, 2004b).

N storage in cryptogam mats. Woodlands or tree-islands of pine with ground vegetation of mat-forming lichens are a common taiga vegetation type. In general, when inorganic N is received in low concentrations, either from natural rainfall (Hyvärinen and Crittenden 1998b) or applied in solution (Crittenden 1998), the estimated uptake efficiency of (non-N_2-fixing) mat-forming lichens has ranged from 90 to 100 percent. Internal recycling of N and P in mat-forming lichens improves nutrient-use efficiency and is likely ecologically important in N- and P-limited environments typical of the taiga (Crittenden et al. 1994, Kytöviita and Crittenden 2007). Much of the eastern portion of the Taiga ecoregion is underlain by the Canadian Shield and soils can be shallow and acidic. During a short-term experimental addition of 40 kg N ha^{-1} yr^{-1} to a small catchment of boreal pine-reindeer lichen (*Pinus-Cladonia*) forest in Ontario, Canada, the higher export of mineral N from lichen-dominated bedrock surfaces compared to treed soil islands was attributed to the lower retention of N deposition in combination with leaching of mineralized N from lichen and moss patches (Lamontagne 1998). Net nitrification increased or remained similar to reference sites in lichen patches, while N-amended forest islands had a strong tendency to consume NO_3^- and produce NH_4^+ (Lamontagne and Schiff 2000). By the second year, lichen-covered bedrock surfaces no longer retained N additions. In contrast, N-amended and reference forest islands retained a similar proportion of N inputs, indicating that forest islands did not become N saturated in this time frame. However, because the components of the boreal shield landscape are hydrologically connected, there is concern that long-term N deposition to such a heterogeneous landscape will ultimately lead to N saturation of habitats with relatively high N retention capacities (Lamontagne and Schiff 1999). Finally, organic forms of N (e.g., free amino acids) serve as important plant N sources, and N deposition can disrupt the ratio between organic and mineral N supply in boreal soils (Näsholm et al. 1998, Nordin et al. 2001).

Epiphytic lichens and algae. Jack pine and black spruce boreal forests of northeastern Alberta were sampled at 5, 10, 15, 20, 25, 30, 50, 60, 80, 100, and 120 km along cardinal directions from the Athabasca Oil Sands operations, a major source of nitrogen oxide (NO_x) and sulfur dioxide (SO_2) emissions for Canada. Nitrogen and S in the mat-forming gray-green reindeer lichen (*Cladina rangiferina*) and in two epiphytes, a tube (*Hypogymnia physodes*) and ring (*Evernia mesomorpha*) lichen, decreased with distance and were elevated within 30 km of the operations. Lichen community composition was weakly correlated with distance: sensitive shrubby beard and horsehair lichens were less abundant and showed dwarfing, hyper-growth of asexual structures, discoloration of the lichen, and increased parasitism by fungi at sites close to the Athabasca Oil Sands (Berryman et al. 2004). Preliminary data indicate that N deposition in canopy throughfall under jack pine forests at clean sites ranges from 0.6 to 2.0 kg ha^{-1} yr^{-1}, increasing to 3.0 kg ha^{-1} yr^{-1} at sites near the mines. A new study is under way to relate deposition measures and modeled estimates of N and S to lichen response and to elucidate the relative roles of SO_2, NO_x, metals, and alkaline dust from mining operations in observed community responses (Berryman and Straker 2008). The correlation of N accumulated by lichen thalli with measures of deposition or distance from a point source is consistent with other studies in boreal forests in Eurasia (Bruteig 1993, Crittenden 2000, Crittenden et al. 1994, Hyvärinen and Crittenden 1998a, Walker et al. 2003). Information on lichen research methodology and terminology can be found in Chapter 4 of this report.

During a 10-year monitoring period in Sweden, patterns for sensitive epiphytic lichens were opposite to those observed for algae (Bråkenhielm and Quinghong 1995). The number of individuals, total cover, and proportion of sensitive lichens decreased with growing season length and with increasing N and S deposition; the first marked decrease occurred as N deposition exceeded 5 to 8 kg N ha^{-1} yr^{-1}. In contrast, colonization rate and colony thickness of epiphytic green algae (mainly *Protococcus viridis*) increased with increases in deposition and growing season length, especially as N deposition exceeded 12 kg ha^{-1} yr^{-1}. Poikolainen et al. (1998) observed increases in the abundance of green algae on conifers at lower deposition levels than did the Swedish researchers. Based on observations from 3009 permanent Finnish forest plots between 1985 and 1995, increased algal cover was associated with N deposition levels as low as 3 kg ha^{-1} yr^{-1}. Nitrogen concentration in the epiphytic tube lichen, *Hypogymnia physodes*, the splendid feather moss (*Hylocomium splendens*), Schreber's big red stem moss, and bark of Scots pine (*Pinus sylvestris*) were also correlated with N deposition. Temperature was confounded with N and S deposition in both studies, as both temperature and deposition decrease in more northerly latitudes.

Additions of N can cause changes in physiology and ultrastructure in common lichens of taiga ecosystems. In an electron microscopy study of the epiphytic horsehair (*Bryoria capillaris*) and tube (*Hypogymnia physodes*) lichens, treatments of 560 µg m^{-3} nitrogen dioxide (NO_2) or 10 mM sodium nitrate ($NaNO_3$), ammonium chloride (NH_4Cl), and ammonium nitrate (NH_4NO_3) induced accumulation of electron-opaque substances in the vacuoles of both the algal and fungal cells and general degeneration of the fungal cells (Holopainen and Karenlampi 1985). This demonstrates that N additions can influence cellular structure and metabolic processes in lichens—an important functional group in both boreal and arctic regions. See Chapter 5 (Tundra) for descriptions of effects on mat-forming and other terricolous lichens.

Ectomycorrhizal fungi. There is no information on ectomycorrhizal community responses to N in the Taiga ecoregion. We postulate that, given the climate, species composition and soils, white and black spruce dominated ecosystems may have similar deposition thresholds to those seen in spruce forests of the same species in coastal Alaska (see Chapter 9, West Coast Marine Forests) and to those of the spruce-fir forests of the northeastern United States (see Chapter 7, Northern Forests).

6.3.3 Ericaceous Shrublands (Heaths)

Heathlands are dwarf shrub communities that form on shallow peat or drained soils. Nitrogen-enrichment responses of heathland plant communities are characterized by increased growth of grasses and decreased growth of dwarf shrubs, lichens, and bryophytes (Allen 2004). Initially, shrubs respond to N additions with increased growth and tissue N concentrations, and the first adverse effects are shade-induced declines in lichen and bryophyte cover (Cornelissen et al. 2001). However, long-term N enrichment decreases root biomass and increases the susceptibility of shrubs to insect attack and frost. These effects, together with increased competition from grasses, cause a deterioration of the dominant shrub community. During a 5-year fertilization study (10.8 kg ha^{-1} yr^{-1} modeled ambient total deposition plus a 10 kg N ha^{-1} yr^{-1} application) of low-alpine heather (*Calluna vulgaris*) heaths in the Cairngorm Mountains of Scotland, species richness was reduced by exposure to added N deposition (Britton and Fisher 2007). The lichen component of the vegetation was most sensitive to N additions, although vascular plants were also affected via interactions with climate (Britton and Fisher 2007). Curtis et al. (2005) used isotope tracers in other European heaths and moorlands to demonstrate that bryophytes and lichens were important sinks for N deposition, reducing the amount of inorganic N available to both higher plants and soil microbes in grassland and ericoid shrub-dominated catchments. However, as N deposition increased from 2 to 30 kg ha^{-1} yr^{-1}, these sinks became saturated and cryptogam biomass decline was accompanied by increased NO_3^- leaching (see also Emmett 2007).

6.3.4 Peatlands

Peatlands are moss-dominated bogs and fens that are prevalent in the Taiga ecoregion. About 43 percent of Alaska can be classified as wetlands, much of that peatlands, contrasting strongly with the contiguous 48 states where wetlands comprise barely 5 percent of the total land area (Hall et al. 1994). The sensitivity of peatlands to N deposition decreases along a poor-to-rich productivity gradient from ombrotrophic bogs, which receive nearly all nutrient inputs from the atmosphere, to poor and rich fens, which receive additional nutrients from slow moving ground water and mineral sources (Vitt et al. 2003). The general progression of N deposition effects is:

1) At 0.7 to 8.1 kg N ha^{-1} yr^{-1} peat accumulation increases with N deposition due to increases in net photosynthesis and growth of previously N-limited mosses (Moore et al. 2004, Vitt et al. 2003). With average bulk deposition of 0.81 kg N ha^{-1} yr^{-1} and 1.14 kg S ha^{-1} yr^{-1} from 2005 to 2008, a dominant sphagnum moss (*Sphagnum fuscum)* in 10 remote bogs across northeastern Alberta was N-limited, and no differences in moss growth or net primary productivity were observed compared to previously published values for this area (Wieder et al. 2010).There are some indications that net photosynthesis in this sphagnum species may peak as early as 3 kg N ha^{-1} yr^{-1} in some Canadian peatlands (Vitt et al. 2003). (Oligotrophic mosses are the predominant N-sink and biomass in peatlands).
2) At 12 to 18 kg N ha^{-1} yr^{-1}, growth rates do not increase further and mosses begin to accumulate foliar N (Lamers et al. 2000, Moore et al. 2004, Vitt et al. 2003).
3) At >18 kg N ha^{-1} yr^{-1}, the natural moss N filter fails and N begins to leach from the saturated moss layer, altering competitive relationships (Lamers et al. 2000). Vegetation changes are characterized by decreases in cover of oligotrophic mosses and carnivorous plants and increases in graminoids, especially cotton grass and certain ericaceous shrubs (Allen 2004).

Chapter 17 (Wetlands) contains a more detailed discussion of these and interrelated responses, especially in relation to P availability, water availability, and climate.

6.3.5 Tundra

Areas of tundra are included in the Taiga ecoregion, notably at the northern boundaries. See Chapter 5 (Tundra) for descriptions of the range of responses.

6.4 Critical Loads Estimates

There are many indications that low levels of N deposition can affect community composition, abundance, net photosynthesis, N accumulation, physiology, and ultrastructure of lichens, mosses, and algae (see Table 6.1). These taxa, especially peatland sphagnum mosses and reindeer lichens, are dominant components of taiga ecosystems. Application here of a model relating epiphytic lichen community composition of Oregon and Washington coniferous forests to N deposition (Chapter 4, Geiser et al. 2010) yields a critical load estimate of 1 to 3 kg ha^{-1} yr^{-1} for Taiga ecoregion forests and woodlands. This value was calculated by substituting a realistic precipitation range of 20 to 80 cm and applying a conservative community-composition response threshold allowing no less than 41 percent oligotrophs or more than 27 percent eutrophs. For perspective, about 85 percent of sites in the western Oregon and Washington study area did not exceed this response threshold (Geiser et al. 2010). Considering this result and those of Moore et al. (2004), Vitt et al. (2003), Strengbom et al. (2003), Berryman et al. (2004), Berryman and Straker (2008), and Poikolainen et al. (1998), we recommend that the critical load for lichen, moss, and algae of the North American Taiga ecoregion be no more than 1 to 3 kg ha^{-1} yr^{-1}. This estimate can be considered fairly reliable, pending results from more definitive work currently in progress in North America. Critical loads are summarized in Table 6.2.

Table 6.1—Responses to N input relevant to the North American taiga. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical load for N dep. *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Epiphytic lichens	1-3	(#)	Community composition shift	Application of model developed for Marine West Coast Forests ecoregion to the Taiga ecoregion	Geiser et al. 2010, Chapter 4
Peatlands, NE Canada	2.7-8.1	#	Increase in peat accumulation	N addition and gradient studies	Moore et al. 2004
Boreal forest, Sweden	<3	(#)	Decreased frequency of the shrub lingonberry, especially in spruce (as opposed to pine) stands	Possible interactions with other biotic and abiotic factors	Strengbom et al. 2003
Black spruce and jack pine forests, NE Alberta	3	(#)	Increased lichen N concentrations, morphological damage to and decreased abundance of sensitive epiphytic lichens	N effects likely confounded and/or amplified by elevated SO_2, alkaline dust and/or metal deposition	Berryman et al. 2004; Berryman and Straker 2008
Boreal forest, Finland	3	(#)	Increased cover of green algae on conifers	Increasing temperature, decreasing S may also be contributing to increased algal cover	Poikolainen et al. 1998
Peatlands, NE Alberta	>3	#	Gradual decrease in net primary photosynthesis of *Sphagnum fuscum*	Combined multiple N- addition studies	Vitt et al. 2003
Boreal forest, Sweden	5-8	(#)	Decreases in the proportion of N-sensitive epiphytic lichens	Confounding temperature effect	Bråkenhielm and Quinghong 1995
Boreal forest, Sweden	6	##	Increase in grass cover, esp. wavy hairgrass; decreased growth of shrubs whortleberry and lingonberry	Long term experiment in area with low background deposition using low N addition rates	Nordin et al. 2005
Boreal forest, Sweden	6	#	Decreased frequency of the shrub, whortleberry, concurrent with rates of parasitism by *Valdensia heterodoxa*	Possible interactions with other biotic and abiotic factors	Strengbom et al. 2003
Low-alpine heather heaths, Cairngorm Mtns, Scotland	5-15	#	Reduced species richness of lichens; also higher plants via interactions with climate		Britton and Fisher 2007
Northern Europe	10-15; 10-20	#	Increased mineralization, nitrification and N leaching of soils		Bobbink et al. 2003, de Vries et al. 2007

Northern Europe	10-15	#	Changes in composition and cover of understory vascular plants, bryophytes, lichens, and free-living algae		Bobbink et al. 2003, de Vries et al. 2007
Northern Europe	10-20	(#)	Reduced sporocarp production, changed/reduced below-ground mycorrhizal species composition		Bobbink 2003, de Vries et al. 2007
Boreal forest, Sweden	<12	#	Increased fungal parasitism of whortleberry by *Valdensia heterodoxa*; enhanced growth of wavy hairgrass from defoliation of parasitized whortleberry and from N addition		Strengbom et al. 2002
Boreal forest, Sweden	12	(#)	Increased abundance of the green alga, *Scoliciosporum chlorococcum*, on conifers	Confounding temperature effect	Bråkenhielm and Quinghong 1995
Red spruce High elevation New Hampshire spruce fir forest	<16	#	First year foliage showed lower membrane instability, increased electrolyte losses, greater susceptibility to frost damage	Similar effects were observed after 12 years of fertilization at 15.7 and 31.4 kg N ha^{-1} yr^{-1}, suggesting that the CL is well below 15.7	Schaberg et al. 2002
Norway spruce stand, southern Finland	25	(#)	Decreased biomass of dominant oligotrophic mosses *Pleurozium schreberi* and *Dicranum polysetum*	4 yr study. 30 kg S also added therefore effect not due to N alone	Mäkipää 1998
Pinus-Cladina boreal forest, Ontario, Canada	<40	##	Increase in nitrification (lichen-dominated bedrock) leading to N leaching; increased production of NH_4^+ in tree islands with deeper soils	Hydrological connectivity in taiga ecosystems may permit cascading N saturation in boreal shield landscapes	Lamontagne 1998, Lamontagne and Schiff 1999

Table 6.2—Empirical critical loads of nutrient N for the Taiga ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Lichen, moss, and algae	1-3	#	Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates		Berryman et al. 2004, Berryman and Straker 2008, Geiser et al. 2010, Moore et al. 2004, Poikolainen et al. 1998, Strengbom et al. 2003, Vitt et al. 2003
Mycorrhizal fungi, spruce-fir forests	5-7	(#)	Change in ectomycorrhizal fungi community structure	Expert judgment extrapolated from Marine West Coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
Shrublands	6	##	Alterations in shrub and grass cover; increased parasitism of shrubs	Long term, low N addition study: shrub cover decreased, grass cover increased	Nordin et al. 2005, Strengbom et al. 2003

Provisional N critical loads using ectomycorrhizal fungal abundance and diversity as indicators ranged from 5 to 7 kg ha^{-1} yr^{-1}, based on critical loads determined using the same indicators in similar forest types in the Marine West Coast Forests and Northern Forests ecoregions (Chapters 9 and 7; Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008).

Based on reliable estimates from European work described previously and in section 6.5, critical loads for alterations in shrub and grass community composition in the Taiga ecoregion could be set at 6 kg ha^{-1} yr^{-1} (Nordin et al. 2005, Strengbom et al. 2003; Table 6.1). However, the higher European critical loads estimates correspond to the levels of N added in experimental manipulations, which may far exceed the level of N input that would eventually induce a response. As deposition levels exceed 5 to 15 kg N ha^{-1} yr^{-1}, the following become evident: changes in woodland, heath, and peatland communities of vascular plant (especially shrubs and grasses) and mycorrhizal communities; increased foliar nutrient imbalances; and increased susceptibility of vegetation to frost, drought, pathogens and pests. At deposition levels exceeding 15 kg N ha^{-1}, changes in nitrification rates, soil saturation and N leaching can be documented, especially when the N-holding capacity of moss and lichen mats are exceeded.

6.5 Critical Load Data from Europe or from Other Ecoregions

European critical loads for boreal forest ecosystems (Bobbink et al. 2003) as updated by the Alterra Rapport 1382 (de Vries et al. 2007) are 10 to 15 kg N ha^{-1} yr^{-1} for soil processes (increased mineralization, nitrification and N leaching); 10 to 20 kg N ha^{-1} yr^{-1} for increased risk of foliar nutrient imbalances (decreased P, K and Mg to N ratios in foliar tissue) in coniferous and deciduous trees and changes in community composition and of ground vegetation, lichens, and mycorrhizae; and 15 to 25 kg N ha^{-1} yr^{-1} for increased susceptibility to frost, drought, pathogens, and pests, and increases in free algae. Based largely on biodiversity changes documented by Nordin et al. 2005 (see section 6.3), de Vries et al. (2007) recommended decreasing the overall critical load for boreal forests from 10 to 20 (Bobbink et al. 2003) to 5 to 10 kg N ha^{-1} yr^{-1}.

European critical loads (Bobbink et al. 2003) for other taiga ecosystem components are 5 to 10 kg ha^{-1} yr^{-1} for tundra with permafrost, 10 to 15 kg ha^{-1} yr^{-1} for alpine and subalpine scrub without permafrost, and 10 to 20 kg ha^{-1} yr^{-1} for wet and dry heaths. Critical loads for Tundra and Northern Forests ecoregions are especially relevant to tundra-covered areas and large river valley areas of the Taiga ecoregion, respectively. All three ecoregions share some floral and faunal species.

6.6 Future Research Directions and Gaps in Data

Research is needed to confirm that European critical loads and study results are applicable to North America. Long-term studies at low levels of experimentally applied N (i.e., 1 to 5 kg ha^{-1} yr^{-1}) are most needed. Although local Alaskan population and emissions sources are relatively small, regional and trans-Pacific sources of N are increasing with massive energy development projects, industrial expansion, and high latitude population growth. Fire frequency and intensity in boreal ecosystems are increasing with global climate change; fire will continue to be a major regional source of NO_x. Because temperature increases are predicted to be greater in northern latitudes, North American studies are needed to elucidate the interplay between climate change, N volatilization, and N deposition on dry- and wet-land biota, communities, and ecosystems. Indeed, climate change may be the most important driver of vegetation changes in most of the Alaskan portion of the ecoregion, considering the low current background levels of N deposition.

Finally, a greater understanding is needed regarding the underlying mechanisms responsible for N-affected changes, in addition to quantification of the functional relationships between N deposition and specific ecological responses. Such a mechanistic understanding of how N addition alters low N ecosystems could be used to inform modeled predictions.

LITERATURE CITED

Aerts, R.; Chapin, F.S. 2000. **The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns.** Advances in Ecological Research. 30: 1-67.

Allen, E. 2004. **Effects of nitrogen deposition on forests and peatlands: A literature review and discussion of the potential impacts of nitrogen deposition in the Alberta Oil Sands region.** Report to the Wood Buffalo Association. Fort McMurray, AB, Canada: Wood Buffalo Assoc. Available at http://wbea.org/index2.php?option=com_docman&task=doc_view&gid=299&Itemid=104 (Accessed May 10, 2010).

Aronsson, A. 1980. **Frost hardiness in Scots pine. II. Hardiness during winter and spring in young trees of different mineral status.** Studia Forestalia Suecica. 155: 1-27.

Balsberg-Påhlsson, A. 1992. **Influence of nitrogen fertilization on minerals, carbohydrates, amino acids and phenolic compounds in beech (*Fagus sylvatica*) leaves.** Tree Physiology. 10: 93-100.

Berryman, S.; Geiser, L.; Brenner, G. 2004. **Depositional gradients of atmospheric pollutants in the Athabasca Oil Sands region, Alberta, Canada: an analysis of lichen tissue and lichen communities.** Lichen Indicator Pilot Program 2002-2003. Final report to the Terrestrial Environmental Effects Monitoring Science Sub-committee of the Wood Buffalo Environmental Association. Available at http://wbea.org/component/option,com_docman/task,cat_view/gid,29/dir,DESC/order,date/Itemid,104/limit,10/limitstart,0/ (Accessed April 20, 2011).

Berryman , S.; Straker, J. 2008. **Nitrogen loading and terrestrial vegetation—Assessment of existing regional vegetation data and recommendations for future monitoring.** Report to the Cumulative Environmental Management Association (CEMA) NO_x-SO_2 Management Working Group (NSMWG) and Eutrophication Task Group. Sydney, BC, Canada: CE Jones and Associates.

Bobbink, R. 2004. **Plant species richness and the exceedance of empirical nitrogen critical loads: an inventory.** Bilthoven, Utrecht University/RIVM. Report Landscape Ecology.

Bobbink, R.; Ashmore, M.R.; Braun, S.; Fluckiger, W.; van der Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R., eds. Empirical critical loads for nitrogen. Environmental Documentation 164. Background document for expert workshop on empirical critical loads for nitrogen on semi-natural ecosystems; 2002 November 11-13; Berne, Switzerland: Swiss Agency for the Environment, Forests and Landscape: 143-170.

Bråkenhielm, S.; Quinghong, L. 1995. **Spatial and temporal variability of algal and lichen epiphytes on trees in relation to pollutant deposition in Sweden.** Water, Air and Soil Pollution. 79: 61-74.

Britton, A.J.; Fisher, J.M. 2007. **Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate *Calluna vulgaris* heathland.** Journal of Applied Ecology. 44: 125-135.

Bruteig, I.E. 1993. **The epiphytic lichen *Hypogymnia physodes* as a biomonitor of atmospheric nitrogen and sulphur deposition in Norway.** Environmental Monitoring and Assessment. 26: 27-47.

CEC (Commision for Environmental Cooperation). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

Cornelissen, J. H. C.; Callaghan, T.V.; Alatalo, J.M.; Michelsen, A.; Graglia, E.; Hartley, A.E.; Hik, D.S.; Hobbie, S.E.; Press, M.C.; Robinson, C.H.; Henry, G.H.R.; Shaver, G.R.; Phoenix, G.K.; Jones, D.G.; Jonasson, S.; Chapin, F.S.; Molau, U.; Neill, C.; Lee, J.A.; Melillo, J.M.; Sveinbjornsson, B.; Aerts, R. 2001. **Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass?** Journal of Ecology. 89: 984-994.

Crittenden, P.D. 1998. **Nutrient exchange in an Antarctic macrolichen during summer snowfall-snow melt events.** New Phytologist. 139(4): 697-707.

Crittenden, P.D. 2000. **Aspects of the ecology of mat-forming lichens.** Rangifer. 20(2-3): 127-139.

Crittenden, P.D.; Kalucka, I.; Oliver, E. 1994. **Does nitrogen supply limit the growth of lichens?** Cryptogamic Botany. 4: 143-155.

Curtis, C.J.; Emmett, B.A.; Grant, H.; Kernan, M.; Reynolds, B.; Shilland, E. 2005. **Nitrogen saturation in UK moorlands: the critical role of bryophytes and lichens in determining retention of atmospheric N deposition.** Journal of Applied Ecology. 42: 507-517.

de Vries, W.; Kros, H.; Reinds, G.; Wamelink, W.; Mol, J.; van Dobben, H.; Bobbink, R.; Emmett, B.; Smart, S.; Evans, C.; Schlutow, A.; Kraft,P.; Belyazid, S.; Sverdrup, H.; van Hinsberg, A.; Posch, M.; Hettelingh, J.-P. 2007. **Developments in deriving critical limits and modeling critical loads of nitrogen for terrestrial ecosystems in Europe.** Alterra Report 1382 [Alterra-rapport 1382]. Wageningen, The Netherlands: Wageningen University, Alterra. 206 p.

Emmett, B.A. 2007. **Nitrogen saturation of terrestrial ecosystems: some recent findings and their implications for our conceptual framework.** Water, Air and Soil Pollution. 7: 99-109.

Geiser, L.H.; Jovan, S.E.; Glavich, D.A.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in western Oregon and Washington forests, USA.** Environmental Pollution. 158: 2412-2421.

Gough, L.; Osenberg, C.W.; Gross, K.L.; Collins, S.L. 2000. **Fertilization effects on species density and primary productivity in herbaceous plant communities.** Oikos. 89: 428-439.

Hall, J. V.; Frayer, W.E.; Wilen, B.O. 1994. **Status of Alaska wetlands.** Anchorage, AK: U.S. Department of the Interior, U.S. Fish and Wildlife Service. 32 p. Available at www.fws.gov/wetlands/_documents/gSandT/StateRegionalReports/Status/AlaskaWetlands.pdf (Accessed March 14, 2011).

Holopainen, T.; Karenlampi, L. 1985. **Characteristic ultrastructural symptoms caused in lichens by experimental exposure to nitrogen compounds and fluorides.** Annales Botanici Fennici. 22: 333-342.

Hyvärinen, M.; Crittenden, P.D. 1998a. **Growth of the cushion-forming lichen, *Cladonia portentosa*, at nitrogen-polluted and unpolluted heathland sites.** Environmental and Experimental Botany. 40: 67-76.

Hyvärinen, M.; Crittenden, P.D. 1998b. **Relationships between atmospheric nitrogen inputs and the vertical nitrogen and phosphorus concentration gradients in the lichen *Cladonia portentosa*.** New Phytologist. 140 (3): 519-530.

Jaffe, D; Zukowski, M.D. 1993. **Nitrate deposition to the Alaskan snowpack.** Atmospheric Environment. 27A: 2935-2941.

Jönsson, A.M. 2000. **Soil treatment effects on bark lesions and frost sensitivity of beech (*Fagus sylvatica*) in southern Sweden.** Forest Ecology and Management. 129:167-175.

Jönsson, A.M.; Ingerslev, M.; Raulund-Rasmussen, K. 2004a. **Frost sensitivity and nutrient status in a fertilized Norway spruce stand in Denmark.** Forest Ecology and Management. 201:199-209.

Jönsson, A.M.; Kivimäenpää, M.; Stjernquist, I.; Sutinen, S. 2001. **Frost hardiness in bark and needles of Norway spruce in southern Sweden.** Trees. 15:171-176.

Jönsson, A.M.; Rosengren-Brinck, U.; Nihlgård, B. 2004b. **Excess nitrogen affects the frost sensitivity of the inner bark of Norway spruce.** Annals of Forestry Science. 61: 293-298.

Kallio, T.K.; Häkkinen, R.; Heinonen, J. 1985. **An outbreak of *Gremmeniella abietina* in central Finland.** European Journal of Forest Pathology. 15: 216-223.

Kellner, P.S.; Redbo-Torstensson, P. 1995. **Effects of elevated nitrogen deposition on the field-layer vegetation in coniferous forests.** Ecological Bulletins. 44: 227-237.

Kytöviita, M.-M.; Crittenden, P.D. 2007. **Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*.** Annals of Botany. 100: 1537-1545.

Lamers, L.P.M.; Bobbink, R.; Roelofs, J.G.M. 2000. **Natural nitrogen filter fails in polluted raised bogs.** Global Change Biology. 6: 583-586.

Lamontagne, S. 1998. **Nitrogen mineralization in upland Precambrian Shield catchments: contrasting the role of lichen-covered bedrock and forested areas.** Biogeochemistry. 41: 53-69.

Lamontagne, S.; Schiff, S.L. 1999. **The response of a heterogeneous upland boreal shield catchment to a short term NO_3^- addition.** Ecosystems. 2: 460-473.

Lamontagne, S.; Schiff, S.L. 2000. **Response of soil microorganisms to an elevated nitrate input in an open *Pinus banksiana-Cladina* forest.** Forest Ecology and Management. 137: 13-22.

Lilleskov, E.A. 1999. **Decline of above- and belowground ectomycorrhizal fungal diversity over an atmospheric nitrogen deposition gradient near Kenai, Alaska.** Ithaca, NY: Cornell University.198 p. Ph.D. dissertation.

Lilleskov, E.A.; Fahey, T.J.; Horton, T.R; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** Ecology. 83: 104-115.

Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient.** Ecological Applications. 11: 397-410.

Lilleskov, E.A.; Wargo, P.M.; Vogt, K.A.; Vogt, D.J. 2008. **Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern US.** Canadian Journal of Forest Research. 38: 1260-1266.

Longton, R.E. 1997. **The role of bryophytes and lichens in polar ecosystems.** In: Woodin, S.J.; Marquiss, M., eds. Ecology of Arctic environments. Oxford, UK: Blackwell Science: 69-96.

Mäkipää, R. 1998. **Sensitivity of understory vegetation to nitrogen and sulfur deposition in a spruce stand.** Ecological Engineering. 10: 87-95.

Moore, T.; Blodau, C.; Turunen, J.; Roulet, N.; Richard, P.J.H. 2004. **Patterns of nitrogen and sulfur accumulation and retention in ombrotrophic bogs, eastern Canada.** Global Change Biology. 11: 356-367.

NADP (National Atmospheric Deposition Program). 2008. **National Atmospheric Deposition Program/ National Trends Network.** Available at http://nadp.sws.uiuc.edu/ (Accessed April 27, 2008).

Näsholm, T.; Ekblad, A.; Nordin, A.; Giesler, R.; Högberg, M; Högberg, P. 1998. **Boreal forest plants take up organic nitrogen.** Nature. 392: 914-916.

Nordin, A.; Näsholm, T.; Ericson, L. 1998. **Effects of simulated N deposition on understorey vegetation of a boreal coniferous forest.** Functional Ecology. 12: 691-699.

Nordin, A.; Högberg, P.; Näsholm, T. 2001. **Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient.** Oecologia. 129: 125-132.

Nordin, A.; Strengbom, J.; Witzell, J.; Näsholm, T.; Ericson, L. 2005. **Nitrogen deposition and the biodiversity of boreal forests: Implications for the nitrogen critical load.** Ambio. 34:20-24.

Poikolainen, J.; Lippo, H.; Hongisto, M.; Kubin, E.; Mikkola, K.; Lindgren, M. 1998. **On the abundance of epiphytic green algae in relation to the nitrogen concentrations of biomonitors and nitrogen deposition in Finland.** Environmental Pollution. 102: 85-92.

Schaberg, P.G.; DeHayes, D.H.; Hawley, G.J.; Murakami, P.F.; Strimbeck, G.R.; McNulty, S.G. 2002. **Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon storage in montane red spruce.** Canadian Journal of Forest Research. 32: 1351-1359.

Strengbom, J.; Nordin, A.; Näsholm, T.; Ericson, L. 2002. **Parasitic fungus mediates change in nitrogen-exposed boreal forest vegetation.** Journal of Ecology. 90: 61-67.

Strengbom, J.; Walheim, M.; Näsholm, T.; Ericson, L. 2003. **Regional differences in the occurrence of understory species reflect nitrogen deposition in Swedish forests.** Ambio. 32: 91-97.

Tamm, C.O.; Aronsson, A.; Popovic, B.; Flower-Ellis, J. 1999. **Optimum nutrition and nitrogen saturation in Scots pine stands.** Studia Forestalia Suecica. 209: 1-126.

Vitt, D.H.; Wider, K.; Halsey, L.A.; Turetsky, M. 2003. **Response of *Sphagnum fuscum* to nitrogen deposition: A case study of ombrogenous peatlands in Alberta, Canada.** The Bryologist. 106(2): 235-245.

Walker, T.R.; Crittenden, P.D.; Young, S.D. 2003. **Regional variation in the chemical composition of winter snow pack and terricolous lichens in relation to sources of acid emissions in the Usa River basin, northeast European Russia.** Environmental Pollution. 125: 401-412.

Wieder, R.K.; Vitt, D.H.; Burke-scoll, M.; Scott, K.D.; House, M.; Vile, M.A. 2010. **Nitrogen and sulphur deposition and the growth of *Sphagnum fuscum* in bogs of the Athabasca Oil Sands Region, Alberta.** In: Aherne, J.; Shaw, D.P., guest eds. Impacts of sulphur and nitrogen deposition in western Canada. Journal of Limnology. 69 (Suppl. 1): 161-170.

Wiedermann, M.M,; Nordin, A.; Gunnarsson, U.; Nilsson, M.B.; Ericson, L. 2007. **Global change shifts vegetation and plant-parasite interactions in a boreal mire.** Ecology. 88: 454-464.

7 NORTHERN FORESTS

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7.1 Ecoregion Description

The Northern Forests ecological region spans much of Canada, from Saskatchewan to Newfoundland; its southern portion extends into the northern United States (CEC 1997). The U.S. component includes the northern hardwood and spruce-fir forest types and encompasses parts of the Northeast (mountainous regions in Pennsylvania, New York, New Jersey, Connecticut, Massachusetts, Maine, and most of Vermont and New Hampshire) and the northernmost parts of the upper Midwest (Minnesota, Wisconsin, Michigan; CEC 1997; see Chapter 2, Figure 2.2). The ecoregion description is adapted from CEC (1997). In Canada, the ecoregion is underlain by ancient Canadian Shield bedrock interspersed with glacial moraine deposits, creating a hilly terrain dotted with numerous lakes. Soils are generally coarse-textured and nutrient-poor, characterized typically by thick organic accumulations in the forest floor and leached layers in the mineral soil below. Shallow soils and exposed bedrock are covered with various plant communities dominated by shrubs, forbs, and lichens. Peatlands are extensive in northern Minnesota. The climate is characterized by long, cold winters (means of -20.5 °C in the west to -1 °C in the east) and short, warm summers (means of 11 to 18 °C). Annual precipitation varies from 400 to 1,000 mm. The ecoregion is more than 80 percent forested, and dominated by conifers, mostly white and black spruce (*Picea glauca* and *P. mariana*), jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*) (CEC 1997). Toward its southern and eastern extremes in the upper midwest and northeastern United States, the ecoregion includes more paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera)*, eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), beech (*Fagus* spp.), red spruce (*Picea rubens*), and various species of oak (*Quercus* spp.).

7.2 Ecosystem Responses to N Deposition

Most northern forests are naturally nitrogen (N) limited; cold temperatures limit rates of decomposition and slow rates of release of N from decomposing organic matter. These low rates of N mineralization limit the supply of N to plants and microbes. There is strong competition for N between plants and microbes and most of the N entering the ecosystem is tightly retained in soils and in vegetation, with little loss of inorganic N to drainage waters. When air pollution increases the supply of N to these ecosystems through N deposition, a range of ecosystem responses, described below, are anticipated. Some of these responses occur as gradual changes, others as cumulative threshold responses in progressive stages of N saturation (cf. Aber et al. 1998). See Chapter 1 for a more detailed explanation of the stages. Briefly, early stages (especially stage 1) are marked by increased supply of N to plants and to microbes, indicated by increasing plant foliar N concentration, growth rate, and soil N mineralization rate. Cumulative N inputs may decrease the carbon:nitrogen (C:N) ratio of soils and change rates of decomposition. Responding to increased N supply and low soil C:N ratios, net nitrification marks a next stage of ecosystem response (stage 2). Nitrification can acidify the soil and produce high levels of nitrate (NO_3^-), a form of N that readily leaches with runoff. This phase of response is marked by increased NO_3^- concentrations in surface water and leaching of N from catchments. When NO_3^- leaches, it removes base cations from the soil and leads to soil and drainage water acidification. Collectively, acidification and nutrient imbalances may cause growth declines or increased mortality rates (stage 3). These direct effects of N deposition may also lead to increased susceptibility to secondary stresses such as winter injury, drought damage, pest outbreak, and diseases, and may reduce cold tolerance (Schaberg et al. 2002). Declining vegetation is likely to take up less N than healthy vegetation, and so losses of NO_3^- are expected to accelerate as N saturation proceeds. In addition to these ecosystem-level responses, N deposition can affect the competitive balance of different species, leading to changes in composition of mycorrhizal fungi, lichen, bryophyte, understory shrub and herb, and tree species composition. In this chapter, we review the evidence for impacts of N deposition on overstory trees, herbaceous vegetation, mycorrhizal fungi, and lichens in the Northern Forests ecoregion.

7.3 Range of Responses Observed

Three types of studies provide empirical information on the effects of N on ecosystem properties: (1) long-term observations at sites receiving increasing or chronically elevated N deposition; (2) long-term, low- to moderate-level N fertilization studies; and (3) observational studies along gradients of N deposition. All three study types are discussed below, and each approach has its strengths and limitations. Long-term observations can reveal trends through time, but also can be influenced by a great many factors in addition to N deposition, factors which are difficult to disentangle. Fertilization studies may provide some additional insight about the timing and nature of responses of forests to elevated N inputs. Often, fertilization studies utilize such high N inputs that they do not help define the actual threshold when a response is induced. Gradient studies examine ecosystem responses along gradients of N deposition, but can also suffer from difficulty in separating out effects of N from effects of other covariates.

7.3.1 Foliar N, Growth, and Mortality

Foliar N concentrations increased in most N fertilization experiments in the Northern Forests ecoregion (Table 7.1). This increase in foliar N might be expected to increase plant growth, since photosynthesis typically increases with foliar N concentration within and across most natural ecosystems. Increased foliar N was accompanied by increased tree growth in fertilized sugar maple stands in Michigan (Pregitzer et al. 2008) and Maine (Elvir et al. 2003). However, fertilized red spruce trees in Maine (Elvir et al. 2003) and black spruce and balsam fir stands in northern Quebec (Houle and Moore 2008) showed no change in growth rates. At a subalpine spruce-fir forest at Mt. Ascutney, Vermont, long-term fertilization with ammonium chloride (NH_4Cl) at 15.7 kg N ha^{-1} yr^{-1} (in addition to ambient wet plus dry N deposition of approximately 10 kg ha^{-1} yr^{-1}) increased foliar N concentration and decreased growth and increased mortality, leading to an approximately 20 percent decline in live basal area after 14 years (McNulty et al. 2005). Other effects observed at this fertilization rate were reductions in foliar membrane-associated Ca, reduced cold tolerance, and increased winter freezing injury (Schaberg et al. 2002). The responses observed at the high treatment plot, where 31 kg N ha^{-1} yr^{-1} above ambient deposition were added, are far more striking. In these plots, mortality is high (40 percent decline in live basal area) and species composition changes were induced after only 14 years of N addition (McNulty et al. 2005).

Overall, these fertilization experiments show modest growth enhancement by some, but not all, species. Sometimes the initial growth enhancement is followed by growth declines or increased mortality in the long-term studies, especially at the highest rates of N inputs or sites with soils containing few base cations. It is unclear precisely where this threshold for detrimental effects occurs, although the experimental work at Mt. Ascutney demonstrated substantial mortality by red spruce in response to just 15.7 kg N ha^{-1} yr^{-1} above the ambient deposition of approximately 10 kg N ha^{-1} yr^{-1}. While Mt. Ascutney clearly represents the sensitive end-member of forest ecosystems in the Northeast, it is instructive because the nonlinear path that the high treatment plots followed may also occur over time at the low treatment plot. It is possible, then, that inputs even lower than 26 kg N ha^{-1} yr^{-1} would lead to N saturation over an extended period of time (e.g., 50 to 100 years).

Gradient studies have shown mixed evidence for foliar N response to atmospheric deposition to northern forest ecosystems. In a broad synthesis of data from 354 plots in upland forests across the Northeast, Aber et al. (2003) did not find patterns of increasing foliar N concentration with deposition, even when controlling for tree species; variation in foliar N was most strongly associated with elevation and climatic variables. In red spruce, foliar lignin:N ratio was related to N deposition, but deposition covaried with elevation

Table 7.1—Response of Northern Forest ecosystems to experimental N fertilization (≤ 50 kg N ha^{-1} yr^{-})

Site Location	Michigan (4 sites)	Mt. Ascutney, Vermont	---- Bear Brook, ---- Maine		Adirondacks, NY (3 sites)	Northwest Ontario	---- Northern ---- Quebec	
Forest type	Sugar maple	Montane spruce-fir	Northern hardwoods	Red spruce	Northern hardwoods	Rock, Jack pine / spruce	Black spruce	Balsam fir
Type of N deposition	Wet + dry	Wet + dry	Wet + dry		Throughfall	Bulk	Wet only	
N Deposition (*kg ha^{-1} yr^{-1}*)	6.8-11.8	10	8.4		4.6-12.0	3.4-6.5	3	5.7
N fertilization rate (*kg ha^{-1} yr^{-1}*)	+30	+15.7, +31.4	+25		+14, +28	+36-40	+9, +30	+18, +60
Form of N fertilizer	$NaNO_3$	NH_4Cl	$(NH_4)_2SO_4$		HNO_3, $(NH_4)_2SO_4$	$NaNO_3$	NH_4NO_3	
Start year	1994	1988	1989		1991	1995	2001	
Duration (years)	10	14	13		3	2	3	3
- Response relative to Control[a] -								
Tree growth	+	–	+	0	ND	ND	0	0
Mortality	+	+	ND	ND	ND	ND	ND	ND
Foliar %N	+	+	+	+	ND	ND	+	0
Foliar %Ca	ND	–	0, –	–	ND	ND	+	0
NO_3^- leaching	+	ND	+		0, 0, +	+	+	+
Cation loss	ND	ND	+		ND	ND	ND	ND
Soil C/N	0	0	0	–	ND	ND	ND	ND
N mineralization	0	0, –	+	+	ND	ND	ND	ND
Nitrification	+	+	+	+	ND	ND	ND	ND
Soil respiration	–	–	0	ND	ND	ND	ND	ND
Microbial biomass	0	–	0	ND	ND	ND	ND	ND
References	1-5	6-7	7-11		12	13	14	14

[a]Responses are indicated as positive (+), negative (–) or no response (0) in fertilized relative to control plots, or no data (ND) in indicated references.

References: 1) Burton et al. 2004; 2) Pregitzer et al. 2004; 3) Pregitzer et al. 2008; 4) Zak et al. 2004; 5) Zak et al. 2006; 6) McNulty et al. 2005; 7) Wallenstein et al. 2006; 8) Elvir et al. 2003; 9) Elvir et al. 2006; 10) Fernandez et al. 2003; 11) Jefts et al. 2004; 12) Mitchell et al. 2001; 13) Lamontagne and Schiff 1999; 14) Houle and Moore 2008.

and climatic variables within this dataset (Aber et al. 2003). However, other studies have shown that foliar N concentration increases with increasing N deposition. McNeil et al. (2007) saw an increase in foliar N concentration for eight of nine canopy tree species across 73 plots spanning an N deposition gradient (3.5 to >7 kg ha^{-1} yr^{-1} of wet-only N deposition) in the Adirondack Park, New York. American beech *(Fagus grandifolia)* did not respond, but yellow birch (*Betula alleghaniensis*), paper birch, red maple (*Acer rubrum*), sugar maple, eastern white pine, eastern hemlock *(Tsuga canadensis)*, balsam fir, and red spruce did. Another regional foliar analysis, which included 2702 foliar samples from 434 plots in the Northeast, found significant correlations between N deposition (5 to 12 kg ha^{-1} yr^{-1} of wet plus dry deposition) and foliar N concentration for both hardwoods and conifers (Pardo et al. 2006). This study also examined foliar $\delta^{15}N$, another measure used to assess the N status of ecosystems because it provides an integrated measure of past N cycling and often increases in response to disturbance (Emmett et al. 1998, Nadelhoffer and Fry 1994). Foliar $\delta^{15}N$ increased with deposition, although correlations were stronger for conifers than for hardwoods (Pardo et al. 2006); in all cases the correlation between N deposition and foliar N concentration was stronger than with foliar

$\delta^{15}N$. In another gradient study evaluating N cycling in red spruce stands from Maine to New York, sampling in 1987 and 1988 (McNulty et al. 1991) and again in 1999 (Boggs et al. 2007) showed an increase in foliar N concentration both over time and with deposition along the gradient from 5 to 11 kg N ha^{-1} yr^{-1} (Pardo et al. 2007). Hardwood foliar N concentration was measured only in 1999 and increased with deposition along the gradient. These relationships were weaker than for spruce, but were statistically significant (Pardo et al. 2007). These studies broadly demonstrate that foliar N concentration in Northern Forests tends to increase with increasing N inputs. Nonetheless, because of the variability in response and the lack of a threshold above which the rate of change is altered, it is difficult to use foliar N concentration alone as an indicator of N saturation.

Until recently, there has been little evidence outside of fertilization experiments for either enhanced growth or mortality in U.S. forests attributable to elevated N deposition. This lack of evidence is largely due to the difficulty of detecting such a signal against the large background variation due to factors that affect growth in natural ecosystems and the relative paucity of such studies. Caspersen et al. (2000) discerned a 2.0 percent enhancement of forest biomass in several states (Minnesota, Michigan, Virginia, North Carolina, and Florida) over the last century, but could not identify which mechanism (e.g., rising atmospheric CO_2 concentrations, climate changes, N deposition) might be responsible for this growth increase. Similarly, Hicke et al. (2002) reported changes in forest growth across North America over the last two decades derived from satellite observations of canopy properties, but saw no trends that were easily attributable to N deposition. In Europe, regional patterns of forest growth are largely driven by forest management decisions, but growth enhancement from N deposition has long been speculated (e.g., Kauppi et al. 1992, Nabuurs et al. 2003). Recently, Magnani et al. (2007) reported a strong correlation between wet N deposition and estimates of net ecosystem production derived from chronosequences and eddy flux towers at 20 temperate forest sites. This correlation implied a very large stimulation of C sequestration with increasing N deposition of approximately 180 to 480 kg C ha^{-1} yr^{-1} per 1 kg ha^{-1} yr^{-1} received in N deposition (Magnani et al. 2007). Several researchers have questioned the plausibility of so large an effect (de Vries et al. 2008, Högberg 2007, Sutton et al. 2008).

In a recent gradient analysis, Thomas et al. (2010) used forest inventory data from plots spanning the northern and eastern forests in the northeastern United States to discern a N deposition-induced tree-growth enhancement in plot-level biomass increment amounting to 5.5 percent per kg N ha^{-1} yr^{-1}, or 61 kg C ha^{-1} yr^{-1} per 1 kg ha^{-1} yr^{-1} received in N deposition. Overall, this plot-level growth enhancement did not saturate or decline within the range of wet + dry deposition experienced in the region (3 to 11 kg N ha^{-1} yr^{-1}). However, different tree species responded in different ways: some species had no response, some showed steady growth increases across the range of N deposition (e.g., yellow-poplar [*Liriodendron tulipifera*], black cherry [*Prunus serotina*], white ash [*Fraxinus americana*]), some showed growth rate peaks at mid-levels of N deposition (quaking aspen, scarlet oak [*Quercus coccinea*]), and one showed growth declines with increasing deposition (red pine). Tree survivorship increased with N deposition for some species (black cherry, red maple) and decreased for others (e.g., quaking and bigtooth aspen [*Populus grandidentata*], yellow birch, basswood [*Tilia* spp.], chestnut oak [*Quercus prinus*], and scarlet oak). Overall, this analysis indicates that current rates of N deposition enhance carbon sequestration in northeastern forests, but that N deposition can have negative impacts on growth and survivorship for some sensitive species.

7.3.2 Nitrate Leaching and Soil N

Conceptual models of N saturation indicate that NO_3^- leaching should increase in response to long-term increases in or chronic exposure to atmospheric N deposition (Aber et al. 1998, Stoddard 1994). In fact, long-term NO_3^- leaching trends in the northeastern United States have been inconsistent. Some sites have shown increases in NO_3^- loss over the last 20 to 30 years, particularly in regions with the highest deposition (10 to 15 kg N ha^{-1} yr^{-1}) such as the Catskill Mountains, New York (Burns et al. 2006) or Fernow Experimental

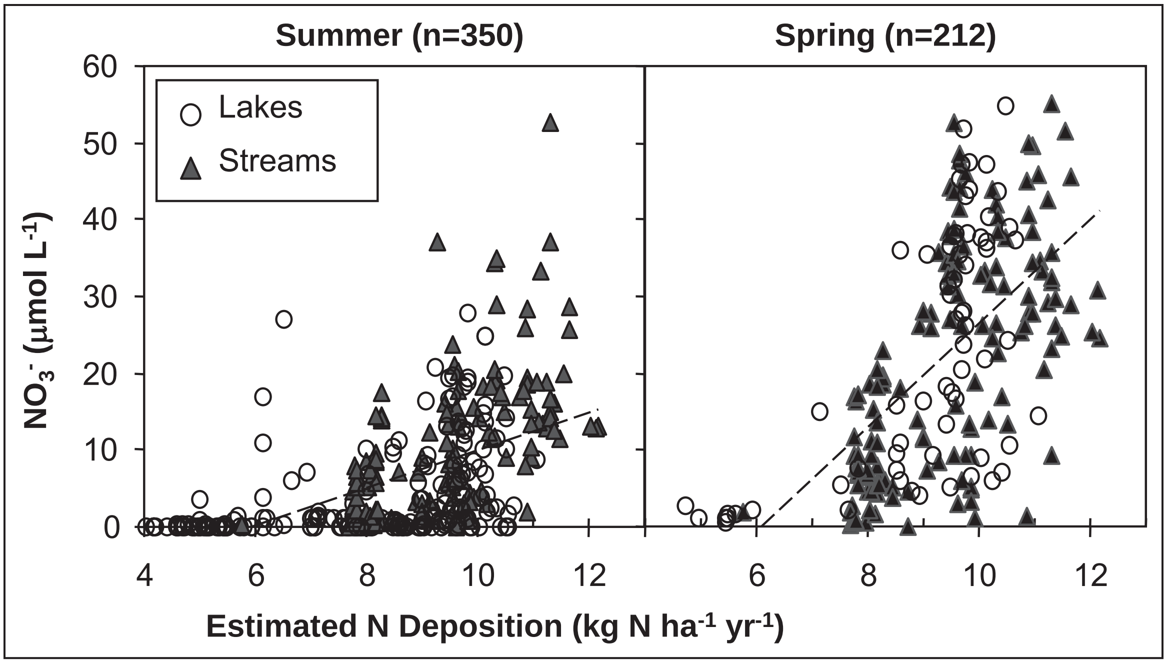

Figure 7.1—Surface water NO_3^- concentrations increase with estimates of N deposition at the base of study watersheds in both summer and spring. N deposition to the entire watershed may be approximately 1 kg ha^{-1} yr^{-1} greater than at the base (From Aber et al. 2003).

Forest, West Virginia (Peterjohn et al. 1996, Adams et al. 2006); however, there is considerable temporal variability within these records. At other sites in the Adirondacks (Driscoll et al. 2003, 2007) and at the Hubbard Brook Experimental Forest (Dittman et al. 2007) and other sites in the White Mountains, New Hampshire (Goodale et al. 2003), surface water NO_3^- concentrations have decreased over the last 20 to 30 years despite near-constant deposition.

The absence of a straightforward relationship between N deposition and surface water NO_3^- leaching over time highlights the value of other approaches for assessing N effects on leaching, such as gradient studies and fertilization experiments. In a synthesis of NO_3^- data across a northeastern N deposition gradient, Aber et al. (2003) report that surface water NO_3^- concentrations in catchments receiving less than ~8 kg N ha^{-1} yr^{-1} rarely exceed 1 μmol L^{-1} (Fig. 7.1). Nitrate concentrations increase on average above this threshold, though with substantial site-to-site variation. The wide range of NO_3^- concentrations observed likely reflect the many factors other than N deposition that impact NO_3^- leaching, such as tree species composition, soil and stand characteristics, land-use history, and hydrology. For example, a high abundance of sugar maple has been associated with elevated nitrification and NO_3^- leaching (Lovett and Rueth 1999, Lovett et al. 2004). Shallow soils at Mt. Ascutney in southern Vermont may be implicated in the site's sensitivity to N inputs and rapid increases in nitrification rates (McNulty and Aber 1993, McNulty et al. 1996, 2005). Old-growth stands have been shown to have higher nitrification rates and NO_3^- leaching than second-growth historically logged or burned stands in the White Mountains of New Hampshire (Goodale and Aber 2001). However, elevated NO_3^- losses at some sites, including the old-growth Bowl Research Natural Area, New Hampshire, may reflect hydrologic flow paths more than biological controls on N saturation (Martin et al. 2000, Pardo et al. 2004). Because so many factors can affect stream NO_3^- losses, determining thresholds for NO_3^- leaching in response to N deposition requires information from a very large number of catchments to discern the leaching signal over variation driven by other factors.

The Aber et al. (2003) N gradient study included a synthesis of soil data from 250 plots in the northeastern United States, yet detected only weak relationships between N deposition and soil N cycling measures (e.g., forest floor C:N, nitrification), due to the great number of additional factors that affect N cycling beyond just N deposition. Stronger relationships were found between forest floor C:N ratio and nitrification, which presumably should lead to increased N availability for NO_3^- leaching. The study evaluating N cycling in red spruce stands across an N deposition gradient from Maine to New York found significant increases in net nitrification potential with increasing deposition in 1987 (McNulty et al. 1991). When the same sites were evaluated in 1999, the relationship between N deposition and net nitrification potential was still observed, although the rate of nitrification had decreased significantly over time (Boggs et al. 2007). Decreasing patterns in stream water NO_3^- and nitrification rate contradict the expectation that an ecosystem exposed to elevated N deposition over an extended period would move toward N saturation. Instead, these data suggest that the other factors beyond N deposition, such as climate, contribute to the observed patterns of ecosystem N cycling and loss.

7.3.3 Herbaceous Layer

There are few studies of N deposition effects on the herb layer in northern forests. In a low-level fertilization study, Hurd et al. (1998) added N in two forms at varying rates at three sites in the Adirondack Mountains of New York: (1) biweekly as dissolved nitric acid (HNO_3) spray at the rate of 14 kg N ha^{-1} yr^{-1} (two times the ambient of 7 kg N ha^{-1} yr^{-1} at the lowest deposition site); and (2) single applications of ammonium sulfate at 14 and 28 kg N ha^{-1} yr $^{-1}$ (two and four times ambient). They found that cover of prominent herbaceous species declined significantly after only 3 years of treatment, particularly in response to ammonium sulfate ($(NH_4)_2SO_4$). This decline resulted from increased shading by ferns, which can substantially reduce light levels to the forest floor. The response to N additions was more pronounced at sites experiencing lower ambient inputs of atmospheric N.

7.3.4 Mycorrhizal Fungi

*Ectomycorrhizal fungi***.** Lilleskov et al. (2008) found that community structure of ectomycorrhizal fungi changed over a regional N deposition gradient from northeastern New York to Maine. Frequency of the different morphotypes varied continuously with increasing root N, and root N was positively related to N deposition. Wet deposition at the low N end of this gradient was estimated at approximately 3 kg N ha^{-1} yr^{-1}; total N deposition would be approximately 4 kg N ha^{-1} yr^{-1} (Ollinger et al. 1993). The estimated level of N deposition resulting in community change is 5 to 7 kg N ha^{-1} yr^{-1}. This is quite similar to patterns found in white spruce forests in Alaska (Lilleskov et al. 2001, 2002) and pitch pine forests in the Pine Barrens of New Jersey (Dighton et al. 2004).

If elevated soil NO_3^- availability is a good indicator of ectomycorrhizal fungal community change in oligotrophic N-limited conifer forests (Lilleskov et al. 2002, Lilleskov 2005), then N deposition thresholds that minimize excess NO_3^- availability should be sufficient to protect ectomycorrhizal fungal diversity in these forest types.

Arbuscular mycorrhizal fungi. We have less empirical data on arbuscular mycorrhizal community response to N in northern forests. One study in sugar-maple-dominated forests in Michigan has found declines of arbuscular mycorrhizal fungal biomass (van Diepen et al. 2007, 2010) and changes in community structure (van Diepen 2008) in response to N addition of 30 kg ha^{-1} yr^{-1} above background deposition of approximately 5 to 12 kg ha^{-1} yr^{-1} wet deposition, but the lower threshold of response to N is not yet known. There is some indication that arbuscular mycorrhizal biomass has declined and community composition has shifted over the N deposition gradient (van Diepen 2008), suggesting a threshold of <12 kg ha^{-1} yr^{-1} of wet deposition, but it is likely that there are interactions with within-site factors, and definitive determination of a response threshold awaits further analysis.

7.3.5 Lichens and Bryophytes

Lichen and bryophyte responses documented in the Taiga and Eastern Temperate Forests ecoregions sections can also be expected in the U.S. portion of the Northern Forests ecoregion (see Chapters 6 and 10). Nearly all northern forest lichens belong either to the boreal or to the eastern flora (Brodo et al. 2001). However, air quality in this ecoregion is much more similar to the densely populated Eastern Forests ecoregion than it is to the relatively pristine Taiga ecoregion (see Chapter 3,

Table 7.2—Critical loads of nutrient N for the Northern Forests ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Trees	>3	#	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		Thomas et al. 2010
Lichens	4-6	(#)	Community composition shift	Application of model developed for Marine West Coast Forests to Northern Forests	Geiser et al. 2010
Ectomycorrhizal fungi	5-7	#	Change in fungal community structure		Lilleskov et al. 2008
Herbaceous species cover	>7 and <21	#	Loss of prominent species	Response observed in low-level fertilization experiment	Hurd et al. 1998
Northern Hardwood and Coniferous Forests	8	##	increased surface water nitrate leaching		Aber et al. 2003
Tree growth and mortality	>10 and <26	#	Decreased growth and/or induced mortality	Response observed in low-level fertilization experiment in old-growth montane red spruce	McNulty et al. 2005
Arbuscular mycorrhizal fungi	<12	(#)	biomass decline and community composition change	Observed along a Michigan N gradient	van Diepen 2008

air quality for the Taiga ecoregion). Responses to combined sulfur dioxide (SO_2^-), acidity, and enhanced N deposition in western Pennsylvania (Showman and Long 1992) and New York (Smiley and George 1974) have included dramatic declines in species diversity and a shifting of community composition favoring acid- and N-tolerant species. Information on lichen research methodology and terminology can be found in Chapter 4 of this report.

7.4 Critical Loads Estimates

Empirical critical loads for both hardwood and coniferous ecosystems within the Northern Forest ecoregion can be set at 8 kg ha^{-1} yr^{-1} (Table 7.2), the observed threshold for surface water NO_3^- leaching from these forests (Aber et al. 2003). This estimate is very reliable because it is based on 354 data points from sites around the northeastern United States (Aber et al. 2003). Rather than threshold responses, foliar N concentration and forest growth and survivorship all tend to show gradual responses with variation in N deposition received in the northern United States, with responses that often vary by species. Some sensitive tree species show declines in growth (red pine) or survivorship (yellow birch, scarlet and chestnut oak, quaking aspen, and basswood) as deposition increases across the Northeast from 3 to 11 kg N ha^{-1} yr^{-1} (Thomas et al. 2010); the critical load for negative tree growth response to N deposition is >3 kg ha^{-1} yr^{-1}. This value is fairly reliable, based on measurements from thousands of trees of each species. Based on the N-addition study in montane spruce-fir systems at Mt. Ascutney, adverse growth and mortality responses are likely to occur at deposition > 10 but <26 kg N ha^{-1} yr^{-1}

(McNulty et al. 2005). Although it only occurred at a single site, this striking and clear response of induced mortality is considered fairly reliable. Similarly, based on an N addition study in the Adirondacks, understory herbaceous composition is likely to be altered at deposition >7 kg N ha^{-1} yr^{-1} but < 21 kg N ha^{-1} yr^{-1} (Hurd et al. 1998). Because this response was observed at a single site, this value is considered fairly reliable. Ectomycorrhizal fungal-based critical loads appear to be about 5 to 7 kg N ha^{-1} yr^{-1} (Lilleskov et al. 2008); the upper end of this range converges with the critical load based on surface water NO_3^- leaching reported above. Arbuscular mycorrhizal fungal critical loads are tentatively set at <12 kg N ha^{-1} yr^{-1} (van Diepen 2008). The value for ectomycorrhizal fungi can be considered fairly reliable, as it is based on the convergence of several studies in this and ecologically similar regions. The value for arbuscular mycorrhizal fungi is considered expert judgment as it is based on one gradient with only four sites.

Application of a model relating epiphytic lichen community composition of Oregon and Washington coniferous forests to N deposition, accounting for precipitation (Chapter 4; Geiser et al. 2010), to the Northern Forests ecoregion yields a critical load estimate of 4 to 6 kg ha^{-1} yr^{-1}. This value was calculated using a precipitation range of 100 to 240 cm modeled by PRISM for the U.S. portion of northern forests, and a lichen community-composition response threshold that allows as few as 30 percent oligotrophs and no more than 34 percent eutrophs. This is the same threshold that was used for western Oregon and Washington coniferous forests by Geiser et al. (2010). Because it relies on data from other ecoregions, the value for lichens is considered expert judgment.

7.5 Comparison to European Critical Loads

Critical loads for comparable forest ecosystems in Europe are reported to range from 10 to 15 kg N ha^{-1} yr^{-1} for boreal and temperate forest, based largely on changes in soil processes and NO_3^- leaching (Bobbink et al. 2003). Critical loads for expected changes in foliar N:P and N:Mg ratios were set at 15 to 20 kg N ha^{-1} yr^{-1}; no critical load was set for growth (Bobbink et al. 2003). For herbaceous species in boreal forests, the critical load may be as low as 7 kg N ha^{-1} yr^{-1}. For ectomycorrhizal fungi, Bobbink et al. (2003) stated an expert judgment for critical loads of 10 to 20 kg N ha^{-1} yr^{-1}. For lichens and epiphytic algae, the critical load is likely not higher than 10 to 15 kg N ha^{-1} yr^{-1} (Bobbink et al. 2003).

7.6 Future Research Directions and Gaps in Data

Fundamental gaps in understanding the regulation of N availability in forest ecosystems remain. Hence, simple relationships between inputs and ecosystem outputs and damage have been difficult to determine. Other factors that may be important include climate events (disturbance and variation), prior land use, species composition, site characteristics, and hydrology. Interactions between different stressors add complexity to the input/output relationship. Low-level fertilization induced substantial mortality in a montane spruce-fir ecosystem at Mt. Ascutney (McNulty et al. 2005), but it is not clear to what extent that research can be extrapolated to the rest of the region, especially to lowland forests. Determining whether this site is unique would be useful to understanding the potential consequences of elevated N deposition in the Northern Forest ecoregion.

Far less research exists for herbaceous vegetation than for trees. Future research might include additional low-level fertilizations with an emphasis on examining the responses of herbaceous species, mycorrhizal fungi, bryophytes (especially in bog ecosystems), and lichens. In addition, diversity and community structure could be included in the parameters measured. Better quantification of N deposition at high elevations would also help improve understanding of the susceptibility of the ecosystems and the thresholds when responses occur.

Finally, the results of this analysis may be useful in improving understanding of the value chosen for critical N concentrations or leaching values in the steady-state mass balance method for calculating critical loads.

LITERATURE CITED

Aber, J.D.; Goodale, C.L.; Ollinger, S.V.; Smith, M.-L.; Magill, A.H.; Martin, M.E.; Hallet, R.A.; Stoddard, J.L. 2003. **Is nitrogen deposition altering the nitrogen status of Northeastern forests?** BioScience. 53(4): 375-389.

Aber, J.; McDowell, W.; Nadelhoffer, K.; Magill, A.; Berntson, G.; Kamakea, M.; McNulty, S.; Currie, W.; Rustad, L.; Fernandez, I. 1998. **Nitrogen saturation in temperate forest ecosystems.** BioScience. 48(11): 921-934.

Adams, M.B; DeWalle, D.R.; Hom, J.L., eds. 2006. **The Fernow watershed acidification study.** Dordrecht, Netherlands: Springer. 279 p.

Bobbink, R.; Ashmore, M.R.; Braun, S.; Fluckiger, W.; van der Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R., eds. Empirical critical loads for nitrogen. Environmental Documentation 164. Background document for expert workshop on empirical critical loads for nitrogen on semi-natural ecosystems; 2002 November 11-13; Berne, Switzerland: Swiss Agency for the Environment, Forests and Landscape: 143-170.

Boggs, J.L.; McNulty, S.G.; Pardo, L.H. 2007. **Changes in conifer and deciduous forest foliar and forest floor chemistry and basal area tree growth across a nitrogen (N) deposition gradient in the northeastern US.** Environmental Pollution. 149: 303-314.

Brodo, I.M.; Duran Sharnoff, S.; Sharnoff, S. 2001. **Lichens of North America.** New Haven, CT: Yale University Press. 795 p.

Burns, D.A.; McHale, M.R.; Driscoll, C.T., Roy, K.M. 2006. **Response of surface water chemistry to reduced levels of acid precipitation: comparison of trends in two regions of New York, USA.** Hydrological Processes. 20: 1611-1627.

Burton A.J.; Pregitzer K.S.; Crawford J.N.; Zogg G.P.; Zak D.R. 2004. **Chronic additions reduce soil respiration in northern hardwood forests.** Global Change Biology. 10: 1080-1091.

Caspersen, J.P.; Pacala, S.W.; Jenkins, J.C.; Hurtt, G.C.; Moorcroft, P.R.; Birdsey, R.A. 2000. **Contributions of land-use history to carbon accumulation in U.S. forests.** Science. 290: 1148-1151.

Commision for Environmental Cooperation (CEC). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf. (Accessed May 24, 2010).

de Vries, W.; Solberg, S.; Dobbertin, M.; Sterba, H.; Laubhahn, D.; Reinds, G.J.; Nabuurs, G.J.; Gundersen, P.; Sutton, M.A. 2008. **Ecologically implausible carbon response?** Nature. 451 (7180): 1-3.

Dighton, J.; Tuininga, A.R.; Gray, D.M.; Huskins, R.E.; Belton, T. 2004. **Impacts of atmospheric deposition on New Jersey pine barrens forest soils and communities of ectomycorrhizae.** Forest Ecology and Management. 201: 131-144.

Dittman, J.A.; Driscoll, C.T.; Groffman, P.M.; Fahey, T.M. 2007. **Dynamics of nitrogen and dissolved carbon at the Hubbard Brook Experimental Forest.** Ecology. 88: 1153-166.

Driscoll, C.T.; Driscoll, K.M.; Roy, K.M.; Dukett; J. 2007. **Changes in the chemistry of lakes in the Adirondack region of New York following declines in acidic deposition.** Applied Geochemistry. 22: 1181-1188.

Driscoll, C.T.; Driscoll, K.M.; Roy, K.M.; Mitchell, M.J. 2003. **Chemical response of lakes in the Adirondack region of New York to declines in acidic deposition.** Environmental Science and Technology. 37: 2036-2042.

Elvir, J.A.; Wiersma, G.B.; Day, M.E.; Greenwood, M.S.; Fernandez, I.J. 2006. **Effects of enhanced nitrogen deposition on foliar chemistry and physiological processes of forest trees at the Bear Brook Watershed in Maine.** Forest Ecology and Management. 221: 207-214.

Elvir, J.A.; Wiersma, G.B.; White, A.; Fernandez, I. 2003. **Effects of chronic ammonium sulfate treatment on basal area increment in red spruce and sugar maple at the Bear Brook Watershed in Maine.** Canadian Journal of Forest Research. 33: 862-869.

Emmett, B.A.; Kjønaas, O.J.; Gundersen, P.; Koopmans, C.; Tietema, A.; Sleep, D. 1998. **Natural abundance of ^{15}N in forests across a nitrogen deposition gradient.** Forest Ecology and Management. 101: 9-18.

Fernandez, I.J.; Rustad, L.E.; Norton, S.A.; Kahl, J.S.; Cosby, B.J. 2003. **Experimental acidification causes soil base-cation depletion at the Bear Brook Watershed in Maine.** Soil Science Society of America Journal. 67: 1909-1919.

Geiser, L.H.; Glavich, D.A.; Jovan, S.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA.** Environmental Pollution. 158: 2412-2421.

Goodale, C.L.; Aber, J.D. 2001. **The long-term effects of land-use history on nitrogen cycling in northern hardwood forests.** Ecological Applications. 11: 253-267.

Goodale, C.L; Aber, J.D.; Vitousek, P.M. 2003. **An unexpected nitrate decline in New Hampshire streams.** Ecosystems. 6: 75-86.

Hicke, J.A.; Asner, G.P.; Randerson, J.T.; Tucker, C.; Los, S.; Birdsey, R.; Jenkins, J.C.; Field, C.; Holland, E. 2002. **Satellite-derived increases in net primary productivity across North America, 1982-1998.** Geophysical Research Letters. 29 (10): 10.1029/2001GL013578.

Högberg, P. 2007. **Nitrogen impact on forest carbon.** Nature. 447: 781-782.

Houle, D.; Moore, J.D. 2008. **Soil solution, foliar concentrations and tree growth response to 3-year of ammonium-nitrate addition in two boreal forests of Québec, Canada.** Forest Ecology and Management. 255 (7): 2049-2060.

Hurd, T.M.; Brach, A.R.; Raynal, D.J. 1998. **Response of understory vegetation of Adirondack forests to nitrogen additions.** Canadian Journal of Forest Research. 28: 799-807.

Jefts, S.; Fernandez, I.J.; Rustad, L.E.; Dail, D.B. 2004. **Decadal responses in soil N dynamics at the Bear Brook Watershed in Maine, USA.** Forest Ecology and Management. 189: 189-205.

Kauppi, P.; Mielikainen, K.; Kuusela, K. 1992. **Biomass and carbon budgets of European forests, 1971-1990.** Science. 256: 70-74.

Lamontagne, S.; Schiff, S.L. 1999. **The response of a heterogeneous upland boreal shield catchment to a short term NO_3^- addition.** Ecosystems. 2: 460-473.

Lilleskov, E.A. 2005. **How do composition, structure, and function of mycorrhizal fungal communities respond to nitrogen deposition and ozone exposure?** In: Dighton, J.; White, J.F;. Oudemans, P., eds. The fungal community: its organization and role in the ecosystem. Boca Raton, FL: Taylor and Francis: 769-801.

Lilleskov, E.A.; Fahey, T.J.; Horton, T.R; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** Ecology. 83: 104-115.

Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community**

change over an atmospheric nitrogen deposition gradient. Ecological Applications. 11: 397-410.

Lilleskov, E.A.; Wargo, P.M.; Vogt, K.A.; Vogt, D.J. 2008. **Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern US.** Canadian Journal of Forest Research. 38: 1260-1266.

Lovett, G.M.; Rueth, H. 1999. **Soil nitrogen transformations in beech and maple stands along a nitrogen deposition gradient.** Ecological Applications. 9(4): 1330-1344.

Lovett, G.M.; Weathers, K.C.; Arthur, M.A.; Schultz, J.C. 2004. **Nitrogen cycling in a northern hardwood forest: Do species matter?** Biogeochemistry. 67: 289-308.

Magill, A.H.; Aber, J.D.; Currie, W.S.; Nadelhoffer, K.J.; Martin, M.E.; McDowell, W.H.; Melillo, J.M.; Steudler, P. 2004. **Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA.** Forest Ecology and Management. 196: 7-28.

Magnani F.; Mencuccini, M.; Borghetti, M.; Berbigier, P.; Berninger, F.; Delzon, S.; Grelle, A.; Hari, P.; Jarvis, P.G.; Kolari, P.; Kowalski, A.S.; Lankreijer, H.; Law, B.E.; Lindroth, A.; Loustau, D.; Manca, G.; Moncrieff, J.B.; Rayment, M.; Tedeschi, V; Valentini, R.; Grace, J. 2007. **The human footprint in the carbon cycle of temperate and boreal forests.** Nature. 447: 848-851.

Martin, C.W.; Driscoll, C.T.; Fahey, T.J. 2000. **Changes in streamwater chemistry after 20 years from forested watersheds in New Hampshire, USA.** Canadian Journal of Forest Research. 30: 1206-1213.

McNeil B.E.; Read, J.M.; Driscoll, C.T. 2007. **Foliar nitrogen responses to elevated nitrogen deposition in nine temperate forest canopy species.** Environmental Science and Technology. 41: 5191-5197.

McNulty, S.G.; Aber, J.D. 1993. **Effects of chronic nitrogen additions on nitrogen cycling in a high-elevation red spruce-fir stand.** Canadian Journal of Forest Research. 23: 1252-1263.

McNulty, S.G.; Aber, J.D.; Boone, R.D. 1991. **Spatial changes in forest floor and foliar chemistry of spruce-fir forests across New England.** Biogeochemistry. 14: 13-29.

McNulty, S.G.; Aber, J.D.; Newman, S. D. 1996. **Nitrogen saturation in a high elevation New England red spruce-fir stand.** Forest Ecology and Management. 84: 109-121.

McNulty, S.G.; Boggs, J.; Aber, J.D.; Rustad, L.; Magill, A. 2005. **Red spruce ecosystem level changes following 14 years of chronic N fertilization.** Forest Ecology and Management. 219: 279-291.

Mitchell, M.J.; Driscoll, C.T.; Owen, J.S.; Schaefer, D.; Michener, R.; Raynal, D.J. 2001. **Nitrogen biogeochemistry of three hardwood ecosystems in the Adirondack Region of New York.** Biogeochemistry. 56 (2): 93-133.

Nabuurs, G.-J.; Schelhaas, M.-J.; Mohren, G.M.J.; Field, C.B. 2003. **Temporal evolution of the European forest sector carbon sink from 1950-1999.** Global Change Biology. 9: 152-160.

Nadelhoffer, K.J.; Fry, B. 1994. **Nitrogen isotope studies in forest ecosystems.** In: Lajtha, K.; Michener, R.H., eds. Stable isotopes in ecology and environmental science. Cambridge, U.K.: Blackwell Scientific Publishers: 22-44.

Ollinger, S.V.; Aber, J.D.; Lovett, G.M.; Millham, S.E.; Lathrop, R.G.; Ellis, J.M. 1993. **A spatial model of atmospheric deposition for the northeastern U.S.** Ecological Applications. 3: 459-472.

Pardo, L.H.; Kendall, C.; Pett-Ridge, J.; Chang, C.C.YR. 2004. **Evaluating the source of streamwater nitrate using $\delta^{15}N$ and $\delta^{18}O$ in nitrate**

in two watersheds in New Hampshire, USA. Hydrological Processes. 18: 2699-2712.

Pardo, L.H.; McNulty, S.G.; Boggs, J.L.; Duke, S. 2007. **Regional pattern in foliar ^{15}N across a gradient of nitrogen deposition in the northeastern U.S.** Environmental Pollution. 149(3): 293-302.

Pardo, L.; Templer, P.; Goodale, C.; Duke, S.; Groffman, P.; Adams, M.; Boeckx, P.; Boggs, J.; Campbell, J.; Colman, B.; Compton, J.; Emmett, B.; Gundersen, P.; Kjønaas, J.; Lovett, G.; Mack, M.; Magill, A.; Mbila, M.; Mitchell, M.; McGee, G.; McNulty, S.; Nadelhoffer, K.; Ollinger, S.; Ross, D.; Rueth, H.; Rustad, L.; Schaberg, P.; Schiff, S.; Schleppi, P.; Spoelstra, J.; Wessel, W. 2006. **Regional assessment of N saturation using foliar and root δ^{15}N.** Biogeochemistry. 80 (2): 143-171.

Peterjohn, W.T.; Adams, M.B.; Gilliam, F.S. 1996. **Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems.** Biogeochemistry. 35: 507-522.

Pregitzer, K.S.; Burton, A.J.; King, J.S.; Zak, D.R. 2008. **Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO_2 and tropospheric O_3.** New Phytologist.180 (1): 153-161.

Pregitzer, K.S.; Zak, D.R.; Burton, A.J.; Ashby, J.A.; MacDonald, N.W. 2004. **Chronic nitrate additions dramatically increase the export of carbon and nitrogen from northern hardwood ecosystems.** Biogeochemistry. 68 (2): 179-197.

Schaberg, P.G.; DeHayes, D.H.; Hawley, G.J.; Murakami, P.F.; Strimbeck, G.R.; McNulty, S.G. 2002. **Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon storage in montane red spruce.** Canadian Journal of Forest Research. 32: 1351-1359.

Showman, R.E.; Long, R.P. 1992. **Lichen studies along a wet sulfate deposition gradient in Pennsylvania.** The Bryologist. 95 (2): 166-170.

Smiley, D.; George, C.J. 1974. **Photographic documentation of lichen decline in the Shawangunk Mountains of New York.** The Bryologist. 77: 179-187.

Stoddard, J.L. 1994. **Long-term changes in watershed retention of nitrogen.** In: Baker, L.A., ed. Environmental chemistry of lakes and reservoirs, advances in chemistry series, Vol. 237. Washington, DC: American Chemical Society: 223-284.

Sutton, M.A.; Simpson, D.; Levy, P.E.; Smith, R.I.; Reis, S.; van Oijen, M.; deVries, W. 2008. **Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration.** Global Change Biology. 14: 1-7.

Thomas, R.Q.; Canham, C.D.; Weathers, K.C.; Goodale, C.L. 2010. **Increased tree carbon storage in response to nitrogen deposition in the US.** Nature Geoscience. 3: 13-17.

van Diepen, L.T.A. 2008. **The role and diversity of arbuscular mycorrhizal fungi in *Acer saccharum* dominated forest ecosystems under natural and N-amended conditions.** Houghton, MI: Michigan Technological University. 99 p. PhD dissertation.

van Diepen, L.T.A.; Lilleskov, E.A.; Pregitzer, K.S.; Miller, R.M. 2007. **Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions.** New Phytologist. 176: 175-183.

van Diepen, L.T.A.; Lilleskov, E.A.; Pregitzer, K.S.; Miller R.M. 2010. **Simulated nitrogen deposition causes a decline of intra- and extraradical abundance of arbuscular mycorrhizal fungi and changes in microbial community structure in northern hardwood forests.** Ecosystems. 13: 683-695.

Wallace, Z.P.; Lovett, G.M.; Hart, J.E.; Machona, B. 2007. **Effects of nitrogen saturation on tree growth and death in a mixed-oak forest.** Forest Ecology and Management. 243: 210-218.

Wallenstein, M.D.; McNulty, S.; Fernandez, I.J.; Boggs, J.; Schlesinger, W.H. 2006. **Nitrogen fertilization decreases forest soil fungal and bacterial biomass in three long-term experiments.** Forest Ecology and Management. 222(1-3): 459-468.

Zak, D.R.; Holmes, W.E.; Tomlinson, M.J.; Pregitzer, K.S.; Burton, A.J. 2006. **Microbial cycling of C and N in northern hardwood forests receiving chronic atmospheric NO_3^-.** Ecosystems. 9(2): 242-253.

Zak, D.R.; Pregitzer, K.S.; Holmes, W.E.; Burton, A.J.; Zogg, G.P. 2004. **Anthropogenic N deposition and the fate of $^{15}NO_3^-$ in a northern hardwood ecosystem.** Biogeochemistry. 69(2): 143-157.

8 NORTHWESTERN FORESTED MOUNTAINS

W.D. Bowman, J.S. Baron, L.H. Geiser, M.E. Fenn, E.A. Lilleskov

8.1 Ecoregion Description

The Northwestern Forested Mountains are ecologically diverse and geographically widespread, encompassing the mountain ecosystems of central and northwestern North America (CEC 1997; Figure 2.2). The ecoregion description is adapted from CEC (1997). Geographically, they extend from the Rocky Mountains and the Sierra Nevada north through the Siskiyous, the east side of the Cascade Range, and then east of the Coast Ranges to interior Alaska. Climatically, the region is characterized by a transition from a moist, maritime climate in the northwest, to a continental and drier climate in the Rockies in the southeast. Orographically generated rainfall creates both rain shadows and wet belts, often in close proximity.

The vegetation of the ecoregion is extremely diverse, with distinct community zonation occurring along elevation gradients. Alpine communities at the highest elevations contain various forb, lichen, and shrub associations. Subalpine communities include lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Pacific silver fir (*Abies amabilis*), grand fir (*Abies grandis*), and Engelmann spruce (*Picea engelmannii*). Mid-elevation forests are characterized by ponderosa pine (*Pinus ponderosa)*, Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), lodgepole pine, and quaking aspen (*Populus tremuloides*) in the east, and by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), and western white pine (*Pinus monticola*) in the west and southwest. White and black spruce (*Picea glauca and P. mariana*) dominate the Alaskan portion of the ecoregion. Vegetation of the interior valleys in the southern portion of the region includes big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), and antelope bitterbrush (*Purshia tridentata*).

8.2 Ecosystem Responses to N Deposition

The wide diversity of communities and climates, along with diverse bedrock geologies, results in substantial variation in ecological responses to nitrogen (N) deposition. Unfortunately, little information exists on the response of many areas in the region. Documented responses to elevated N deposition within this bioregion include alteration of soils (carbon:nitrogen (C:N) ratios, base cation composition, and N cycling rates, including mineralization and nitrification), plant, lichen, and algal chemistry (N concentration and nitrogen:calcium (N:Ca), nitrogen:magnesium (N:Mg), nitrogen: phosphorus (N:P), and C:N ratios; lichen thallus N concentrations), surface water N concentration and acid-neutralizing capacity, catchment N leaching rate, and changes in the community composition of plants, lichens, and phytoplankton. The region provides several important ecosystem services that may be compromised by N deposition, including water supply for much of western North America, timber, forage for livestock, and recreation.

8.3 Range of Responses Observed

8.3.1 Forest

Much of the research on ecological responses to N deposition in this ecoregion has been conducted in the Colorado Front Range of the Rocky Mountains, where a strong connection between regional urban and agricultural emissions and adjacent wildlands responses has been documented (e.g., Rocky Mountain National Park; Baron et al. 2000, Gebhart et al. 2011). Responses to N deposition are shown in Table 8.1. Rueth and Baron (2002) evaluated characteristics of subalpine Engelmann spruce stands spanning the Continental Divide across a N deposition gradient from 1-2 to 3-5 kg ha^{-1} yr^{-1}. Deposition reported is total (wet + dry) at the eastern end of the deposition

Table 8.1—Observed and modeled responses to N inputs for the Northwestern Forested Mountains ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem	Site	N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Coniferous forest	Alaska	1.2-3.7	(#)	Lichen community composition	Application of western Oregon and Washington model	Geiser et al. 2010
Alpine lake	S. Rockies/Loch Vale RMNP	1.5	##	Diatom assemblages	Wet deposition estimate	Baron 2006
Coniferous forest	Northwestern Forested Mountains, non-Alaska	2.5-7.1	##	Lichen community composition	Application of western Oregon and Washington model, Sierra thresholds	Geiser et al. 2010
Alpine	S. Rockies/ Rocky Mountain National Park	3-4	(#)	Soil chemistry		Baron et al. 1994
Coniferous forest	Sierra Nevada	3.1-5.2	##	Lichen community composition	N measured as canopy throughfall	Fenn et al. 2008
Subalpine Forest	S.Rockies/12 stands of paired high and low N deposition	<4	##	Foliar chemistry, mineralization, nitrification, initial increases in N leaching below the organic layer	Effects are cumulative over time	Rueth and Baron 2002
Subalpine Forest	S. Rockies/fertilized plots in Fraser and Loch Vale	<4	##	Foliar chemistry, mineralization, nitrification	Effects are cumulative over time	Rueth et al. 2003
Alpine vegetation	S. Rockies/ Niwot Ridge	4	##	Species composition ; individual species responses		Bowman et al. 2006
Alpine lake	S. Rockies/Niwot	4.0	#	Episodic freshwater acidification		Williams and Tonnesson 2000
Hardwood and coniferous forests	Columbia River Gorge	4-5	#	Lichen community composition	N measured as canopy throughfall	Geiser et al. in 2010
Alpine stream	S. Rockies/Loch Vale RMNP	5	(#)	Episodic freshwater acidification		Baron and Hartman[a], model results
Alpine and subalpine lakes and streams	Sierra Nevada	> 5	##	NO_3^- leaching	Increased NO_3^-leaching not observed at the highest deposition (5 kg ha^{-1} yr^{-1})	Sickman et al. 2001

Alpine stream	S. Rockies/Loch Vale RMNP	7.3	(#)	Chronic freshwater acidification		Baron and Hartman[a], model results
Alpine stream	S. Rockies/Loch Vale RMNP	8	(#)	Freshwater acidification	ANC=20 μeq/L	Sullivan et al. 2005 (modeled)
Alpine vegetation	S. Rockies/ Niwot Ridge	10	##	Species composition; whole community		Bowman et al. 2006
Subalpine stream/lake	S. Rockies/Loch Vale RMNP	12	(#)	Freshwater acidification	ANC=20 μeq/L	Sullivan et al. 2005 (modeled)
Alpine stream	S. Rockies/Loch Vale RMNP	14	(#)	Freshwater acidification	ANC=0 μ/L	Sullivan et al. 2005 (modeled)
Mixed conifer forest	Sierra Nevada	17	##	NO_3^- leaching; reduced fine root biomass	Critical load not exceeded in NW forests; critical load based on SW Sierra Nevada and San Bernardino Mts	Fenn et al. 2008
Alpine terrestrial	S. Rockies / Niwot Ridge	>20	#	NO_3^- leaching, soil nitrogen fluxes		Bowman et al. 2006
Subalpine stream/lake	S. Rockies/Loch Vale RMNP	21	(#)	Freshwater acidification	ANC=0 μeq/L	Sullivan et al. 2005 (modeled)

[a] Baron, J.S.; Hartman, M.D. Unpublished data. On file with Jill Baron, Research ecologist, U.S. Geological Survey, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins CO 80523-1499

gradient; wet deposition only is reported in the west where dry deposition was assumed to be insignificant (Rueth and Baron 2002). At the eastern, high end of the deposition gradient, forest stands had significantly lower organic soil horizon C:N, higher N mineralization rates, higher potential net nitrification rates and foliar N concentration, and higher N:P, N:Ca, and N:Mg ratios. Nitrate (NO_3^-) leaching was elevated at the eastern, high end of the deposition gradient (Baron[6], Rueth and Baron 2002). An earlier study reported elevated foliar N:P ratios in high elevation bristlecone pine (*Pinus aristata)* stands receiving N deposition of 6 kg N ha^{-1} yr^{-1} (Williams et al. 1996).

Four years of low-level (25 kg ha^{-1} yr^{-1}) ammonium nitrate (NH_4NO_3) fertilization to old-growth coniferous forests with different initial levels of atmospheric N deposition showed different responses based on initial conditions (Rueth et al. 2003). The low deposition site with initial organic horizon C:N of 36 and N pool of 605 kg N ha^{-1} showed no significant increase in N mineralization rates. At this low deposition site, foliar and soil organic horizon C:N decreased significantly with fertilization. In contrast, N mineralization rates and extractable inorganic N in soil increased significantly at the higher N deposition site with greater initial soil N (C:N of 24, N pool of 991 kg N ha^{-1}). At this higher N deposition site, foliar and soil organic horizon percentages of N did not change (Rueth et al. 2003).

In mixed conifer forests of the southwestern Sierra Nevada (See Chapter 13, Mediterranean California), NO_3^- leaching increases at a deposition of 17 kg N ha^{-1} yr^{-1}, as determined from empirical data and from biogeochemical modeling (Fenn et al. 2008). At this level of N deposition, fine root biomass was reduced by 26 percent. The highest throughfall N deposition inputs reported for the northern and eastern regions of the Sierra Nevada range are 7 kg ha^{-1} yr^{-1} (Fenn et al. 2008). Mixed conifer forests in California with these levels of N deposition are highly conservative of N, with no appreciable hydrologic NO_3^- leaching or gaseous N losses from soil (Fenn et al. 2008). Effects on soils and vegetation could be occurring in the most polluted northern and eastern regions, but are likely to be subtle and may not have been observed for lack of in-depth study. However, Community Multi-scale Air Quality (CMAQ) simulations of N deposition indicate that N inputs may be as high as 11 to 17 kg ha^{-1} yr^{-1} along portions of the western edge of the central and northern Sierra Nevada range (Fenn et al. 2010). If deposition actually occurs at these levels in some sites, N enrichment of soil and plants are expected. Increased NO_3^- leaching and gaseous N loss may also occur at the upper end of this deposition range (Fenn et al. 2008). Effects of N deposition on biodiversity of understory or shrub communities in the Sierra Nevada range have not been studied, although plant community composition of many nutrient-poor low biomass ecosystems in California are likely impacted by deposition levels ≤10 kg ha^{-1} yr^{-1} (Weiss 2006). Weiss (2006) estimated that 10,000 km^2 in California are vulnerable to plant community impacts from N deposition >10 kg ha^{-1} yr^{-1}.

The most notable effect of N deposition in the low to moderately polluted forested regions of the Sierra Nevada range (N deposition of 3 to 7 kg ha^{-1} yr^{-1}) is the highly significant alteration of lichen communities (Fenn et al. 2008).

Ectomycorrhizal fungi. There is no information on ectomycorrhizal community responses to N in the Northwestern Forested Mountains ecoregion. We postulate that, given the climate, species composition and soils, white and black spruce dominated ecosystems may have similar deposition thresholds to those seen in spruce forests of the same species in coastal Alaska (see Chapter 9, West Coast Marine Forests). Similarly, deposition thresholds for Engelmann spruce-subalpine fir dominated ecosystems may be similar to those of the spruce-fir forests of the northeastern United States (see Chapter 7, Northern Forests).

Forest Lichen Communities. In the California Sierra Nevada range, a strong ammonia (NH_3) deposition gradient was positively correlated with NH_3 indicator lichen species, or eutrophs (r = 0.93). The greatest lichen

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community impacts were observed in the portions of the Sierra Nevada range in the southwest and near the Tahoe Basin, and the Modoc Plateau, near urban areas and at popular recreation areas in Sequoia and Yosemite National Parks (Jovan and McCune 2006). Increased N content of the lichen epiphyte *Letharia vulpina*, as defined by a threshold concentration of 1.0 percent, was also observed in these areas (Jovan and Carlberg 2006). Thallus N concentrations above this threshold are correlated with decreasing representation of oligotrophic species relative to mesotrophic and eutrophic species within epiphytic macrolichen communities of the Sierra Nevada (Fenn et al. 2008). Thallus N concentrations below the threshold represent the clean site range; at these sites no community shifts are detected. Information on lichen research methodology and terminology can be found in Chapter 4 of this volume.

Within the mixed conifer forests in California, which extend from the west side of the California Sierra Nevada from Tahoe National Forest south through Sequoia-Kings Canyon National Park, simple indices of three N-indicator groups—the oligotrophs (adapted to low nutrient availability), the mesotrophs (requiring moderate nutrient levels and tolerating some anthropogenic enhancement but not extreme levels of N deposition) and the eutrophs (nitrophilous species that respond favorably to enhanced N deposition)—were used to identify N loads that correspond with major shifts in Sierra Nevada lichen communities. At 3.1 kg N ha^{-1} yr^{-1} (95 percent confidence interval: 0.70 to 5.5 kg ha^{-1} yr^{-1}; Fenn et al. 2008; see also Table 8.2), the N concentration threshold in the lichen *Letharia vulpina* was exceeded, and the lichen community composition was already shifting from oligotrophic to more N-tolerant mesotrophic and eutrophic species. At an estimated N deposition of 5.7 kg ha^{-1} yr^{-1} the lichen community had shifted from the natural state of oligotroph dominance. This change is of particular concern because oligotrophic species are important components of winter food webs, hydrologic and nutrient cycles, and wildlife habitat (McCune et al. 2007, McCune and Geiser 2009). The data from this study predict a complete extirpation of oligotrophs from the lichen community at an N load of about 10.2 kg N ha^{-1} yr^{-1}. This work demonstrates that known biological impacts are occurring at N deposition levels as low as 3 to 5 kg ha^{-1} yr^{-1}, levels which are exceeded over large areas of the forests of California: most of the forested region of the San Bernardino and San Gabriel Mountains, the western portions of the Sierra Nevada, and large portions of other mountain ranges in southern California (Fenn et al. 2003a, b; Fenn et al. 2008, Fenn et al. 2010).

Geiser et al. (2010) applied a model developed for Oregon and Washington forests to Sierra Nevada lichen communities, using the same response thresholds as Fenn et al. (2008) and median site precipitation (111 cm). At 2.5 to 3.8 kg N ha^{-1} yr^{-1}, some sensitive oligotrophic species were modeled to be absent; at 4.6 to 5.7 kg N ha^{-1} yr^{-1}, the lichen community would shift away from oligotroph dominance. These results are very close to the results obtained by Fenn et al. (2008). Fenn et al. (2008) did not account for precipitation in the Sierra Nevada study, as recommended by Geiser et al. (2010) for Oregon and Washington forests. Because mean annual precipitation across Sierra Nevada study sites varied only twofold (79 to 165 cm), it was probably less influential there than in Oregon and Washington, where precipitation varied tenfold. If the entire precipitation range in the ecoregion were considered, the Geiser et al. 2010 model predicts a lichen response threshold of 2.5 to 7.1 kg N ha^{-1} yr^{-1} for the Northwestern Forested Mountains ecoregion in the contiguous United States(30 to 203 cm), and 1.2 to 3.7 kg N ha^{-1} yr^{-1} (30 to 80 cm) for Alaska (See Table 4.1 for details).

Along the Snake River and its tributaries in Idaho and Oregon, within Hells Canyon National Recreation Area, comparatively high NH_4NO_3 in fine particulates originating from the agriculturally intensive Snake River basin accounted for increased lichen N throughout the Recreation Area relative to other remote sites in Oregon, Washington, Wyoming, and Colorado. Average seasonal NH_3 concentrations between 4.2 and 7.7 parts per billion (ppb), with 2-week averages peaking at 9 to 18 ppb, were associated with significantly higher cover of the nitrophilous lichens *Xanthomendoza* and *Xanthoria*,

Table 8.2—Responses to N input for lichens of the Northwestern Forested Mountains ecoregion.

Ecosystem	Site	N levels generating observed response	Measured response	Comments	Study
Coniferous forest	Central-southern Sierra Nevada	3.1 kg N ha^{-1} yr^{-1}	Some sensitive lichen species absent	Critical load based on exceedance of a N concentration threshold in the lichen *Letharia vulpina*	Fenn et al. 2008
Coniferous forest	Central-southern Sierra Nevada	2.5-3.8 kg N ha^{-1} yr^{-1}	Some sensitive lichen species absent	Application of Oregon/ Washington model using Fenn et al. 2008 response threshold and median precipitation	Geiser et al. 2010
Coniferous forests	Sierra Nevada (Tahoe)	4-5 kg N ha^{-1} yr^{-1}	Lichen N >1.03% (*Letharia vulpina*).	In the SW Sierras, Tahoe and Modoc Plateau	Jovan and Carlberg 2006, Jovan and McCune 2006
Coniferous forest	Central-southern Sierra Nevada	5.7 kg N ha^{-1} yr^{-1}	50 % sensitive lichen species absent	Critical load based on exceedance of a N concentration threshold in the lichen *Letharia vulpina*	Fenn et al. 2008
Coniferous forest	Central-southern Sierra Nevada	4.6-5.7 kg N ha^{-1} yr^{-1}	50 % sensitive lichen species absent	Application of Oregon/ Washington model using Fenn et al. 2008 response threshold and median precipitation	Geiser et al. 2010
Coniferous forests	Sierra Nevada (Sequoia NP)	6-15 kg N ha^{-1} yr^{-1}	Lichen N > 1.03% (*Letharia vulpina*).	N was mostly NH3; N content was elevated in the SW Sierras, Tahoe and Modoc Plateau	Jovan and Carlberg 2006, Jovan and McCune 2006
Coniferous forest	Central-southern Sierra Nevada	10.2 kg N ha^{-1} yr^{-1}	Extirpation of all sensitive lichen species	Critical load based on exceedance of a N concentration threshold in the lichen *Letharia vulpina*	Fenn et al. 2008
Coniferous forest	Columbia River Gorge OR/WA	<11.5 kg ha^{-1} in 4.5 months	Loss of sensitive species; lichen N >1.5% (*Xanthoparmelia cumberlandia*).	Lichen N and measured N in throughfall were correlated. Lichen N concentration exceeded the threshold at all sites	Fenn et al. 2007
Deciduous riparian forests	Hells Canyon NRA, Snake River OR/ID	4.2-7.7 µg NH_3 m^{-3} annual mean; 5-20 µg NH_3 m^{-3} summer biweekly peaks	Increased cover of eutrophs; lichen N >1.5% (*Xanthoparmelia cumberlandia*)	4.2-7.7 µg NH_3 m^{-3} annual mean; 5-20 µg NH_3 m^{-3} summer biweekly peaks	Geiser et al. 2008

and higher lichen N concentrations in *Xanthoparmelia cumberlandia* (Geiser et al. 2008). Similarly, abundance of the lichen epiphyte, *Xanthomendoza fallax,* in northern Utah and southern Idaho, increased with proximity to peak urban (Logan, Utah) and agricultural NH_3 emission centers, where summertime NH_3 ranged from 7.3 to 92.2 µg m^{-3}. Much of the effect was attributed to long distance transport and deposition of NH_4^+ (Rogers et al. 2009).

Topographic and meteorological conditions make the Columbia River Gorge a conduit for N-containing pollutants generated by the Portland, Oregon to Vancouver, Washington metropolis to the west and the agriculturally intensive Columbia Basin to the east. Nitrogen pollution contributes to decreased visibility and highly acidic fog events and potentially impacts valuable historic petroglyphs (Fenn et al. 2007, Geiser et al. 2008). Lichen N and measured N in throughfall were correlated throughout the Columbia River Gorge, and elevated levels were measured, especially at eastern- and western-most sites. Lichens indicating N-enriched environments were more abundant and lichen N concentrations were two to three times higher in the Columbia River Gorge than surrounding national forests; throughfall N deposition ranged from 11.5 to 25.4 kg ha^{-1} over 4.5 months (Fenn et al. 2007). Lichen N concentrations exceeded regional background ranges.

8.3.2 Alpine Terrestrial

Alpine ecosystems are particularly sensitive to increased availability of N due to inherently low rates of N cycling, low rates of primary production, and thin, poorly weathered soils (Fenn et al. 1998). Most of the studies examining the responses of alpine ecosystems come from the Colorado Front Range of the Rocky Mountains. Baron et al. (1994) used the CENTURY model to estimate N uptake by plants and soils. They estimated that increases in the export of NO_3^- began at lower inputs (3 to 4 kg ha^{-1} yr^{-1}) in the alpine than adjacent subalpine ecosystems, which had larger biological sinks for N.

Bowman et al. (2006) used an experimental approach to examine N impacts on alpine vegetation. Noting that previous studies using high N inputs resulted in modest increases in production and large changes in species composition, they established experimental plots in dry meadow tundra with an ambient control of 6 kg ha^{-1} yr^{-1} and experimental N additions of 20, 40, and 60 kg ha^{-1} yr^{-1}. Diversity increased at all levels of N treatment relative to the control, while changes in net N mineralization, nitrification, and leaching occurred at inputs greater than 20 kg N ha^{-1} yr^{-1} (Bowman et al. 2006). Nearly identical results were obtained from a similar study in Rocky Mountain National Park (Bowman and Murgel[7]). Changes in plant species composition associated with N deposition have the potential to enhance rates of N cycling, leading to a nonlinear increase in N leaching and acidification of soils (Bowman and Steltzer 1998).

8.3.3 Alpine Freshwater Lakes and Streams

Because many alpine freshwaters are strongly N-limited, they are highly responsive to even slight changes in nutrient availability (Elser et al. 2009a, b). Nutrient data collected from regional lake surveys and analyzed as part of the Surface Water Chapter (18) of this monograph indicate that 45 percent of Rocky Mountain lakes and 35 percent of Sierra Nevada/Cascade lakes were N limited in 1985 (see Table 18.1). Slight amounts of additional N from deposition or experiments have elicited an increase in algal biomass and changes in the composition of Rocky Mountain and Sierra Nevada lake species assemblages (Bergström and Jansson 2006; Goldman 1988; Interlandi and Kilham 1998; Lafrancois et al. 2003a, 2003b; Michel et al. 2006; Morris and Lewis 1988; Nydick et al. 2004). Lake sediment records, including algal diatoms, organic compounds, and stable isotopes, indicated that the onset of change due to N fertilization from atmospheric deposition occurred in the decade 1950-1960 (Das et al. 2005; Enders et al. 2008; Wolfe et al. 2001, 2003).

Two species of diatom that are favored by high N availability, *Asterionella formosa* and *Fragilaria crotonensis*, now dominate the flora of at least several

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[7] Bowman, W.D.; Murgel, J. Unpublished data on file with William Bowman, Professor, Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309-0334

alpine and montane Rocky Mountain lakes (Baron et al. 2000, Interlandi and Kilham 1998, Saros et al. 2003, Saros et al. 2005, Wolfe et al. 2001, Wolfe et al. 2003). Other species have shown negative growth responses to increased N; two of these, *Tetracyclus glans* and *Staurosirella pinnata*, were reported by Michel et al. (2006). In studies of remains of diatoms in lake sediment, typical oligotrophic species such as *Aulacoseria perglabra*, *Cyclotella steligera*, and *Achnanthes spp*. declined coincident with the rise in dominance of *A. formosa* and *F. crotonensis* (Wolfe et al. 2001, 2003).

Several studies have noted higher surface water NO_3^- concentrations in the Colorado Front Range compared with other lakes of the Southern Rocky Mountains, especially lakes east of the Continental Divide (Baron et al. 2000, Elser et al. 2009b, Musselman et al. 2004). Another study reported acid neutralizing capacity (ANC) in surface water < 0 µmol/L as a result of acidifying inputs of N deposition, suggesting that current deposition levels are having an observable impact on catchments in the Front Range (Williams and Tonnesson 2000).

In contrast to the elevated NO_3^- leaching observed with relatively low N deposition inputs in the Colorado Front Range, similar N deposition levels (2 to 5 kg ha^{-1} yr^{-1}) in Sierra Nevada high elevation catchments have not been reported to increase NO_3^- leaching or NO_3^- levels in lakes. Even when atmospheric deposition is low, high elevation watersheds in the Sierra Nevada appear to naturally export low levels of NO_3^- during early snowmelt, particularly in catchments with low amounts of soil cover (Fenn et al. 2003b, Sickman et al. 2001). The greater response of Rocky Mountain catchments to atmospheric deposition may be due to climatic differences. For example, the greater extent of soil freezing in the Rockies likely reduces the N retention capacity of these watersheds (Sickman et al. 2002). However, the combination of a snowmelt NO_3^- pulse, coupled with a short growing season and limited soils and vegetation, results in temporal asynchrony between N availability and N demand, suggesting that high elevation ecosystems in the Sierra Nevada will respond quickly to increased N deposition (Fenn et al. 2003b).

8.4 Critical Load Estimates

8.4.1 Forest

The empirical N critical load for subalpine forests of the Rocky Mountains is ≤ 4 kg N ha^{-1} yr^{-1}, based on the incipient effects of N saturation (organic horizon and foliar N enrichment, higher potential net N mineralization rates, and NO_3^- leaching; more information about N saturation can be found in Chapter 7) reported by Rueth and Baron (2002) and Baron.[6] We expect that more productive forest types with deeper soils in the Pacific Northwest, e.g., Douglas-fir, would have higher critical load thresholds. A modeling study conducted for subalpine forests of the Colorado Front Range projected an increase in forest soil N leachate to streams at N deposition values > 4 kg ha^{-1} yr^{-1} (Baron et al. 1994). In mixed conifer forests of the Sierra Nevada, the empirical critical load for incipient NO_3^- leaching is 17 kg ha^{-1} yr^{-1} (Fenn et al. 2008). Critical loads are summarized in Table 8.3.

Critical loads for lichens ranged from 1.2 to 7.1 kg N ha^{-1} yr^{-1}. The western Sierra Nevada critical loads range, 3.1 to 5.2 kg N ha^{-1} yr^{-1} (Fenn et al. 2008), is considered reliable. The most protective response threshold was based on N concentrations above the threshold value in the lichen, *Letharia vulpina,* in mixed conifer forests of California (Fenn et al. 2008). At this level of N deposition, community composition of epiphytic macrolichens was already shifting from oligotrophic to more N-tolerant species. The higher threshold marked a shift to domination by eutrophic species. Using the Sierra Nevada (Fenn et al. 2008) response thresholds, a more conservative response threshold for Alaska (justified in Table 4.1), and relevant precipitation ranges, the western Oregon and Washington model (Geiser et al. 2010) predicted critical loads of 2.5 to 7.1 for the Northwestern Forested Mountains ecoregion in the contiguous United States and 1.2 to 3.7 kg N ha^{-1} yr^{-1} for Alaska.

Provisional N critical loads using ectomycorrhizal fungal abundance and diversity as indicators ranged from 5 to 10 kg ha^{-1} yr^{-1}, based on critical loads determined using the same indicators in similar forest types in the marine west coast forests and northern forests ecoregions

Table 8.3—Empirical critical loads of nutrient N for the Northwestern Forested Mountains ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Alpine lakes	1.5	##	Changes in diatom assemblages	Wet deposition estimate	Baron 2006
Lichens	1.2-3.7	(#)	Community change in mixed-conifer forests in Alaska	Application of western Oregon and Washington model	Geiser et al. 2010
	2.5-7.1	##	Community change in mixed-conifer forests		Fenn et al. 2008, Geiser et al. 2010
Subalpine forest	4	##	Increase in organic horizon N, foliar N, potential net N mineralization, and soil solution N, initial increases in N leaching below the organic layer		Baron et al. 1994, Rueth and Baron 2002
Alpine lakes	4.0	#	Episodic freshwater acidification		Williams and Tonnesson 2000
Alpine vegetation	4-10	##	Plant species composition		Bowman et al. 2006
Ectomycorrhizal fungi	5-10	(#)	Ectomycorrhizal fungi community structure in white, black, and Engelmann spruce forests	Expert judgment extrapolated from Marine West coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
Mixed conifer forest	17	##	NO_3^- leaching	Critical load based on SW Sierra Nevada and San Bernardino Mts	Fenn et al. 2008
	17	#	Reduced fine root biomass	Critical load based on SW Sierra Nevada and San Bernardino Mts	Fenn et al. 2008

(Chapters 9 and 7; Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008).

8.4.2 Alpine Terrestrial

Using the rates of changes in species abundances, Bowman et al. (2006) estimated individual plant species responded to inputs at 4 kg ha^{-1} yr^{-1}, while whole community responses were detectable at 10 kg N ha^{-1} yr^{-1}. Estimates of critical load based on changes in net N mineralization, nitrification, and NO_3^- leaching were above 20 kg N ha^{-1} yr^{-1} (Bowman et al. 2006), higher than the 3 to 4 kg N ha^{-1} yr^{-1} predicted by Baron et al. (1994) using a modeling approach.

8.4.3 Alpine Freshwater Lakes and Streams

A hindcasting technique suggested the tipping point for change for aquatic diatoms occurred at about 1.5 kg N ha^{-1} yr^{-1} as wet deposition (Baron 2006). A meta-analysis of lakes across the northern hemisphere, including alpine lakes of the western United States, suggests lake productivity increases at deposition values of 2.5 kg N ha^{-1} yr^{-1} (Bergström and Jansson 2006). Williams and Tonnessen (2000) compared catchment yields of N with deposition in the Green Lakes Valley, and estimated a N critical load for acidification of 4 kg ha^{-1} yr^{-1} wet deposition. Aquatic critical loads for alpine and other lakes are discussed in greater detail in Chapter 18.

8.5 Comparison to European Critical Loads

8.5.1 Forest

Northwestern forests can most easily be compared to the Scandinavian forests, which were the subject of a recent workshop (Nordin 2007). Using empirical results from

N fertilization experiments, a critical load for changes in understory plant species composition of less than 10 kg N ha^{-1} yr^{-1} was suggested for forest ecosystems, while for more sensitive parts of the ecosystem, such as bogs and poor minerotrophic mires, a critical load of less than 8 kg ha^{-1} yr^{-1} was suggested (Nordin 2007). Bobbink et al. (2003) recommended a critical load of 10 to 15 kg N ha^{-1} yr^{-1} for forests based on increased N mineralization and nitrification.

8.5.2 Alpine Terrestrial

The synthesis by Bobbink et al. (2003) included estimates of critical loads for alpine ecosystems based on vegetation responses in fertilization experiments. For ecosystems on soils derived from granitic parent material, an estimated critical load of 10 kg N ha^{-1} yr^{-1} was reported, while for soils on basic parent material, a critical load of 15 to 20 kg N ha^{-1} yr^{-1} was estimated. These estimates are 2 to 5 times higher than those estimated for alpine sites in the southern Rockies discussed above.

8.6 Future Research Directions and Gaps in Data

Improved methods for quantifying N deposition and increased efforts to monitor trends over time are critically important for the Northwestern Forested Mountains ecoregion (Fenn et al. 2009), especially considering the projected increase in atmospheric N deposition to the region. Given the highly variable terrain, orographic effects, difficulties of measuring winter deposition in alpine sites, potentially high inputs of dry deposition (particularly to coniferous stands), and isolated or concentrated emission source areas, deposition rates are often underestimated. As a result, it is difficult to extrapolate deposition rates, even to areas that are physically close to each other but different in climate, elevation, or vegetation. Using wet-only estimates for deposition, and the problems associated with underestimating current deposition rates, may result in setting critical loads too low. In contrast, empirical critical loads are often based on linking observed responses with shorter-term N additions and the time lag in ecological responses to N deposition could lead us to set critical loads too high. The results of long-term fertilization studies would improve understanding of the rate of change possible in these high elevation ecosystems. Effects of N deposition on plant biodiversity and mycorrhizae have not been studied over most of the Northwestern Forested Mountains ecoregion. Plant biodiversity often responds to low to moderate levels of chronic N deposition. Such sensitive indicators will be most valuable, considering the low to moderate N deposition levels that occur over most of this region.

Far more is known for the more heavily impacted Colorado Front Range than for other parts of the Rocky Mountains. Additional studies are needed to better understand the sensitivity of alpine ecosystems in other parts of the west, particularly in the Teton and Wind River Ranges, which may have elevated N deposition due to agricultural activities and oil and gas extraction. Existing plant and lichen data collected systematically by the U.S. Forest Service Forest Inventory and Analysis program in California, Oregon, Washington, Idaho, Montana, Wyoming, Utah, Colorado, and New Mexico can potentially provide further insights into regional critical loads if community composition responses can be correlated with N deposition estimates.

Fire is an essential component of western forests, and many stands have suffered severe dieback due to bark beetle irruptions. More research is needed on the interactions between fire, bark beetle attack, and atmospheric deposition (Grulke et al. 2009). For freshwaters, surveys and experiments are needed to determine the effects of N deposition on algal biodiversity in N-limited lakes. No studies to date have adequately addressed this question. Finally, climate change will affect every aspect of the N cycle, from emissions and agricultural practices to climate-mediated ecological and biogeochemical N response rates. Modeling and empirical studies should be used to address whether the already low estimates of critical loads for the Northwestern Forested Mountains ecoregion will need to be adjusted to changes in temperature and precipitation regimes.

LITERATURE CITED

Baron, J.S. 2006. **Hindcasting nitrogen deposition to determine ecological critical load.** Ecological Applications. 16(2): 433-439.

Baron, J.S.; Ojima, D.S.; Holland, E.A.; Parton, W.J. 1994. **Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: Implications for aquatic systems.** Biogeochemistry. 27: 61-82.

Baron, J.S.; Rueth, H.M.; Wolfe, A.M.; Nydick, K.R.; Allstott, E.J.; Minear, J.T.; Moraska, B. 2000. **Ecosystem responses to nitrogen deposition in the Colorado Front Range.** Ecosystems. 3: 352-368.

Bergström, A.; Jansson, M. 2006. **Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere.** Global Change Biology. 12: 635-643.

Bobbink, R.; Ashmore, M.R.; Braun, S.; Fluckiger, W.; van der Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R., eds. Empirical critical loads for nitrogen. Environmental Documentation 164. Berne, Switzerland: Swiss Agency for the Environment, Forests and Landscape: 143-170.

Bowman, W.D.; Larson, J.R.; Holland, K.; Wiedermann, M.; Nieves, J. 2006. **Nitrogen critical loads for alpine vegetations and ecosystem response: are we there yet?** Ecological Applications. 16(3): 1183-1193.

Bowman, W.D.; Steltzer, H. 1998. **Positive feedbacks to anthropogenic nitrogen deposition in Rocky mountain alpine tundra.** Ambio 27: 514-517.

CEC (Commision for Environmental Cooperation). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf. (Accessed May 24, 2010).

Das, B.; Vinebrooke, R.D.; Sanchez-Azofeifa, A.; Rivard, B.; Wolfe, A.P. 2005. **Inferring sedimentary chlorophyll concentrations with reflectance spectroscopy: a novel approach to reconstructing historical changes in the trophic status of mountain lakes.** Canadian Journal of Fisheries and Aquatic Science. 62: 1067-1078.

Elser, J.J.; Anderson, T.; Baron, J.S.; Bergström, A-K; Kyle, M.; Nydick, K.R.; Steger, L.; Hessen, D.O. 2009a. **Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition.** Science. 326: 835-837.

Elser, J.J.; Kyle, M.; Steger, L.; Nydick, K.R.; Baron, J.S. 2009b. **Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition.** Ecology. 90: 3062-3072.

Enders, S.K.; Pagani, M.; Pantoja, S.; Baron, J.S.; Wolfe, A.P.; Pedentchouk, N.; Nuñez, L. 2008. **Compound-specific stable isotopes of organic compounds from lake sediments track recent environmental changes in an alpine ecosystem, Rocky Mountain National Park (United States of America).** Limnology and Oceanography. 53(4): 1468-1478.

Fenn, M.E.; Allen, E.B.; Weiss, S.B.; Jovan, S.; Geiser, L.; Tonnesen, G.S.; Johnson, R.F.; Rao, L.E.; Gimeno, B.S.; Yuan, F.; Meixner, T.; Bytnerowicz, A. 2010. **Nitrogen critical loads and management alternatives for N-impacted ecosystems in California.** Journal of Environmental Management. 91(12): 2404-2423.

Fenn, M.E.; Geiser, L.; Bachman, R.; Blubaugh, T.J.; Bytnerowicz, A. 2007. **Atmospheric deposition inputs and effects on lichen chemistry and indicator species in the Columbia River Gorge, USA.** Environmental Pollution. 146(1): 77-91.

Fenn, M.E.; Haeuber, R.; Tonnesen, G.S.; Baron, J.S.; Grossman-Clarke, S.; Hope, D.; Jaffe, D.A.;

Copeland, S.; Geiser, L.; Rueth, H.M.; Sickman, J.O. 2003a. **Nitrogen emissions, deposition, and monitoring in the western United States.** BioScience. 53: 391-403.

Fenn, M.E.; Jovan, S.; Yuan, F.; Geiser, L.; Meixner, T.; Gimeno, B.S. 2008. **Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests.** Environmental Pollution. 155: 492-511.

Fenn, M.E.; Poth, M.A.; Aber, J.D.; Baron, J.S.; Bormann, B.T.; Johnson, D.W.; Lemly, A.D.; McNulty, S.G.; Ryan, D.F.; Stottlemyer, R. 1998. **Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies.** Ecological Applications. 8: 706-733.

Fenn, M.E.; Poth, M.A.; Bytnerowicz, A.; Sickman, J.O.; Takemoto, B.K. 2003b. **Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada.** In: Bytnerowicz, A.; Arbaugh, M.J.; Alonso, R., eds. Developments in environmental science, volume 2: Ozone air pollution in the Sierra Nevada: distribution and effects on forests. Amsterdam, The Netherlands: Elsevier: 111-155.

Fenn, M.E.; Sickman, J.O.; Bytnerowicz, A.; Clow, D.W.; Molotch, N.P.; Pleim, J.E.; Tonnesen, G.S.; Weathers, K.C.; Padgett, P.E.; Campbell., D.H. 2009. **Methods for measuring atmospheric nitrogen deposition inputs in arid and montane ecosystems of western North America.** In: Legge, A.H. ed. Developments in environmental science, Vol. 9: Relating atmospheric source apportionment to vegetation effects: establishing cause effect relationships. Amsterdam, The Netherlands: Elsevier: 179-228.

Gebhart, K.A.; Schichtel, B.A.; Malm, C.W.; Barna, M.G.; Rodriguez,M.A.; Collett, J.L., Jr. 2011. **Back-trajectory-based source apportionment of airborne sulfur and nitrogen concentrations at Rocky Mountain National Park, Colorado, USA.** Atmospheric Environment. 45(3): 621-633

Geiser, L.H.; Ingersoll, A.R.; Bytnerowicz, A.; Copeland, S.A. 2008. **Evidence of enhanced atmospheric ammoniacal nitrogen in Hell's Canyon National Recreation Area: Implications for natural and cultural resources.** Journal of the Air and Waste Management Association. 58: 1223-1234.

Geiser, L.H.; Glavich, D.A.; Jovan, S.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA.** Environmental Pollution. 158: 2412-2421.

Goldman, C.R. 1988. **Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada.** Limnology and Oceanography. 33(6): 1321-1333.

Grulke, N.E.; Minnich, R.A.; Paine, T.D.; Seybold, S.J.; Chavez, D.J.; Fenn, M.E.; Riggan, P.J.; Dunn, A. 2009. **Air pollution increases forest susceptibility to wildfires: A case study in the San Bernardino Mountains in southern California.** In: Bytnerowicz, A.; Arbaugh, M.J.; Riebau, A.R.; Andersen, C., eds. Developments in environmental science, volume 8: Wildland fires and air pollution. Amsterdam, The Netherlands: Elsevier: 365-403.

Interlandi, S. J.; Kilham, S.S. 1998. **Assessing the effects of nitrogen deposition on mountain waters: A study of phytoplankton community dynamics.** Water Science and Technology. 38: 139-146.

Jovan, S; Carlberg, T. 2006. **Nitrogen content of *Letharia vulpina* tissue from forests of the Sierra Nevada, California: Geographic patterns and relationships to ammonia estimates and climate.** Environmental Monitoring and Assessment. 129: 243-251.

Jovan, S; McCune, B. 2006. **Using epiphytic macrolichen communities for biomonitoring ammonia in forests of the greater Sierra Nevada, California.** Water, Air and Soil Pollution. 170: 69-93.

Lafrancois, B.M.; Carlisle, D.M.; Nydick, K.R.; Johnson, B.M.; Baron, J.S. 2003a. **Environmental characteristics and benthic invertebrate assemblages in Colorado mountain lakes.** Western North American Naturalist. 63(2): 137-154.

Lafrancois, B.M.; Nydick, K.R.; Caruso, B. 2003b. **Influence of nitrogen on phytoplankton biomass and community composition in fifteen Snowy Range Lakes (Wyoming, USA).** Arctic Antarctic Alpine Research. 35: 499-508.

Lilleskov, E.A. 1999. **Decline of above- and belowground ectomycorrhizal fungal diversity over an atmospheric nitrogen deposition gradient near Kenai, Alaska.** Ithaca, NY: Cornell University. 198 p. Ph.D. dissertation.

Lilleskov, E.A.; Fahey, T.J.; Horton, T.R.; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** Ecology. 83: 104-115.

Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient.** Ecological Applications. 11: 397-410.

Lilleskov, E.A.; Wargo, P.M.; Vogt, K.A.; Vogt, D.J. 2008. **Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern US.** Canadian Journal of Forest Research. 38: 1260-1266.

McCune, B.; Geiser, L. 2009. **Macrolichens of the Pacific Northwest. 2nd edition.** Corvallis, OR: Oregon State University Press. 448 p.

McCune, B.; Grenon, J.; Mutch, L.S.; Martin, E.P. 2007. **Lichens in relation to management issues in the Sierra Nevada national parks.** Pacific Northwest Fungi. 2: 1-39.

Michel, T.J.; Saros, J.E.; Interlandi, S.J.; Wolfe, A.P. 2006. **Resource requirements of four freshwater diatom taxa determined by in situ growth bioassays using natural populations from alpine lakes.** Hydrobiologia. 568: 235-243.

Morris, D. P.; W. M. Lewis, Jr. 1988. **Phytoplankton nutrient limitation in Colorado mountain lakes.** Freshwater Biology. 20: 315-327.

Musselman, R.C.; Hudnell, L.; Williams, M.W.; Sommerfeld, R.A. 2004. **Water chemistry of Rocky Mountain Front Range aquatic ecosystems.** RM-RP-325. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Research. 13 p.

Nordin, A. 2007. **Nitrogen critical loads for terrestrial ecosystems in low deposition areas.** Background document for an expert workshop of the Convention on Long-range Transboundary Air Pollution. 2007 March 29-30: Stockholm, Sweden: Swedish Environmental Protection Agency. Available at http://www.scarp.se/workshopsandmeetings/workshopsandmeetings/workshopn.4.4a4d22a41128e56161b800014617.html (Accessed on July 15, 2010).

Nydick, K.R.; Lafrancois, B.M.; Baron, J.S.; Johnson, B.M. 2004. **Nitrogen regulation of algal biomass, productivity, and composition in shallow mountain lakes, Snowy Range, Wyoming, USA.** Canadian Journal of Fisheries and Aquatic Science. 61: 1256-1268.

Rogers, P.C.; Moore, K.D.; Ryel, R.J. 2009. **Aspen succession and nitrogen loading: a case for epiphytic lichens as bioindicators in the Rocky Mountains, USA.** Journal of Vegetation Science. 20: 498-510.

Rueth, H.M.; Baron, J.S. 2002. **Differences in Englemann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA.** Ecosystems. 5: 45-57.

Rueth, H.M.; Baron, J.S.; Allstott, E.J. 2003. **Responses of Engelmann spruce forests to nitrogen fertilization in the Colorado Rocky Mountains.** Ecological Applications. 13(30): 664-673.

Saros, J.E.; Interlandi, S.J.; Wolfe, A.P.; Engstrom, D.R. 2003. **Recent changes in the diatom community structure of lakes in the Beartooth Mountain Range, USA.** Arctic Antarctic and Alpine Research. 35: 18-23.

Saros, J.E.; Michel, T.J.; Interlandi, S.J.; Wolfe, A.P. 2005. **Resource requirements of *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations.** Canadian Journal of Fisheries and Aquatic Science. 62: 1681-1689.

Sickman, J.O.; Melack, J.M.; Stoddard, J.L. 2002. **Regional analysis of nitrogen yield and retention in high-elevation ecosystems of the Sierra Nevada and Rocky Mountains.** Biogeochemistry. 57: 341-374.

Sickman, J.O.; Leydecker, A.; Melack, J.M. 2001. **Nitrogen mass balances and abiotic controls on N retention and yield in high-elevation catchments of the Sierra Nevada, California, United States.** Water Resources Research. 337: 1445-1461.

Sullivan, T.J.; Cosby, B.J.; Tonnessen, K.A; Clow, D.W. 2005. **Surface water acidification responses and critical loads of sulfur and nitrogen deposition in Loch Vale watershed, Colorado.** Water Resources Research. 41: WO1021.

Weiss, S.B. 2006. **Impacts of nitrogen deposition on California ecosystems and biodiversity.** California Energy Commission, PIER Energy-Related Environmental Research. CEC-500-2005-165. Santa Barbara, CA: University of California. 91 p.

Williams, M.W.; Baron, J.S.; Caine, N.; Sommerfeld, R.; Sanford, R., Jr. 1996. **Nitrogen saturation in the Rocky Mountains.** Environmental Science and Technology. 30(2): 640-646.

Williams, M. W.; Tonnessen, K.A. 2000. **Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA.** Ecological Applications. 10: 1648-1665.

Wolfe, A.P.; Baron, J.S.; Cornett, R.J. 2001. **Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA).** Journal of Paleolimnology. 25: 1-7.

Wolfe, A.P.; Van Gorp, A.C.; Baron, J.S. 2003. **Recent ecological and biogeochemical changes in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to anthropogenic nitrogen deposition.** Geobiology. 1(2): 153-168.

9 MARINE WEST COAST FORESTS

S.S. Perakis, L.H. Geiser, E.A. Lilleskov

9.1 Ecoregion Description

The Marine West Coast Forests ecoregion encompasses the Pacific Coast from central Alaska and the Aleutian Islands south through northern California (CEC 1997; Fig. 2.2). The ecoregion description is adapted from CEC (1997). Topography is mountainous bordered by coastal plains. Soils range from very nutrient rich to nutrient poor; nitrogen (N) is the nutrient most commonly limiting to plant productivity, although some areas are naturally very rich in N. The maritime influence of the Pacific Ocean results in high precipitation (600 to 5000 mm yr^{-1}), a long growing season, and moderate mean annual temperatures (5 to 9 °C). Within North America, all of the wettest climates, many of the most productive forests, and all temperate rain forests occur in this ecoregion. Many lowland aquatic ecosystems in this region sustain a diversity of anadromous salmonids that can be a significant source of marine-derived N to rivers and lakes, whereas upland aquatic ecosystems are often nutrient poor. Terrestrial ecosystems range from mild, humid coastal rain forest to boreal forests, to cool sub-alpine forests and alpine conditions at higher elevations. Tree species composition of the temperate coastal forests varies by latitude, and from north to south, and includes white spruce (*Picea glauca*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), Nootka cypress (Alaska yellow cedar; *Callitropsis nootkatensis*), red alder (*Alnus rubra*), western red cedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), and California redwood (*Sequoia sempervirens*). Many of these trees can reach large size and live to great age. In the drier rain-shadow areas, Oregon white oak (Garry oak; *Quercus garryana*) and Pacific madrone (*Arbutus menziesii*) occur with Douglas-fir. Mountain hemlock (*Tsuga mertensiana*) and Pacific silver fir (*Abies amabilis*) dominate subalpine forests; alpine tundra is dominated by shrubs, herbs, mosses, and lichens.

9.2 Ecosystem Responses to N Deposition

Data are sparse on Marine West Coast Forests ecosystem responses to N deposition, with information available on lichen responses in Oregon, Washington, and southeastern Alaska, and for plant, soil and mycorrhizal responses in white spruce dominated ecosystems in south-central Alaska. Two of the best understood lichen responses to N deposition across the Marine West Coast Forests ecoregion are changes in lichen community composition and accumulation of N in lichen thalli. Declines in the growth and photosynthesis of rare aquatic lichens have also been associated with elevated streamwater nitrate (NO_3^-) concentrations.

Responses to N emissions from an industrial fertilizer facility by coastal white spruce forests in south-central Alaska include declines in tree health (thinning crowns, chlorotic foliage), changes in forest understory composition, foliar nutritional imbalances (elevated nitrogen:magnesium and nitrogen:calcium), elevated NO_3^- in forest floor and mineral soil, and declines in ectomycorrhizal fungal diversity and ectomycorrhizal fungal community change (sporocarp and root-tip level; Lilleskov et al. 2001, 2002; Whytemare et al. 1997). A suite of other responses typical of forested regions (see Chapters 7, 8, and 10) are also likely to be important in the Marine West Coast Forests ecoregion, including: increases in plant foliar N, soil N cycling and NO_3^- leaching; decreases in soil carbon:nitrogen; changes in species composition; and increased likelihood of pest outbreak (Brozek 1990, Compton et al. 2003, Perakis et al. 2006, Perakis and Sinkhorn in press, Prescott et al. 1993, 1995).

9.3 Range of Responses Observed

9.3.1 Forest Lichens

Lichen community composition and chemistry are currently the best indicators for assessing ecosystem responses to N deposition across the Marine West Coast Forests ecoregion (Fenn et al. 2003, 2007; Geiser and Neitlich 2007; Glavich and Geiser 2008; Geiser et al. 2010; Jovan 2008); information on lichen research methodology and terminology can be found in Chapter 4 of this report.

A recent analysis by Geiser and Neitlich (2007) of 1470 epiphytic lichen surveys in western Oregon and Washington shows that lichen community composition and thallus N concentrations shift continuously across the regional N deposition gradient of 0.8 to 8 kg N ha^{-1} yr^{-1} (Porter 2007). Oligotrophs and mesotrophs, encompassing nearly all of the larger bodied, endemic, and ecologically important species, comprised more than 90 percent of species richness at 865 of the sites (Geiser et al. 2010). Oligotroph detections peak at N deposition ranges up to 2.5 kg N ha^{-1} yr^{-1} (McCune and Geiser 2009). As N deposition increases, the relative proportion of mesotrophic species increases, peaking at deposition rates between 2.5 and 4.0 kg N ha^{-1} yr^{-1}. At deposition rates of 4.5 kg N ha^{-1} yr^{-1}, smaller, eutrophic species dominate and oligotrophs and mesotrophs decline to less than 12 percent of species. Oligotrophs play important ecological roles as forage, nesting material, habitat for mollusks and invertebrates, and contribute to N_2-fixation, nutrient cycling, and moderation of humidity; these roles are not filled by eutrophs (McCune and Geiser 2009). Therefore, shifts in lichen community composition, particularly in old-growth forests where lichen biomass is highest, can have broader effects on forest ecosystems and food webs. Responses to N inputs are summarized in Table 9.1.

Lichen community-based air quality scores have been linearly correlated with N deposition estimates from Interagency Monitoring of Protected Visual Environments (IMPROVE), National Atmospheric Deposition Program (NADP), and Community Multiscale Air Quality (CMAQ; see Chapter 4 for descriptions). Geiser and Neitlich (2007) used a nonmetric multi-dimensional scaling ordination technique to separate climate from pollution effects on lichen communities and score air quality at each of the western Oregon and Washington survey sites. In this analysis, air score increased as air quality worsened. Air scores were directly and positively correlated with N concentrations in ammonium ion (NH_4^+) wet deposition at eight NADP sites (mg L^{-1} yr^{-1}; $r^2 = 0.55$, $p < 0.0001$; Geiser and Neitlich 2007), and with ammonium sulfate ($(NH_4)_2SO_4$) and ammonium nitrate (NH_4NO_3) concentrations in fine particulates at 12 IMPROVE sites in the study area (µg m^{-3} yr^{-1}; $r^2 = 0.93$, $p < 0.0001$; Geiser et al. 2010). After accounting for precipitation, lichen air scores were also positively correlated with total kg N ha^{-1} yr^{-1} in wet deposition measured by NADP ($r^2 = 0.64$, $p = 0.006$) and modeled by CMAQ ($r^2 = 0.23$, $p < 0.005$). CMAQ deposition estimates were matched to each of 1470 air scores by overlaying lichen survey coordinates on 36 x 36 km CMAQ grid cell modeled output. When dry deposition was included to estimate total deposition, still accounting for precipitation volume, the strength of correlations between air scores and CMAQ output improved ($r^2 = 0.35$, $p<0.005$).[8] Responses of lichens to N concentrations are summarized in Table 9.2.

Field exposure of the air-pollution tolerant epiphytic lichens *Parmelia sulcata* and *Platismatia glauca* to 2 kg wet N ha^{-1} yr^{-1} in the western Oregon and Washington Cascades resulted in mainly beneficial effects (shifts in carbon balance between cellular compartments, stimulation of carbon uptake, and improved protection from chlorophyll degradation), though some sensitive lichens were sparse at these sites (Ra et al. 2004, 2005). This deposition rate, while relatively low in comparison to polluted areas, is more than double the estimated background deposition of 0.8 kg N ha^{-1} yr^{-1} for Oregon and Washington (Porter 2007).

The sensitive and conspicuous epiphytic macrolichen, Menzies' cartilage (*Ramalina menziesii)*, is distributed throughout the Coast Ranges and inland valleys from southern California to southeastern Alaska. Fumigation with nitric acid (HNO_3) at levels from 7 to 25 µg

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[8] The 36 x 36 km resolution for deposition estimates is low. Point measurements, especially in grid cells that include urban areas or steep deposition gradients, can be very different than the grid cell mean. Therefore correlations of 0.35 seem reasonable, and, because of statistical power generated by 1470 measurements, the equation for the linear relationship is expected to be reliable. Uncertainty lies primarily in the accuracy of the model output.

Table 9.1—Responses to N input for Marine West Coast Forests ecoregion.

Ecosystem	Site	N input *kg N ha^{-1} yr^{-1}*	Indicator	Response	Study
Coniferous forest	Western OR; WA	~1-8	Lichens	Defined regional indicator oligotroph, mesotroph, and eutroph species response to N deposition range	Jovan 2008
Coniferous forest	Western OR; WA	<1.5->4.5	Lichens	Defined regional indicator oligotroph, mesotroph, and eutroph species response to N deposition range	McCune and Geiser 2009
Coniferous forest	Western OR; WA	2.7-9.2 CMAQ 0-7.0 NADP (wet) 0.4-4.4 CMAQ (wet)	Lichens	Regional scale lichen community composition shifts from oligotroph dominance to mesotroph and eutroph dominance with increasing lichen thallus N; N input increases with precipitation	Geiser et al. 2010
Coniferous forest	Western OR; WA Cascades	2 (wet)	Lichens	N tolerant lichens *Parmelia sulcata* and *Platismatia glauca* from moderately polluted sites had increased chlorophyll and lipid content, cytoplasmic lipid droplets, and algal cell wall thickness, indicating altered storage allocation among cellular compartments	Ra et al. 2004
Coniferous forest	Western OR; WA Cascades	2 (wet)	Lichens	Positive physiological effect on tolerant lichens but some sensitive lichens were sparse. *Platismatia glauca* exposed to moderate levels of fertilizing air pollutants had increased N, S, K, Na; increased chlorophyll and carotenoids; increased OD435/415 ratios; and, in summer, increased CO_2 uptake and decreased thallus density	Ra et al. 2005
Coniferous forest	S. Central Alaska	5	Tree	Crown thinning, chlorotic foliage	Lilleskov et al. 2001, 2002; Whytemare et al. 1997
Coniferous forest	S. Central Alaska	5	Tree foliar chemistry	Elevated N:Mg and N:Ca ratios	Lilleskov et al. 2002, Whytemare et al. 1997
Coniferous forest	S. Central Alaska	5	Understory and ground cover	Compositional shifts	Lilleskov et al. 2001, Whytemare et al. 1997
Coniferous forest	S. Central Alaska	5	Ectomycorrhizal fungi	Loss of diversity	Lilleskov et al. 2001, 2002
Coniferous forest	S. Central Alaska	5	Ectomycorrhizal fungi	Compositional shifts towards nitrophilic taxa	Lilleskov et al. 2001, 2002
Coniferous forest	S. Central Alaska	5	Soils	Elevated available NO_3^-	Lilleskov et al. 2001, 2002; Whytemare et al. 1997

Table 9.2—Range of responses to N concentrations for lichen in Marine West Coast Forests ecoregion.

Ecosystem component	Site	N input	Indicator	Response	Study
Coniferous forest	Western OR; WA	>0.06 mg wet NH_4^+ L^{-1} from NADP	Lichens	Declines in sensitive and increases in tolerant and eutrophic epiphytic lichens, increases in lichen thallus N. Lichen N thresholds for *Platismatia glauca* (0.59% N dry weight)	Geiser and Neitlich 2007
Mountain streams	Coast, Cascade, and Siskiyou Ranges of w OR WA and n CA	Up to 0.1 to 0.33 mg L^{-1} during summer field visits	Lichens	Presence of the aquatic lichens *Peltigera hydrotheria* and *Leptogium rivale*	Glavich 2009
Mountain streams	Western Cascades, OR	6.3-12.6 mg L^{-1} annual mean as NO_3^-	Lichens	Declines in rate of photosynthesis of *Peltigera hydrotheria* after 1 year exposure	Davis et al. 2000
Coniferous forest	Western OR and WA	0.51 µg m^{-3} or 0.26-0.33 kg N ha^{-1} yr^{-1}in fine particulate N from $(NH_4)_2SO_4$ and NH_4NO_3 (IMPROVE)	Lichens	Shifts in lichen community composition dominance from oligotrophs to eutrophs	Geiser et al. 2010; Glavich and Geiser 2008
Deciduous forest	CA Coast Range	7-25 µg HNO_3 m^{-3} fumigation	Lichens	Increased membrane permeability, decomposition of photosynthetic pigments, and decreased carbon exchange capacity in *Ramalina menziesii*	Riddell et al. 2008

m^{-3} (equivalent to concentrations observed in the Los Angeles basin) were unequivocally damaging and associated with increased membrane permeability, decomposition of photosynthetic pigments, and decreased carbon exchange capacity (Riddell et al. 2008).

In southeastern Alaska, response thresholds for N concentration in the epiphytic macrolichens witch's hair (*Alectoria sarmentosa*, 0.56 percent), tube lichen (*Hypogymnia enteromorpha*, 0.75 to 0.89 percent), inactive tube lichen (*Hypogymnia inactiva*, 0.76 percent), and ragged lichen (*Platismatia glauca*, 0.59 to 0.80 percent) have been used to detect hotspots of N deposition in forests near cruise ship docks in Juneau and Skagway's Klondike Goldrush National Historic Park, near popular anchorages for marine fishing vessels at Warren and Coronation Island Wildernesses, and at Greens Creek Gold mine (Dillman et al. 2007, Furbish et al. 2000). Increasing N concentrations in lichens during the past 15 years were attributed to additional N deposition from transpacific sources and increased regional marine traffic (Dillman et al. 2007).

9.3.2 Other Forest Responses

General information on the response of the Marine West Coast Forests to N deposition, beyond information derived from lichens, is relatively sparse. Adverse effects of excess N resulting from industrial NH_3 emissions have been observed in plants, soils, and mycorrhizae along a gradient of N deposition (range: 0.7 to 21.0 kg N ha^{-1} yr^{-1}) in coastal white spruce forests of south-central Alaska. Although estimates of N deposition along this gradient are not well constrained, and likely varied over ~30 years of industrial emissions, strong gradients in forest response to N were observed. Bulk N deposition of approximately 5 kg ha^{-1} yr^{-1} at the time of sampling was associated with declines in tree health (thinning crowns, chlorotic foliage), changes in forest understory composition, foliar nutritional imbalances (elevated N:Mg and N:Ca), elevated NO_3^- in forest floor and mineral soil, and declines in ectomycorrhizal fungal diversity and ectomycorrhizal fungal community change (sporocarp and root-tip level; Lilleskov et al. 2001, 2002; Whytemare et al. 1997). Most changes were correlated with increased soil NO_3^-

availability, which appears to be a useful indicator of long-term response to N inputs in this ecosystem.

Other pathways of N input to forests of the Marine West Coast Forests ecoregion provide insight into forest responses to added N. High rates of biological N_2-fixation by alder and ceanothus (*Ceanothus* spp.) are a distinguishing feature of many forested ecosystems in the region, and commercial forest fertilization with N is also widely practiced. While such N inputs differ from atmospheric deposition in their mode, timing, and rates, they can nevertheless be useful for developing a qualitative understanding of the impacts of elevated N. Forest N fertilization usually occurs as a large dose of urea exceeding 200 kg N ha^{-1}, typically applied once or twice over 40 to 80 years of plantation growth (Stegemoeller et al. 1990). Pure stands of red alder can sustain N_2-fixation rates of 100 to 300 kg N ha^{-1} yr^{-1}over 50 to 75 years of growth, adding fixed N to ecosystems primarily in organic forms via above- and belowground tissue turnover, as well as some leakage of NH_4^+ from nodules (Binkley et al. 1994). Many of the observed effects of N addition by fertilization and biological fixation qualitatively resemble those associated with atmospheric N deposition, including: elevated tissue N content (Brozek 1990), increased nitrification and NO_3^- leaching to soils and streams (Compton et al. 2003), loss of divalent base cations from soil and increased soil acidification (Van Miegroet and Cole 1984), and changes in forest understory composition (Prescott et al. 1993, 1995). However, it remains difficult to assess how high rates of N input from biological N_2-fixation and N fertilization translate quantitatively into response thresholds under chronic N deposition.

Responses to atmospheric N inputs in Marine West Coast Forests are likely to be shaped by wide variation in N status across the region. Site N status in the region ranges from ultra N-poor soils developed on young volcanic ash and glacial outwash to extremely N-rich soils that escaped the last glaciation and which rank among the most N-rich areas on Earth. Sites with high N status, particularly in coastal regions, often show negative or no response to N fertilization (Hopmans and Chappell 1994, Peterson and Hazard 1990). Responses to N fertilization can also vary depending on the dominant tree species considered, for example, with Douglas-fir being more N responsive than western hemlock (Edmonds and Chappell 1993). Variation in N status influences ecosystem response to N_2-fixation and forest fertilization (Binkley et al. 1992, Edmonds and Hsiang 1987), and is therefore likely to shape response to atmospheric N deposition as well. Previous site occupancy by woody N_2-fixers, fire history, and climate all contribute to variations in site N status across the region. Legacy effects of N_2-fixing red alder are particularly significant and can result in addition of >10,000 kg N ha^{-1} during the 75-year lifespan of a pure stand of red alder. In the moist Oregon Coast Range, historic N_2-fixation by red alder is a proximate cause of exceptionally high soil N accumulation (~30 Mg ha^{-1}), and ultimately yields coniferous forests that exhibit elevated nitrification (80 kg N ha^{-1} yr^{-1}), NO_3^- leaching (25 kg N ha^{-1} yr^{-1}), soil acidification, base cation depletion, and aluminum (Al) mobilization (Perakis et al. 2006, Perakis and Sinkhorn in press). High foliar N also predisposes large areas of Douglas-fir plantation forests to outbreaks of pathogenic Swiss needle cast fungi (*Phaeocryptopus gaeumannii*) (El Hajj et al. 2004). Further N additions to such areas may have the potential to rapidly intensify symptoms of N saturation; the stages of N saturation in forested ecosystems are described in Chapter 7. Disturbances such as fire and forest harvest can remove ~1,000 kg N ha^{-1} from a site and may ameliorate some effects of excess N, although N losses may be reversed within several decades where alder or ceanothus dominate early succession.

9.3.3 Aquatic Systems

Currently there is limited information on how atmospheric N deposition shapes aquatic ecosystem N status across the Marine West Coast Forests ecoregion. Transpacific transport of pollutants from Asia to western North America is an issue of increasing concern in the region (Jaffe et al. 1999, Wilkening et al. 2000). Short-lived spikes in N deposition have been associated with increased streamwater NO_3^- in old-growth forested watersheds of Olympic National Park, raising concentrations from baseline values < 5 µg N L^{-1} up to 40 µg N L^{-1}, and illustrating the potential sensitivity of old-growth forests in the region to added N (Edmonds et al. 1998). The infrequent and highly pulsed nature of these inputs, however, makes it difficult to understand long-term ecological effects and develop watershed N input-output relationships.

Variation in the cover of N_2-fixing red alder across watersheds of the Oregon coast range is related positively to streamwater fluxes of NO_3^- and major base cations. Assuming an N_2-fixation rate of 150 kg ha^{-1} yr^{-1} for pure alder stands (Binkley et al. 1994), approximately 25 to 30 percent of fixed N is lost as streamwater N export (Compton et al. 2003). These losses correspond to maximum flow-weighted streamwater N concentrations of 2.5 mg L^{-1}, mostly (>90 percent) as NO_3^-. Studies of N_2-fixing red alder forests in Oregon and Washington (Binkley et al. 1992) and of conifer forests in Oregon (Perakis and Sinkhorn in press) further suggest that the susceptibility of sites to NO_3^- leaching increases with soil N status and nitrification rates. Collectively, these results suggest a high potential for atmospheric N deposition to increase NO_3^- leaching across some N-rich coastal areas of the Marine West Coast Forests ecoregion, and that some streams are already exposed to naturally elevated NO_3^-. In colder and more inland areas that support less active N_2-fixation, however, streamwater fluxes of NO_3^- remain low, with unknown sensitivity to atmospheric N inputs.

A lichen-indicated critical level for stream-water NO_3^- would appear to be between 6.3 to 12.6 mg N L^{-1}. The critical level is the concentration above which adverse effects to sensitive vegetation may occur (UBA 2004). This estimate is based on a year-long laboratory study of the growth and photosynthetic responses of the submerged aquatic hydrothyria lichen (*Peltigera hydrothyria*) collected from the Oregon Cascades and exposed to NO_3^- concentrations between 1.6 and 94.5 mg N L^{-1} (Davis et al. 2000). These levels greatly exceed typical summer NO_3^- levels (< 0.05 mg L^{-1}) in the native habitat of this lichen; however stream N could be higher during fall flushes. During a 2-year field study of randomly selected watersheds in western Oregon, western Washington, and northern California, the highest summer stream total N concentrations associated with occurrence of the aquatic skin (*Leptogium rivale*) and hydrothyria lichens were 0.1 and 0.33 mg N L^{-1}, respectively (Glavich 2009). Gilbert et al. (1997) observed a lower biological diversity in aquatic lichen communities in waters of England where total inorganic N concentrations were just above 0.6 mg L^{-1}.

9.4 Critical Loads Estimates

The onset of elevated soil nitrification and NO_3^- availability, conifer nutrient imbalance and decline, declines in ectomycorrhizal fungal diversity, and ectomycorrhizal fungal community change are expected at bulk N deposition of approximately 5 kg ha^{-1} yr^{-1} in the northern forests of this region (Lilleskov et al. 2001, 2002; Whytemare et al. 1997). This critical load must be considered expert opinion because historic unrecorded N inputs were likely to have been higher than inputs recorded at the time of study. In addition, it is based on only one study system in southeast Alaska that is almost certainly not representative of all forest types, soils, and climates across the region.

Geiser et al. (2010) created regression models relating lichen-based air scores to NADP and CMAQ measures of N deposition, accounting for precipitation. At an air score response threshold of 0.21, oligotrophs comprised as little as 30 percent, and eutrophs up to 34 percent, of species richness (see Table 4.1). The resulting critical loads were 2.7 to 9.2 kg N ha^{-1} yr^{-1} for total deposition (and 0.7 to 4.4 kg N ha^{-1} yr^{-1} for wet-only deposition). Because hardwood forests growing on valley floors favor eutrophs by providing a more nutrient-rich canopy drip and higher pH bark substrates compared to the dominant coniferous forests, the response threshold was selected to allow for a natural range in N-availability among clean sites. Critical loads increased with precipitation, which varied approximately tenfold across the study area, because high precipitation volumes dilute the impact of N loading on lichens. The 95 percent confidence interval for the 2.7 to 9.2 kg N ha^{-1} yr^{-1} critical load range was 0 to 13.5 kg N ha^{-1} yr^{-1}. The critical load range can be considered reliable because the systematic sampling design yielded high quality, spatially extensive data. However, while the data for

Table 9.3—Empirical critical loads of nutrient N for the Marine West Coast Forests ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Western OR and WA forests	2.7-9.2	##	Lichen community composition	Critical load increases with regional range in mean annual precipitation from 45-450 cm	Geiser et al. 2010
SE Alaska forests	5	(#)	Fungal community change; declines in ectomycorrhizal fungal diversity		Lilleskov 1999; Lilleskov et al. 2001, 2002; Whytemare et al. 1997

total deposition are also extensive, they are based on a fairly coarse grid (36 km) with some uncertainties regarding accuracy of the modeled data. Critical loads are summarized in Table 9.3.

9.5 Comparison to Critical Loads from Europe and Other Ecoregions

Many vascular plants and cryptogams of the Tundra, Taiga, and Northern Forests ecoregions also occur in the Marine West Coast Forests ecoregion. For example, extensive peatlands in the Alaskan portion of the Marine West Coast Forests ecoregion support mat-forming lichens and bryophytes and ericaceous shrubs (heaths) typical of boreal ecoregions; alpine areas, especially in Alaska, support tundra species. Therefore, references to Eurasian vegetation responses in these three preceding chapters are potentially relevant to parts of the Marine West Coast Forests. The estimated critical load range for Marine West Coast Forests (2.7 to 9.2 kg N ha^{-1} yr^{-1}) is consistent with all other U.S. lichen-based estimates reported in this document. The upper-end estimate is consistent with European values, and the lower-end estimate is more than threefold greater than background deposition in the region. For mycorrhizal fungi, the results for this region correspond well with those expected for spruce-fir forests for the northeastern United States (5 to 7 kg N ha^{-1} yr^{-1}) and are lower than those reported for European forests (10 to 20 kg N ha^{-1} yr^{-1}).

9.6 Future Research Directions and Gaps in Data

There is a need to understand how the response of forest soils, streams, and their biota will be mediated by underlying variations in site N status in the region. Generally, lowland coastal Oregon and Washington forests and streams possess the highest N status in the region, yet may escape significant elevated N inputs in the near-term due to the lack of significant population and industrial activity along upwind coastal areas. Potential increases in N transport from Asia, however, could make these areas susceptible. On the other hand, naturally N-poor areas of the Oregon and Washington Cascades and glaciated montane forests of the Olympic Peninsula may be sensitive to added N originating from anthropogenic sources in the Willamette Valley and Puget Sound. The wide range in forest ages and in natural and anthropogenic disturbances (e.g., fire, logging) across the region is likely to interact with N status in unknown ways to shape ecosystem responses to N deposition. A better understanding of the relative sensitivity of lichens and other ecosystem response indicators to different forms of atmospheric N deposition would allow more accurate apportionment and prediction of the effects from different emissions sources. Analysis of existing Forest Inventory and Analysis and other U.S. Forest Service lichen community data from southeastern and south-central Alaska will test their application to the northern parts of the ecoregion.

LITERATURE CITED

Binkley, D.; Cromack K., Jr.; Baker, D.D. 1994. **Nitrogen fixation by red alder: biology, rates, and controls.** In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 57-72.

Binkley, D.; Sollins, P.; Bell, R.; Sachs, D.; Myrold,D. 1992. **Biogeochemistry of adjacent conifer and alder-conifer stands.** Ecology. 73: 2022-2033.

Brozek, S. 1990. **Effect of soil changes caused by red alder (*Alnus rubra*) on biomass and nutrient status of Douglas-fir (*Pseudotsuga menziesii*) seedlings.** Canadian Journal of Forest Research. 20: 1320-1325.

CEC (Commision for Environmental Cooperation). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/fi les/pdf/BIODIVERSITY/eco-eng_EN.pdf. (Accessed May 24, 2010).

Compton, J.E.; Church, M.R.; Larned, S.T.; Hogsett, W.E. 2003. **Nitrogen saturation in forested watersheds of the Oregon Coast Range: The landscape role of N_2-fixing red alder.** Ecosystems. 6: 773-785.

Davis, W.C.; Gries, C.; Nash, T.H. III. 2000. **The ecophysiological response of the aquatic lichen, *Hydrothyria venosa* to nitrates in terms of weight and photosynthesis over long periods of time.** Bibliotheca Lichenologica. 75: 201-208.

Dillman, K.; Geiser, L.; Brenner, G. 2007. **Air quality biomonitoring with lichens on the Tongass National Forest.** Final Report. Petersburg, AK: Tongass National Forest, Air Resource Management Program. Available at http://gis.nacse.org/lichenair/?page=reports#R10 (Accessed August 4, 2010).

Edmonds, R.L.; Chappell, H.N. 1993. **Relationships between soil organic matter and forest productivity in western Oregon and Washington.** Canadian Journal of Forest Research. 24: 1101-1106.

Edmonds, R.L.; Hsiang, T. 1987. **Influence of forest floor and soil properties on response of Douglas-fir to urea.** Soil Science Society of America Journal. 57: 1332-1337.

Edmonds, R.L.; Blew, R.D.; Marra, J.L.; Blew, J.; Barg, A.K.; Murray, G.; Thomas, T.B. 1998. **Vegetation patterns, hydrology, and water chemistry in small watersheds in the Hoh River Valley, Olympic National Park.** NPS Scientific Monograph NPSD/NRUSGS/NRSM-98/02. Washington, D.C.: U.S. Department of Interior, National Park Service. 131 p.

El-Hajj, Z.; Kavanaugh, K.; Rose, C.; Kanaan-Atallah, Z. 2004. **Nitrogen and carbon dynamics of a foliar biotrophic fungal parasite in fertilized Douglas-fir.** New Phytologist. 163: 139-147.

Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W.; Neitlich, P. 2003. **Ecological effects of nitrogen deposition in the Western United States.** BioScience. 53(4): 404-420.

Fenn, M.E.; Geiser, L.; Bachman, R.; Blubaugh, T.J.; Bytnerowicz, A. 2007. **Atmospheric deposition inputs and effects on lichen chemistry and indicator species in the Columbia River Gorge, USA.** Environmental Pollution. 146: 77-91.

Furbish, C.E.; Geiser, L.; Rector, C. 2000. **Lichen-air quality pilot study for Klondike Gold Rush National Historical Park and the city of Skagway, Alaska.** Final Report. Skagway, AK: U.S. Department of Interior: National Park Service, Klondike Goldrush National Historic Park. 47 p. Available at http://gis.nacse.org/lichenair/?page=reports#R10 (Accessed May 12, 2010)

Geiser, L.H.; Jovan, S.E.; Glavich, D.A.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA.** Environmental Pollution. 158: 2412-2421.

Geiser, L.H.; Neitlich, P.N. 2007. **Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens.** Environmental Pollution. 145: 203-218.

Gilbert, O.L.; Giavarini, V.J. 1997. **The lichen vegetation of acid watercourses in England.** The Lichenologist. 29: 347-367.

Glavich, D.A. 2009. **The distribution, rarity, and habitats of three aquatic lichens in the US Pacific Northwest.** The Bryologist. 112: 54-72.

Glavich, D.A.; Geiser, L.H. 2008. **Potential approaches to developing lichen-based critical loads and levels for nitrogen, sulfur and metal-containing atmospheric pollutants in North America.** The Bryologist. 111: 638-649.

Hopmans, P.; Chappell, H.N. 1994. **Growth response of young, thinned Douglas-fir stand to nitrogen fertilizer in relation to soil properties and tree nutrition.** Canadian Journal of Forest Research. 24: 1684-1688.

Jaffe, D.; Anderson, T.; Covert, D.; Kotchenruther, R.; Trost, B.; Danielson, J.; Simpson, W.; Berntsen, T.; Karlsdottir, S.; Blake, D.; Harris, J.; Carmichael, G.; Uno, I. 1999. **Transport of Asian air pollution to North America.** Geophysical Research Letters. 26(6): 711-714.

Jovan, S. 2008. **Lichen bioindication of biodiversity, air quality, and climate: baseline results from monitoring in Washington, Oregon, and California.** Gen.Tech. Rep. PNW-GTR-737. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 115 p.

Lilleskov, E.A. 1999. **Decline of above- and belowground ectomycorrhizal fungal diversity over an atmospheric nitrogen deposition gradient near Kenai, Alaska.** Ithaca, NY: Cornell University. 198 p. Ph.D. dissertation.

Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient.** Ecological Applications. 11: 397-410.

Lilleskov, E.A.; Fahey, T.J.; Horton, T.R.; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** Ecology. 83: 104-115.

McCune, B.M.; Geiser, L.H. 2009. **Macrolichens of the Pacific Northwest. 2nd edtion.** Corvallis, OR: Oregon State University Press. 400 p.

Perakis, S.S.; Maguire, D.A.; Bullen, T.D.; Cromack, K.; Waring, R.H.; Boyle, J.R. 2006. **Coupled nitrogen and calcium cycles in forests of the Oregon Coast Range.** Ecosystems. 9: 63-74.

Perakis, S.S.; Sinkhorn, E.R. In press. **Biogeochemistry of a temperate forest nitrogen gradient.** Ecology.

Peterson, C.E.; Hazard, J.W. 1990. **Regional variation in growth response of coastal Douglas-fir to nitrogen fertilizer in the Pacific Northwest.** Forest Science. 36: 625-640.

Porter, M.K. 2007. **Regional modeling of nitrogen, sulfur, and mercury atmospheric deposition in the Pacific Northwest.** Pullman, WA: Washington State University. 127 p. M.S. thesis.

Prescott, C.E.; Coward, L.P.; Weetman, G.F.; Gessel, S.P. 1993. **Effects of repeated nitrogen fertilization on the ericaceous shrub, salal (*Gaultheria shallon*) in two coastal Douglas-fir forests.** Forest Ecology and Management. 61: 45-60.

Prescott, C.E.; Kumi, J.W.; Weetman, G.F. 1995. **Long-term effects of repeated N fertilization and straw application in a jack pine forest. 2. Changes in the ericaceous ground vegetation.** Canadian Journal of Forest Research. 25: 1984-1990.

Ra, H.S.Y.; Geiser, L.H.; Crang, R.F.E. 2005. **Effects of season and low-level air pollution on physiology and element content of lichens from the U.S. Pacific Northwest.** Science of the Total Environment. 343: 155-167.

Ra, H.-S.Y.; Rubin, L.; Crang, R.F.E. 2004. **Structural impacts on thallus and algal cell components of two lichen species in response to low-level air pollution in Pacific Northwest forests.** Microscopy and Microanalysis. 10(2): 270-279.

Riddell, J.; Nash, T.H. III; Padgett, P. 2008. **The effect of HNO_3 gas on the lichen *Ramalina menziesii*.** Flora. 203: 47-54.

Stegemoeller, K.A.; Chappell, H.N.; Bennett, W.S. 1990. **Regional forest nutrition research project analysis history: objectives and achievements.** RFNRP Rep. No. 12. Seattle, WA: University of Washington, College of Forest Resources. 33 p.

UBA (UmweltBundesAmt). 2004. **Manual on methodologies and criteria for modeling and mapping critical loads and levels and air pollution effects, risks, and trends.** Berlin: Federal Environmental Agency (UmweltBundesAmt). Available at http://icpmapping.org/cms/zeigeBereich/11/manual-english.html (Accessed May 12, 2010).

Van Miegroet, H.; Cole, D.W. 1984. **Impact of nitrification on soil acidification and cation leaching in a red alder ecosystem.** Journal of Environmental Quality. 13: 586-590.

Whytemare, A.B.; Edmonds, R.L.; Aber, J.D.; Lajtha, K. 1997. **Influence of excess nitrogen deposition on a white spruce (*Picea glauca*) stand in southern Alaska.** Biogeochemistry. 38: 173-187.

Wilkening, K.E.; Barrie, L.A.; Engle, M. 2000. **Trans-Pacific air pollution.** Science. 290: 65-67.

10 EASTERN TEMPERATE FORESTS

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10.1 Ecoregion Description

The Eastern Temperate Forests ecoregion extends from the Atlantic Coast westward into eastern Texas, Oklahoma, Missouri, Iowa, and Minnesota. The ecoregion description is adapted from CEC (1997). Eastern Temperate Forests are comprised of two fairly distinct ecosystems: eastern hardwood forests and the Southeastern Coastal Plain. The former includes mixed wood plains and central plains, as well as Ozark and Ouachita-Appalachian forests of the northeastern and midwestern states and Appalachian Mountains. The latter is composed of the southeastern and coastal plains extending from Cape Cod and Long Island to Florida, inland to and around the Appalachian mountains (Fig. 2.2; CEC 1997).

The Eastern Temperate Forests ecoregion is distinguished by its temperate, humid climate; dense, diverse forest cover; and dense human population (>160 million). Coastal plains underlain by sedimentary bedrock in the southeast abut older sedimentary, metamorphic, and igneous bedrock of the Appalachian Mountains (peaking at > 2,000 m). Mixed limestone-dolomite plains and hills dominate the west central parts, sedimentary rock dominates the northwest plains and plateaus, and glacial activity shaped northern landscapes. Soils are mostly leached, being nutrient-poor to calcium-rich. Surface waters include abundant perennial streams, areas of high lake density, diverse wetlands, and rich maritime ecosystems. The climate grades latitudinally from cool, continental to subtropical. Summers are hot and humid (27 °C to 32 °C daily maxima); winters are mild to cool (-12 °C to 4 °C). Precipitation (100 to 150 cm yr^{-1}) is relatively even throughout the year, with summer or spring peaks.

10.2 Eastern Hardwood Forest

10.2.1 Ecosystem Description

Eastern hardwood forests, as originally described by Braun (1950) and further characterized by Greller (1988), are among the most diverse forests of North America, particularly those of the mixed mesophytic forest region (Hinkle et al. 1993). Forest types range from beech-maple and maple-basswood in the east to mixed oak-hickory in the upper Midwest, and oak-hickory-pine in the Appalachians southward. Ashes (*Fraxinus* spp.), elms (*Ulmus* spp.), black cherry (*Prunus serotina*), yellow-poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), basswood (*Tilia* spp.), hackberry(*Celtis occidentalis*), persimmon (*Diospyros virginiana*), eastern red cedar (*Juniperus virginiana*), and dogwood (*Cornus* spp.) are also wide ranging. The complex and diverse forest regions include: (1) the mixed mesophytic forest region; (2) the western mesophytic forest region; (3) the oak-hickory forest region; (3) the former oak-chestnut forest region; and (4) the oak-pine forest region (Braun 1950). Each of these regions displays an impressive number of canopy co-dominant species, and occupies widely ranging topography on numerous soil types derived from sharply contrasting parent materials. The herbaceous layer, most often defined as the stratum of vascular plants ≤1 m in height (Gilliam and Roberts 2003), can represent >90 percent of vascular plant species richness of temperate deciduous forest ecosystems in this ecoregion (Gilliam 2007).

10.2.2 Ecosystem Responses to N Deposition

Responses of eastern hardwood forests to excess nitrogen (N) deposition include increases in tissue N, soil N cycling, nitrate (NO_3^-) leaching, decreases in soil carbon:nitrogen (C:N) ratio, and shifts in community composition, including declines in species richness and abundance. The stages of N saturation are described in Chapter 7. Some ecosystem responses occur as a result of acidification and therefore are caused by sulfate (SO_4^-) as well as NO_3^-. These responses include soil nutrient cation imbalances (particularly calcium (Ca) and magnesium (Mg)) from enhanced leaching of NO_3^-, especially in soils derived from intermediate to acidic classes of parent material (Bailey et al. 2005). As the result of decreases in soil nutrient cation availability, decreases in net primary productivity of forest ecosystems (i.e., forest decline) can occur. At the interface between terrestrial and aquatic habitats, excess N can cause increases in NO_3^- in streams and lakes and, particularly in extreme cases, increases in the mobilization of aluminum (Al^{3+}) in freshwater ecosystems (Driscoll et al. 2003).

Excess N deposition can also cause a loss of biodiversity. Gilliam (2006) identified five mechanisms to explain such loss: (1) alteration of interspecific competition; (2) increases in herbivory; (3) decreases in mycorrhizal infection; (4) increases in pathogenic fungal infection; and (5) enhanced likelihood of invasions by nonnative species. Herbaceous, epiphytic lichen, and bryophyte layers are generally most sensitive to a variety of disturbances, including chronically elevated N deposition.

Herbaceous species. Gilliam (2006) reported that the response of the forest herbaceous layer to increasing N may include the following: (1) initial increases in cover of the herb layer; (2) decreases in species richness resulting from loss of numerous N-efficient species; (3) decreases in species evenness resulting from increasing dominance of a few high N-requiring species; and (4) declines in forest biodiversity as a result of decreases in both richness and evenness. In addition, these studies suggest that the response time of herb layer species to increases in N availability is more rapid when ambient N deposition is low. Thus, a rapid response should occur in areas receiving low levels of atmospheric deposition of N, such as that found for Hurd et al. (1998) in the Adirondacks**,** whereas a delayed response would be expected in areas receiving high N deposition, such as that found by Gilliam et al. (2006a). This response pattern has been reported for other sites in eastern hardwood forests (Fraterrigo et al. 2009, Royo et al. 2010). The relationship between plant response time to added N and ambient N deposition could arise because the effect is ultimately a function of relative amounts of N added. For a given amount of N added, the relative addition would be higher for a site receiving lower amounts of ambient N deposition.

Still other work has focused on the importance of the herb layer in mediating N cycling (Gilliam 2007). Recent work (Moore et al. 2007, Muller 2003, Welch et al. 2007) has demonstrated that plants of the herb layer facilitate N cycling in a disproportionately large way compared to their minimal biomass. This is primarily because herb layer foliage is generally higher in nutrient content and more decomposable than tree foliage.

Lichens. Lichen community-level responses to changing sulfur dioxide (SO_2), acidity, and nutrient N deposition regimes vary. Increased deposition in low deposition areas results in species composition shifts to tolerant species, while in high deposition areas species richness, abundance, and total landscape diversity decline dramatically. Lichen thallus concentrations of N and sulfur (S) also increase or decrease, corresponding to changes in deposition.

10.2.3 Range of Responses Observed

Eastern hardwood forest regions with higher levels of N deposition (US EPA 2002; Table 10.1) exhibit some of the ecosystem responses previously described in this chapter. For example, the long-term reference watershed at the Fernow Experimental Forest, West Virginia, exhibited a 20-year pattern of increasing NO_3^-, Ca^{2+}, and Mg^{2+} export in streamwater; throughfall deposition was 17.5 kg N ha^{-1} yr^{-1} (Peterjohn et al. 1996). At the Great Smoky Mountains National Park, export of streamwater N is elevated (Garten 2000, Van Miegroet et al. 2001) at sites within the park receiving deposition of about 32 kg N ha^{-1} yr^{-1} (Pardo and Duarte 2007, Weathers et al. 2006). In a broad synthesis of data from 354 upland forest catchments across the Northeast, Aber et al. (2003) reported that for catchments receiving less than 8 kg N ha^{-1} yr^{-1}, surface water NO_3^- concentration rarely exceeded 1 μmol L^{-1}; above that threshold NO_3^- concentrations in surface water increased. The cross-catchment analysis covered both Eastern Temperate Forests and Northern Forests (Chapter 7). Tree growth response from Wisconsin to Maine and south to Virginia show general increases in net growth and carbon storage as N deposition increases from 3 to 11 kg N ha^{-1} yr^{-1}, reflecting an overall fertilization effect of N deposition on eastern and northern forests (Thomas

Table 10.1—Responses to N input for the Eastern Temperate Forests ecoregion

Site	N inputs *kg ha^{-1} yr^{-1}*	Response	Comments	Study
New Jersey Pine Barrens	<8	Decreasing ectomycorrhizal fungi morphotype richness		Dighton et al. 2004
North Carolina and West Virginia deposition gradient	>7	Stream NO_3^- > DON		Brookshire et al. 2007
Northeastern Forest catchments	8	Surface water NO_3^- ≥ 1 μmol L^{-1}		Aber et al. 2003
Southeastern deposition gradient	9-15	Increasing foliar N concentration		Boggs et al. 2005
North Carolina and West Virginia deposition gradient	<10	Soil C:N <20		Brookshire et al. 2007
Michigan deposition gradient	<12	Arbuscular mycorrhizal fungal biomass decline and community composition change		van Diepen et al. 2008, 2010
Fernow Experimental Forest, WV	<17.5	Herb layer changes		Gilliam et al. 2006a
Fernow Experimental Forest, WV	17.5	Increasing streamwater Ca^{2+}, Mg^{2+}, NO_3^-	Deposition as ambient throughfall	Peterjohn et al. 1996
Cedar Creek LTER, MN	<28	Ectomycorrhizal fungi community response		Avis et al. 2008
Great Smoky Mountains National Park	32	Export of streamwater N		Garten 2000, Pardo and Duarte 2007, Van Miegroet et al. 2001, Weathers et al. 2006
Michigan deposition gradient	<35	Declines in fungal biomass		van Diepen et al. 2007, 2010
Cedar Creek LTER, MN	<50	Ectomycorrhizal fungi community response		Avis et al. 2003

et al. 2010). However, responses vary considerably by species. All hardwood tree species with arbuscular mycorrhizal associations (red maple [*Acer rubrum*], sugar maple, white ash [*Fraxinus americana*], yellow-poplar, and black cherry) as well as six tree species with ectomycorrhizal associations (balsam fir [*Abies balsamea*], pignut hickory [*Carya glabra*], eastern white pine [*Pinus strobus*], quaking aspen [*Populus tremuloides*], northern red and scarlet oak [*Quercus rubra* and *Q. coccinea*]) had marked increases in growth with increasing deposition. In contrast, red pine (*Pinus resinosa*), red spruce (*Picea rubens*), and northern white cedar (*Thuja occidentalis*) all had statistically significant decreases in growth with increasing deposition, and eight tree species (yellow birch [*Betula alleghaniensis*], eastern white pine, basswood, quaking aspen, bigtooth aspen [*Populus grandidentata*], scarlet oak, chestnut oak [*Quercus prinus*], and northern red oak; all ectomycorrhizal) all had decreased survivorship with increasing deposition. These declines in survivorship could be due to multiple factors, including: direct effects of N itself, spatial covariation between N deposition and exposure to other pollutants (e.g., O_3, SO_4^{2-}), N-induced nutrient imbalances, interactions between N loading and secondary stressors such as drought or insect outbreaks, or suppression by competition from other tree species (Thomas et al. 2010).

Table 10.2—Response of Eastern Temperate Forests ecosystems to experimental N fertilization (≤ 50 kg ha^{-1} yr^{-1})

	Site Location	Harvard Forest, Massachusetts		Millbrook, New York	Fernow Forest, West Virginia
	Forest Type	Red pine plantation	Black oak & red maple	Chestnut & northern red oak	Mixed central hardwoods
	Type of N Deposition	Wet + dry		Wet + dry	Wet + dry
	N Deposition *kg ha^{-1} yr^{-1}*	9		10	15
	N fertilization rate *kg ha^{-1} yr^{-1}*	+50		+50[b]	+35
	Form of N Fertilizer	NH_4NO_3		NH_4NO_3	$(NH_4)_2SO_4$
	Start year	1988		1996	1989
	Duration (years)	14		9	11
--Response relative to Control[a]--	Tree growth	0/–	0/+	+	–
	Mortality	+	0	+	0,+
	Foliar %N	+	+	ND	+, 0
	Foliar %Ca	0	0	ND	-, 0
	NO$_3^-$ leaching	+	0	+	+
	Cation loss	+	0	+	+
	Soil C/N	0	0	ND	0
	N mineralization	0	0	ND	0
	Nitrification	+	0	ND	0
	Soil respiration	–	0	ND	ND
	Microbial biomass	–	–	ND	ND
	References	1-6	1-6	7	8-11

[a] Responses are indicated as increase (+), decrease (–), or no response (0) in fertilized relative to control plots, or no data (ND) in indicated references.

[b] Started at 100 kg ha^{-1} yr^{-1} for 1996-1999, then reduced to 50 kg ha^{-1} yr^{-1} thereafter.

References: 1) Magill et al. 2000; 2) Magill et al. 2004; 3) Frey et al. 2004; 4) Bowden et al. 2004; 5) Minocha et al. 2000; 6) Venterea et al. 2004; 7) Wallace et al. 2007; 8) May et al. 2005; 9) Adams et al. 2006; 10) Edwards et al. 2006; 11) DeWalle et al. 2006; 12) Gilliam and Adams 1996.

Experimental N additions indicate broadly similar responses to the gradient studies above (Table 10.2). At the Fernow Experimental Forest, experimental additions of N (35 kg ha^{-1} yr^{-1}) increased NO$_3^-$ leaching (Edwards et al. 2006), decreased soil nutrient cation availability (Gilliam et al. 1996), and decreased tree growth by some species but not others (May et al. 2005, DeWalle et al. 2006). These results resemble those from fertilization experiments at an oak stand at Millbrook, New York (Wallace et al. 2007), and at a red pine stand and an oak-maple stand at Harvard Forest, Massachusetts (Table 10.1; Bowden et al. 2004, Frey et al. 2004, Magill et al. 2000, Magill et al. 2004, Minocha et al. 2000, Venterea et al. 2004). In all but the oak-maple stand at Harvard Forest, moderate rates of long-term fertilization induced NO$_3^-$ leaching, which led to losses of soil base cations. Foliar N content increased at both the red pine and oak-maple stands at Harvard Forest for the duration of that experiment (Magill et al. 2004), whereas the increase in foliar N concentration at the Fernow Experimental Forest was transient in some species (black cherry, red maple) and persistent in others (yellow-poplar; DeWalle et al. 2006, May et al. 2005). These changes in foliar N have had mixed consequences for tree growth. At Harvard Forest, fertilization enhanced growth in the oak-maple stand, but stimulated mortality in the mature red pine stand following a drought in 1995 (Magill et al. 2004). At

Millbrook, New York, chronic N fertilization induced significant mortality in a 60- to 100-year-old chestnut oak/northern red oak stand, but also increased the relative growth rate of the remaining trees, for a net effect of an overall decrease in live basal area in five of six treatment plots after 8 years (Wallace et al. 2007). The most oak mortality occurred at fertilized sites that also had low Ca:Al ratios in surface organic layers (Wallace et al. 2007). At the Fernow Experimental Forest, some tree species (red maple, river birch [*Betula nigra*]) had no response to fertilization, whereas others (black cherry, yellow-poplar) increased growth during the first 7 years, then had decreased growth relative to control trees in years 9 - 12 (DeWalle et al. 2006). Soil processes also often respond to chronic fertilization. Although none of these studies had detectable changes in soil C:N ratio (Magill et al. 2004, Adams et al. 2006), fertilization resulted in higher net nitrification rates at Fernow Forest (Gilliam et al. 2001) and at the Harvard Forest red pine plots (Magill et al. 2000, Venterea et al. 2004). After more than a decade of N addition, both the red pine and the oak-maple stands at the Harvard Forest had decreases in microbial biomass (Frey et al. 2004) and depressed rates of soil respiration relative to the control plot (Bowden et al. 2004).

In a gradient study spanning a range of N deposition rates across North Carolina and Virginia, Boggs et al. (2005) found an increase in foliar N concentration in American beech, sugar maple, and yellow birch as wet N deposition increased from 9 to 15 kg N ha^{-1} yr^{-1}. Foliar Ca:Al ratios were not affected. Forest floor pH and C:N ratios decreased and rates of net N mineralization and nitrification increased with increasing deposition. In an independent gradient study spanning N deposition rates from 5 to 32 kg N ha^{-1} yr^{-1} in North Carolina and West Virginia, Brookshire et al. (2007) found that stream NO_3^- and dissolved organic N (DON) concentrations both increased with increasing N deposition, although NO_3^- increased most dramatically. Nitrate concentrations exceeded DON concentrations with >7 kg N ha^{-1} yr^{-1} of deposition. They also observed a steep decrease in surface soil C:N ratio from 30 to 17 as deposition increased from 5 to 10 kg N ha^{-1} yr^{-1}, after which soil C:N ratio did not decrease further with increasing deposition.

The impact of excess N via acidification was assessed by both Fox et al. (1989) and Adams et al. (1991) using a “Green-Yellow-Red” screening model to determine levels of acid deposition (N and S) that would impact Class 1 wilderness areas. At the green line value, vegetation health and vigor would be protected; at the red line value, changes in N cycling, species composition, or other ecosystem features could occur (Fox et al. 1989). For Joyce Kilmer, North Carolina, and Slick Rock, Tennessee, the green line value for total N deposition was 7 to 10 kg N ha^{-1} yr^{-1}; damage would occur at 15 kg N ha^{-1} yr^{-1} (red line). In Otter Creek, West Virginia, the green line value was 7 kg N ha^{-1} yr^{-1}; the red line value was 10 to 15 kg N ha^{-1} yr^{-1} (Fox et al. 1989). Adams et al. (1991) used the same approach to determine N and S deposition levels that would prevent foliar injury and fish species shifts. They set green line values of 5 to 8 kg N ha^{-1} yr^{-1} for Dolly Sods, West Virginia; Hercules Glade, Missouri; and Otter Creek, West Virginia. Significant ecosystem damage could be expected at total N deposition level >20 kg N ha^{-1} yr^{-1} (Adams et al. 1991).

Herbaceous layer. Responses of the herb layer to excess N vary among temperate deciduous forest sites. A northern forest (Adirondack) ecosystem had large shifts in herb cover in response to modest N additions (Hurd et al. 1998). At the Watershed Acidification Study at Fernow Experimental Forest, West Virginia, which has ambient deposition of approximately 17.5 kg N ha^{-1} yr^{-1} in throughfall (Adams et al. 1993), addition of 35 kg N ha^{-1} yr^{-1} via aerial application has led to changes in herbaceous species composition. Recently, similar changes in herbaceous species composition have been observed over time on the adjacent reference (control) watershed, which receives only atmospheric deposition[9]. Previous research (Gilliam et al. 2006a) at the same watershed had shown no significant differences in herb cover, composition, or several diversity indicators between treatment and control watersheds for any of the years sampled (1991, 1992, and 1994). Gilliam et al. (2006a) suggested that the initial lack of observed

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[9] Gilliam, F.S. Unpublished data. Professor, Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510.

response to N addition was due to high background levels of N deposition that had already saturated watershed soils. Because the ecosystem had already been altered by N inputs, changes in the herb layer had already occurred. This is consistent with the conclusion of Hurd et al. (1998) that sensitivity of the herb layer to N additions was largely a function of ambient N deposition.

Ectomycorrhizal fungi. Ectomycorrhizal fungi form associations with many of the dominant trees of drier or nutrient-poor sites in the region, including oak, hickory, beech, birch, and basswood (*Quercus*, *Carya*, *Fagus*, *Betula*, *Tilia*). There has been less research on ectomycorrhizal response to N deposition in hardwood than in conifer forests. We expect hardwood forest types that have a strong ecological overlap with conifer forest types of this region (e.g., oligotrophic beech-dominated northern hardwoods and oligotrophic oak forests) to have similar community responses to N deposition, but at this time, this supposition is unsupported by data. In an oak savannah forest in east-central Minnesota, ectomycorrhizal fungal community response (reduced species richness of sporocarps, changes in communities seen on root tips and sporocarps) was seen with addition of 50 and 170 kg ha^{-1} yr^{-1} over 18 to 20 years (Avis et al. 2003). The treatments also involved fertilization with other nutrients, so are not strictly equivalent to N deposition. In an N-only fertilization experiment Avis et al. (2008) also found a change in oak forest ectomycorrhizal fungal communities with deposition plus additions of N of approximately 28 kg N ha^{-1} yr^{-1}. However, we do not know the lower threshold for this response. Studies of other ectomycorrhizal community types (e.g., *Betulaceae, Salicaceae*) are lacking.

Arbuscular mycorrhizal fungi. Arbuscular mycorrhizal fungi form associations with many tree taxa dominant in this forest type, including maple, ash, yellow-poplar, sweet gum, and cherry (*Acer*, *Fraxinus*, *Liriodendron*, *Liquidambar*, and *Prunus)*. We have very little empirical data on arbuscular mycorrhizal community response to N in forests. One study in sugar maple dominated forests in Michigan has found declines of arbuscular mycorrhizal fungal biomass and change in community composition in response to addition of 30 kg^{-1} ha^{-1} yr^{-1} over and above background deposition across a gradient ranging from approximately 5 to12 kg ha^{-1} yr^{-1} wet deposition (van Diepen et al. 2007, 2010; van Diepen 2008). There is some indication that arbuscular mycorrhizal biomass has declined and community composition has shifted over the N deposition gradient (van Diepen et al. 2007, 2010; van Diepen 2008), suggesting a threshold of <12 kg ha^{-1} yr^{-1} of wet deposition, but it is likely that there are interactions with within-site factors, and definitive determination of a response threshold awaits further analysis.

Lichens. Air pollution has been a major factor in the depauperization of the lichen flora in the eastern hardwoods region during the past 100 years (e.g., see Murphy et al. (1999; Massachusetts), Smiley and George (1974; New York), Showman and Long (1992; Pennsylvania); Wetmore (1989) and Showman (1975; Ohio); Wetmore (1988) and McCune (1988; Indiana and Michigan); or Lawrey and Hale (1988; Virginia)). Historically, the most damaging pollutants have been SO_2, sulfuric acid (H_2SO_4), nitrogen oxides (NO_x), and nitric acid (HNO_3). As an example, declines in lichen species diversity exceeding 80 percent in Cuyahoga National Park (Ohio) and Indiana Dunes National Lake Shore, between 1895 and 1988, were attributed to SO_2 (Wetmore 1988,1989). Nutrient N, especially in the form of ammonium (NH_4^+), is a newly recognized concern.

It is entirely possible that a widespread modification of native lichen flora has taken place across the eastern forests due to air pollution and habitat loss. In 2007, after substantial, regionwide decreases in SO_2 and NO_x emissions, total wet N deposition was still 2 to 5 times higher throughout the eastern hardwoods ecoregion compared to background western U.S. localities. In some regions, NH_4^+ is a significant portion of deposition (NADP 2009). Although species richness remains high in parts of the southern Appalachians and southeastern Georgia (McCune et al. 1997), north central Florida (DeBolt et al. 2007), and Maine (Hinds and Hinds 1998), the paucity of historical records complicates confirmation of intact lichen community composition, species richness, cover, and/or landscape-level diversity in most locations.

Table 10.3—Previously determined critical loads of nutrient N for the Eastern Temperate Forests ecoregion

Site	Critical load for nutrient N *kg N ha^{-1} yr^{-1}*	Comments	Study
Great Smoky Mountains National Park	3-7	Determined using steady state mass balance method	Pardo and Duarte 2007
Great Smoky Mountains National Park	2.5-9	Determined using steady state mass balance method	Oja and Arp 1998

Declines in SO_2 and NO_x emissions in response to the Clean Air Act have been linked to improvements in epiphytic lichen diversity and cover in the upper Ohio Valley (Showman 1981, 1990, 1998) and south central Pennsylvania (McClenahen et al. 2007) and lower tissue S concentrations in Virginia (Lawrey and Hale 1988). For the Ohio and Pennsylvania study areas, 2007 total wet N deposition was still between 6.2 and 7.2 kg N ha^{-1} yr^{-1} in 2007 (NADP 2009). As a result, the returning species are moderately acid- and SO_2-sensitive, but N tolerant (Geiser et al. 2010). This response is consistent with substantial regional decreases in acidity but increasing N in wet deposition between 1980 and 2007 (NADP 2009).

More information on lichen research methodology and terminology can be found in Chapter 4 of this volume.

10.2.4 Critical Loads Estimates

The critical load for decreased tree growth and survivorship in response to N deposition is >3 kg N ha^{-1} yr^{-1}, while the critical load for herbaceous species is <17.5 kg N ha^{-1} yr^{-1}. Empirical critical loads for nutrient N in eastern hardwood forest ecosystems can be set at 8 kg N ha^{-1} yr^{-1} for NO_3^- leaching (Table 10.5). This threshold applies for surface water NO_3^- leaching in the northeastern United States (Aber et al. 2003), as well as for select forests in the southeastern United States, where Brookshire et al. (2007) observed stream NO_3^- concentrations to exceed those of dissolved organic N above 7 kg N ha^{-1} yr^{-1}. Similarly, Lewis (2002) used 10 kg N ha^{-1} yr^{-1} as a deposition criterion for "minimally disturbed" watersheds in a compilation of N yield from watersheds across the United States.

Critical loads for nutrient N calculated using the steady-state mass balance method (Pardo 2010, UBA 2004) were reported (Table 10.3) for Great Smoky Mountains National Park as ranging from 3 to 7 kg ha^{-1} yr^{-1} (Pardo and Duarte 2007). Earlier calculations of critical loads for N nutrient within Great Smoky Mountains National Park made using data from the Integrated Forest Study (Johnson and Lindberg 1992) ranged from 2.5 to 9 kg N ha^{-1} yr^{-1} (Oja and Arp 1998).

Critical loads for ectomycorrhizal fungi, arbuscular mycorrhizal fungi, and lichens have not been reported previously. The critical load for ectomycorrhizal fungi is expected to be much less than the N input level of 28 kg ha^{-1} yr^{-1} reported by Avis et al. (2008); the critical load for arbuscular mycorrhizal fungi is also expected to be less than the 35 kg ha^{-1} yr^{-1} that caused a mycorrhizal response in research by van Diepen et al. (2007), and may be less than 12 kg N ha^{-1} yr^{-1} (van Diepen 2008). Arbuscular mycorrhizal fungal critical loads are tentatively set at <12 kg N ha^{-1} yr^{-1} (van Diepen 2008). The value for arbuscular mycorrhizal fungi is considered expert judgment, as it is based on one gradient with only four sites.

Lichen community-based critical loads are difficult to pinpoint in the eastern hardwoods region due to the confounding effect of acidity from sulfur-containing pollutants, habitat alterations, and changing climate. However, N critical loads are probably similar to those proposed for epiphytic macrolichens in other temperate forests of the United States (northwest forested mountains (3.1 to 5.2 kg N ha^{-1} yr^{-1}), west coast marine forests (2.7 to 9.2 kg N ha^{-1} yr^{-1}), Mediterranean

Table 10.4—Previously determined critical loads of acidity for the Eastern Temperate Forests ecoregion

Site	Critical load for N acidity *kg N ha^{-1} yr^{-1}*	Response	Study
Joyce Kilmer, NC; Slick Rock, TN	7-10	Vegetation health and vigor	Fox et al. 1989
Otter Creek, WV	7	Vegetation health and vigor	Fox et al. 1989
Otter Creek, WV; Hercules Glade, MO; Dolly Sods, WV	5-8	ANC = 25	Adams et al. 1991

California (3.3 to 5.5 kg N ha^{-1} yr^{-1})), due to species overlap and physiological/ecological similarities among epiphytic macrolichens. Application of the western Oregon and Washington model relating epiphytic lichen community composition to N deposition (Chapter 4, Geiser et al. 2010), to eastern hardwoods yields a critical load estimate of 4 to 8 kg N ha^{-1} yr^{-1}. This value was calculated using a precipitation range of 71 to 305 cm, and a lichen community-composition response threshold that allows as few as 25 percent oligotrophs and no more than 47 percent eutrophs. This response threshold is higher than that used for Oregon and Washington to allow for the higher nutrient content of leaf exudates and more neutral bark substrates in hardwood forests, which favor eutrophs. (Coniferous forests predominate in western Oregon and Washington.)

A number of estimates of critical loads for acidity have also been set for the region and are summarized in Table 10.4. Critical loads for N associated with acidity often tend to be higher than those for nutrient N; for this ecoregion, they were of similar magnitude. The red line/green line approach of Fox et al. (1989) has been used to establish critical loads for acidity for eastern forests. Using the green line value determined for Joyce Kilmer, North Carolina, the critical load for acidity for the overstory and herb layer was 7 kg N ha^{-1} yr^{-1}. This is consistent with calculations made for this region by McNulty et al. (2007), who made coarse estimates for critical loads for total acidity across the United States. Based on those calculations, the contribution of N to those critical loads for acidity is ~10 kg ha^{-1} yr^{-1}. Earlier assessments in this region suggest that the critical load for acidity has been exceeded for both terrestrial and aquatic ecosystems (Fox et al. 1989, Sullivan and Cosby 2002, Sullivan and Cosby 2004, Sullivan et al. 2003).

10.2.5 Comparison to European Critical Loads

These estimates for critical loads are somewhat lower than for comparable ecosystems in Europe. Critical loads for European deciduous forests are set at 10 to 15 kg N ha^{-1} yr^{-1} for increased NO_3^- leaching and increased N mineralization and nitrification; at 15 to 20 kg N ha^{-1} yr^{-1} for alterations in tissue chemistry and increased susceptibility to pest outbreak; and at 10 to 20 kg N ha^{-1} yr^{-1} for alterations in mycorrhizal community composition (UBA 2004). In a review and synthesis on effects of atmospheric ammonia (NH_3) on terrestrial vegetation that included critical load estimates, Krupa (2003) reported a critical load range of 15 to 20 kg N ha^{-1} yr^{-1} for deciduous forests of Europe.

Herbaceous layer. Critical loads for ground vegetation in temperate forests are set at 10 to 15 kg N ha^{-1} yr^{-1} in Europe (UBA 2004). Critical loads research in Europe often employs gradients in N deposition (Brunet et al. 1998, Strengbom et al. 2003). Most such work is done in conifer forests of Europe, limiting direct comparisons to the herb layer of temperate deciduous forests in the eastern United States. Brunet et al. (1998) employed multivariate methods to assess potential effects of N deposition on herb layer species of oak forests by sampling along a gradient of N deposition in southern Sweden. Species that increased in cover with increased N deposition were generally both nitrophilous and acid

Table 10.5—Empirical critical loads of nutrient N for the Eastern Temperate Forests ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem	Ecosystem component	Critical load for nutrient N kg N ha^{-1} yr^{-1}	Reliability	Response	Comments	Study
Eastern hardwood forests	Trees	>3	#	Decreased growth of northern white cedar, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		Thomas et al. 2010
Eastern hardwood forests	Lichens	4-8	(#)	Changes in epiphytic lichen community composition		Geiser et al. 2010
Eastern hardwood forests	Forests	8	##	Increased surface water loading of NO_3^-		Aber et al. 2003
Eastern hardwood forests	Arbuscular mycorrhizal fungi	<12	(#)	Arbuscular mycorrhizal fungal biomass decline and community composition change	Observed along a Michigan N gradient	van Diepen 2008
Eastern hardwood forests	Herbs	<17.5	(#)	Herb layer changes	Observed at Fernow Experimental Forest, WV	Gilliam 2006, 2007, Gilliam et al. 2006a
Southeastern Coastal Plain	Lichens	4-6	(#)	Changes in epiphytic lichen community composition		Appliation of Geiser et al. 2010
Southeastern Coastal Plain	Ectomycorrhizal fungi	5-10	(#)	Ectomycorrhizal fungi community response		Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008

tolerant. They concluded that N deposition influenced vegetation directly by increasing N availability and indirectly by increasing soil acidity.

10.2.6 Future Research Directions and Gaps in Data

Research on critical loads for eastern hardwood forests of the United States lags far behind research for similar forests in Europe. Particularly lacking are empirical data on community responses to gradients of ambient N deposition. Plot-scale fertilizer studies have been conducted, but these are not as numerous as similar studies in Europe, and carry with them the inherent difficulty of scaling up from the plot to the landscape scale. Studies that employ whole-watershed treatment with N, such as that at Fernow Experimental Forest, are extremely rare. Additional complexities affecting responses to N loading include interactions between N addition and climate events (disturbance and variation), prior land use, species composition, site characteristics, and hydrology. For example, the coincidence of increased N availability, drought, and soil nutrient cation depletion appear to have led to significant tree mortality at sites in Massachusetts (Magill et al. 2004) and eastern New York (Wallace et al. 2007), suggesting that the incipient N saturation at the site made the trees more susceptible to secondary stresses. Multi-factor experimental manipulations that addressed N interactions with climate and other stressors could help address some of these uncertainties.

Also useful would be more studies focusing on gradients in N deposition (e.g., Boggs et al. 2005, Brookshire et al. 2007) and on forests of varying stand age (Castro et al. 2007). Gradient studies would be especially useful in filling the large data gaps that exist on the response of mycorrhizal fungal communities to realistic levels of N deposition in this region, especially in the development of response functions to N deposition that would permit establishment of critical loads.

A framework grid system has been systematically surveyed for lichens in New England and Mid-Atlantic states (Maine through Virginia) by the U.S. Forest Service Forest Inventory and Analysis/Forest Health Monitoring (FIA/FHM) program (McCune 2000, Will-Wolf et al. 2006); matching deposition estimates and supplementary sites are needed to interpret these data to estimate critical loads. Despite major reductions in SO_2 and NO_x, critical loads for nutrient N for epiphytic lichens are probably still exceeded in much of the region. Lichen floras dating back to about 1900, where available, would help elucidate the changes that have already taken place. Research is also needed to separate H_2SO_4 and HNO_3 acidification effects from fertilizing N effects on lichen community composition, diversity, and physiology, with consideration to the influences of habitat alteration and climatic changes. Forests of Minnesota and Wisconsin, where hydrogen ion (H^+) and SO_4^- deposition are close to background levels but NO_3^- and NH_4^+ deposition are elevated, may offer an opportunity for such studies when compared to forests of Ohio, Pennsylvania, West Virginia, and New York with high acidity, S deposition, and N deposition.

10.3 Southeastern Coastal Plain

10.3.1 Ecosystem Description

Forest ecosystems of the Southeastern Coastal Plain have evolved under conditions of relatively high frequency of fire and hurricanes (Gilliam et al. 2006b). The forests of the coastal plain contrast with other forest types in the Eastern Temperate Forests ecoregion in that: (1) coastal plain forests tend to comprise pine-dominated overstories of low biodiversity and herb-dominated understories often of very high biodiversity (Gilliam 2007, Platt et al. 2006); and (2) coastal plain forests experience lower levels of atmospheric deposition of N.

10.3.2 Ecosystem Responses to N Deposition

Coastal Plain forest responses to N deposition are not well studied. Generally, we would expect the same responses to excess N as seen in eastern hardwood forests: increases in tissue N concentration, declines in biodiversity, shifts in soil N cycling and NO_3^- leaching, decreases in soil C:N ratio, and shifts in community composition (section 10.2.2). Interactions of N deposition with ecosystem processes in the Southeastern Coastal Plain are complicated by a changing N deposition regime, spatially variable fire dynamics, and disturbances caused by large tropical storms. Historically, many pine-dominated forests of the Coastal

Plain have been fire maintained. Fire varies in frequency throughout the region and alters the N status of the ecosystem (Boerner et al. 2004). In a meta-analysis, Wan et al. (2001) found that fire invariably caused substantial loss of N from fuels (i.e., forest litter). For example, as much as 50 percent of litter N was lost in a single fire for conifer forests.

Tropical storms are an important disturbance regime in forest ecosystems of the coastal plain (Gilliam et al. 2006b). These disturbances can have a substantial impact of nutrient cycling in these ecosystems. It is possible that the frequency/intensity of tropical storms is increasing as a result of global warming.

10.3.3 Range of Responses Observed

Although the effect of S deposition on coastal plain ecosystems has been studied (Janicki et al. 1995), little research has been done on responses of the coastal plain ecosystem to excess N deposition.

Ectomycorrhizal fungi. One study in the Pine Barrens region of New Jersey found a trend of decreasing morphotype richness with increasing N deposition (Dighton et al. 2004). There was significantly lower mycorrhizal morphotype richness at a site with bulk deposition of 8 kg N ha^{-1} yr^{-1} than at a site with approximately 4 kg N ha^{-1} yr^{-1} (Dighton et al. 2004). Low number of sample points in the gradient weakens the evidence for causal linkages, but this evidence is consistent with that from other oligotrophic conifer-dominated ecosystems that suggest thresholds of somewhere between 5 and 10 kg ha^{-1} yr^{-1} for community response (Lilleskov et al. 2001, 2002, 2008). More productive pine or deciduous ecosystems in the southern part of this ecosystem type, on richer soils or with significant N removals via harvest and/or fire, might have a higher deposition threshold. However, no data are available from the region with which to test this hypothesis.

Lichens. Acidifying and fertilizing pollutants in deposition (N and S), primarily from urban/industrial emissions, have strongly influenced lichen communities in the Southeastern Coastal Plain. The characteristic response has been loss of sensitive species resulting in sharply reduced species richness and reduced lichen cover. For example, even by 1966, epiphytic lichen diversity was low (14 species per plot) on the north shore of Long Island, up to 62 km from Brooklyn (New York City; Brodo 1966). There was complete extirpation of all lichens within 19 km of Brooklyn's industrial center, even though Brooklyn and the north shore of Long Island shared the same flora historically (Brodo 1966). Of 70 species detected around 1900 on Plummer's Island, a protected habitat 15 km south of Washington, D.C., only 20 could be found in the early 1990s (Lawrey 1993). Such extreme de-pauperization of the lichen flora is less pervasive in the southeastern states. In an analysis of FIA/FHM epiphytic macrolichen data from forests of Georgia, the Carolinas, eastern Tennessee, and Virginia, McCune et al. (1997) observed pollution-tolerant species and lower species richness in urban and industrial areas, but pollution-sensitive and 'luxuriant and diverse' lichens (up to 40 species per plot) in many rural areas. The richer flora is consistent with generally lower deposition of S and N in states of the southeastern compared to the northeastern United States. However, lacking historic flora, it is not possible to confirm whether species are missing from communities in the southeast that are experiencing lower S and N deposition. Some aspects of the flora hint at a widespread loss of species due to air pollution: only one fruticose genus was detected and cyanolichens were rare.

Fire has less influence on the N regimes of forest lichens compared to soil-rooted plants in the Southeastern Coastal Plain. Lichens that are not consumed or heat-killed during forest fire become a propagule source for recolonization without long term shifts in community composition (Johansson et al. 2006, Sillet and Goslin 1997). However, increased fire frequency and short timber harvest cycles favors faster growing species over those with greater dispersal or growth rate limitations, shifting community composition and reducing diversity (DeBolt et al. 2007).

More information on lichen research methodology and terminology can be found in Chapter 4 of this volume.

10.3.4 Critical Loads Estimates

Until more research has been done in Southeastern Coastal Plain forests, we can only offer provisional critical loads. Our best estimate of the critical load for ectomycorrhizal community integrity is 5 to 10 kg N ha^{-1} yr^{-1}, and even this must be regarded as highly uncertain and only applicable to low productivity pine barrens forests (Table 10.5). In other ecosystem types, critical loads for mycorrhizal fungi appear to be roughly equivalent to those for other receptors, but definitive characterization of critical loads for other receptors and responses awaits further research.

Application of the western Oregon and Washington model relating epiphytic lichen community composition to N deposition (Chapter 4, Geiser et al. 2010) to Southeastern Coastal Plains yields a critical load estimate of 4 to 6 kg ha^{-1} yr^{-1}. This value was calculated using a precipitation range of 102 to 178 cm, and a lichen community-composition response threshold that allows as few as 30 percent oligotrophs and no more than 34 percent eutrophs. This response threshold represents the upper end of the response threshold range used for Oregon and Washington to allow for potential favoring of the mesotrophs and eutrophs by warmer temperature. These species are generally more drought resistant than oligotrophs.

10.3.5 Comparison to European Critical Loads

The concept of critical loads for N was originally developed for forest ecosystems of Europe (Nilsson and Grennfelt 1988). Whereas most of these forests have long been altered by human use (Dambrine et al. 2007), they generally do not experience frequent natural disturbances, such as fire and extreme wind events. Thus, it is difficult to compare Southeastern Coastal Plain ecosystems to European ecosystems.

10.3.6 Future Research Directions and Gaps in Data

More research is needed on the effects of N deposition to ecosystems of the Southeastern Coastal Plain. Potential research areas include watershed and plot scale fertilization studies and deposition gradient studies. In addition, research should be conducted to examine how the interaction of frequent disturbance and N deposition affect the N status of the Coastal Plain. Research is also needed to separate H_2SO_4 and HNO_3 acidification effects from fertilizing N effects on lichen community composition, diversity, and physiology, with consideration to the influences of habitat alteration, climatic changes and changes in fire frequency. Southern Georgia and north-central Florida, with the lowest N and S deposition, may be good locations for field-based N addition studies.

LITERATURE CITED

Aber, J.D.; Goodale, C.L.; Ollinger, S.V.; Smith, M-L.; Magill, A.H.; Martin, M.E.; Hallet, R.A.; Stoddard, J.L. 2003. **Is nitrogen deposition altering the nitrogen status of Northeastern forests?** BioScience. 53(4): 375-389.

Adams, M.B.; Nichols, D.S.; Federer, C.A.; Jensen, K.F.; Parrott, H. 1991. **Screening procedure to evaluate effects of air pollution on eastern region wildernesses cited as class I air quality areas.** Gen. Tech. Rep. NE-151. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 33 p.

Adams, M.B.; Edwards, P.J.; Wood, F.; Kochenderfer, J.N. 1993. **Artificial watershed acidification on the Fernow Experimental Forest, USA.** Journal of Hydrology. 150: 505-509.

Adams, M.B.; DeWalle, D.R.; Peterjohn, W.T.; Gilliam, F.S.; Sharpe, W.E.; Williard, K.W.J. 2006. **Soil chemical responses to experimental acidification treatments.** In: Adams, M.B.; DeWalle, D.R.; Hom, J.L., eds. The Fernow Watershed acidification study. Dordrecht, The Netherlands: Springer: 41-69.

Avis, P.G.; McLaughlin, D.J.; Dentinger, B.C.; Reich, P.B. 2003. **Long-term increase in nitrogen supply alters above- and below-ground ectomycorrhizal communities and increases the dominance of *Russula* spp. in a temperate oak savanna.** New Phytologist. 160: 239-253.

Avis, P.G.; Mueller, G.M. ; Lussenhop, J. 2008. **Ectomycorrhizal fungal communities in two North American oak forests respond to nitrogen addition.** New Phytologist.179: 472-483.

Bailey, S.W.; Horsley, S.B.; Long, R.P. 2005. **Thirty years of change in forest soils of the Allegheny Plateau, Pennsylvania.** Soil Science Society of America Journal. 69: 681-690.

Boerner, R.E.J.; Brinkman, J.A.; Sutherland, E.K. 2004. **Effects of fire at two frequencies on nitrogen transformations and soil chemistry in a nitrogen-enriched forest landscape.** Canadian Journal of Forest Research. 34: 609-618.

Boggs, J.L.; McNulty, S.G.; Gavazzi, M.J.; Moore, J. 2005. **Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forests.** Canadian Journal of Forest Research. 35: 1901-1913.

Bowden, R.D.; Davidson, E.; Savage, K.; Arabia, C.; Steudler, P. 2004. **Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest.** Forest Ecology and Management. 196: 43-56.

Braun, E.L. 1950. **Deciduous forests of eastern North America.** New York: Hafner Press.

Brodo, I.M. 1966. **Lichen growth and cities: A study on Long Island, New York.** The Bryologist. 69(4): 427-449.

Brookshire, E.N.J.; Valett, H.M.; Thomas, S.A.; Webster, J.R. 2007. **Atmospheric N deposition increases organic N loss from temperate forests.** Ecosystems. 10: 252-262.

Brunet, J.; Diekmann, M.; Falkengren-Grerup, U. 1998. **Effects of nitrogen deposition on field layer vegetation in south Swedish forests.** Environmental Pollution. 102: 35-40.

Castro, M.S.; Eshleman, K.N.; Pitelka, L.F.; Frech, G.; Ramsey, M.; Currie, W.S.; Kuers, K.; Simmons, J.A.; Pohlad, B.R.; Thomas, C.L.; Johnson, D.M. 2007. **Symptoms of nitrogen saturation in an aggrading forested watershed in western Maryland.** Biogeochemistry. 84: 333-348.

CEC (Commision for Environmental Cooperation). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/fi les/pdf/BIODIVERSITY/eco-eng_EN.pdf. (Accessed May 24, 2010).

Dambrine, E.; Dupouey, J.-L.; Laüt, L.; Humbert, L.; Thinon, M.; Beaufils, T.; Richard, H. 2007. **Present forest biodiversity patterns in France related to former Roman agriculture.** Ecology. 88: 1430-1439.

DeBolt, A.M.; Rosentreter, R.; Martin, E.P. 2007. **Macrolichen diversity in subtropical forests of north-central Florida.** The Bryologist. 110(2): 254-265.

DeWalle, D.R.; Kochenderfer, J.N.; Adams, M.B.; Miller, G.W.; Gilliam, F.S.; Wood, F.; Odenwald-Clemens, S.S.; Sharpe, W.E. 2006. **Vegetation and acidification.** In: Adams, M.B.; DeWalle, D.R.; Hom, J.L., eds. The Fernow Watershed Acidification Study. Dordrecht, The Netherlands: Springer: 137-188.

Dighton, J.; Tuininga, A.R.; Gray, D.M.; Huskins, R.E.; Belton, T. 2004. **Impacts of atmospheric deposition on New Jersey pine barrens forest soils and communities of ectomycorrhizae.** Forest Ecology and Management. 201: 131-144.

Driscoll, C.T.; Whitall, D.; Aber, J.D.; Boyer, E.W.; Castro, M.S.; Cronan, C.; Goodale, C.L.; Groffman, P.M.; Hopkinson, C.; Lambert, K.; Lawrence, G.; Ollinger, S.V. 2003. **Nitrogen pollution in the northeastern United States: Sources, effects, and management options.** BioScience. 53: 357-374.

Edwards, P.J.; Williard, K.W.J.; Wood, F.; Sharpe, W.E. 2006. **Soil water and stream water chemical responses.** In: Adams, M.B.; DeWalle, D.R.; Hom, J.L., eds. The Fernow Watershed Acidification Study. Dordrecht, The Netherlands: Springer: 71-136.

Fox, D.G.; Bartuska, A.M.; Byrne, J.G.; Cowling, E.; Fisher, R.; Likens, G.E.; Lindberg, S.E.; Linthurst, R.A.; Messer, J.; Nichols, D.S. 1989. **A screening procedure to evaluate air pollution effects on Class I wilderness areas.** Gen. Tech. Rep. RM-168. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 36 p.

Fraterrigo, J.M.; Pearson, S.M.; Turner, M.G. 2009. **The response of understory herbaceous plants to nitrogen fertilization in forests of different land-use history.** Forest Ecology and Management. 257: 2182-2188.

Frey, S.D., Knorr, M., Parrent, J.L., Simpson, R.T. 2004. **Chronic nitrogen enrichment affects the structure and function of the soil microbial community in temperate hardwood and pine forests.** Forest Ecology and Management. 196: 159-171.

Garten, C.T. 2000. **Nitrogen saturation and soil N availability in a high-elevation spruce and fir forest.** Water, Air, and Soil Pollution. 120: 295-313.

Geiser, L.H.; Jovan, S.E.; Glavich, D.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA.** Environmental Pollution. 158: 2412-2421.

Gilliam, F.S. 2006. **Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition.** Journal of Ecology. 94: 1176-1191.

Gilliam, F.S. 2007. **The ecological significance of the herbaceous layer in forest ecosystems.** BioScience. 57: 845-858.

Gilliam, F.S.; Adams, M.B. 1996. **Wetfall deposition and precipitation chemistry for a central Appalachian forest.** Journal of Air and Waste Management Association. 46: 978-984.

Gilliam, F.S.; Adams, M.B.; Yurish, B.M. 1996. **Ecosystem nutrient responses to chronic nitrogen inputs at Fernow Experimental Forest, West Virginia.** Canadian Journal of Forest Research. 26: 196-205.

Gilliam, F.S.; Hockenberry, A.W.; Adams, M.B. 2006a. **Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest.** Journal of the Torrey Botanical Society. 133: 240-254.

Gilliam, F.S.; Platt, W.J.; Peet, R.K. 2006b. **Natural disturbances and the physiognomy of pine savannas: a phenomenological model.** Applied Vegetation Science. 9: 83-96.

Gilliam, F.S.; Roberts M.R. 2003. **The herbaceous layer in forests of eastern North America.** New York: Oxford University Press. 408 p.

Gilliam, F.S.; Yurish, B.M.; Adams, M.B. 2001. **Temporal and spatial variation of nitrogen transformations in nitrogen-saturated soils of a Central Appalachian hardwood forest.** Canadian Journal of Forest Research. 31: 1768-1785.

Greller, A.M. 1988. **Deciduous forest. Chapter 10.** In: Barbour, M.G.; Billings, W.D., eds. North American vegetation. Cambridge, UK: Cambridge University Press: 288-316.

Hinds, J.W.; Hinds, P.L. 1998. **An annotated checklist of Maine macrolichens.** In: Glenn, M.G.; Harris, R.C.; Dirig, R.; Cole, M.S., eds. Lichenographia Thomsoniana: North American Lichenology in Honor of John W. Thomson. Ithaca, NY: Mycotaxon Ltd.: 345-376.

Hinkle, C.R.; McComb, W.C.; Safley Jr., J.M.; Schmalzer, P.A. 1993. **Mixed mesophytic forests. Chapter 5.** In: Martin, W.H.; Boyce, S.G.; Echternacht, A.C., eds. Biodiversity of the southeastern United States: Upland terrestrial communities. New York, NY: John Wiley and Sons: 203-254.

Hurd, T.M.; Brach, A.R.; Raynal, D.J. 1998. **Response of understory vegetation of Adirondack forests to nitrogen additions.** Canadian Journal of Forest Research. 28: 799-807.

Janicki, A.; Wade, D.; Wilson, H.; Heimbuch, D. 1995. **Maryland critical loads study: Critical loads assessment for Maryland streams; Volume 1.** Report CBRM-AD-95-9. Annapolis, MD: Maryland Dept. of Natural Resources, Chesapeake Bay Research and Monitoring Division.

Johansson, P.; Wetmore, C.M.; Carlson, D.J.; Reich, P.B.; Thor, G. 2006. **Habitat preference, growth form, vegetative dispersal and population size of lichens along a wildfire severity gradient.** The Bryologist. 109(4): 527-540.

Johnson, D.W.; Lindberg, S.E., eds. 1992. **Atmospheric deposition and forest nutrient cycling—A synthesis of the integrated forest study.** New York: Springer-Verlag. 707 p.

Krupa, S.V. 2003. **Effects of atmospheric ammonia (NH_3) on terrestrial vegetation: a review.** Environmental Pollution. 124: 179-221.

Lawrey, J.D. 1993. **Lichens as monitors of pollutant elements at permanent sites in Maryland and Virginia.** The Bryologist. 96(3): 339-341.

Lawrey, J.D.; Hale, M.E., Jr. 1988. **Lichen evidence for changes in atmospheric pollution in Shenandoah National Park, Virginia.** The Bryologist. 91(1): 21-23.

Lewis, W.M. 2002. **Yield of nitrogen from minimally disturbed watersheds of the United States.** Biogeochemistry. 57/58: 375-385

Lilleskov, E.A.; Fahey, T.J.; Horton, T.R.; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** Ecology. 83: 104-115.

Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient.** Ecological Applications. 11: 397-410.

Lilleskov, E.A.; Wargo, P.M.; Vogt, K.A.; Vogt, D.J. 2008. **Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern US.** Canadian Journal of Forest Research. 38: 1260-1266.

Magill, A.H.; Aber, J.D.; Berntson, G.M.; McDowell, W.H.; Nadelhoffer, K.J.; Melillo, J.M.; Steudler, P. 2000. **Long term nitrogen additions and nitrogen saturation in two temperate forests.** Ecosystems. 3: 238-253.

Magill, A.H.; Aber, J.D.; Currie, W.S.; Nadelhoffer, K.J.; Martin, M.E.; McDowell, W.H.; Melillo, J.M.; Steudler, P. 2004. **Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA.** Forest Ecology and Management. 196: 7-28.

May, J.D.; Burdette, E.; Gilliam, F.S.; Adams M.B. 2005. **Interspecific divergence in foliar nutrient dynamics and stem growth in a temperate forest in response to chronic nitrogen inputs.** Canadian Journal of Forest Research. 35: 1023-1030.

McClenahen, J.R.; Davis, D.D.; Hutnik, R.J. 2007. **Macrolichens as biomonitors of air-quality change in western Pennsylvania.** Northeastern Naturalist. 14(1): 15-26.

McCune, B. 2000. **Lichen communities as indicators of forest health.** The Bryologist. 103(2): 353-356.

McCune, B. 1988. **Lichen Communities along O_3 and SO_2 Gradients in Indianapolis.** The Bryologist. 91(3): 223-228.

McCune, B.; Dey, J.; Peck, J.; Heiman, K.; Will-Wolf, S. 1997. **Regional gradients in lichen communities of the southeast United States.** The Bryologist. 100(2): 145-158.

McNulty, S.G.; Cohen, E.C.; Moore Myers, J.A.; Sullivan, T.J.; Harbin, L. 2007. **Estimates of critical acid loads and exceedances for forest soils across the conterminous United States.** Environmental Pollution. 149: 281-292.

Minocha, R.; Long, S.; Magill, A.H.; Aber, J.; McDowell, W.H. 2000. **Foliar free polyamine and inorganic ion content in relation to soil and soil solution chemistry in two fertilized forest stands at the Harvard Forest, Massachusetts.** Plant and Soil. 222: 119-137.

Moore, P.T.; Van Miegroet, H.; Nicholas. 2007. **Relative role of understory and overstory carbon and nitrogen cycling in a southern Appalachian spruce-fir forest.** Canadian Journal of Forest Research. 37: 2689-2700.

Muller, R.N. 2003. **Nutrient relations of the herbaceous layer in deciduous forest ecosystems.** In: Gilliam, F.S.; Roberts, M.R., eds. The herbaceous layer in forests of eastern North America. New York: Oxford University Press: 15-37.

Murphy, K.J.; Alpert, P.; Cosentino, D. 1999. **Local impacts of a rural coal-burning generating station on lichen abundance in a New England forest.** Environmental Pollution. 105: 349-354.

NADP (National Atmospheric Deposition Program). 2009. **NADP maps and data.** Available at http://nadp.sws.uiuc.edu/data/. (Accessed February 9, 2009.)

Nilsson, J.; Grennfelt, P., eds. 1988. **Critical loads for sulphur and nitrogen.** Miljorapport 1988:15. Copenhagen, Denmark: Nordic Council of Ministers.

Oja, T.; Arp, P.A. 1998. **Assessing atmospheric sulfur and nitrogen loads critical to the maintenance of upland forest soils.** In: Maynard, D., ed. Sulfur in the environment. New York, NY: Marcel Dekker: 337-363.

Pardo, L. H. 2010. **Approaches for estimating critical loads of N and S deposition for forest ecosystems on U.S. federal lands.** Gen. Tech. Rep. NRS-71. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 25 p.

Pardo, L.H.; Duarte, N. 2007. **Assessment of effects of acidic deposition on forested ecosystems in Great Smoky Mountains National Park using critical loads for sulfur and nitrogen.** A report prepared for Tennessee Valley Authority, Knoxville, TN and Great Smoky Mountains National Park, Gatlinburg, TN. 141 p.

Peterjohn, W.T.; Adams, M.B.; Gilliam, F.S. 1996. **Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems.** Biogeochemistry. 35: 507-522.

Platt, W.J.; Carr, S.M.; Reilly, M.; Fahr, J. 2006. **Pine savanna overstorey influences on ground-cover biodiversity.** Applied Vegetation Science. 9: 37-50.

Royo, A.A.; Collins, R.; Adams, M.B.; Kirschbaum, C.; Carson, W.P. 2010. **Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity.** Ecology. 91(1): 93-105.

Showman, R.E. 1975. **Lichens as indicators of air quality around a coal-fired power generating plant.** The Bryologist. 78: 1-6.

Showman, R.E. 1981. **Lichen recolonization following air quality improvement.** The Bryologist. 84: 492-497.

Showman, R.E. 1990. **Lichen recolonization in the upper Ohio River valley.** The Bryologist. 93(4): 427-428.

Showman, R.E.1998. **Continuing lichen recolonization in the upper Ohio River Valley.** The Bryologist. 100(4): 478-481.

Showman, R.E.; Long, R.P. 1992. **Lichen studies along a wet sulfate deposition gradient in Pennsylvania.** The Bryologist. 95(2): 166-170.

Sillet, S.C.; Goselin, M.N. 1999. **Distribution of epiphytic macrolichens in relation to remnant trees in a multiple-age Douglas-fir forest.** Canadian Journal of Forest Research. 29: 1204-1215.

Smiley, D.; George, C.J. 1974. **Photographic documentation of lichen decline in the Shawangunk Mountains of New York.** The Bryologist. 77: 179-187.

Strengbom, J.; Walheim, M.; Näsholm, T.; Ericson, L. 2003. **Regional differences in occurrences of understorey forest species reflect differences in N deposition.** Ambio. 32: 91-97.

Sullivan, T.J.; Cosby, B.J. 2002. **Critical loads of sulfur deposition to protect streams within Joyce Kilmer and Shining Rock Wilderness Areas from future acidification.** Report prepared for the USDA Forest Service, Ashville, NC. Corvallis, OR: E&S Environmental Chemistry, Inc.

Sullivan, T.J.; Cosby, B.J. 2004. **Aquatic critical load development for the Monongahela National Forest, West Virginia.** Report for the USDA Forest Service, Monongahela National Forest. Corvallis, OR: E&S Environmental Chemistry, Inc.

Sullivan, T.J.; Cosby, B.J.; Laurence, J.A.; Dennis, R.L.; Savig, K.; Webb, J.R.; Bulger, A.J.; Scruggs, M.; Gordon, C.; Ray, J.; Lee, H.; Hogsett, W.E.; Wayne, H.; Miller, D.; Kern, J.S. 2003. **Assessment of air quality and related values in Shenandoah National Park.** Tech. Rep. NPS/NERCHAL/NRTR-03/090. Philadelphia, PA: U.S. Department of Interior, National Park Service, Eastern Region. 66 p. Available at www.nps.gov/nero/science/FINAL/shen_air_quality/shen_airquality.html (Accessed May 12, 2010).

Thomas, R.Q.; Canham, C.D.; Weathers, K.C.; Goodale, C.L. 2010. **Increased tree carbon storage in response to nitrogen deposition in the US.** Nature Geoscience. 3: 13-17.

UBA (UmweltBundesAmt). 2004. **Manual on methodologies and criteria for modeling and mapping critical loads and levels and air pollution effects, risks, and trends.** Berlin: Federal Environmental Agency (UmweltBundesAmt). Available at http://icpmapping.org/cms/zeigeBereich/11/manual-english.html (Accessed May 12, 2010).

US EPA (U.S. Environmental Protection Agency). 2002. **Nitrogen: multiple and regional impacts.** EPA-430-R-01-006. Washington, D.C.: U.S. Environmental Protection Agency, Clean Air Markets Division. 39 p.

van Diepen, L.T.A. 2008. **The role and diversity of arbuscular mycorrhizal fungi in *Acer saccharum* dominated forest ecosystems under natural and N-amended conditions.** Houghton, MI: Michigan Technological University. 99 p. Ph.D. dissertation.

van Diepen, L.T.A.; Lilleskov, E.A.; Pregitzer, K.S. Miller, R.M. 2007. **Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions.** New Phytologist. 176: 175-183.

van Diepen, L.T.A.; Lilleskov, E.A., Pregitzer, K.S.; Miller, R.M. 2010. **Simulated nitrogen deposition causes a decline of intra- and extraradical abundance of arbuscular mycorrhizal fungi and changes in microbial community structure in northern hardwood forests.** Ecosystems. 13: 683-695.

Van Miegroet, H.; Creed, I.F.; Nicholas, N.S.; Tarboton, D.G.; Webster, K.L.; Shubzda, J.; Robinson, B.; Smoot, J.; Johnson, D.W.; Lindberg, S.E.; Lovett, G.; Nodvin, S.; Moore, S. 2001. **Is there synchronicity in nitrogen input and output fluxes at the Noland Divide Watershed, a small N-saturated forested catchment in Great Smoky Mountains National Park?** The Scientific World. 1: 480-492.

Venterea, R.T.; Groffman, P.M.; Verchot, L.V.; Magill, A.H.; Aber, J.D. 2004. **Gross nitrogen process rates in temperate forest soils exhibiting symptoms of nitrogen saturation.** Forest Ecology and Management. 196: 129-142.

Wallace, Z.P.; Lovett, G.M.; Hart, J.E.; Machona, B. 2007. **Effects of nitrogen saturation on tree growth and death in mixed-oak forest.** Forest Ecology and Management. 243: 210-218.

Wan, S.; Hui, D.; Luo, YR. 2001. **Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis.** Ecological Applications. 11: 1349-1365.

Weathers, K.C.; Simkin, S.M.; Lovett, G.M.; Lindberg, S.E. 2006. **Empirical modeling of atmospheric deposition in mountainous landscapes.** Ecological Applications. 16(4): 1590-1607.

Welch, N.T.; Belmont, J.M.; Randolph, J.C. 2007. **Summer ground layer biomass and nutrient contribution to aboveground litter in an Indiana temperate deciduous forest.** American Midland Naturalist. 157: 11-26.

Wetmore, C.M. 1988. **Lichens and air quality in Indian Dunes National Lakeshore.** Mycotaxon. 33: 25-39.

Wetmore, C.M. 1989. **Lichens and air quality in Cuyahoga Valley National Recreation Area, Ohio.** The Bryologist. 92(3): 273-281.

Will-Wolf, S.; Geiser, L.H.; Neitlich, P.; Reis, A.H. 2006. **Forest lichen communities and environment—how consistent are relationships across scales?** Journal of Vegetation Science. 17: 171-184.

11 GREAT PLAINS

C.M. Clark

11.1 Ecoregion Description

The North American Great Plains are the largest contiguous ecoregion in North America, covering 3.5 million square km^2, or 16 percent of the continental area (CEC 1997). In the United States, the Great Plains ecoregion encompasses a roughly triangular region (Figure 2.2), bordered on the west by the Rocky Mountains and the southwestern deserts in Texas and northern Mexico, on the east by the Eastern Temperate and Northern Forests ecoregions, and extending well into Canada to the north. Precipitation decreases from east to west, and the dry climate, combined with historical fire and grazing regimes, generally limits tree expansion except in localized riparian areas (Briggs and Knapp 1995, Wells 1965). Savannas and local forest cover are also possible in the wetter eastern Great Plains, though periodic fire and grazers play an important role in determining the balance of herbaceous and woody vegetation across the Great Plains (Briggs and Knapp 1995). Precipitation ranges from 320 to 1020 mm per year, and temperatures range from -5 to 30 °C; both peak during the summer growing season (Bailey 1998). Topography is generally flat, with some plateaus and slightly rolling plains. Soils are generally deep and fertile, with little leaching of minerals and strong buffering potential.

Due to the dry climate, Great Plains ecoregion vegetation is primarily composed of herbaceous species, with grasses dominant, and forbs, sedges, and shrubs subdominant. However, in the drier areas to the west and south, shrubs can codominate; in the east and north, as well as along riverbanks and depressions, trees can dominate. The Great Plains usually are subdivided into three subregions based on precipitation. From west to east (drier to wetter), these are the shortgrass prairie, mixed-grass prairie, and tallgrass prairie (CEC 1997, Samson and Knopf 1994). Shortgrass prairie is primarily dominated by the C_4 (warm season)[10] grasses blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), interspersed with succulents and dwarf shrubs. Tallgrass prairie is primarily dominated by the taller C_4 grasses: big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*), interspersed with C_3 (cool season)[11] grasses, forbs, and shrubs. Mixed-grass prairie is a mixture of the two and can shift dramatically in composition with variation in climate (Samson and Knopf 1994). The historical combination of low precipitation, frequent fires, and coevolution with native herbivores (e.g., North American bison, *Bison bison*) maintains the persistence of this generally grass-dominated ecoregion (CEC 1997, Knapp et al. 1999, Samson and Knopf 1994). More recently, reductions in fire frequency and grazing have contributed to encroachment by more woody vegetation across the Great Plains (Briggs et al. 2005).

Human activity has greatly modified the structure and function of the Great Plains. Because of its fertile soil, the Great Plains have been and continue to be heavily used for agriculture and rangelands. It is estimated that of the approximately 120 million ha of historical U. S. prairie, nearly 96 percent, 59 percent, and 50 percent, respectively, of the tallgrass, mixed-grass, and shortgrass prairie, have been lost as a result of human activity (Samson and Knopf 1994). The remaining areas exist mostly as a patchwork of prairie remnants. Many of the species on these remnants are still considered at risk due to long-term fire suppression, alteration of grazing regimes, and isolation, leading to unfavorable conditions for persistence (Briggs et al. 2005, Leach and Givnish 1996). In the Great Plains States, 61 plant species are

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[10] C_4 grass: Any species of grass that uses the C_4 photosynthetic pathway, which initially produces a 4-carbon intermediary during fixation of carbon dioxide. This process is more energetically expensive but enables more efficient water usage and less degradation of photosynthetic enzymes.

[11] C_3 grass: Any species of grass that uses the C_3 photosynthetic pathway, which initially produces a 3-carbon intermediary during fixation of carbon dioxide. This process is less energetically expensive but is also less efficient at using water and leads to more degradation of photosynthetic enzymes.

listed as Federally protected (threatened, endangered, or extirpated), and 1029 are listed as state protected (NRCS 2009). The short-, mixed-, and tallgrass prairie generally correspond to the western rangelands, the wheat belt, and the corn/soybean regions (CEC 1997). Wet N deposition generally ranges from 1 to 7 kg N ha^{-1} yr^{-1}, increasing from west to east in roughly equal proportions of ammonium (NH_4^+) and nitrate (NO_3^-): 1.3:1 ratio of NH_4^+: NO_3^- (NADP 2009[12]). Dry deposition is poorly defined for the area, but site-specific studies indicate that dry deposition can account for at least half of total deposition (Gilliam 1987, Knapp et al. 1998). Consequently, we estimate total N deposition over the Great Plains at 2 to 14 kg N ha^{-1} yr^{-1}.

11.2 Ecosystem Responses to N Deposition

Grasslands characteristic of the Great Plains are commonly N-limited or co-limited by N and other resources (e.g., water, phosphorus (P)), and are dominated by plants capable of rapid response to changing conditions (Hooper and Johnson 1999, Knapp and Smith 2001, Vitousek and Howarth 1991). As such, the Great Plains are expected to be sensitive to elevated N input. Following N deposition, there is a complex cascade of potential ecosystem responses which fall into three broad categories: biogeochemical and soil microbial responses, plant population and community responses, and responses at higher trophic levels (Galloway et al. 2003).

Biogeochemical and soil microbial responses:

- Increase in N availability in the soil for microbial immobilization and plant growth
- Change in microbial community structure and activity (often more bacteria)
- Increase or decrease in decomposition based on litter chemistry and other factors
- Increase in NH_3 volatilization (depending on soil pH)
- Increase in N leaching
- Increase soil acidification

Plant individual, population, and community responses:

- Increase in plant growth and allocation to aboveground structures
- Increase in tissue N content
- Decrease in light levels and alteration of germination conditions
- Shifts in competitive interactions and community composition
- Loss of species; often of rare, short, long-lived, native, and N-fixing species

Higher trophic level responses:

- Short-term increase in production at higher trophic levels due to consumption of more aboveground structures that are more nutritionally rich
- Long-term increase or decrease depending on whether plant community shifts toward or away from herbivore-preferred plant species

The above responses are general, and likely to be affected by several factors important in the Great Plains. Indeed, the structure and function of the Great Plains ecosystem is co-regulated by a complex interaction among multiple-resources, co-evolution with large populations of herbivores, and frequent punctuated disturbances, such as wildfire, that have effects on (and are affected by) responses at multiple hierarchical levels (Knapp et al.1998, Risser et al. 1981, Seastedt and Knapp 1993). As such, analysis of the effects of N deposition on the Great Plains is incomplete without incorporation of disturbance, especially from fire, herbivory, and climatic vulnerability. Unfortunately, the paucity of studies examining the effects of N addition at levels comparable to N deposition (discussed in the next section) means that little can be concluded about potential interactions with these important regulatory factors. One might expect that the removal of N via fire and/or herbivores would enhance N-limitation and therefore sensitivity to N deposition, though this likely depends on regional climatic factors, the intensity of

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[12] Data from Great Plains sites were averaged over all available years to estimate N deposition and the average ratio of NH_4^+: NO_3^-.

herbivory, and the dominant mechanism regulating ecosystem structure and function (Knapp et al. 1998). Because of these uncertainties, we focus our analysis on known effects of relatively low input rates of N comparable to deposition, with some extrapolation to higher levels.

11.3 Range of Responses Observed

Few studies in the Great Plains have explicitly examined the impact of rates of N input similar to ambient N deposition rates. Indeed, of the 108 papers reviewed for this chapter that examined the effects of N enrichment on the Great Plains, only 17 included treatments ≤30 kg N ha^{-1} yr^{-1}, relevant for direct assessment of critical loads (range: 10 to 25 kg N ha^{-1} yr^{-1}). Furthermore, 9 of these 17 included other nutrient amendments in addition to N (e.g., Tilman 1987), and 12 of these 17 are from only two geographic locations (Cedar Creek Ecosystem Science Reserve, Minnesota, and the Center for Subsurface and Ecological Assessment Research, Oklahoma). These limitations warrant caution when drawing conclusions. It is unclear whether studies that also add non-N resources would underestimate the effect of N deposition (because other effects such as soil acidification and cation loss might not occur) or overestimate effects of N deposition (because co-limiting nutrients were also added). However, because (1) studies that add only N but at higher rates show qualitatively similar patterns; and (2) the site that added non-N resources is not co-limited and is largely unresponsive to addition of non-N resources (Tilman 1984, 1987), we are confident in using these studies in this review. The sections that follow in this chapter are structured by ecosystem responses, with all three prairie types grouped, owing to the small number of studies. The first few paragraphs describe the effects from low-N studies (≤30 kg N ha^{-1} yr^{-1}) and the last paragraph in each section extends the review to include notable high-N studies (>30 kg N ha^{-1} yr^{-1}).

11.3.1 Biogeochemical and Soil Microbial Responses in the Great Plains

Jorgensen et al. (2005) added N at 16.3 kg ha^{-1} yr^{-1} to a mixed-grass prairie with a background total deposition of 11 kg N ha^{-1} yr^{-1} in Oklahoma for 5 years and measured several key ecosystem responses. Soil NO_3^- increased within 1 year and remained elevated by an average of 250 percent over the next 5 years. This N was not efficiently retained in the system. Indeed, leaching of N increased nearly twelvefold, and the dominant form of N-loss shifted from dissolved organic N (DON) (75 percent of N-losses in control plots) to NO_3^- (85 percent of N-losses in fertilized plots). Although litter decomposition was not strongly affected by N addition, there was a tendency for litter N loss to be inhibited after 180 days in fertilized plots. Denitrification was not generally stimulated by added N except after large rain events or with supplemental carbon (C), thus this process appeared to be C-limited and oxygen-inhibited more than N-limited. Gross N transformation rates were not sampled within fertilized plots.

Tilman (1987) added N at a range of rates (0, 10, 20, 34, 54, 95, 170, and 270 kg N ha^{-1} yr^{-1}) to four Minnesota sites near the ecotone of mesic prairie and mixed woodland (background wet deposition 6 kg N ha^{-1} yr^{-1}). We focus our assessment on the two old fields (fields abandoned from agriculture) that most closely represent native prairie of the Great Plains, though patterns exhibited following N addition to all four fields were qualitatively similar. This experiment also included addition of non-N mineral nutrients (P, potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), and trace metals), and was resampled several times in its 28-year history to assess the impacts of eutrophication. Nitrogen addition at 10 and 20 kg N ha^{-1} yr^{-1} for 12 years did not generally increase soil NO_3^- or net N mineralization rates except in the more N-poor field, though both were elevated at higher treatment rates in both fields (Wedin and Tilman 1996). After 22 years, low rates of N addition (10 and 20 kg N ha^{-1} yr^{-1}) in the previously unresponsive old-field increased net N mineralization rates and soil extractable NO_3^- tended to increase at all treatment rates (Clark et al. 2009). The other field was not examined in this later study. Finally, although much of the added N at low rates was retained after 12 years in both fields (Wedin and Tilman 1996), this retention efficiency was diminished after 22 years, as N sinks became saturated and species composition shifted at lower treatment rates (Clark and Tilman 2008, Clark et al. 2009).

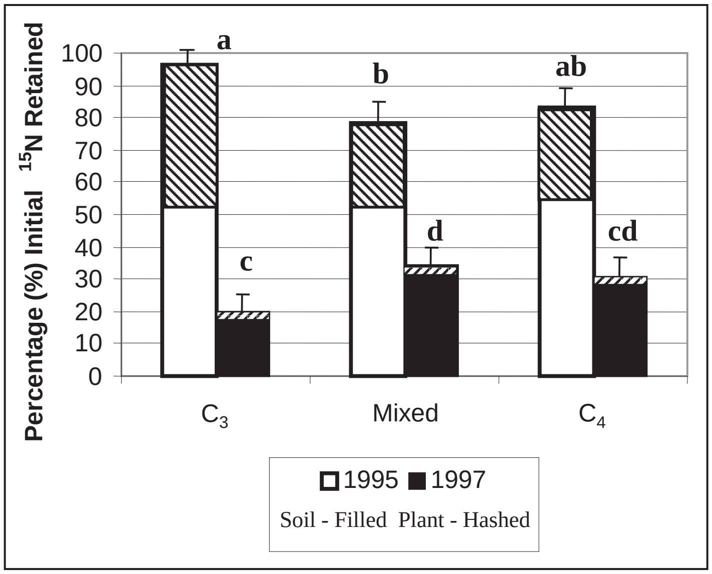

Figure 11.1—Percentage initial ^{15}N retained in soil (solid) and plant compartments (hatched) for three different plant communities (C3, mixed, C4) in 1995 (1 month after addition) and in 1997 (three growing seasons after addition). Bars are +1 SE. Difference letters represent statistically significant differences ($P<0.05$) (Epstein et al. 2001, reprinted with kind permission of Springer Science+Business Media).

The bulk of the nutrients and C in prairie ecosystems are found in the soil, suggesting the ultimate fate of deposited N is likely in complex organic matter stored in the soil. To explore this, Epstein et al. (2001) added 10 kg N ha^{-1} yr^{-1} of ^{15}N to three shortgrass steppe communities (C_3, C_4, and mixed communities) in northeastern Colorado, and sampled various pools over 3 years (background wet deposition not reported). They found that, although the C_3 community initially retained more ^{15}N after the first year (especially in plant material, Fig. 11.1), after the third year retention efficiencies were fairly low (range: 20 to 35 percent). In addition, after 3 years, more ^{15}N was retained in the C_4 and mixed C_3-C_4 communities primarily in the fine particulate organic matter fraction of the soil (Epstein et al. 2001). Another study added 25 kg N ha^{-1} yr^{-1} to five sites across the Great Plains (Table 11.1), and found after 3 years that 46 to 84 percent of the added N was retained primarily in the fine particulate organic matter of the top 20 cm of the soil, with increasing retention in soils with higher soil organic C and finer texture (Barret and Burke 2002). The lower retention efficiencies found in Epstein et al. (2001) compared with Barrett and Burke (2002; as well as others) was explained by higher losses to grazing in Epstein et al. (2001), though it is unknown whether higher herbivory led to a redistribution of ^{15}N or actual losses (i.e., increased volatilization, denitrification). Numerous tracer studies from forests corroborate the evidence that added N often resides in the soil organic or mineral layer rather than in plant tissue (Aber et al. 1998, Currie et al. 2004, Nadelhoffer et al. 2004).

Studies using higher rates of N addition than those already discussed generally confirm the above dynamics and further elucidate responses following N addition. Nitrogen addition (40 kg ha^{-1} yr^{-1}) to monocultures of prairie grassland species in Minnesota increased net N mineralization (46 percent), and respiration rates of the labile (21 percent) and recalcitrant (10 percent) soil C, and significantly decreased soil labile C (31 percent) and microbial N (20 percent) (Dijkstra et al. 2006, Reich et al. 2001). The same experiment demonstrated that although N addition also increased gross N mineralization rates (West et al. 2006) and plant tissue quantity and quality (discussed in next section), there was not an observed increase in the rate of decomposition (Knops et al. 2007). Meta-analyses have found few general relationships between N addition and decomposition, though decomposition is often inhibited in low quality tissue (high lignin:N) and when N addition rates are low compared with ambient N deposition (Knorr et al. 2005). Detailed decomposition studies using higher rates of N addition (100 kg ha^{-1} yr^{-1}) have found that fine-scale soil-substrate interactions, for example from possible shifts in microbial community composition and activity, likely determine whether N addition will generally

Table 11.1—Site characteristics and percentage of N retained 3 years after adding ^{15}N (25 kg N ha^{-1} yr^{-1}) to five prairie communities across the Great Plains. The bulk of the retention was in fine-textured soil with greater organic C content, with less N retention in plant biomass (average of 25 percent in plants across sites) (Barret and Burke 2002, reprinted with permission).

Site	State	System	MAP (cm)[a]	MAT (°C)[b]	Total N retention (%)
Comanche National Grassland	Colorado	shortgrass	41	11.9	84
Thunder Basin National Grasslands	Wyoming	mixed-grass	32	7.9	76
Pawnee National Grasslands	Colorado	shortgrass	37	9.1	64
Fort Keogh Livestock and Range Research Laboratory	Montana	mixed-grass	35	7.1	61
Muleshoe National Wildlife Refuge	Texas	shortgrass	45	14.3	46

[a] MAP – mean annual precipitation
[b] MAT – mean annual temperature

increase or decrease decomposition (Hobbie 2005, 2008; Keeler et al. 2009). In tallgrass prairie where N addition (100 kg ha^{-1} yr^{-1}) was studied in combination with fire and simulated grazing (mowing), N availability was unaffected by burning, was elevated with burning plus N addition, and was not decreased with additional mowing (Collins et al. 1998).

Mycorrhizal responses to N deposition in the Great Plains ecoregion have been documented in gradient studies and fertilization experiments. Using grassland soil data from an N gradient in the Chicago area, Egerton-Warburton[13] reported a decline in both mycorrhizal colonization and spore density as total extractable N increased. There was a steep decline in arbuscular mycorrhizal fungal activity between 5-10 μg g^{-1} extractable soil inorganic N. While N deposition values were not available for all of these sites, National Atmospheric Deposition Program (NADP) values of 9.7 kg ha^{-1} yr^{-1} were reported from the site with highest arbuscular mycorrhizal fungal activity, and 12.4 kg ha^{-1} yr^{-1} from a site with reduced activity. Other studies using higher rates of N inputs (≥40 kg N ha^{-1} yr^{-1}) generally confirm the effects of N on microbial populations, reporting shifts in microbial communities from fungal to bacterial dominance (Bradley et al. 2006, Chung et al. 2007), increased activity for several key soil enzymes (phosphatase, β-glucosidase, and peroxidase) (Chung et al. 2007), and decreased symbiotic microbial populations (Johnson 1993, Johnson et al. 2003). These effects appear to be especially pronounced when soils are more P-rich (Egerton-Warburton et al. 2007, Johnson et al. 2003).

11.3.2 Plant Community Responses in the Great Plains

Nitrogen addition for 4 years at 16.3 kg ha^{-1} yr^{-1} to a mixed-grass prairie in Oklahoma (background total deposition of 11 kg N ha^{-1} yr^{-1}) increased total plant biomass and led to a fivefold increase in tall fescue (*Festuca arundinacea*) cover, although total cover was relatively unaffected (Clark et al. 2003, Jorgensen et al. 2005). Tall fescue cover was weakly, and often not significantly, correlated with cover of other plant functional groups (negatively with native C_4 grasses and positively with non-leguminous forbs). Species richness decreased with increased tall fescue cover in the second and third years of the study (this effect was not seen in year 1, and was not examined in later years), and was unrelated to litter biomass.

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[13] Egerton-Warbuton, L.M. Unpublished data. Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL, 60022

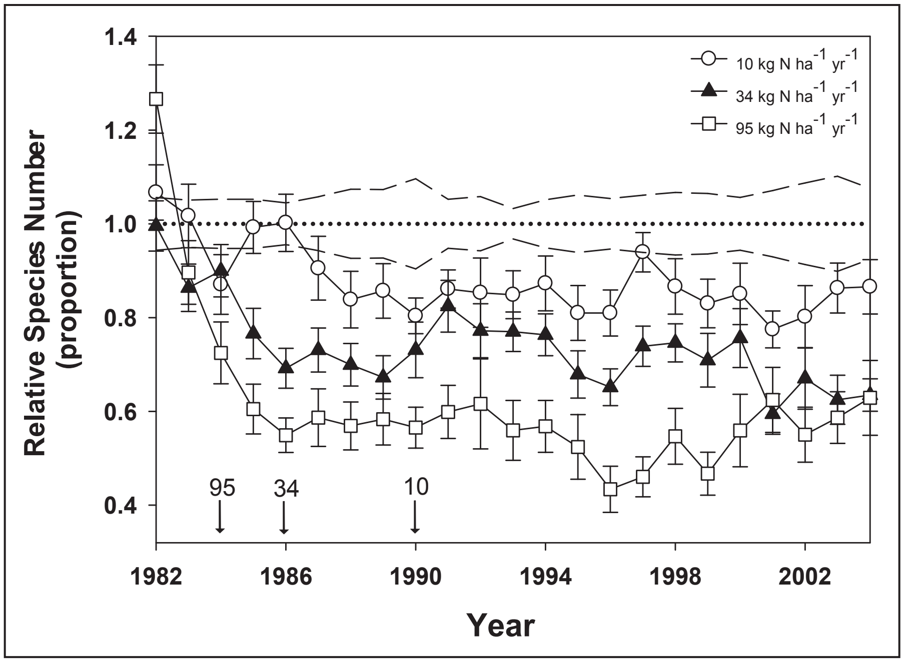

Figure 11.2—Shown are the species numbers (relative to controls) for plots receiving N at three difference rates averaged over three Minnesota fields from 1982-2004. Dashed lines correspond to annual standard errors in control plots and arrows indicate the year of first significant ($P < 0.01$) detection of species loss for that treatment rate (Clark and Tilman 2008).

Wedin and Tilman (1996) examined the impacts of 12 years of N addition at a range of rates (0 to 270 kg N ha^{-1} yr^{-1}, background wet deposition of 6 kg N ha^{-1} yr^{-1}) to two Minnesota old fields dominated by a diverse mixture of prairie grasses and forbs near the ecotone of prairie and mixed woodland. Even low rates of N addition (10 and 20 kg ha^{-1} yr^{-1}) decreased the percent abundance of C_4 grasses (dominated by the native bunchgrass little bluestem) by nearly 20 percent, and increased the abundance of C_3 grasses (primarily the invasive rhizomatous grasses Kentucky bluegrass [*Poa pratensis*] and quackgrass [*Agropyron repens*]) (Wedin and Tilman 1996). Knops and Reinhard (2000) found that the specific leaf area for all three of these grasses tended to increase with N across the N addition gradient. However, quackgrass specific leaf area increased the most at the lowest N addition rate (10 kg N ha^{-1} yr^{-1} plus 6 kg N ha^{-1} yr^{-1} background wet deposition) and demonstrated the largest proportional increase on average (86 percent for quackgrass as opposed to 40 percent and 28 percent for little bluestem and Kentucky bluegrass respectively) (Knops and Reinhart 2000). This pattern suggests plasticity as a key factor influencing compositional changes. Compositional shifts toward more productive N-rich species decreased root and litter C:N ratios, increased litter mass, decreased light penetration, and decreased species richness (Tilman 1993, Wedin and Tilman 1996). Though these changes were not readily apparent after the first few years (Clark and Tilman 2008, Tilman 1987), the losses of species and shifts in community structure increased through time, especially at lower N input levels, with a 17 percent reduction in species number at the 10 kg N ha^{-1} yr^{-1} rate after 22 years (Fig. 11.2, Clark and Tilman 2008). Tilman (1993) suggested that the loss of species was driven primarily by increased litter mass, reducing light and germination rates—a hypothesis supported by the weaker response found in the annually burned field at the same research site (Tilman 1993) and from other related studies (Foster and Gross 1998). Other research suggests light limitation from competing neighbors drives the reduction in species (Hautier et al. 2009).

Studies using high rates of N addition generally confirm the dynamics discussed above. Nitrogen addition (> 50 kg ha^{-1} yr^{-1}) to a newly restored tallgrass prairie (Baer et al. 2003) increased productivity and decreased species richness, purportedly through the same mechanism of reduced light and increased aboveground biomass and litter. Nitrogen addition at 40 kg ha^{-1} yr^{-1} to assembled prairie communities in Minnesota led to similar responses as in natural communities (increased biomass, increased plant N concentration, increased aboveground:belowground biomass ratios), and also led to decreased lignin:N ratios, increased root cellulose concentration, and short-term increases in photosynthesis (Dijkstra et al. 2006, Knops et al. 2007, Lee et al. 2001, Reich et al. 2001). Lee et al. (2001) reported that the small increases in rates of net photosynthesis for 13 prairie species in the first year of treatment did not generally continue, even though leaf N content remained elevated. Nitrogen addition for 8 years at 50 kg ha^{-1} yr^{-1} to a restored tallgrass prairie community increased annual net primary productivity, root N, and root tissue quality, but root C:N ratios remained high enough to prevent net mineralization of N (Baer and Blair 2008). Similar to the long-term studies in Minnesota (Clark et al. 2009), there was little evidence that N enrichment increased root biomass, soil C or N accrual rates, or storage of C in total, microbial, or mineralizable pools within this time frame (Baer and Blair 2008).

Higher rates of N addition (100 kg ha-1 yr-1) have been studied extensively in many sites, with qualitatively similar results. One notable study is from the tallgrass prairie, that added high rates of N addition in combination with burning and mowing. They found that N addition greatly reduces species richness in combination with burning (especially of the diverse C_3 forb group), a decline that is mitigated with additional mowing (Collins et al. 1998).

11.3.3 Other trophic responses in the Great Plains

Nitrogen addition for 2 years (16.3 kg ha^{-1} yr^{-1}, background total deposition of 11 kg N ha^{-1} yr^{-1}) to a mixed-grass prairie in Oklahoma had variable effects on mammalian herbivores (Clark et al. 2003, Clark et al. 2005, Jorgensen et al. 2005). Nitrogen addition increased the abundance of one species of harvest mouse (*Reithrodontomys montanus*) primarily during the winter, had no effect on a second species of harvest mouse (*Reithrodontomys fulvescens*), and increased the abundance of cotton rats (*Sigmodon hispidus*) only in combination with reduced predation (i.e., fencing) (Clark et al. 2003, Jorgensen et al. 2005).

Haddad et al. (2000) examined the impacts on insect communities from fertilizer addition at a range of rates to a Minnesota old-field (0 to 270 kg N ha^{-1} yr^{-1}; background wet deposition 6 kg N ha^{-1} yr^{-1}). Nitrogen addition at low rates (≤20 kg ha^{-1} yr^{-1}) for 14 years decreased insect species diversity and increased insect numbers and biovolume. This resulted from a decrease in the diversity of food sources and oviposition sites as plant species richness declined and two species (quackgrass and Kentucky bluegrass) came to dominate. Changes in the number of insect individuals at low N addition rates (≤20 kg ha^{-1} yr^{-1}) also varied by functional type, with decreases in parasitoids and increases in herbivores (esp. dominant herbivores) (Haddad et al. 2000). Another study used a detailed biogeochemical process model to examine the effect of N deposition (1 to 5 kg N ha^{-1} yr^{-1}) and insect herbivory on ecosystem level C and N dynamics (Throop et al. 2004). Researchers found that although total C storage was less sensitive to herbivory than to N deposition, herbivory reduced production and soil organic C more as N deposition increased, influencing whether ecosystem C sequestration saturated at lower or higher N deposition rates (Fig. 11.3) (Throop et al. 2004). Short-term and long-term trophic responses to N deposition are likely to differ, and they remain understudied (Throop and Lerdau 2004). Over the short term, N addition increases plant quantity and quality without large changes in composition, which should increase insect populations. But over longer periods, compositional changes can increase or decrease herbivore activity, depending on whether there is a shift toward or away from a community dominated by herbivore-preferred species (Throop and Lerdau 2004).

Studies using higher rates of N addition than those discussed above generally confirm the aforementioned dynamics, with some notable exceptions. In particular, Lau et al. (2008) found no effect of N addition (40 kg ha^{-1} yr^{-1}) on herbivory of a common N-fixing prairie legume (roundhead lespedeza [*Lespedeza capitata*]). This suggests that higher trophic responses to N deposition are likely to depend on specific plant-herbivore interactions. Nonetheless, a review of studies on the effect of high rates of N addition on insect herbivory found a generally stimulatory effect through increased foliar N and decreased secondary compounds (Throop and Lerdau 2004). Macroinvertebrates in the tallgrass prairie of Kansas yielded complex treatment responses between N addition (100 kg ha^{-1} yr^{-1}) and other treatments (burning, mowing, and P addition).

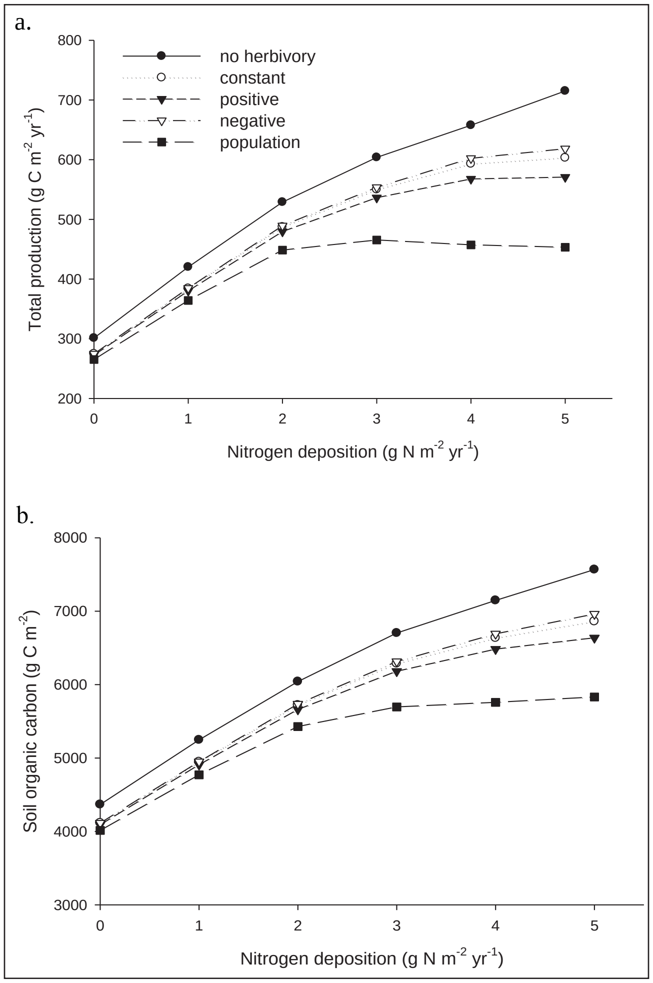

Figure 11.3—Influences of N deposition and the four herbivore functions on C dynamics. The four functions describe whether the intensity of herbivory is independent of the rate of N deposition (constant), increases linearly with N deposition (positive), decreases linearly with N deposition (negative), increases multiplicatively with N deposition (population), or whether herbivory is absent (no herbivory). Values are from the final year of a simulation run that included a 2500-year climate stabilization, 30 years of N deposition, and 30 years of herbivory and N deposition. (a) Total annual biomass production (sum of above-and belowground production) in terms of C accumulation in g m^{-2} yr^{-1}; (b) Total pools of soil organic C (Throop et al. 2004, reprinted with permission of John Wiley and Sons).

Generally, exotic earthworms and herbivorous beetle larvae tended to increase with fertilization, while cicadas were relatively unresponsive (Callaham et al. 2002, 2003). Nitrogen addition (80 kg ha^{-1} yr^{-1}) to a tallgrass prairie in Texas led to a decrease in arthropod richness as a result of an increase in nonpreferred woody species (Hartley et al. 2007). One of the few long-term studies to date of small mammal responses found a long-term decrease in the population of voles after 9 years of high-N treatment (336 kg ha^{-1} yr^{-1}) to an Ohio old-field (Hall et al. 1991).The decrease in the vole population was attributed to a shift in the plant population from edible species (70 percent edible species such as Canada goldenrod [*Solidago canadensis*] and clover [*Trifolium* spp.] in control plots) to inedible species (63 to 99 percent inedible species such as annual ragweed [*Ambrosia artemisiifolia*] and great ragweed [*Ambrosia trifida*] in fertilized plots).

11.4 Critical Loads Estimates

We estimate the critical loads for shifts in ecosystem structure and function at 10 to 25 kg N ha^{-1} yr^{-1} for mixed- and shortgrass prairie and 5 to 15 kg N ha^{-1} yr^{-1} for tallgrass prairie. These overall estimates are based on observed shifts in several key biogeochemical, plant, and trophic indicators following N inputs just above these levels (Table 11.2, 11.3). Total N input at 27.3 kg ha^{-1} yr^{-1} (16.3 kg N ha^{-1} yr^{-1} treated and 11.0 kg N ha^{-1} yr^{-1} of ambient N deposition) to a mixed-grass prairie site increased plant community biomass, increased NO_3^- leaching, and had variable effects on higher trophic levels, suggesting that the N critical load must be below this level. Thus, we set the critical load at 10 to 25 kg N ha^{-1} yr^{-1}. It is difficult to assign a lower value to this range, as we do not have a treatment level for which there was no negative effect, nor do we know whether ambient N deposition has caused alterations in the ecosystem from a prior unimpacted condition. We regard this estimate as fairly reliable rather than reliable because of this uncertainty and because it is based on the only known empirical study examining the response of mixed-grass prairie to such low levels of N. We use the same estimate for the shortgrass prairie (10 to 25 kg N ha^{-1} yr^{-1}) because we expect these ecosystems to respond similarly and we have no other empirical studies to consult. This reduces the reliability for the shortgrass prairie critical loads to expert judgment. The critical load for shortgrass prairie may be slightly higher or co-dependent on water availability, as this system is less sensitive to high rates of N addition (100 kg ha^{-1} yr^{-1}) than the tallgrass prairie (Clark et al. 2007), and likely has a greater tendency for water limitation or co-limitation of water and N (Hooper and Johnson 1999, Lauenroth et al. 1978). However, we urge caution due to the lack of studies and suggest using the 10 to 25 kg

Table 11.2—Responses to low rates of N addition (N-add; ≤25 kg N ha^{-1} yr^{-1}) for the Great Plains ecoregion. Rates of N deposition (N-dep) are shown for comparison.

Ecosystem component	Site	N input *kg N ha^{-1} yr^{-1}* N-add/N-dep	Indicator	Measured Response	Study
Ecotone (tallgrass prairie and oak woodland)	Cedar Creek Ecosystem Science Reserve LTER, MN	10-20/6[a]	Biogeochemical and microbial	Elevated net N mineralization rates after 22 years, not after 12 years	Clark et al. 2009, Wedin and Tilman 1996
Ecotone (tallgrass prairie and oak woodland)	Cedar Creek Ecosystem Science Reserve LTER, MN	10-20/6[a]	Plant community	Increased biomass, C_3 (cool season grass) abundance, litter mass, decreased C_4 (warm season grass) biomass, light penetration, tissue C:N, and species richness	Clark and Tilman 2008, Wedin and Tilman 1996, Tilman 1993, Tilman 1987
Ecotone (tallgrass prairie and oak woodland)	Cedar Creek Ecosystem Science Reserve LTER, MN	10-20/6[a]	Higher trophic levels	Decreased insect diversity, and number of parasitoids, increase in total numbers of insects and number of herbivorous insects	Haddad et al. 2000
Shortgrass prairie (3)	Short-grass steppe LTER, CO	10/3[a]	Biogeochemical	Retention of ^{15}N in organic soil layers more than in plants after 3 years	Epstein et al. 2001
Arbuscular mycorrhizal fungi	Chicago, IL area N gradient	12[a]	microbial	Decline in both mycorrhizal colonization and spore density	Egerton-Warburton[c]
Mixed-grass prairie	Center for Ecological Assessment Research, OK	16.3/11[b]	Biogeochemical and microbial	Increased soil NO_3^- and leaching, inconclusive effects on decomposition, no effect on denitrification	Jorgensen et. al. 2005
Mixed-grass prairie	Center for Ecological Assessment Research, OK	16.3/11[b]	Plant community	Increased plant biomass and tall fescue cover, decreased richness, weaker effects on cover of other species	Jorgensen et. al. 2005
Mixed-grass prairie	Center for Ecological Assessment Research, OK	16.3/11[b]	Higher trophic levels	Increases of harvest mouse (*Reithrodontomys montanus*) in winter, no effects on other mammals	Jorgensen et. al. 2005
Mixed-grass (2) and shortgrass (3) prairies	Various (Table 11.1)	25/1-4[a]	Biogeochemical	Retention of ^{15}N in organic soil layers more than in plants	Barret and Burke 2002

[a] Locally measured wet deposition
[b] Total (wet+dry) N deposition
[c] See footnote 13 on page 121

Table 11.3—Critical loads for nutrient N for the Great Plains ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Tallgrass prairie	5-15	#	Biogeochemical N cycling, plant and insect community shifts	Need more low-N studies without other nutrients	Clark et al. 2009, Clark and Tilman 2008, Tilman 1993, Tilman 1987, Wedin and Tilman 1996
Mixed-grass prairie	10-25	#	Soil NO_3^- pools, leaching, plant community shifts	More studies needed	Clark et al. 2003, 2005; Jorgenson et al. 2005
Shortgrass prairie	10-25	(#)		Inferred from mixed grass	Barret and Burke 2002, Epstein et al. 2001
Mycorrhizal fungi	12	(#)	Decline in arbuscular mycorrhizal fungal activity		Egerton-Warburton[a]

[a] See footnote 13 on page 121

N ha^{-1} yr^{-1} level as the critical load. Total N input at 16 kg N ha^{-1} yr^{-1} (10 kg N ha^{-1} yr^{-1} treated and 6 kg N ha^{-1} yr^{-1} ambient N deposition) to a northeastern tallgrass prairie site led to reductions in plant richness, shifts in biogeochemical cycling, and changes in the insect community, suggesting that the N critical load must be below this level. Researchers at this site estimated the critical threshold to these old fields at 5.3 kg N ha^{-1} yr^{-1}. However, due to the extremely low N status of this site, resulting from its geomorphology and past use for agriculture, we think this estimate is likely low for the tallgrass prairie as a whole. Thus, we estimate the critical load for tallgrass prairie at 5 to 15 kg N ha^{-1} yr^{-1}. We regard this estimate as fairly reliable rather than reliable because the only available study also added non-N resources, and because the site is nutrient poor compared to other tallgrass prairie sites (Grigal et al. 1974).

Based on research by Egerton-Warburton[13] and NADP wet deposition, we suggest a provisional N critical load of 12 kg ha^{-1} yr^{-1} for mycorrhizal effects in this ecoregion. However, the lack of sites with lower N deposition in the gradient studied may give us an unrealistically high value for the critical load, as communities in the low deposition sites may have already been altered. Clearly, additional factors such as soil type, fire history, and agricultural and other land-use history will have a large influence on the N status of the Great Plains grassland ecosystem types, and thus on the responsiveness of mycorrhizal fungi to N deposition.

11.5 Comparison to Critical Loads for Other Regions

The European ecosystems most comparable to the U.S. Great Plains are the EUNIS (European Nature Information System) coded habitats E1.2 (perennial calcareous grassland and basic steppes) and E1.7 (non-Mediterranean dry acid and neutral grassland) (European Environmental Agency 2010). Bobbink et al. (2003) estimated a moderately reliable critical load for perennial calcareous grassland and basic steppes at 15 to 25 kg N ha^{-1} yr^{-1}, and a reliable critical load for non-Mediterranean dry acid and neutral grassland at 10 to 20 kg N ha^{-1} yr^{-1} (Bobbink et al. 2003). Other ecosystems comparable to the U.S. Great Plains (especially short- and mixed-grass prairie) include the Eurasian steppe that stretches from Asia into Eastern Europe. Nitrogen addition at 17.5 kg N ha^{-1} yr^{-1} to a representative site in rural China led to increases in plant biomass and reductions in species richness (critical load less than 20 kg N ha^{-1} yr^{-1}) (Bai et al. 2010). Our estimates for the Great Plains are similar to those from China and slightly lower than those from Europe, as we have long-term field experiments in these lower ranges, and it is likely that responses in Europe may be somewhat attenuated due to higher historical levels of N deposition (Galloway et al. 2004). Indeed, several observational studies across current N deposition gradients (Stevens et al. 2004) and at different time periods (Bennie et al. 2006, Smart et al. 2005) suggest that current and historical N deposition may lower species richness across European systems, though more research is sorely needed.

11.6 Future Research Directions and Gaps in Data

Currently, native communities of the Great Plains are highly fragmented as a result of extensive agricultural activity across this large region and are threatened by several global-change factors in addition to N deposition, including continued land-use change, alterations of historic fire and grazing regimes, and regional climate change. Although fire and grazing are expected to alter ecosystem sensitivity to N deposition, no studies to date have examined these critical interactions at rates comparable to deposition levels. The few high N addition studies suggest that ecosystems may be maximally sensitive if fire regimes alone are restored, suggesting effective conservation likely requires the re-establishment of multiple regulating factors (Collins et al. 1998, Suding et al. 2004). Elevated carbon dioxide (CO_2) under future global change has been hypothesized to both favor and disfavor the currently subordinate C_3 grasses in this ecoregion, depending on the dominant ecological response. On one hand, C_3 grasses may be favored if the fertilization effect of CO_2 predominates and water does not become limiting, resulting in dramatic reductions of ecosystem C-sequestration (Knapp et al. 1998). However, several other lines of research suggest that elevated CO_2 may actually favor the continued dominance of the C_4 grasses of this system through their elevated water use efficiency during dry years (Ham et al. 1995; Knapp et al.1993, 1996), an effect that is likely dependent on future climate patterns (Knapp et al. 1998). Each of these dynamics requires further investigation, but is beyond the scope of this report. Nevertheless, there are several future research directions that will improve our ability to predict the impacts of N deposition. Most importantly, we stress the need for more empirical studies in more geographic locations examining the long term (≥10 years) impacts from low rates of N input (≤ 20 kg N ha^{-1} yr^{-1}) comparable to N deposition over this region. This should be pursued both in isolation and in combination with the multiple factors that regulate ecosystem structure and function across the Great Plains. This experimental work, however, is not enough, and should be coordinated with dynamic ecosystem-vegetation models to direct limited resources towards areas of greater sensitivity. The wide range of ecosystem responses to high rates of N addition observed (Clark et al. 2007) demonstrate that not all ecosystems are equally N sensitive. Prior research suggests that fine-scale as well as regional-scale factors likely moderate ecosystem responses (Gough et al. 2000). Nonetheless, there are several specific areas that would benefit from additional study as they relate to N deposition:

- Shifts in phenology: A few studies in other systems have examined changes in the timing of ecological interactions with added N which can greatly influence ecosystem functioning (Cleland et al. 2006).
- Decomposition: The impact of N addition on decomposition is still unresolved and largely unstudied at low input rates (Hobbie 2008, Keeler 2010, Knorr et al. 2005).
- Shifts in belowground communities and processes: Although fungal:bacterial population ratios often decrease with N addition (e.g., Bradley et al. 2006), no studies to date have addressed these dynamics at low rates.
- Modulating responses to N deposition: Historical and altered regimes of fire and herbivory are likely to modulate ecosystem sensitivity to N deposition. In addition, grasslands are known to often be co-limited by other resources in addition to N (primarily water), though it is unknown whether critical thresholds for N deposition will decrease or increase under changing climatic regimes (Bobbink et al. 1998).
- Higher-order responses to N deposition: Most of the research to date has focused on plant and soil responses to N deposition. However, higher order responses, such as N-induced shifts in herbivory, pathogens, and drought stress, as well as modulating influences from fire,

herbivory, and climatic variability, are likely to greatly modify the total ecosystem response to N deposition (Bobbink et al. 1998, Knapp et al. 1998, Throop and Lerdau 2004).

- Predictive modeling: As briefly mentioned above, more effort directed to predictive modeling of ecosystem sensitivity to N addition needs to be pursued across ecosystem types and indicators (Heil and Bobbink 1993).

LITERATURE CITED

Aber, J.; McDowell, W.; Nadelhoffer, K.; Magill, A.; Berntson, G.; Kamakea, M.; McNulty, S.; Currie, W.; Rustad, L.; Fernandez, I. 1998. **Nitrogen saturation in temperate forest ecosystems - Hypotheses revisited.** BioScience. 48: 921-934.

Baer, S.G.; Blair, J.M. 2008. **Grassland establishment under varying resource availability: A test of positive and negative feedback.** Ecology. 89: 1859-1871.

Baer, S.G.; Blair, J.M.; Collins, S.L.; Knapp, A.K. 2003. **Soil resources regulate productivity and diversity in newly established tallgrass prairie.** Ecology. 84: 724-735.

Bai, Y.F.; Wu, J.G.; Clark, C.M.; Naeem, S.; Pan, Q.M.; Huang, J.H.; Zhang, L.X.; Han, X.G. 2010. **Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands.** Global Change Biology. 16: 358-372.

Bailey, R.G. 1998. **Ecoregions: The ecosystem geography of the oceans and continents.** New York, NY: Springer-Verlag. 176 p.

Barret, J.E.; Burke, I.C. 2002. **Nitrogen retention in semiarid ecosystems across a soil organic-matter gradient.** Ecological Applications. 12: 878-890.

Bennie, J.; Hill, M.O.; Baxter, R.; Huntley, B. 2006. **Influence of slope and aspect on long-term vegetation change in British chalk grasslands.** Journal of Ecology. 94: 355-368.

Bobbink, R.; Ashmore, M.; Braun, S.; Flückinger, W.; van den Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R., eds. Empirical critical loads for nitrogen. Environmental Documentation No. 164. Berne, Switzerland: Swiss Agency for the Environment, Forests, and Landscape: 43-170.

Bobbink, R.; Hornung, M.; Roelofs, J.G.M. 1998. **The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation.** Journal of Ecology. 86: 717-738.

Bradley, K.; Drijber, R. A.; Knops, J. 2006. **Increased N availability in grassland soils modifies their microbial communities and decreases the abundance of arbuscular mycorrhizal fungi.** Soil Biology & Biochemistry. 38: 1583-1595.

Briggs, J.M.; Knapp, A.K. 1995. **Interannual variability in primary production in tallgrass prairie: Climate, soil moisture, topographic position, and fire as determinants of aboveground biomass.** American Journal of Botany. 82: 1024-1030.

Briggs, J.M.; Knapp, A.K.; Blair, J.M.; Heisler, J.L.; Hoch, G.A.; Lett, M.S.; McCarron, J.K. 2005. **An ecosystem in transition. Causes and consequences of the conversion of mesic grassland to shrubland.** BioScience. 55: 243-254.

Callaham, M.A.; Blair, J.M.; Todd, T.C.; Kitchen, D.J.; Whiles, M.R. 2003. **Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass.** Soil Biology & Biochemistry. 35: 1079-1093.

Callaham, M. A.; Whiles, M.R.; Blair, J.M. 2002. **Annual fire, mowing and fertilization effects on**

two cicada species (Homoptera : Cicadidae) in tallgrass prairie. American Midland Naturalist. 148: 90-101.

CEC (Commision for Environmental Cooperation). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

Chung, H.G.; Zak, D.R.; Reich, P.B.; Ellsworth, D.S. 2007. **Plant species richness, elevated CO2, and atmospheric nitrogen deposition alter soil microbial community composition and function.** Global Change Biology. 13: 980-989.

Clark, C.M.; Cleland, E.E.; Collins, S.L.; Fargione, J.E.; Gough, L.; Gross, K.L.; Pennings, S.C.; Suding, K.N.; Grace, J.B. 2007. **Environmental and plant community determinants of species loss following nitrogen enrichment.** Ecology Letters. 10: 596-607.

Clark, C.M.; Hobbie, S.; Venterea, R.; Tilman, D. 2009. **Long-lasting effects on N cycling 12 years after treatments cease despite minimal N retention.** Global Change Biology. 15: 1755-1766.

Clark, C. M.; Tilman, D. 2008. **Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands.** Nature. 451: 712-715.

Clark, J.E.; Hellgren, E.C.; Jorgensen, E.E.; Leslie, D.M. 2005. **Population dynamics of harvest mice (Reithrodontomys fulvescens and R. montanus) across a nitrogen-amended old field.** American Midland Naturalist. 154: 240-252.

Clark, J.E.; Hellgren, E.C.; Jorgensen, E.E.; Tunnell, S.J.; Engle, D.M.; Leslie, D.M. 2003. **Population dynamics of hispid cotton rats (Sigmodon hispidus) across a nitrogen-amended landscape.** Canadian Journal of Zoology-Revue Canadienne De Zoologie 81: 994-1003.

Cleland, E.E.; Chiariello, N.R.; Loarie, S.R.; Mooney, H.A.; Field, C.B. 2006. **Diverse responses of phenology to global changes in a grassland ecosystem.** Proceedings of the National Academy of Sciences. 103: 13740-13744.

Collins, S.L.; Knapp, A.K.; Briggs, J.M.; Blair, J.M.; Steinauer, E.M. 1998. **Modulation of diversity by grazing and mowing in native tallgrass prairie.** Science. 280: 745-747.

Currie, W.S.; Nadelhoffer, K.J.; Aber, J.D. 2004. **Redistributions of N-15 highlight turnover and replenishment of mineral soil organic N as a long-term control on forest C balance.** Forest Ecology and Management. 196: 109-127.

Dijkstra, F.A.; Hobbie, S.E.; Reich, P.B. 2006. **Soil processes affected by sixteen grassland species grown under different environmental conditions.** Soil Science Society of America Journal. 70: 770-777.

Egerton-Warburton, L.M.; Johnson, N.C.; Allen, E.B. 2007. **Mycorrhizal community dynamics following nitrogen fertilization: A cross-site test in five grasslands.** Ecological Monographs. 77: 527-544.

Epstein, H.E.; Burke, I.C.; Mosier, A.R. 2001. **Plant effects on nitrogen retention in shortgrass steppe 2 years after ^{15}N addition.** Oecologia. 128: 422-430.

European Environmental Agency. 2010. **EUNIS - Welcome to EUNIS biodiversity database.** Copenhagen, Denmark: European Environmental Agency. Available at http://eunis.eea.europa.eu/. (Accessed August 20, 2010).

Foster, B.L.; Gross, K.L. 1998. **Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter.** Ecology. 79: 2593-2602.

Galloway, J.N.; Aber, J.D.; Erisman, J.W.; Seitzinger, S.P.; Howarth, R.W.; Cowling, E.B.; Cosby, B.J. 2003. **The nitrogen cascade.** BioScience. 53: 341-356.

Galloway, J.N.; Dentener, F.J.; Capone, D.G.; Boyer, E.W.; Howarth, R.W.; Seitzinger, S.P.; Asner, G.P.; Cleveland, C.C.; Green, P.A.; Holland, E.A.; Karl, D.M. ; Michaels, A.F.; Porter, J.H.; Townsend, A.R.; Vorosmarty, C.J. 2004. **Nitrogen cycles: past, present, and future.** Biogeochemistry. 70: 153-226.

Gilliam, F.S. 1987. **The chemistry of wet deposition for a tallgrass prairie ecosystem - inputs and interactions with plant canopies.** Biogeochemistry. 4: 203-217.

Gough, L.; Osenberg, C.W.; Gross, K.L.; Collins, S.L. 2000. **Fertilization effects on species density and primary productivity in herbaceous plant communities.** Oikos. 89: 428-439.

Grigal, D.F.; Chamberlain, L.M.; Finney, H.R.; Wroblewski, D.W.; Gross, E.R. 1974. **Soils of the Cedar Creek Natural History Area.** Misc. Rep. 123. St. Paul, MN: University of Minnesota Agriculture Experiment Station. 47 p.

Haddad, N.M.; Haarstad, J.; Tilman, D. 2000. **The effects of long-term nitrogen loading on grassland insect communities.** Oecologia. 124: 73-84.

Hall, A.T.; Woods, P.E.; Barrett, G.W. 1991. **Population-dynamics of the meadow vole (*Microtus-Pennsylvanicus*) in nutrient-enriched old-field communities.** Journal of Mammalogy. 72: 332-342.

Ham, J.M.; Owensby, C.E.; Coyne, P.I.; Bremer, D.J. 1995. **Fluxes of CO_2 and water-vapor from a prairie ecosystem exposed to ambient and elevated atmospheric CO_2.** Agricultural and Forest Meteorology. 77: 73-93.

Hartley, M.K.; Rogers, W.E.; Siemann, E.; Grace, J. 2007. **Responses of prairie arthropod communities to fire and fertilizer: Balancing plant and arthropod conservation.** American Midland Naturalist. 157: 92-105.

Hautier, Y.R.; Niklaus, P.A.; Hector, A. 2009. **Competition for Light Causes Plant Biodiversity Loss After Eutrophication.** Science. 324: 636-638.

Heil, G.W.; Bobbink, R. 1993. **Calluna, a simulation-model for evaluation of impacts of atmospheric nitrogen deposition on dry heathlands.** Ecological Modelling. 68: 161-182.

Hobbie, S.E. 2005. **Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition.** Ecosystems. 8: 644-656.

Hobbie, S.E. 2008. **Nitrogen effects on decomposition: a five-year experiment in eight temperate sites.** Ecology. 89: 2633-2644.

Hooper, D.U.; Johnson, L. 1999. **Nitrogen limitation in dryland ecosystems: Response to geographical and temporal variation in precipitation.** Biogeochemistry. 46: 247-293.

Johnson, N.C. 1993. **Can fertilization of soil select less mutualistic mycorrhizae?** Ecological Applications. 3: 749-757.

Johnson, N.C.; Rowland, D.L.; Corkidi, L.; Egerton-Warburton, L.M.; Allen, E.B. 2003. **Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands.** Ecology. 84: 1895-1908.

Jorgensen, E.E.; Holub, S.M.; Mayer, P.M.; Gonsoulin, M.E.; Silva, R.G.; West, A.E.; Tunnell, S.J.; Clark, J.E.; Parsons, J.L.; Engle, D.M.; Hellgren, E.C.; Spears, J.D.H.; Bulter, C.E.; Leslie, D.M. Jr. 2005. **Ecosystem stress from chronic exposure to low levels of nitrate.** EPA/600/R-05/087. Washington, DC: U.S. Environmental Protection Agency, National Risk Management Research Laboratory. 35 p.

Keeler, B.L.; Hobbie, S.E.; Kellogg, L.E. 2009. **Effects of long-term nitrogen addition on microbial enzyme activity in eight forested and grassland**

sites: Implications for litter and soil organic matter decomposition. Ecosystems. 12: 1-15.

Knapp, A.K.; Blair, J.M.; Briggs, J.M.; Collins, S.L.; Hartnett, D.C.; Johnson, L.C. ; Towne, E.G. 1999. **The keystone role of bison in north American tallgrass prairie - Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes.** BioScience. 49: 39-50.

Knapp, A.K.; Briggs, J.M.; Hartnett, D.C.; Collins, S.L.; eds. 1998. **Grassland dynamics: Long-term ecological research in tallgrass prairie.** New York, NY: Oxford University Press. 386 p.

Knapp, A.K.; Hamerlynck, E.P.; Ham, J.M.; Owensby, C.E. 1996. **Responses in stomatal conductance to elevated CO_2 in 12 grassland species that differ in growth form.** Vegetatio. 125: 31-41.

Knapp, A.K.; Hamerlynck, E.P.; Owensby, C.E. 1993. **Photosynthetic and water relations responses to elevated CO_2 in the C_4 grass *Andropogon-Gerardii*.** International Journal of Plant Sciences. 154: 459-466.

Knapp, A.K.; Smith, M.D. 2001. **Variation among biomes in temporal dynamics of aboveground primary production.** Science. 291: 481-484.

Knops, J.M.H.; Naeemw, S.; Reich, P.B. 2007. **The impact of elevated CO_2, increased nitrogen availability and biodiversity on plant tissue quality and decomposition.** Global Change Biology. 13: 1960-1971.

Knops, J.M.H.; Reinhart, K. 2000. **Specific leaf area along a nitrogen fertilization gradient.** American Midland Naturalist. 144: 265-272.

Knorr, M.; Frey, S.D.; Curtis, P.S. 2005. **Nitrogen additions and litter decomposition: A meta-analysis.** Ecology. 86: 3252-3257.

Lau, J.A.,; Strengbom, J.; Stone, L.R.; Reich, P.B.; Tiffin, P. 2008. **Direct and indirect effects of CO_2, nitrogen, and community diversity on plant-enemy interactions.** Ecology. 89: 226-236.

Lauenroth, W.K.; Dodd, J.L.; Simms, P.L. 1978. **The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland.** Oecologia. 36: 211-222.

Leach, M.K.; Givnish, T.J. 1996. **Ecological determinants of species loss in remnant prairies.** Science. 273: 1555-1558.

Lee, T.D.; Tjoelker, M.G.; Ellsworth, D.S.; Reich, P.B. 2001. **Leaf gas exchange responses of 13 prairie grassland species to elevated CO_2 and increased nitrogen supply.** New Phytologist. 150: 405-418.

NADP (National Atmospheric Deposition Program). 2009. **NADP maps and data.** Available at http://nadp.sws.uiuc.edu/data/ (Accessed May 5, 2010).

NRCS (Natural Resources Conservation Service). 2011. **The PLANTS database.** Baton Rouge, LA: U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Center. Available at http://plants.usda.gov. (Accessed April 12, 2010).

Nadelhoffer, K.J.; Colman, B.P.; Currie, W.S.; Magill, A.; Aber, J.D. 2004. **Decadal-scale fates of N-15 tracers added to oak and pine stands under ambient and elevated N inputs at the Harvard Forest (USA).** Forest Ecology And Management. 196: 89-107.

Reich, P.B.; Tilman, D.; Craine, J.; Ellsworth, D.; Tjoelker, M.G.; Knops, J.; Wedin, D.; Naeem, S.; Bahauddin, D.; Goth, J.; Bengtson, W.; Lee, T.D. 2001. **Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO_2 and N availability regimes? A field test with 16 grassland species.** New Phytologist. 150: 435-448.

Risser, P.G.; Birney, C.E.; Blocker, H.D.; May, S.W.; Parton, W.J.; Wiens, J.A. 1981. **The true prairie**

ecosystem. Stroudsberg, PA: Hutchinson Ross Publishing. 557 p.

Samson, F.; Knopf, F. 1994. **Prairie conservation in North America.** BioScience. 44: 418-421.

Seastedt, T.R.; Knapp, A.K. 1993. **Consequences of nonequilibrium resource availability across multiple time scales: The transient maxima hypothesis.** American Naturalist. 141: 621-633.

Smart, S.M.; Bunce, R.G.H.; Marrs, R.; LeDuc, M.; Firbank, L.G.; Maskell, L.C.; Scott, W.A.; Thompson, K.; Walker, K.J. 2005. **Large-scale changes in the abundance of common higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: Tests of hypothesised changes in trait representation.** Biological Conservation. 124: 355-371.

Stevens, C.J.; Dise, N.B.; Mountford, J.O.; Gowing, D.J. 2004. **Impact of nitrogen deposition on the species richness of grasslands.** Science. 303: 1876-1879.

Suding, K.N.; Gross, K.L.; Houseman, G.R. 2004. **Alternative states and positive feedbacks in restoration ecology.** Trends in Ecology & Evolution. 19: 46-53.

Throop, H.L.; Holland, E.A.; Parton, W.J.; Ojima, D.S.; Keough, C.A. 2004. **Effects of nitrogen deposition and insect herbivory on patterns of ecosystem-level carbon and nitrogen dynamics: results from the CENTURY model.** Global Change Biology. 10: 1092-1105.

Throop, H.L.; Lerdau, M.T. 2004. **Effects of nitrogen deposition on insect herbivory: Implications for community and ecosystem processes.** Ecosystems. 7: 109-133.

Tilman, D. 1984. **Plant dominance along an experimental nutrient gradient.** Ecology. 65: 1445-1453.

Tilman, D. 1987. **Secondary succession and the pattern of plant dominance along experimental nitrogen gradients.** Ecological Monographs. 57: 189-214.

Tilman, D. 1993. **Species richness of experimental productivity gradients: How important is colonization limitation.** Ecology. 74: 2179-2191.

Vitousek, P.M.; Howarth, R.W. 1991. **Nitrogen limitation on land and in the sea - How can it occur?** Biogeochemistry. 13: 87-115.

Wedin, D.A.; Tilman, D. 1996. **Influence of nitrogen loading and species composition on the carbon balance of grasslands.** Science. 274: 1720-1723.

Wells, P.V. 1965. **Scarp woodlands transported grassland soils and concept of grassland climate in great plains region.** Science. 148 : 246-9.

West, J.B.; Hobbie, S.E.; Reich, P.B. 2006. **Effects of plant species diversity, atmospheric [CO2], and N addition on gross rates of inorganic N release from soil organic matter.** Global Change Biology. 12: 1400-1408.

12 NORTH AMERICAN DESERTS

E.B. Allen, L.H. Geiser

12.1 Ecoregion Description

North American deserts and semi-deserts extend from British Columbia to Mexico (CEC 1997). The ecoregion description is adapted from CEC (1997). They are characterized by aridity (130 to 380 mm annual precipitation); shrub and succulent vegetation with trees in riparian areas and higher elevation woodlands; and dry, low organic matter soils that are high in calcium carbonate ($CaCO_3$) in some regions. The ecoregion can be subdivided into cold northern deserts and semi-deserts (Columbia Plateau, Snake River Basin, Great Basin, greater Colorado Plateau) and warm southern deserts (Mojave, Sonoran, Chihuahuan) (see Table 12.1).

The cold deserts and semi-deserts are arid to semi-arid with marked seasonal temperature extremes, a winter moisture regime and some snow. They lie in the rain shadow of the Cascade and Sierra Mountains to the west, and are blocked from moist Gulf Coast air masses by the Rocky Mountains to the east. The Columbia/Snake River Plateaus are loess- and volcanic ash-covered plains; their expansive grassland and sagebrush steppes have been largely converted to agriculture. The Great Basin contains hundreds of north-south mountain ranges separated by broad valleys, whereas the Colorado and Arizona/New Mexico plateaus consist of canyons, cliffs, buttes, and mesas of sedimentary rock. Sagebrush (*Artemisia* spp.) dominates these deserts, with saltbush (*Atriplex* spp.) and greasewood (*Sarcobatus* spp.) on more alkaline soils.

The warm deserts have higher temperatures and greater evaporation rates. The Mojave is the driest and hottest of the North American deserts; its recorded high temperature, in Death Valley, California, is 57 °C. Characteristic plants are the creosote bush (*Larrea tridentata*) and Joshua tree (*Yucca brevifolia*). The Sonoran Desert of Arizona and California is subtropical and receives most of its precipitation in the summer monsoon season; gentler rains may occur in the winter months. Its structurally diverse vegetation includes the paloverde tree (*Parkinsonia* spp.), saguaro cactus (*Cereus gigantea*), cholla (*Cylindropuntia* spp.), and agave (*Agave* spp.). The Chihuahuan Desert extends into southern New Mexico from Mexico. Rain occurs primarily in the summer, and supports smaller scrub vegetation characterized by American tarwort (tarbush; *Flourensia cernua*), creosote bush (*Larrea tridentata*),

Table 12.1—Location of North American Deserts of the United States.

Level 2 Ecoregion[a]	Desert	Location	Level 3 Ecoregion[a]
Cold deserts	Columbia Plateau	Eastern Washington	Columbia Plateau
	Snake River Plain	Southern Idaho	Snake River Plain
	Great Basin	Southern Oregon, extreme southern Idaho, north and central Nevada, western Utah	Northern Basin and Range, Central Basin and Range
	Greater Colorado Plateau	Western Wyoming, western Colorado, eastern Utah, northern Arizona, northern New Mexico	Wyoming Basin, Colorado Plateau, Arizona/New Mexico Plateau
Warm deserts	Mojave	Southeastern California, southern Nevada, northeastern Arizona	Mojave Basin and Range
	Sonoran	Southwestern Arizona, extreme southern California	Sonoran Basin and Range
	Chihuahuan	Southern New Mexico	Chihuahuan Desert

[a] CEC 1997

soaptree yucca (*Yucca elata*), grama grasses (*Bouteloua* spp.), and tobosagrass (*Pleuraphis mutica*). Piñon-juniper woodlands occur at the higher elevations above both cold and warm deserts.

Small mammals, birds, and reptiles are the most abundant wildlife of the ecoregion. Livestock grazing is widespread and, together with irrigated agriculture and population growth, has had significant ecological and hydrological effects. Major urban areas with higher nitrogen (N) deposition, which affects the adjacent and downwind deserts, are Phoenix, Salt Lake City, Las Vegas, Tucson, Albuquerque, Spokane, and Los Angeles (Fenn et al. 2003).

12.2 Ecosystem Responses to N Deposition

Responses to N deposition in deserts include alterations of species composition, often increases in biomass of exotic species, and decreases in native species. In this ecoregion of altitudinal, latitudinal, and landform diversity, vegetation types vary, but low growing shrubs and grasses predominate. Recently, invasive exotic species have been increasing in desert ecosystems (Allen et al. 2009, Brooks 2003). This may be due to increased N deposition, as exotic grasses may respond to higher soil N levels differently than native species (Allen et al. 2009). Such changes can have serious management implications. For example, in the agriculturally intensive Snake River Plain and in the Great Basin, extensive cheatgrass (*Bromus tectorum*) invasions contribute to increased fire frequency, that in turn favors even greater cover of cheatgrass. Loss of native plants adapted to longer fire intervals and the poorer nutritional quality of cheatgrass in turn reduces the carrying capacity of lands (Whisenant 1990). Fire frequency has similarly increased in the Mojave Desert in areas undergoing exotic grass invasions (Brooks et al. 2004, Brooks and Matchett 2006). Experimental N fertilization resulted in a depletion of soil moisture in sagebrush steppe, which could potentially affect future plant production (Inouye 2006).

Biotic soil crusts (consisting of bacteria, green algae, microfungi, and crustose lichens) and mycorrhizal fungi constitute important parts of desert ecosystems. Responses to increased N deposition include reductions in photosynthesis and nitrogen fixation rates; reductions in photosynthetic pigments and ultraviolet (UV) protective pigments such as scytonemin; increases in electrolyte leakage, increases in microbial N and denitrification; shifts in community composition favoring eutrophs; and increases in microbial activity in nonvegetated soils.

12.3 Range of Responses Observed

Several studies have used N fertilizer in the desert to measure a biomass response and then compared this response to N inputs along N deposition gradients (Allen et al. 2009, Baez et al. 2007). Responses to N inputs are summarized in Table 12.2. A response to a certain level of N fertilization is assumed to be similar to the response along the gradient, assuming that factors besides N inputs are equal. The difficulty with this approach is that gradients may have multiple factors that change among sites in addition to N inputs, making interpretation of results difficult. The combination of N fertilization plus gradient approaches provide the most reliable information currently available. The most useful N fertilization studies for setting critical loads are those in the range of threshold responses, as reported below. For instance, N fertilizer of 72 kg ha^{-1} yr^{-1} at the Jornada Long-Term Ecological Research (LTER) site in New Mexico showed growth increases by native winter annual forbs and decreases by summer annual forbs (Gutierrez and Whitford 1987), but this value is well above the response threshold determined from studies reviewed below. Similarly, 60 kg N ha^{-1} yr^{-1} increased mineralization rates at the Central Arizona Project (CAP-LTER; Hall et al. 2009). Alternatively, input of 40 kg N ha^{-1} yr^{-1} over 3 years did not increase creosote bush biomass at the Mojave Global Change Facility near Las Vegas (Barker et al. 2006) and the authors concluded that annual variability in precipitation was the most important variable for creosote bush productivity.

12.3.1 Plant Community Responses

Baez et al. (2007) used an increase in the biomass of the dominant native blue grama grass (*Bouteloua gracilis*) as an indicator of elevated N in desert grassland at the

Table 12.2—Responses to N input for North American Deserts ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Response threshold *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Riparian habitat, Hells Canyon NRA, Columbia Plateau	3	(#)	High cover of eutrophic lichens, enhanced N concentrations in lichen thalli	Uncertainty regarding modeled N estimate	Geiser et al. 2008, Porter et al 2007
Piñon-juniper and creosote scrub, Joshua Tree National Park, Sonoran and Mojave Desert	8.4	#	Increased biomass of invasive grasses	N fertilization of 5 kg ha-1 y-1 plus background N deposition of 3 kg ha-1 y-1 in wet year	Allen et al. 2009
Creosote scrub, Joshua Tree National Park, Sonoran Desert	3-8	#	Production of fine fuel of Mediterranean splitgrass sufficient for fire	DayCent model	Rao et al. 2010
Piñon-juniper Joshua Tree National Park, Mojave Desert	3-6	#	Production of fine fuel of red brome sufficient for fire	DayCent model	Rao et al. 2010
Desert grassland Sevilleta LTER	2.5-22	#	Increase in blue grama biomass	Response observed at 20 kg N ha-1 y-1 fertilization; ambient is 2.45 kg N ha-1 y-1	Baez et al. 2007
Sagebrush steppe	7.4	#	Depletion of soil moisture	No increase in aboveground production	Inouye 2006
Desert grassland, Colorado Plateau	22	Not reliable: fertilization level too high	Increase in tiller density of the dominant cool season grass species Indian ricegrass	No increase in warm season galleta grass. Fertilizer addition of 20 kg N ha-1 y-1; ambient deposition 2 kg N ha-1 y-1	Schwinning et al. 2005
	42	Not reliable: fertilization level too high	Increase in biomass of the invasive species Russian thistle	Short term—2 yrs fertilization	
Desert scrub, Mohave Desert	32	Not reliable: fertilization level too high	Increase in exotic invasive grasses and a decline in native forbs	Creosote bush dominated ecosystem	Brooks et al. 2003

Sevilleta LTER site in New Mexico. Plots fertilized with 20 kg N ha^{-1} for one season had increased biomass of blue grama compared to controls. Bulk N deposition increased from 1.7 to 2.4 kg ha^{-1} yr^{-1} in the control plots between 1989 to 2004, adding an additional total of 5.9 kg N ha^{-1} to the control plots from increased N deposition during these 16 years. However, there was no change in biomass of blue grama over this period, suggesting that 5.9 kg N ha^{-1} over 16 years was below the threshold for increased biomass in this species. Thus, Baez et al. (2007) concluded that the threshold for elevated biomass of blue grama lies somewhere between 2.45 and 20 kg N ha^{-1} yr^{-1}; including ambient deposition raises the upper response threshold to approximately 22 kg N ha^{-1} yr^{-1}.

Zhu et al. (2006) calculated 72.3 kg ha^{-1} N content in urban Phoenix soils compared to exurban desert soils that had 9.4 kg N ha^{-1}, accompanied by elevated carbon (C) in urban soils. This increase in soil N and C was hypothesized to have occurred during the last several decades of rapid urban expansion. A more recent study also showed elevated N and C in remnant native vegetation fragments within the urban Phoenix CAP-LTER site that promoted changes in N cycling, such as increased denitrification potential and higher microbial N (Hall et al. 2009). Nitrogen deposition in the Phoenix area was measured using wet and dry bucket collectors. The highest measured values were less than 6 kg N ha^{-1} yr^{-1}, which the investigators describe as an underestimate because the dry bucket technique is not accurate (Lohse et al. 2008). The Community Multiscale Air Quality (CMAQ) model, which includes both wet and dry deposition, showed a maximum deposition of 26 kg N ha^{-1} yr^{-1} for the Phoenix area (Fenn et al. 2003). Impacts of N deposition on vegetation were not reported in these studies in the Phoenix area, although the PALS (Patch Arid Land Simulator) model showed nearly a doubling in total plant production with simulated N addition between 2 and 26 kg ha^{-1} yr^{-1} (Shen et al. 2008). The model shows that even a small increase in N can increase biomass, but it is not clear how this can be used to determine a response threshold. However, measurements comparing urban to rural areas show no significant change in plant biomass due to elevated N, likely because of multivariate gradients that include elevated ozone (O_3), temperature, and other factors.[14] Additional research on responses to fertilizer N are under way at the CAP-LTER site.

Schwinning et al. (2005) used fertilizer levels of 0, 10, 20, and 40 kg N ha^{-1} for 2 years in a desert grassland on the Colorado Plateau and measured an increase in tiller (grass shoot) density of the dominant cool season grass species, Indian ricegrass (*Oryzopsis hymenoides*), at 20 kg N ha^{-1} yr^{-1}. This increase was not observed in the warm season grass species, galleta grass (*Hilaria jamesii*). The most noticeable change in this study was an increase in biomass of the invasive species Russian thistle (*Salsola iberica*) at the highest N level. The authors concluded that elevated N deposition will promote an invasion of Russian thistle and a shift in dominance to cool season grasses. However, current N deposition at this site may be as low as 2 kg ha^{-1} yr^{-1}. Because the study was carried out for only 2 years, the levels of N inputs may be higher than threshold response levels for long-term N deposition.

Working in creosote bush desert scrub, Brooks (2003) fertilized at a rate of 32 kg N ha^{-1} yr^{-1} for 2 years and found an increase in exotic invasive grasses and a decline in native forbs. Allen et al. (2009) studied the impacts of elevated N by fertilization along an N deposition gradient in Joshua Tree National Park in creosote bush scrub and piñon-juniper woodland. The N deposition rates along the gradient ranged from 3.4 to 12.4 kg N ha^{-1} yr^{-1} as measured by bulk deposition samplers and also as modeled (Tonnesen et al. 2007). Fertilization rates were 5 and 30 kg N ha^{-1} between 2003 and 2005. There were no vegetation biomass responses in 2003, a dry year. In 2004, a year with moderate precipitation, two of the four sites had increased invasive grass biomass at the treatment of 30 kg N ha^{-1}, but not with 5 kg N ha^{-1}. The strongest response to N occurred in the wettest year, 2005, when invasive grass biomass increased under both 5 and 30 kg N ha^{-1} fertilizer in the lowest and highest N deposition sites. Conversely, native

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[14] Hall, S.J. Unpublished data comparing plant response to N deposition in urban and rural areas. On file with: Department of Ecology, Evolution, and Environmental Science, School of Life Sciences, Arizona State University, Tempe, AZ 85287-4701

forbs decreased in production at these sites following fertilization. However, another site with low N deposition and sparse invasive grass cover had a positive response by native forbs to N fertilization, suggesting that native forbs can respond to N in the absence of grasses (Allen et al. 2009).

To determine the N input level that results in vegetation change, the biogeochemical model daily Century (DayCent; Rao et al. 2010) was used to model invasive grass and forb productivity under varying levels of N deposition, soil texture, and precipitation between 2003 and 2008 (Rao et al. 2009, 2010). Fires have become more frequent in the Mojave and Sonoran Deserts, and there may be a relationship between fire and increased grass biomass under enhanced N deposition (Allen et al. 2009, Brooks 2003, Brooks and Matchett 2006). Fire risk, which was calculated as the probability of producing enough fine fuels to carry a fire (1 T ha^{-1} fine fuel), increased exponentially when deposition was above 3.0 kg N ha^{-1}yr^{-1}; fire risk leveled at 5.7 kg N ha^{-1} yr^{-1} in piñon-juniper woodland, and at 8.2 kg N ha^{-1} yr^{-1} in creosote bush scrub (Rao et al. 2010).

Elevated N may also increase soil water use by plants, as reported by Inouye (2006) for big sagebrush (*Artemisia tridentata*) fertilized at 6 and 12 kg N ha^{-1} yr^{-1} for six years in Great Basin semi-desert in southern Idaho. Soil moisture was depleted to 140 cm and was not recharged except in the wettest years. No aboveground increase in productivity was measured, so the moisture depletion may have been due to increased root productivity. The site receives 1.4 kg N ha^{-1} yr^{-1} wet deposition as measured at a nearby NADP (National Atmospheric Deposition Program) station, but dry deposition is not known. Since there was no significant difference between the two fertilizer levels, the lower level of 6 kg N ha^{-1} yr^{-1} (plus the background 1.4 kg N ha^{-1} yr^{-1} wet deposition) can be considered the response threshold for moisture depletion by sagebrush. Schwinning et al. (2005) observed an earlier onset of drought stress and increased water use with 20 kg N ha^{-1} yr^{-1} of fertilizer plus the estimated background deposition of 2 kg N ha^{-1} yr^{-1}, confirming the observations that elevated N can promote increased water use in desert vegetation.

12.3.2 Arbuscular Mycorrhizal Fungi

Mycorrhizal fungi are important for plant nutrient acquisition, drought stress tolerance, and the hydraulic lifting of water, which are critical in arid lands (Allen 2007). Their diversity, abundance, and functioning are altered by N deposition. A Phoenix-area study showed shifts in mycorrhizal species composition in urban and exurban sites that were dominated by different plant species, but did not relate these species shifts to N deposition (Bills and Stutz 2009). Data from the Sevilleta LTER site, which is located at the junction of cold desert, warm desert, and shortgrass steppe, suggest that long-term N fertilization at 100 kg ha^{-1} yr^{-1} can lead to changes in the community structure and function of arbuscular mycorrhizal fungi associated with grasses from semi-arid environments (Corkidi et al. 2002, Egerton-Warburton et al. 2007). However, this level of N fertilization is well beyond the critical load, greatly exceeds current deposition amounts (wet plus dry), and exceeds the threshold for changes in mycorrhizal functioning observed in Mediterranean California ecosystems. Results of mycorrhizal response to N deposition in the Great Plains and Mediterranean ecoregions (Chapters 11 and 13) also have relevance for the more mesic end of the cold and warm desert ecosystem types.

12.3.3 Lichens, Biotic Soil Crusts, and Soil Microbes

Lichens make a significant contribution to biological diversity in North American deserts and semi-deserts; a recent compendium documented 1971 species from the greater Sonoran Desert alone (Nash et al. 2002, 2004, 2008). However, the long periods of metabolic inactivity due to insufficient hydration, dominance of communities by crustose forms with minimal surface exposure, minimal dry deposition inputs from canopy drip, and lower growth rates, can make it difficult to detect community-level shifts. Even after a decade of exposure, Marsh and Nash (1979) found no evidence of community effects on lichens in the vicinity of the large Four Corners Power Plant in the Colorado Plateau. Nevertheless, physiological measurements indicate that wetted desert lichens can be as sensitive to air pollution as lichens from other climates. Lichens in the vicinity of a coal-fired power plant in Page, Arizona, a major point source of sulfur dioxide(SO_2), nitrogen oxides (NO_x), and metals, exhibited increased electrolyte leakage, chlorophyll degradation, and reduced N fixation (Belnap 1991).

Enhanced concentrations of N in thalli of the saxicolous lichen, *Xanthoparmelia cumberlandia*, and high cover of eutrophic lichens on netleaf hackberry (*Celtis laeviagata* var. *reticulata*), a small tree of riparian areas, were observed throughout Hells Canyon National Recreation Area (Geiser et al. 2008). Interagency Modeling of Protected Visual Elements (IMPROVE) data show that Hells Canyon is a regional hot spot for ammonium (NH_4^+) and nitrate (NO_3^-) deposition from the Snake River valley and possibly as far away as California. Other pollutants—SO_2, NO_x, O_3, hydrogen sulfide (H_2S), and fine particulate ammonium sulfate ($(NH_4)_2SO_4$)—were low and comparable to other remote areas. Mean annual deposition of total N from CMAQ in this area between 1990 and 1999 was 2.6 to 3.0 kg N ha^{-1} yr^{-1} (Porter 2007), with some uncertainty surrounding the reliability of the deposition estimate. Significantly higher thallus N concentrations and eutroph cover occurred within 0.2 km of the Snake River. Ammonia (NH_3) emissions were especially high at these sites in spring and summer (5 to19 ppb biweekly averages), presumably volatilizing from the fertilizer-laden Snake River. Average annual NH_3 concentrations at five year-long monitoring sites along the Snake River ranged from 1.4 to 4.7 ppb. In a review of European studies, Cape et al. (2009) suggested a long-term mean annual critical level for ammonia of 1 µg m^{-3} (1.4 ppb), based on lichen and bryophyte responses; local data support that estimate.

Biotic soil crusts are well developed in cold deserts and, in pristine areas, can account for as much surface cover as vascular plants (Davidson et al. 2002). Consisting of cyanobacteria-dominated mats of intricately enmeshed bacteria, green algae, microfungi, and crustose lichens, they play vital ecological roles by improving topsoil stabilization, soil fertility, surface water holding capacity, and seedling survival (Harper and Belnap 2001). Biotic soil crusts are responsive to N deposition, but because component species are physically inextricable from each other, measurements reflect the response of the combined biota, along with climate, soil chemistry, and other environmental variables. Some examples:

1) An aqueous solution of 0.5 g N L^{-1} was added to biotic crusts from Canyon Lands National Park in the Colorado Plateau (Belnap et al. 2008). Reductions in quantum yield, b-carotene, nitrogenase activity, scytonemin pigments, and UV protective xanthophyll pigments due to N alone were observed in early- and mid- but not late-successional crusts. Higher temperatures, more UV, and more frequent precipitation had adverse effects on all crust types. In these cases, N positively moderated some adverse effects of UV, but only in the late successional crusts.

2) In a gradient study in the Sonoran Desert near Phoenix (McCracken et al. 2008), microbes of wetted soils between plants responded (increased carbon dioxide (CO_2) flux) readily to N deposition, whereas microbes of wetted soils under plants did not. The authors postulated that anthropogenic N could essentially decouple microbes from reliance on shrubs for nutrients, resulting in increased activity in open spaces between plants. In other words, whereas native desert microbial activity is primarily confined to zones influenced by plant root exudates, if adequate water and anthropogenic N are available, microbial activity can occur in soils outside these zones. Major shifts in microbial metabolism, community composition, and biomass in extensive bare soil surface areas are implied effects.

12.4 Critical Loads Estimates

Fertilization studies in the Sevilleta grasslands of the Chihuahuan Desert (Baez et al. 2007) indicate a critical load greater than 2.45 and less than 22 kg N ha^{-1} yr^{-1}, based on alteration in species composition and biomass observed at 22 kg N ha^{-1} yr^{-1} after 1 year and no changes under ambient deposition (2.45 kg N ha^{-1} yr^{-1}). Fertilization studies by Schwinning et al. (2005) and Brooks (2003) were not used to set the

Table 12.3—Empirical critical loads of nutrient N for North American Desert ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Lichens	3	(#)	Lichen community shifts, increase in thallus N concentration	Uncertainty regarding modeled N estimate	Geiser et al. 2008, Porter 2007
Shrubland, woodland, and desert grassland	3-8.4	#	Vegetation response, community change. Increased biomass of invasive grasses; decrease of native forbs		Allen et al. 2009, Inouye 2006, Rao et al. 2010

critical load, as the high levels of N inputs over both short-term experiments could not accurately determine the critical load for long-term N deposition. At Joshua Tree National Park in the Mojave Desert, Allen et al. (2009) found that vegetation response was determined by a combination of factors, including soil properties and precipitation. These experimental studies indicated that a critical load for invasive grass biomass response may be as low as 8.4 kg N ha^{-1} yr^{-1} (3.4 kg N ha^{-1} yr^{-1} deposited, plus 5 kg N ha^{-1} yr^{-1} fertilized), as measured in the cleanest site (Allen et al. 2009). Their results suggest a critical load of 8.4 kg N ha^{-1} yr^{-1} in wet years to prevent an increase of invasive grasses in the desert ecosystem (Allen et al. 2009). The results from the biogeochemical DayCent model compared well with the experimental fertilization studies, and suggested a critical load of 3.1 to 8.2 kg N ha^{-1} yr^{-1} for lower elevation desert dominated by the invasive common Mediterranean grass (*Schismus barbatus*), and a critical load of 3.0 to 5.7 kg N ha^{-1} yr^{-1} in higher elevations with red brome (*Bromus rubens*) as the invasive grass (Rao et al. 2010). The model shows that at levels higher than 5.7 to 8.1 kg N ha^{-1}yr^{-1} the fire risk is controlled by precipitation, i.e., these values exceed the critical load for N. The critical load was determined by the amount of N modeled to produce 1 T ha^{-1} of fine fuel to carry a fire, as these are regions subject to increasing grass-fire cycle impacts (Brooks and Matchett 2006). The critical load for vegetation response to N deposition is set at 3.0 to 8.4 kg ha^{-1} yr^{-1}, based on the research by Allen et al. (2009) and Rao et al. (2010), and supported by evidence (Table 12.3) of soil moisture depletion in that range (Inouye 2006). This critical load is considered fairly reliable; the empirical study (Allen et al. 2009) is supported by a biogeochemical model (Rao et al. 2010). Further research in various desert study locations would increase the reliability of this critical load for the North American Deserts ecoregion. No critical load specific to arbuscular mycorrhizal fungi can be estimated currently. A tentative estimate of 3.0 kg N ha^{-1} yr^{-1} based on data from Geiser et al. (2008) and Porter (2007) is suggested for lichen thallus N concentration and lichen community shifts in the Columbia Plateau. This value is considered expert judgment, as there was uncertainty associated with the deposition estimate.

12.5 Comparison to Critical Loads for Other Regions

No critical loads have been calculated for Europe, as desert regions do not occur in Europe. We are not aware of critical loads estimated for other continents with desert systems. The European critical level for lichen and bryophyte response to NH_3 (1.0 µg m^{-3} or 1.4 ppb; Cape et al. 2009) appears to be consistent with increases in cover of eutrophic lichens and elevated N in lichen thalli observed in the Hells Canyon National Recreation Area in the Columbia Plateau, where annual average NH_3 was 1.4 to 4.7 ppb (Geiser et al. 2008).

12.6 Future Research Directions and Gaps in Data

More research is needed to determine the range of critical loads in the North American Deserts ecoregion. Finer resolution fertilization studies could more closely pinpoint critical loads, as could research along

N deposition gradients. In addition, current research does not encompass the full range of diversity in North American desert ecosystems or flora. Only the far western section of the Sonoran Desert ecosystem downwind of Los Angeles has been studied. This is a region that contains great biological diversity and which is also subject to high rates of increased N deposition around the urban area of Phoenix. In addition, future research should examine the effects of N deposition on ecosystem components with longer generation times, including tree and cactus species. Long-term observations are under way in some of the fertilizer studies cited (Allen et al 2009).

12.6.1 Lichens and biotic crusts

Establishing critical loads is challenging for epiphytic lichens, biotic crusts, and other cryptogamic communities of the North American Deserts compared to other ecoregions, due to slow growth rates, the complex ecology of biotic crusts, and interactions of N deposition with changing climate and soil chemistry. Further research is needed to link accurately measured or modeled estimates of deposition with physiological data for indicator species, threshold N concentrations, or with lichen community responses. Studies that measure physiological responses to fertilization may hold the most promise.

LITERATURE CITED

Allen, E.B.; Rao, L.E.; Steers, R.J.; Bytnerowicz, A.; Fenn, M.E. 2009. **Impacts of atmospheric nitrogen deposition on vegetation and soils in Joshua Tree National Park.** In: Webb, R.H.; Fenstermaker, L.F.; Heaton, J.S.; Hughson, D.L.; McDonald, E.V.; Miller, D.M., eds. The Mojave Desert: Ecosystem processes and sustainability. Las Vegas: University of Nevada Press: 78-100.

Allen, M.F. 2007. **Mycorrhizal fungi: highways for water and nutrients in arid soils.** Vadose Zone. 6: 291-297.

Baez, S.; Fargione, J.; Moore, D.I.; Collins, S.L.; Gosz, J.R. 2007. **Atmospheric nitrogen deposition in the northern Chihuahuan desert: Temporal trends and potential consequences.** Journal of Arid Environments. 68: 640-651.

Barker, D.H.; Vanierm C.; Naumburg, E.; Charlet, T. N.; Nielsen, K.M.; Newingham, B. A.; Smith, S.D. 2006. **Enhanced monsoon precipitation and nitrogen deposition affect leaf traits and photosynthesis differently in spring and summer in the desert shrub *Larrea tridentata*.** New Phytologist. 169: 799-808.

Belnap, J. 1991. **Sensitivity of desert cryptogams to air pollutants: soil crusts and rock lichens.** In: Mangis, D.; Baron, J.; Stolte, K., eds. Acid rain and air pollution in desert park areas. Tech. Rep. NPS/NRAQD/NRTR-91/02. Washington, DC: U.S. Department of the Interior, National Park Service: 112-119.

Belnap, J.; Phillips, S.L.; Flint, S.; Money, J.; Caldwell, M. 2008. **Global change and biological soil crusts: effects of ultraviolet augmentation under altered precipitation regimes and nitrogen additions.** Global Change Biology. 14: 670-686.

Bills, R.J.; Stutz, J.C., 2009. **AMF Associated with indigenous and non-indigenous plants at urban and desert sites in Arizona.** In: AzconAguilar, C.; Barea, J.M.; GianinazziPearson, V.; Gianinazzi, S., eds. Mycorrhizas - Functional processes and ecological impact. Berlin, Germany: Springer-Verlag: 207-220.

Brooks, M.L. 2003. **Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert.** Journal of Applied Ecology. 40: 344-353.

Brooks, M.L.; D'Antonio, C.M.; Richardson, D.M.; Grace, J.B.; Keeley, J.E.; DiTomaso, J.M.; Hobbs, R.J.; Pellant, M.; Pyke, D. 2004. **Effects of invasive alien plants on fire regimes.** BioScience. 54: 677-688.

Brooks, M.L.; Matchett, J.R. 2006. **Spatial and temporal patterns of wildfires in the Mojave**

Desert, 1980-2004. Journal of Arid Environments. 67: 148-164.

Cape, J.N.; van der Eerden, L.J.; Sheppard, L.G.; Leith, I.D.; Sutton, M.A. 2009. **Evidence for changing the critical level for ammonia.** Environmental Pollution. 157: 1033-1037.

CEC (Commission for Environmental Cooperation). 1997. **Ecological regions of North America. Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

Corkidi, L.; Rowland, D.L.; Johnson, N.C.; Allen, E.B. 2002. **Nitrogen fertilization alters the functioning of arbuscular mycorrhizas at two semiarid grasslands.** Plant and Soil. 240: 299-310.

Davidson, D.W.; Bowker, M.; George, D.; Phillips, S.L.; Belnap, J. 2002. **Treatment effects on performance of N-fixing lichens in disturbed soil crusts of the Colorado Plateau.** Ecological Applications. 12(5): 1391-1405.

Egerton-Warburton, L.M.; Johnson, N.C.; Allen, E.B. 2007. **Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands.** Ecological Monographs. 77: 527-544.

Fenn, M.E.; Haeuber, R.; Tonnesen, G.S.; Baron, J.S.; Grossman-Clarke, S.; Hope, D.; Jaffe, D.A.; Copeland, S.; Geiser, L.; Rueth, H.M.; Sickman, J.O. 2003. **Nitrogen emissions, deposition, and monitoring in the western United States.** BioScience. 53: 391-403.

Geiser, L.H.; Ingersoll, A.R.; Bytnerowicz, A.; Copeland, S.A. 2008. **Evidence of enhanced atmospheric ammonicacal nitrogen in Hells Canyon NRA: Impications for natural and cultural resources.** Air and Waste Management Association. 58: 1223-1234.

Gutierrez, J.R.; Whitford, W.G. 1987. **Chihuahuan Desert annuals - importance of water and nitrogen.** Ecology. 68: 2032-2045.

Hall, S.J.; Ahmed, B.; Ortiz, P.; Davies, R.; Sponseller, R.A.; Grimm, N.B. 2009. **Urbanization alters soil microbial functioning in the Sonoran Desert.** Ecosystems. 12: 654-671.

Harper, K.T.; Belnap, J. 2001. **The influence of biological soil crusts on mineral uptake by associated vascular plants.** Journal of Arid Environments. 47: 347-357.

Inouye, R.S. 2006. **Effects of shrub removal and nitrogen addition on soil moisture in sagebrush steppe.** Journal of Arid Environments. 65: 604-618.

Lohse, K.A.; Hope, D.; Sponseller, R.; Allen, J.O.; Grimm, N.B. 2008. **Atmospheric deposition of carbon and nutrients across an and metropolitan area.** Science of the Total Environment. 402: 95-105.

Marsh, J.E.; Nash, T.H. III. 1979. **Lichens in relation to the Four Corners Power Plant in New Mexico.** The Bryologist. 82: 20-28.

McCrackin, M.L.; Harms, T.K.; Grimm, N.B.; Hall, S.J.; Kaye, J.P. 2008. **Responses of soil microorganisms to resource availability in urban, desert soils.** Biogeochemistry. 87: 143-155.

Nash, T.H. III; Gries, C.; Bungartz, F., eds. 2008. **Lichen flora of the greater Sonoran Desert. Volume 3.** Tempe, AZ: Arizona State University. Lichens Unlimited. 567 p.

Nash, T.H. III; Ryan, B.D.; Diederich, P.; Gries, C.; Bungartz, F., eds. 2004. **Lichen flora of the greater Sonoran Desert. Volume 2.** Tempe, AZ: Arizona State University. Lichens Unlimited. 776 p.

Nash, T.H. III; Ryan, B.D.; Gries, C.; Bungartz, F., eds. 2002. **Lichen flora of the Greater Sonoran Desert.**

Volume 1. Tempe, AZ: Arizona State University. Lichens Unlimited. 532 p.

Porter, M.K. 2007. **Regional Modeling of nitrogen, sulfur and mercury atmospheric deposition in the Pacific Northwest.** Pullman, WA: Washington State University. 127 p. M.S. thesis.

Rao, L.E.; Allen, E.B.; Meixner, T. 2010. **Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts.** Ecological Applications. 20: 1320-1335.

Rao, L.E.; Parker, D.R.; Bytnerowicz, A.: Allen, E.B. 2009. **Nitrogen mineralization across an atmospheric nitrogen deposition gradient in southern California deserts.** Journal of Arid Environments. 73: 920-930.

Schwinning, S.; Starr, B.I.; Wojcik, N.J.; Miller, M.E.; Ehleringer, J.E.; Sanford, R.L. 2005. **Effects of nitrogen deposition on an arid grassland in the Colorado plateau cold desert.** Rangeland Ecology and Management. 58: 565-574.

Shen, W.; Wu, J.; Grimm, N.B.; Hope, D. 2008. **Effects of urbanization-induced environmental changes on ecosystem functioning in the Phoenix Metropolitan Region, USA.** Ecosystems. 11: 138-155.

Tonnesen, G.; Wang, Z.; Omary, M.; and Chien, C.J. 2007. **Assessment of nitrogen deposition: Modeling and habitat assessment.** CEC-500-2005-032. Sacramento, CA: California Energy Commission, PIER Energy-Related Environmental Research. Available at http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF (Accessed May 12, 2010).

Whisenant, S.G. 1990. **Changing fire frequencies on Idaho's Snake River plains: ecological and management implications.** In: McArthur, E.D.; Romney, E.M.; Smith, S.D.; Tueller, P.T., comps. Proceedings - symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5-7; Las Vegas, NV. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4-10.

Zhu, W.X.; Hope, D.; Gries, C.; Grimm, N.B. 2006. **Soil characteristics and the accumulation of inorganic nitrogen in an arid urban ecosystem.** Ecosystems. 9: 711-724.

13 MEDITERRANEAN CALIFORNIA

M.E. Fenn, E.B. Allen, L.H. Geiser

13.1 Ecoregion Description

The Mediterranean California ecoregion (CEC 1997; Fig 2.2) encompasses the greater Central Valley, Sierra foothills, and central coast ranges of California south to Mexico and is bounded by the Pacific Ocean, Sierra Nevada Mountains and Mojave Desert. The ecoregion description is adapted from CEC (1997). It is distinguished by its warm, mild Mediterranean climate, chaparral vegetation, agriculturally productive valleys, and a large population (>30 million). The Coast Ranges crest at 600 to 1200 m. The broad, flat, Central Valley is drained by the Sacramento and San Joaquin Rivers into the Sacramento Delta and San Francisco Bay. Rugged Transverse Ranges, peaking at 3506 m, border the Los Angeles basin. Soils are complex, mostly dry, and weakly developed with high calcium (Ca) concentrations. Summers are hot and dry (>18 ºC), winters are mild (>0 ºC) with precipitation from winter Pacific Ocean storms; coastal fog is common May through July. Annual precipitation (200 to 1000 mm) is highly variable and droughts are common. Vegetation is characterized by chaparral, patches of oak woodland, grassland, and some coniferous forest on upper mountain slopes. The chaparral has thickened, hardened foliage resistant to water loss and forms a cover of closely spaced, mostly evergreen shrubs 1 to 4 m tall. Common shrubs include chamise (*Adenostoma fasciculatum*), buckbrush (*Ceanothus cuneatus*), and manzanita (*Arctostaphylos* spp.). Coastal sagebrush (*Artemisia californica*) and summer-deciduous plants that tolerate more xeric conditions are found at lower elevations. A blue oak-California foothills pine (*Quercus douglasii-Pinus sabiniana*) woodland community forms a ring around the Central Valley, which once had extensive grasslands and riparian forests. The southern oak woodland extends into the Transverse and Peninsular Ranges and includes Southern California walnut (*Juglans californica*) and Engelmann oak (*Quercus englemannii*). Mixed-conifer forests (Minnich 1999) occur at a higher elevation than chaparral and include a variety of species mixes depending on elevation and site conditions, but are typically characterized by dense mixed-aged stands composed of coniferous (pine [*Pinus* spp.] and often fir [*Abies* spp.] and incense cedar [*Calocedrus decurrrens*]) and broadleaved species (commonly oaks).

13.2 Coastal Sage Scrub

13.2.1 Ecosystem Description

Coastal sage scrub is a semi-deciduous shrubland that occurs in the Mediterranean-type climate of southern and central coastal California, extending southward to Baja California, Mexico. The United States portion of coastal sage scrub covers some 684,000 ha (CDFFP 2007). Coastal sage scrub is very diverse. Unfortunately, it is subject to extensive human impacts in rapidly developing coastal California. Dominant species throughout the range are coastal sagebrush (*Artemisia californica*), Eastern Mojave buckwheat (*Eriogonum fasciculatum*), sage (*Salvia* spp.), brittlebush (*Encelia* spp.), and other shrub species, with highest shrub diversity occurring in the southern range. The forbs, primarily annual, are especially diverse, with many species of concern under the Endangered Species Act occurring throughout the range of coastal sage scrub in California.

13.2.2 Ecosystem Responses to N Deposition

Ecosystem responses to elevated nitrogen (N) in coastal sage scrub include increases in exotic invasive annual grasses, loss of native shrub and forb cover, reduced diversity of native annual forbs and arbuscular mycorrhizal fungi, and elevated N mineralization. Plants in this low-productivity ecosystem respond quickly to N; thus changes in species abundance are excellent indicators of ecosystem response to N pollution. This is unlike ecosystems with long-lived vegetation, such as forests or chaparral, where initial ecosystem responses to N are measured by changes in biogeocycling or nutrient runoff (Aber et al. 1989, Section 13.3.3).

13.2.3 Range of Ecosystem Responses Observed

Studies along anthropogenic N deposition gradients and in experimental N-fertilized plots have shown alterations in soil N cycling, plant cover and diversity, and arbuscular mycorrhizal fungi. Nitrogen cycling studies include field and laboratory N mineralization measurements that show higher turnover of inorganic N under high N deposition or fertilization (Sirulnik et al. 2007, Vourlitis et al. 2007a, Vourlitis et al. 2007b). Plant cover and diversity studies were done along an N deposition gradient and show threshold losses of native annual forb species of 45 percent (a decrease from 67 to 37 species per site) under 10 kg N ha^{-1} yr^{-1} of modeled and 7.8 kg ha^{-1} yr^{-1} measured N deposition.[15] A study of arbuscular mycorrhizal fungi was made on the same gradient and showed similar threshold losses of mycorrhizal root infection and diversity at many of the same sites showing plant loss under 9 kg N ha^{-1} yr^{-1} of modeled N deposition (Egerton-Warburton and Allen 2000), as described below.

Nitrogen mineralization and nitrification. Several fertilization studies conducted in coastal sage scrub used high levels of N fertilizer, 50 to 60 kg N ha^{-1} yr^{-1} (Allen et al. 1998, Vourlitis et al. 2007a). However, two studies on N mineralization (production of ammonium (NH_4^+) and nitrate (NO_3^-)) along an N deposition gradient in coastal sage scrub showed increased rates of N mineralization in soils receiving 10 compared to 4 kg N ha^{-1} yr^{-1} (Vourlitis et al. 2007b, Vourlitis and Zorba 2007). Another field experiment (Sirulnik et al. 2007) tested the effects of elevated N on net N mineralization and nitrification in coastal sage scrub in sites with modeled (14.7 and 8.7, as modeled by Tonnesen et al. [2007]) and inferential (20.2 vs. 6.6 kg N ha^{-1} yr^{-1}; Table 13.3) N deposition rates. Few changes in N mineralization were observed, but nitrification (production of NO_3^-) was significantly higher in high deposition than control plots on at least one date in all 3 years (Sirulnik et al. 2007). Because the studies by Vourlitis et al. (2007b) and Vourlitis and Zorba (2007) detected changes in soil N dynamics at a lower level of N deposition (10 versus 4 kg N ha^{-1} yr^{-1}) than the study by Sirulnik et al. (2007) (20.2 versus 6.6 kg N ha^{-1} yr^{-1}), the former are used to report the N deposition response threshold for mineralization.

Vegetation cover and species richness. Coastal sage scrub is subject to levels of total N deposition up to 20 kg ha^{-1} yr^{-1}, as estimated by the U.S. Environmental Protection Agency's Community Multiscale Air Quality (CMAQ) model (Tonnesen et al. 2007) in inland Riverside and San Bernardino Counties, an area that has been rapidly converted to exotic annual grassland in the past 30 to 40 years (Allen et al. 1998, Talluto and Suding 2008). The conversion to grassland is likely caused by a combination of elevated N deposition that promotes increased grass biomass and frequent fire that prevents establishment of native shrubs (Allen et al. 1998, Minnich and Dezzani 1998, Talluto and Suding 2008).

Vegetation-type conversion studies in coastal sage scrub have examined patterns of vegetation change, but have not determined the N deposition response threshold. Research in the adjacent North American Deserts ecoregion related N deposition, exotic grass biomass, and fuel for fire to determine the N deposition response threshold (Fenn et al. 2010, Rao et al. 2010, Chapter 12).

A field survey in 2003[15] determined the effects of N on the native and exotic vegetation along a gradient of seven sites that ranged in N deposition from 8.7 to 19 kg N ha^{-1} yr^{-1} (Fenn et al. 2010; Table 13.1). Nitrogen deposition values reported are modeled wet plus dry deposition on a 4-km grid (Tonnesen et al. 2007). In addition, inferential calculations of N deposition are reported for three sites (Table 13.1). The inferential method is used to calculate dry deposition to surfaces (plant canopies and soil) based on atmospheric concentrations of N pollutants, the deposition velocities of each pollutant, surface areas, and other factors (Fenn et al. 2009). Measurements of air quality, soil N, and short-term deposition to leaf surfaces (Padgett et al. 1999) confirm this air pollution gradient. Extractable soil N (NO_3^- plus NH_4^+) ranged from 10 μg g^{-1} at the low end of the N gradient to 38 μg g^{-1} at the high

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Table 13.1—Percent cover and richness (per 3 ha) of plant groups along an N deposition gradient in western Riverside County, California. Sites are arranged from north to south along an urban to rural gradient. Forb species richness in bold shows a rapid drop in richness, suggesting a critical load of 10 kg N ha^{-1} yr^{-1} by the CMAQ model (between 9.0 and 11.1 kg N ha^{-1} yr^{-1}), and 7.8 kg N ha^{-1} yr^{-1} by the inferential method (between 6.6 and 8.9 kg N ha^{-1} yr^{-1}).

Site	Exotic grass % cover	Native forb % cover	Shrub % cover	Native forbs *no. of species per 3 ha*	soil N *µg g^{-1}*	N deposition *kg N ha^{-1} yr^{-1}*	
						CMAQ[a]	Inferential[b]
Jurupa Hills	63.5	4.0	2.2	16	37.7	19.6	
Box Springs	69.2	18.5	2.4	31	32.6	14.7	20.2
Botanic Garden	36.0	25.4	0.2	20	28.9	13.4	
Lake Perris	0.5	26.1	2.8	30	20.3	11.1	
Mott Reserve	6.7	14.3	11.2	**37**	30.6	**11.1**	**8.9**
Lopez Canyon	11.1	19.6	19.3	**67**	9.6	**9.0**	**6.6**
Tucalota Hills	1.5	35.7	35.0	50	10.5	8.7	

[a]N deposition using the CMAQ model is reported as modeled wet plus dry deposition (Tonnesen et al. 2007).

[b]Deposition calculated with the inferential method also includes wet plus dry deposition to vegetation and soil; see footnote 20 on page 161.

end. Percentage cover of exotic grasses was positively correlated with soil N and atmospheric N deposition, while percentage cover of native shrubs and forbs was inversely correlated with N deposition ($P < 0.001$). Native forb richness ranged from 67 to 16 species across the deposition gradient; the rapid drop in native forb richness from 67 to 37 species per site between 9 and 11 kg N ha^{-1} yr^{-1} indicates impacts on plant community richness occur at 10 kg N ha^{-1} yr^{-1}. Chosen sites had not burned in the previous 10 years, and were thus in a similar successional stage. However, the high deposition sites (modeled as 13 to 19 kg N ha^{-1} yr^{-1}) have a history of two or more fires since the 1960s, while the low deposition sites (8 to 11 kg N ha^{-1} yr^{-1}) have burned only once since the 1960s. The two sites with deposition of 11 kg N ha^{-1} yr^{-1} have reduced native cover and richness even without frequent fires, which suggests a direct effect of N on native species, such as increased competition by nitrophilous exotic grasses (Yoshida and Allen 2004).

Arbuscular mycorrhizal fungi. Both mycorrhizal root infection and mycorrhizal spore species density decreased greatly between 8.7 and 9.6 kg N ha^{-1} yr^{-1} of modeled N deposition (Tonnesen et al. 2007) along the same N deposition gradient reported above in coastal sage scrub vegetation in southern California (Egerton-Warburton and Allen 2000, Fenn et al. 2010). The decrease in mycorrhizal fungi occurred between inferential values of 6.6 and 8.9 kg N ha^{-1} yr^{-1}; inferential values were not available for all sites (Table 13.2). Mycorrhizal root infection indicates the extent to which plants may depend on mycorrhizae for their nutrient uptake, and is typically reduced in extent by elevated soil nutrients, while spore density is an indication of the amount of carbon flowing from the plant to the fungus and indicates the strength of the mutualistic relationship.

13.2.4 Estimated Critical Loads

A summary of critical loads for ecosystem responses in coastal sage scrub is given in Table 13.3. Given the rapid decrease in native species cover and forb richness between 9 and 11 kg N ha^{-1} yr^{-1}, 10 kg N ha^{-1} yr^{-1} may be estimated as the critical load for loss of native diversity and cover in coastal sage scrub based on modeled N deposition, while 7.8 kg N ha^{-1} yr^{-1} may be calculated using inferential data (Table 13.1). Percent colonization and spore counts of arbuscular mycorrhizal fungi in coastal sage scrub decline steeply at deposition levels of 9.2 kg N ha^{-1} yr^{-1} using the modeled data and 7.8 kg N ha^{-1} yr^{-1} using inferential data at many of the same sites. A critical load for loss of arbuscular mycorrhizal activity is estimated at 9.2 kg

Table 13.2—Spore counts and percent root infection of arbuscular mycorrhizal fungi along an N deposition gradient in western Riverside County, California. Sites are arranged from north to south along an urban to rural gradient (data from Egerton-Warburton and Allen 2000). Values in bold show a change in spore density and root infection and are interpreted to represent a critical load.

Site	Spores/g soil	% root infection	soil N $\mu g\ g^{-1}$	N deposition $kg\ N\ ha^{-1}\ yr^{-1}$	
				CMAQ[a]	Inferential[b]
Jurupa Hills	23	19	86.2	19.6	
Waterman Rd.	54	18	15.6	16.9	
Box Springs Mt.	66	17	26.4	14.7	20.2
Mockingbird Cyn	74	24	56.8	12.5	
Lake Mathews	70	23	39.5	**11.1**	
Motte Reserve	80	27	26.1	**11.1**	**8.9**
Hemet	**78**	**22**	12.8	**9.6**	
Lake Skinner	**103**	**39**	7.5	**8.7**	**6.6**
Santa Margarita	105	45	9.7	8.7	

[a] N deposition using the CMAQ model is reported as modeled wet plus dry deposition (Tonnesen et al. 2007).

[b] Deposition calculated with the inferential method also includes wet plus dry deposition to vegetation and soil; see footnote 20 on page 161.

N ha^{-1} yr^{-1} using modeled data, and 7.8 kg N ha^{-1} yr^{-1} using the inferential method (inferential data are not available for all modeled areas). The addition of more sample sites to the analysis along the gradient allows more precise values of critical loads to be estimated, as in the case of modeled N for mycorrhizal fungi. One challenge in setting critical loads for this system is that the lowest modeled N deposition is 8.7 kg N ha^{-1} yr^{-1}, and the lowest value for the inferential method is 6.6 kg N ha^{-1} yr^{-1}, values that are already significantly elevated above pre-industrial background deposition. Therefore, the critical load as defined from our study should be considered an upper limit. The threshold might actually be lower than these values. The critical load, with the limitations described above, is considered fairly reliable.

13.3 Chaparral and Oak Woodlands and the Central Valley

13.3.1 Ecosystem Description

Chaparral and oak woodland ecosystems are widespread over the Mediterranean California ecoregion. In this section, the term chaparral refers specifically to California chaparral, an ecosystem type composed of evergreen shrublands occupying most of the hills and lower mountain slopes of California. Chaparral has no commercial value, yet it forms an important cover that helps maintain the integrity of the watershed. Chaparral encompasses about 2.5 million ha, or 6.1 percent of the state (Keeley and Davis 2007). Shrubs common to chaparral include manzanita, Ceanothus (California lilac; *Ceanothus* spp.), buckbrush, chamise, and toyon (*Heteromeles arbutifolia*). Hardwood woodlands include several species of deciduous and live oaks (*Quercus* spp.), box elder (*Acer negundo*) and big leaf maple (*Acer macrophyllum*), California buckeye (*Aesculus californica*), California ash (*Fraxinus latifolia*), Oregon ash (*Fraxinus latifolia*), southern California walnut, and Fremont cottonwood (*Populus fremontii*). Occasional conifers are California foothill pine and Douglas-fir (*Pseudotsuga menziesii*). The Central Valley, now largely converted to agricultural production, was chiefly a grassland and forbland ecosystem, with riparian belts of hardwood trees (CEC 1997) and expansive tule (*Schoenoplectus acutus*) sedge wetlands along rivers and streams (Munz 1973).

13.3.2 Ecosystem Responses to N Deposition

Chaparral ecosystem responses to N deposition include elevated NO_3^- leaching in streamwater and nitric oxide (NO) emissions from soil, increased direct transport

Table 13.3—Empirical critical loads of nutrient N for coastal sage scrub ecosystems of the Mediterranean California ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical load for N deposition[a] *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Coastal sage scrub, W. Riverside Co.	7.8-10	#	Increase in exotic grass cover, decrease in native richness and cover	See Table 13.1	Allen unpublished[b]; Fenn et al. 2010
Coastal sage scrub, W. Riverside Co.	7.8-9.2	#	Decrease in arbuscular-mycorrhizal spore density, richness, and percent root infection	Table 13.2	Egerton-Warburton and Allen 2000; Fenn et al. 2010
Coastal sage scrub, W. Riverside Co.	10	#	Increase in N mineralization rate	Comparison of sites with 4 and 10 kg N ha^{-1} yr^{-1}deposition	Vourlitis and Zorba 2007, Vourlitis et al. 2007b

[a] N deposition is modeled as total wet plus dry N (Tonnesen et al. 2007)

[b] See footnote 15 on page 144

of atmospheric NO_3^- from polluted catchments, N enrichment of soil and vegetation, increased N cycling rates in soil, and decreased diversity, species richness, and productivity of arbuscular mycorrhizal communities. In chaparral and oak woodlands, lichen communities have been severely altered by N deposition. Elevated NO_3^- leaching often follows high atmospheric N inputs to the catchment due to limited biological assimilation or retention. The N response of chaparral ecosystems is not known to be confounded by co-occurring ozone (O_3) effects as it is in forested areas (see section 13.4). Chaparral vegetation is highly O_3 tolerant (Stolte 1982, Temple 1999), and even if some species were O_3 sensitive, California chaparral vegetation is quiescent in summer, when O_3 levels are high.

Factors predisposing both California chaparral and forests to N loss are the active nitrifying characteristics of the soils (Fenn et al. 1998, Fenn et al. 1993, Riggan et al. 1985, Vourlitis and Zorba 2007). Chaparral soils exposed to chronic N deposition exhibit elevated N cycling, as evidenced by lower carbon:nitrogen (C:N) ratios, higher N mineralization rates, and increased $\delta^{15}N$ (Vourlitis and Zorba 2007). The high nitrification capacity of these soils is evidenced by virtually complete net nitrification of mineralized N. Although N responses at low to moderate N input levels have not been evaluated in grasslands in the Central Valley, N deposition in serpentine grasslands near San Jose, California, has been shown to cause the displacement of native herbaceous species by exotic invasive annual grasses (Weiss 1999).

13.3.3 Range of Ecosystem Responses Observed

Data on N deposition effects on chaparral are primarily available from the south coast (Los Angeles) air basin and a watershed study in Sequoia National Park in central California. Although short-term N addition studies have been done, little is known about the long-term effects of N enrichment on vegetation.

Nitrate leaching and nitrification. Because of the virtually complete nitrification of mineralized N in chaparral and forested soils in southern California, approximately 95 percent of the inorganic N in soil occurs in the form of NO_3^- (Fenn et al. 1998, Fenn et al. 1993, Vourlitis et al. 2007b). Nitrification in chaparral and coastal sage scrub soils increases in response to nitrogen deposition (Vourlitis et al. 2007b). Data relating atmospheric deposition and streamwater NO_3^- in chaparral watersheds are available for three areas of California: in several catchments in the San Dimas Experimental Forest, located in the San Gabriel Mountains 45 km northeast of Los Angeles; eight streams in the Devil Canyon watershed, in the western San Bernardino Mountains; and Chamise Creek, a catchment located along the southwestern slope of the Sierra Nevada Mountains within Sequoia and Kings Canyon National Parks (Fenn et al. 2003b). In addition, 56 chaparral streams were sampled for NO_3^- concentrations in a regional survey in March 1982 across the greater Los Angeles Basin and in northern San Diego County over a wide range of N deposition exposures, demonstrating the relationship between N deposition and NO_3^- concentrations in streamwater in these ecosystems (Riggan et al. 1985).

Over 20 years of atmospheric deposition and streamwater NO_3^- data are available from San Dimas Experimental Forest watersheds (Meixner et al. 2006; Riggan et al. 1985, 1994). Atmospheric and streamwater NO_3^- data over shorter periods are available from Devil Canyon (Fenn and Poth 1999, Meixner and Fenn 2004). The Chamise Creek watershed was sampled continuously from 1983 to 1998 (Fenn et al. 2003a). In all three of these study areas, the catchments can be considered to be at Stage 2 of Stoddard's watershed N saturation model (Stoddard 1994) based on the seasonal NO_3^- export patterns and peak NO_3^- concentrations. More information on N saturation can be found in Chapter 1.

Nitrate concentrations in streamwater from chaparral watersheds in California are the highest reported from North America; peak concentrations greater than 200 to 300 µeq L^{-1} are common in catchments receiving elevated N deposition while peaks as high as 700 µeq L^{-1} have been reported (Fenn et al. 2003a, 2003b; Fenn and Poth 1999; Riggan et al. 1985, 1994). On the other hand, total NO_3^- export is often less than in N saturated mesic forests, presumably because of the high evapotranspiration fluxes relative to annual precipitation inputs. Nitrogen export in N-saturated chaparral catchments typically ranges from 1 to 10 kg ha^{-1} yr^{-1}, varying greatly from year to year because of highly variable precipitation (Fenn and Poth 1999, Riggan et al. 1985).

The proportion of NO_3^- exported from chaparral catchments in the Transverse Ranges of southern California that was direct throughput of atmospheric NO_3^- (e.g., without biological assimilation or retention within the watersheds) was quantified using a state-of-the-art isotopic method developed at the University of California in San Diego ($\Delta^{17}O$ as a tracer for atmospheric NO_3^-) (Michalski et al. 2004). During peak flow following storm events, about 40 percent of the stream NO_3^- was found to originate from atmospheric sources that are transported through the watershed without any prior biological assimilation. All soil and aquatic NO_3^- samples in the study had positive $\Delta^{17}O$ values, unambiguously showing that every sample of soil and water (including groundwater) collected exhibited a signal of direct atmospheric NO_3^- inputs (Michalski et al. 2004), thus highlighting the N-saturated condition of these catchments. Nonetheless, on average, only about 10 percent of total N deposition is exported in streamwater from N-saturated catchments in the San Dimas Experimental Forest and in Devil Canyon (Fenn and Poth 1999, Meixner and Fenn 2004, Meixner et al. 2006, Riggan et al. 1985).

Trace gas losses of N. Nitrogen-saturated chaparral ecosystems also exhibit trace N gas emissions, primarily as NO, but nitrous oxide (N_2O) emissions can also be quantitatively important during the relatively short periods when soils are sufficiently wetted (Anderson and Poth 1989). In more anaerobic zones of the groundwater system and near riparian zones, losses of reduced N gases are also expected to be important in N saturated chaparral catchments. Fluxes of NO from soil over a 6-month period from July to December 1986 were estimated to be 1 kg N ha^{-1} in an unburned site and 3 kg N ha^{-1} in a burned chaparral site in the San Dimas Experimental Forest (Anderson and Poth 1989). Data are not available on trace gas losses from the near-riparian zone, or from phreatic zones in chaparral or forested watersheds in California with elevated N deposition. However, very high levels of dissolved N_2O were found in groundwater samples collected from a fault line (Fenn and Poth 1999) within the chaparral zone of the N-saturated Devil Canyon watershed.[16] This pattern suggests that large amounts of excess N may be lost from these catchments via degassing of dissolved N trace gases (Bowden and Bormann 1986).

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Fire effects on N losses. Ecosystem responses to chronic N deposition must be considered within the context of regular fire occurrence in chaparral. Stand-replacing fire return intervals in these ecosystems are generally on the order of 40 to 60 years (Minnich and Bahre 1995). Over time, N from atmospheric deposition accumulates in soil, organic matter, necromass, and biomass. During a burn, much of the N in the aboveground N-enriched vegetation and detritus is released to the atmosphere or deposited on the soil surface, where it is mobilized via nitrification, N trace gas emissions, NO_3^- leaching, and erosion, thus resulting in large pulses of N losses (Anderson and Poth 1989, Riggan et al. 1994). Such losses are of much shorter duration and are more muted in burned chaparral catchments not exposed to elevated N deposition (Riggan et al. 1985, 1994). However, fire removes only a minor component of the large N pools in the mineral soil. As a result, a large pool of N remains in the ecosystem even after a stand-replacing fire. This, combined with continuing atmospheric inputs, results in continued long-term elevated NO_3^- leaching in surface runoff and groundwater (Meixner et al. 2006). Thus, fire alone does not appear to be an effective tool for mitigating N saturation, although simulation studies suggest that N losses from higher elevation forested regions can be mitigated if N deposition is decreased and prescribed fire is applied periodically (Gimeno et al. 2009).

Soil acidification. The pH of chaparral soils measured at more than 700 San Gabriel Mountain sites in the 1970s was compared to measurements taken at more than 300 sites in the 1990s. Surface soil pH values decreased considerably over this period (Wood et al. 1992). Values of pH in the 1970s typically ranged from 6.0 to 7.4 compared to a typical range of 4.6 to 5.6 in the 1990s.[17]

Arbuscular mycorrhizal fungi. In a retrospective study from the San Dimas Experimental Forest, historical trends in biodiversity of the arbuscular mycorrhizal community were evaluated in pure stands of Eastern Mojave buckwheat and chamise established in the 1940s on a homogenized fine sandy loam soil (Egerton-Warburton et al. 2001). This analysis was done by evaluating the diversity of arbuscular mycorrhizal fungal spores in archived soils collected periodically from 1937 to 1999, and from examinations of mycorrhizae on root samples in 1999. It was observed that N enrichment of the soils increased over the same period in which mycorrhizal communities experienced dramatic changes (Egerton-Warburton et al. 2001). Diversity, species richness, and productivity of the arbuscular mycorrhizal community had deteriorated severely by 1969. Three previously common mycorrhizal genera disappeared from the mycorrhizal spore community in soil, and one large-spored genus (*Gigasopora*) was no longer found in the rhizosphere soil. Nitrogen enrichment also enhanced the proliferation of potentially less mutualistic species of small-spored *Glomus*, which may have implications for plant community succession in the face of chronic N deposition (Egerton-Warburton et al. 2001). Throughfall N fluxes in the San Dimas Experimental Forest in the early 1980s were 23 kg N ha^{-1} yr^{-1} (Riggan et al. 1985) and total deposition was estimated at 35 kg N ha^{-1} yr^{-1} (Meixner et al. 2006).

Lichen responses. About half the epiphytic lichen species known to occur during the late 1800s and early 1900s on coast live oak throughout the chaparral and oak vegetation zones of the Los Angeles basin (Hasse 1913) have subsequently disappeared (Ross 1982). This dramatic reduction in species richness was initially attributed solely to oxidizing pollutants, chiefly O_3 (Nash and Sigal 1999, Ross and Nash 1983), but recent research provides unequivocal evidence for an N deposition effect (Riddell et al. 2008). In the Los Angeles air basin, throughfall N deposition in forests downwind of the urban areas can reach 25 to 70 kg ha^{-1} yr^{-1} (Fenn et al. 2008). This deposition includes nitric acid (HNO_3), a strong gas-phase acid which exhibits diurnal patterns paralleling O_3 concentrations. In the mountains downwind of Los Angeles, 24-hr means of up to 27.3 ppb have been recorded, whereas remote location means have been ≤0.1 ppb (Bytnerowicz and Fenn 1996). Unlike O_3, once HNO_3 is produced, it rapidly deposits to surfaces. Menzies' cartilage lichen (*Ramalina menziesii* Tayl.*),* a dominant epiphyte of oaks throughout the Coast Ranges of California and

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[17] Wood, H.B. Unpublished data on file with Mark Fenn, Research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

historically common in the Los Angeles basin (Hasse 1913) was treated with nitric acid at 7 to 25, and 19.9 to 25 μg m^{-3} during month-long fumigations to mimic diurnal patterns in Los Angeles (Riddell et al. 2008). All specimens in both treatments experienced marked declines in chlorophyll content, carbon exchange capacity, and membrane integrity compared to controls. In addition to oxidant and acidic air pollutants, Riddell et al. (2008) also recognized habitat loss, lower humidity due to urbanization, and increased fire incidence as factors in the disappearance of Menzies' cartilage and other lichens from the Los Angeles basin.

Epiphytic lichen communities in more northerly parts of the ecoregion are also showing a clear response to N. The Greater Central Valley, comprising the Central Valley proper and the surrounding chaparral- and oak woodland-dominated central Coast Ranges and Sierra foothills, encompasses many urban centers and is among the most agriculturally intensive regions of the United States. Using a nonmetric multidimensional scaling procedure and vector overlays of environmental variables, Jovan and McCune (2005) ordinated and scored lichen communities surveyed between 1998 and 2001 at 118 sites in the Greater Central Valley along an NH_3 emissions gradient (Fig. 13.1). There were strong correlations between NH_3 and percentages of eutrophic lichen richness and abundance. In addition, total N deposition and other N species, including HNO_3, NO_3^-, and NO_2, were all positively correlated with lichen scores, suggesting that multiple N-containing compounds, not just NH_3, are impacting lichens in the Greater Central Valley (Jovan 2008). Eutrophic lichens benefited from increasing N availability, comprising >50 percent of total abundance in lichen communities at air scores <0.0 (Fig. 13.2). Higher air scores indicate better air quality. Eutroph abundance at sites with the best air quality ranged from 20 to 50 percent. Therefore an air score of 0.0 may be a reasonable lichen response threshold. CMAQ data were not available to the authors at the time of publication, but overlay of a 4-km grid of modeled 2002 CMAQ data (Tonnesen et al. 2007) over lichen survey site coordinates provides a more complete understanding of N deposition at the Jovan and McCune (2005) sites. Of the 53 lichen survey sites in the dataset with clean air scores (>0.0), only three occurred in grid cells where CMAQ predicted >5.5 kg ha^{-1} yr^{-1} total N deposition.

13.3.4 Estimated Critical Loads

In chaparral catchments exhibiting the symptoms of N excess discussed above, N input values range from 5 to 33 kg ha^{-1} yr^{-1} as throughfall (Meixner and Fenn 2004), except for the case of the chaparral/oak woodland lichen response studies in the greater Central Valley, where N deposition was simulated with the CMAQ model (Tonnesen et al. 2007). In the seven catchments sampled in Devil Canyon, throughfall N deposition ranged from 14 to 33 kg ha^{-1} yr^{-1}. Because all seven sites had elevated NO_3^- concentrations in stream water, the lowest deposition value can be considered to be at or above the critical load. Chamise Creek in Sequoia National Park is an N-saturated site based on elevated NO_3^- leaching (Fenn et al. 2003a, 2003b); throughfall N deposition[18] was 10 kg ha^{-1} yr^{-1}. Lichen survey sites with clean air scores suggest a preliminary critical load of 5.5 kg N ha^{-1} yr^{-1}. In a test of the broader applicability of a model developed from western Oregon and Washington lichen community data to temperate forests in general, Geiser et al. (2010), essentially replicated this estimate. For the Greater Central Valley dataset (Jovan and McCune 2005) and response threshold (50 percent eutrophs), Geiser et al. (2010) calculated a critical load of 3 to 6 kg N ha^{-1} yr^{-1} for the study area, increasing with mean annual precipitation from 17 to156 cm. An N critical load for serpentine grassland invasion by exotic annual grasses was determined along a roadside deposition gradient at a site downwind of San Jose, California, and west of the Central Valley. The critical load of 6 kg N ha^{-1} yr^{-1} was based on the N deposition level at the point where the grass invasion was visibly diminished (Fenn et al. 2010, Weiss 1999). Considering the deposition and response data from all the ecosystem components considered here, we suggest a deposition range for the critical load of 3.1 to 14 kg N ha^{-1} yr^{-1}. All the reported responses (see Table 13.4) occur within this range.

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[18] Homyak, P.M. 2009. Personal communication. Graduate research associate, Department of Environmental Sciences, University of California, Riverside, CA 92521.

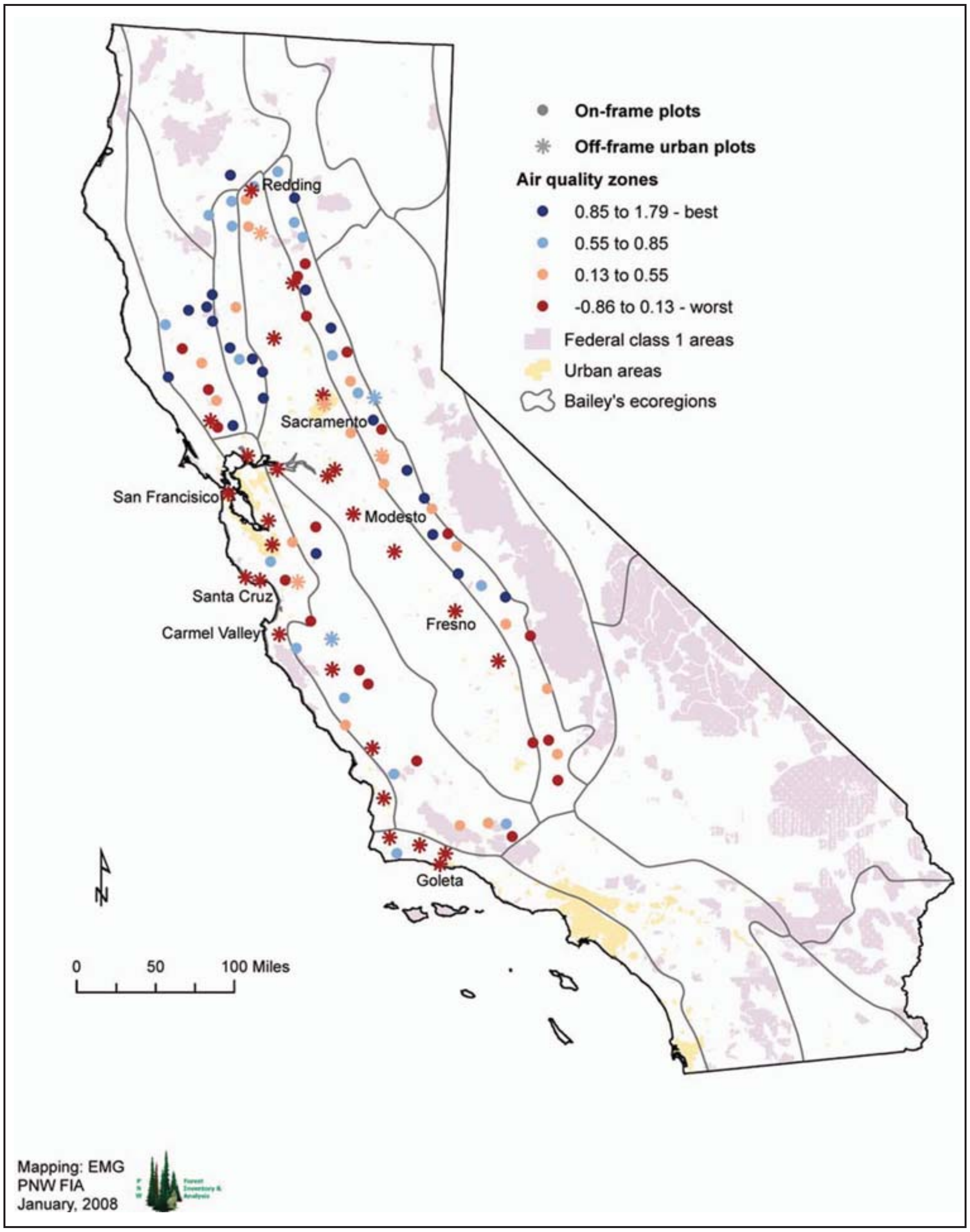

Figure 13.1—Air quality scores for the greater Central Valley divided into air quality zones. Reprinted from Jovan 2008.

In the San Dimas Experimental Forest, with a reported throughfall N deposition of 23 kg ha^{-1} yr^{-1}, the critical load is exceeded for NO_3^- leaching, changes in mycorrhizal spore community changes, and elevated NO emissions from soil. The critical load for NO_3^- leaching is known to be much lower than the deposition at San Dimas as discussed above, but the critical load for mycorrhizal community changes and for N trace gas emissions cannot be determined because we only have data from San Dimas. Likewise, the critical load for increased nitrification has not been established due to insufficient corresponding deposition data at sites where nitrification has been measured. Thus, the critical load for these responses are not included in the critical loads tables.

13.4 Mixed-conifer Forest

13.4.1 Ecosystem Description

Air pollution effects studies in California forests have focused largely on the mixed-conifer forests found at mid-elevation sites in the Transverse Ranges (particularly the San Bernardino Mountains) in the Los Angeles air basin and in the southwestern Sierra Nevada (Fenn et al. 2003b). Because of the high sensitivity to

Table 13.4—Empirical critical loads of nutrient N for chaparral and Central Valley ecosystems of the Mediterranean California ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical load for N deposition[a] *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Sacramento & San Joaquin Valleys, Coast Ranges & Sierra Foothills	3-6	#	Change in lichen communities	Shift to eutroph dominance, precipitation range of 17-156 cm.	Geiser et al. 2010
San Francisco Peninsula, near San Jose, California	6	##	Annual grass invasion, replacing native herbs in a serpentine grassland	Critical load based on a local roadside gradient; Serpentine grassland site is actually west of the Central Valley.	Weiss 1999, Fenn et al. 2010
Sacramento & San Joaquin Valleys, Coast Ranges & Sierra Foothills	5.5	#	Changes in lichen communities	Eutrophic lichens increased at expense of species adapted to lower N availability.	Fenn et al. 2010, Jovan and McCune 2005, Jovan 2008, this chapter
Chamise Creek, Sequoia NP	10	#	Streamwater [NO_3^-] > 14 µM	This NO_3 threshold indicates the beginning of N saturation.	Fenn et al. 2003b, Fenn et al. 2003a, Fenn et al. 2010
Devil Canyon, San Bernardino Mountains	14	#	Streamwater [NO_3^-] > 14 µM	Estimated N deposition in throughfall in the 7 catchments was 14-33, so critical load is lowest value.	Meixner and Fenn, 2004, Fenn and Poth 1999, Fenn et al. 2010
Los Angeles Basin	Atmospheric concentrations of 7-25 µg HNO_3 m^{-3}	#	Loss of lichen species richness and harm to physiological processes	About half of the 1900 lichen flora in the Los Angeles basin is currently extirpated, attributed to O_3 and N pollutants.	Riddell et al. 2008; Hasse 1913; Ross, 1982; Sigal and Nash 1983

[a] N deposition is reported as throughfall (Fenn and Poth 2004, Fenn et al. 2008) except for the serpentine grassland study and lichen studies in chaparral. In the Los Angeles Basin the range of atmospheric concentrations shown for HNO_3 indicate the concentrations at which lichens are impacted. For changes in lichen communities in the Central California valleys, coast ranges and Sierra foothills, N deposition values for determining the critical loads were simulated using the CMAQ model (Tonnesen et al. 2007). Deposition data for Chamise Creek, Sequoia National Park provided by P.M. Homyak; see footnote 18 on page 150

O_3 of ponderosa pine (*Pinus ponderosa*) and the closely related Jeffrey pine (*Pinus jeffreyi*), most of the research has been carried out in sites with a predominant component of these species. Associated tree species that co-occur in varying mixes with ponderosa and Jeffrey pine include white fir (*Abies concolor*), sugar pine, (*Pinus lambertiana*), incense-cedar, and California black oak (*Quercus kelloggii*). In parts of the southwest Sierra Nevada, Douglas-fir and giant sequoia (*Sequoiadendron giganteum*) are also found (Minnich 1999, Peterson and Arbaugh 1992). Shrub understory in mixed-conifer forest is mostly open or absent (cover <20 percent), depending on altitude and climatic gradients. Bracken fern (*Pteridium aquilinum* var. *pubescens*) is common in more mesic sites. See Minnich (1999) for a more complete description of common understory species in mixed-conifer forests.

13.4.2 Ecosystem Responses to N Deposition

Research on air pollution effects in mixed-conifer forests began in the 1960s after the initial discovery in the 1950s of unusual symptoms in ponderosa pine that were later confirmed to be caused by O_3. Studies on N deposition effects in forests began in the San Bernardino Mountains (Fenn 1991) in some of the original O_3 study plots established in the 1970s (Arbaugh et al. 2003). Ecosystem responses to N deposition include NO_3^- leaching, trace gas losses of N, soil acidification, lichen community change, altered forest nutrient cycling, and loss of understory diversity. Because of the co-occurrence of O_3 and N deposition in the mixed-conifer forest of California, the ecological effects of N deposition cannot be evaluated in isolation from the significant impacts of O_3 on nutrient cycling and plant growth, development, community succession, and phenology. The combined ecological effects of N and O_3 are dramatic in areas of high pollution exposure (Fenn et al. 2003b, Grulke et al. 2009).

13.4.3 Range of Ecosystem Responses Observed

Most characteristics which predispose an ecosystem to NO_3^- leaching (e.g., climatic conditions, actively nitrifying soils) discussed for chaparral ecosystems in section 13.3 also apply to forested catchments, as many mixed-conifer catchments grade into chaparral vegetation at lower elevations. Indeed, 4 of 11 catchment streams monitored to determine the relationship between N deposition and NO_3^- leaching in the mixed-conifer forest were accessible for sampling only at the lower elevation chaparral portion of the catchment (Fenn et al. 2008). In both chaparral and mixed-conifer forests, a key factor predisposing these ecosystems to N loss with chronic N deposition is the temporal asynchrony between the period of greatest biotic demand (spring and early summer) and the winter when approximately 85 percent of the precipitation and the greatest surface runoff occurs (Fenn and Poth 1999).

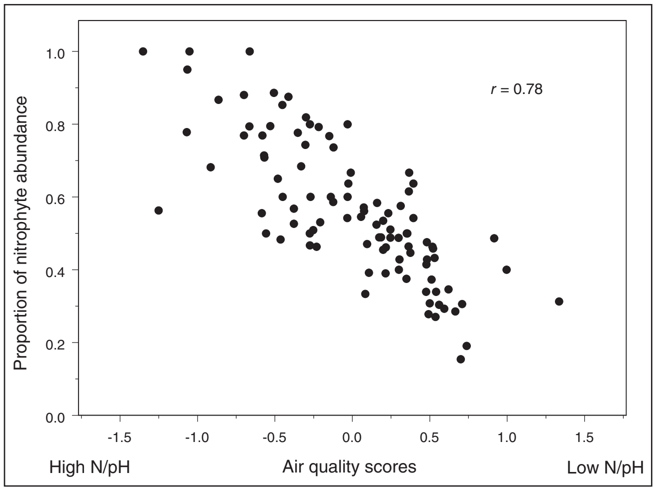

Figure 13.2—The relationship between air quality score and the proportion of nitrophyte (eutroph) abundance in California's greater Central Valley. Reprinted from Jovan 2008.

Nitrate leaching. A threshold streamwater NO_3^- concentration for a site experiencing relatively low atmospheric N deposition (14 μM) was empirically determined to identify watersheds that are exporting elevated levels of NO_3^- (see Fenn et al. 2008, 2010 for more details on these methods and rationale). Based on regression analysis of throughfall N deposition versus streamwater NO_3^- concentrations, the N deposition level at which NO_3^- leaching exceeds the "unpolluted" -site threshold is approximately 17 kg ha^{-1} yr^{-1} (Fenn et al. 2008). This level of N deposition has been measured in the regions of the Transverse Ranges in southern California most exposed to air pollution and along the western edge of the Sierra Nevada (Breiner et al. 2007; Fenn et al. 2008, 2010).

Although many factors affect N loss rates, the available data suggest that within a given catchment, N deposition fluxes to the higher elevation forested portions of catchments are greater than to the lower chaparral and scrub vegetation portions (Meixner and Fenn 2004). This is presumably because of the much greater surface area of forested stands, which are efficient collectors of dry and cloud water deposition, and because of greater occurrence of fog and cloud deposition at the upper levels of these catchments (Fenn et al. 2000, Meixner and Fenn 2004). However, the greater input to the forested portion of the catchment is likely counterbalanced, to some degree, by greater biotic N demand of the forest. Soil leachate and streams in the mixed-conifer zone are known to export high levels of unassimilated NO_3^- (Michalski et al. 2004). In catchments covered by mixed-conifer forests at higher elevations, NO_3^- concentrations in streamwater decrease within the lower elevation chaparral zone because of in-stream and near-stream N uptake and consumptive processes along the descending course of the stream (Meixner and Fenn 2004).

Trace gas losses of N. Fluxes of trace gas emissions from soil of N-saturated sites in the mixed-conifer forest appear to be very similar to those from N-saturated chaparral sites. Annual fluxes of NO in high N deposition chaparral and forested sites generally range from 2 to 3 kg ha^{-1} yr^{-1} (Anderson and Poth 1989, Fenn and Poth 2001), although there is considerable uncertainty because of temporal and spatial heterogeneity in flux measurements. Emissions from soil are higher after a burn and after soil wetting. In short-term measurements, fluxes of NO and N_2O increase markedly after soil wet-up, particularly in N saturated sites (Anderson and Poth 1989, Fenn et al. 1996). Annual flux rates are probably greater in high precipitation years than the estimates given above.

Soil acidification. Because of the Mediterranean climate and typical high base saturation of soils in semi-arid forests, the possible soil acidification effects of N deposition in California have not received nearly as much attention as the effects of N as a nutrient. However, soils have acidified at an accelerated rate in high deposition sites. At Camp Paivika in the western San Bernardino mountains, soil pH values in the top 25 cm of soil ranged from 4.8 to 5.6 in the early 1970s, compared to recent values ranging from 3.1 to 4.3[19] (Fenn and Poth 1996, Wood et al. 2007). The unusually low pH values and rapid acidification at Camp Paivika are due to high throughfall N deposition (70 kg ha^{-1} yr^{-1}) and underlying stone lines at 40 to 60 cm and 130 to 170 cm depths which control the spatial and temporal flow of soil percolates containing high concentrations of NO_3^-. At another site with the stone lines but much lower throughfall N deposition (6 kg ha^{-1} yr^{-1}), soil acidity was relatively constant (pH 5.1 in 1975; pH 5.0 in 2004) during the last 30 years (Wood et al. 2007).

Soil pH is highly correlated ($r^2 = 0.99$) with throughfall N deposition in the San Bernardino Mountains (Breiner et al. 2007). Based on this regression, soil pH is estimated to be 4.8 when deposition is 17 kg ha^{-1} yr^{-1}. Soil base saturation is also much lower at high N deposition sites (30 to 80 percent) compared to low deposition sites (85 to 100 percent) in the San Bernardino Mountains[19] (Fenn et al. 1996). The low pH and lower base saturation of the mineral soil does not inhibit active nitrification, but a recent study suggests that nitrification is dominated by heterotrophic nitrifiers (Jordan et al. 2005).

Ectomycorrhizal fungi. Fungal communities of ectomycorrhizae were studied from November 2005 to June 2007 at a high (71 kg N ha^{-1} yr^{-1}; Camp Paivika) and low (7 kg N ha^{-1} yr^{-1}; Camp Osceola) deposition site in the San Bernardino Mountains east of Los Angeles (Sirajuddin 2009). The effects of added N (150 kg ha^{-1} yr^{-1}) within each of the plots over a 9-year period were also investigated.

Basidiomycetes tended to decline with both N fertilization and at the high N deposition plot. *Russula* (five species) and *Rhizopogon* (three species) were present at Camp Osceola, but were lost with N fertilization and were not found at Camp Paivika. *Cortinarius* spp.

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[19] Wood, Y.A. Unpublished data on file with Mark Fenn, Research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

also decreased with N fertilization. The exceptional basidiomycete was a *Lactarius* sp., which increased in N fertilized plots at both locations. In general, ascomycetes increased with N availability; *Cenococcum geophilum* in particular increased quite dramatically. *Wilcoxinia rehmii* was the exception, in that this ascomycete declined with N enrichment, both via deposition and fertilization. In summary, N deposition and N fertilization shifted the ectomycorrhizal fungal communities in a similar direction, toward ascomycetes. Basidiomycetes generally declined and some key species disappeared with N fertilization or deposition (Sirajuddin 2009).

Lichen responses. Lichen-based responses to N deposition for the mixed-conifer zone of the Sierra Nevada (Northwest Forested Mountains ecoregion) likely have application to the mixed-conifer zone of the Mediterranean California ecoregion, especially in the southwest Sierras and Transverse Ranges, where there was a historic species overlap. The Sierra study (Fenn et al. 2008) utilized a threshold N concentration in the wolf lichen (*Letharia vulpina* (L.) Hue), an epiphyte on tree trunks and branches, from a low N deposition site. As the threshold is exceeded with increasing N deposition, the abundance of ecologically important oligotrophic species begins to decline, shifting lichen community composition from oligotroph-dominated to mesotroph- and eutroph-dominated (Fenn et al. 2008). Oligotrophs are sensitive to even small increases in N; mesotrophs tolerate moderate inputs; eutrophs are fast growing, ‘weedy’ species of small ecological importance that thrive under conditions of high N availability. Lichen surveys in the Sierra Nevada mixed-conifer zone were co-located with or near throughfall deposition monitoring sites. Similar studies can no longer be done in the San Bernardino Mountains because most air pollution sensitive species have long since disappeared (Nash and Sigal 1999, Sigal and Nash 1983). In relatively low N deposition sites in the Sierras (<3.1 kg N ha^{-1} yr^{-1}), oligotrophic lichen species still predominate. At a throughfall N deposition level of 5.2 kg N ha^{-1} yr^{-1}, the lichen community completely shifts from oligotroph to mesotroph/eutroph dominance. Oligotrophs are extirpated at 10.2 kg N ha^{-1} yr^{-1} (Fenn et al. 2008). Conservation of oligotrophic species is important because they make integral contributions to food webs, nesting material and insect habitat, and nutrient and hydrologic cycles (McCune et al. 2007).

Forest sustainability. Nitrogen deposition, in concert with O_3 injury effects, is contributing to a decrease in the sustainability of mixed-conifer forests in the San Bernardino Mountains. Nitrogen deposition increases aboveground growth of coniferous and deciduous species of the mixed-conifer forest (Fenn and Poth 2001). Ozone and increased N fertility result in decreases in both C allocation belowground and fine root biomass (Grulke et al. 1998). Ozone causes premature foliar senescence and abscission. The combined effects of O_3 and elevated N deposition are increased C storage in the bole and woody aboveground biomass and accelerated foliar turnover and litter production (Arbaugh et al. 1999). This also results in increased accumulation of C and N in the forest floor. In these O_3-impacted and N-saturated mixed-conifer stands (N deposition 25 to 71 kg ha^{-1} yr^{-1}) (Fenn et al. 2008), aboveground N pools are much higher than in stands in areas receiving relatively low deposition (Arbaugh et al. 1999, Fenn et al. 2005, Grulke et al. 2009). For example, at an N-saturated site (N deposition 71 kg ha^{-1} yr^{-1}) in the San Bernardino Mountains about 30 percent of ecosystem N is stored in the thick forest floor, compared to about 11 percent at an N-limited site (N deposition approximately 7 kg ha^{-1} yr^{-1}) (Arbaugh et al. 1999, Fenn et al. 2005).

Ozone and elevated N deposition cause specific changes in forest tree C, N, and water balance that enhance individual tree susceptibility to drought, bark beetle attack, and disease, and when combined, contribute to whole ecosystem susceptibility to wildfire (Grulke et al. 2009). The N deposition levels at which these effects begin to occur are not well defined, but regression analysis indicates a 25 percent reduction in fine root biomass at 17 kg ha^{-1} yr^{-1} (Fenn et al. 2008); dramatic shifts in tree phenology and C allocation are evident at a site with N deposition of 39 kg ha^{-1} yr^{-1} (Fenn et al. 2008, Grulke and Balduman 1999). Uncharacteristically deep litter layers develop in mixed-conifer forests impacted by air pollution. Elevated O_3 and N deposition decrease the proportion of whole tree biomass in foliage and roots, the latter effect increasing tree susceptibility to drought and beetle attack. Because both foliar and root mass are compromised, carbohydrates are stored in the bole over winter. Elevated O_3 increases drought stress by significantly reducing plant control of water loss. The resulting increase in canopy transpiration, combined with O_3 and N deposition-induced decreases in root mass, significantly increases tree susceptibility to drought stress. The combination of these effects with increased sequestration of bole carbohydrates may contribute to successful host colonization and population increases of bark beetles (Jones et al. 2004) and possible enhancement of dwarf mistletoe infections, although the latter response has not been confirmed.

Understory. Understory diversity in mixed-conifer forests in the San Bernardino Mountains in southern California was recently compared to studies done 30 years prior, in 1973 (Allen et al. 2007). Both O_3 concentrations and particularly N deposition decline from west to east along the air pollution gradient. Nitrogen deposition in throughfall ranges from 9 to 71 kg ha^{-1} yr^{-1} at the understory study sites (Fenn et al. 2008). Biodiversity loss was pronounced in the sites receiving the highest N deposition and is due to the establishment of exotic invasive species that have become abundant. In three of six sites, including the two westernmost polluted sites, 20 to 40 percent of species were lost between 1973 and 2003. In the highest deposition sites, understory cover equaled 30 to 45 percent and was equally divided between native and exotic species. At lower deposition sites, understory cover was 3 to 13 percent and was dominated by native species. Because of confounding factors such as precipitation and possibly local disturbances, a simple correlation between air pollution and patterns of native and invasive species cover and richness was not found. However, observational evidence and expert opinion suggest that increased N deposition and precipitation in the westernmost sites are the primary factors contributing to reduced biodiversity and increased cover by invasive species (Allen et al. 2007).

Co-occurring O_3 may be indirectly contributing to the establishment of exotic species as well. Ozone causes premature foliage loss in pine, while N deposition stimulates foliar growth, leading to greater litter production and accumulation in the forest floor (Fenn et al. 2003b, 2005). Many native plant species are not able to establish where dense litter accumulates. However, stickywilly (*Galium aparine*), a weedy annual with both native and introduced forms, thrives under these conditions, which include the acidified N-rich soils that underlie the thick litter layer. Portions of the high-pollution study sites in the western San Bernardino Mountains burned in October 2003. Formerly shady sites in the burned areas are now covered by exotic annual brome grasses. Subsequent clearing of dead trees and brush is further exposing the soil to invasive species (Allen et al. 2007).

13.4.4 Critical Loads Estimates

The N deposition input values for the sites included in this synthesis range from 1.2 to 71.1 kg ha^{-1} yr^{-1} as throughfall, with the lowest values in the northern Sierra Nevada and the highest deposition in the western San Bernardino mountains in the Los Angeles air basin. The best defined empirical critical loads are for lichen effects, developed for forests of the Sierra Nevada, with the most protective critical load for incipient effects on lichens of 3.1 kg N ha^{-1} yr^{-1}. This lower critical load is based on the low N deposition-site threshold concentration of N (1.0 percent N) in the widespread wolf lichen; at higher tissue concentrations of N, lichen community effects begin to increase (Fenn et al. 2008). Two additional lichen-based critical loads were determined for mixed-conifer forests in California: at throughfall N deposition of 5.2 kg ha^{-1} yr^{-1}, oligotroph dominance shifts to mesotroph/eutroph dominance, and at 10.2 kg ha^{-1} yr^{-1} oligotrophic species are extirpated. These critical load estimates are considered as reliable (Table 13.5). In applying lichens critical loads, the highest threshold—that of oligotroph extirpation—would not be used under conditions where the integrity of the lichen community was considered important. We do not include it in the summary of lichens for the U.S. (Table 19.4). Application of the western Oregon and Washington model (Geiser et al. 2010; Table 4.1) to the mixed-conifer forests yields a critical load estimate of 4 to 6 kg ha^{-1} yr^{-1} over a precipitation range of 41 to 127 cm. This estimate uses the mid-range response threshold (oligotroph dominance shift) instead of the lowest threshold, as it assumes that eutrophs naturally

Table 13.5—Empirical critical loads of nutrient N for mixed-conifer forest ecosystems of the Mediterranean California ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical load for N deposition[a] *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Sierra Nevada range	3.1-10.2[b]	##	Lichen community changes	Critical load of 3.1 for exceedance of a N concentration threshold in *Letharia vulpina*; critical load of 5.2 for shift from oligotroph to mesotroph/eutroph dominance of lichen communities; critical load of 10.2 for extirpation of oligotrophs	Fenn et al. 2008, 2010
Sierra Nevada range	4-6	#	Lichen community changes	Modeled estimate using the oligotroph to mesotroph/eutroph dominance shift as response threshold and 41-127 cm precipitation range	Geiser et al. 2010
San Bernardino mountains and southern Sierra Nevada range	17	##	$[NO_3^-] > 14$ µM	Based on regression of throughfall vs. peak streamwater NO_3^- concentrations. A threshold of 0.2 mg NO_3-N L^{-1} (14.3 µ*M*) identified catchments beginning to "leak" N. Daycent simulations gave similar results	Fenn et al. 2008, 2010
San Bernardino mountains	17	#	Reduced fine root biomass	Based on regression of throughfall N deposition and fine root biomass in ponderosa pine	Fenn et al. 2008, Grulke et al. 1998
San Bernardino mountains	25.9	#	Soil acidification	Based on regression of throughfall N deposition and mineral soil H+. Soil pH of 4.6 was chosen as the critical value.	Breiner et al. 2007
San Bernardino mountains	24-33	(#)	Biodiversity of understory: percent cover and no. of species/ha	Based on plant surveys in 1970s and 2003. N deposition data: Fenn et al., 2008 and unpublished data	Allen et al. 2007
San Bernardino mountains	39	(#)	Forest sustainability	Based on dramatic shifts in plant phenology and C allocation. Caused by combined effects of O_3 and N deposition. Leads to increased bark beetle mortality and wildfire risk. N deposition data from Fenn et al. 2008	Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004

[a] N deposition is reported as throughfall for all of the critical loads in this table.

[b] Utilizing this critical load value would lead to a condition where lichen community composition had shifted toward dominance by eutrophs to the exclusion of oligotrophic (N-sensitive) species. Throughout this document, we use a threshold that limits shifts toward dominance by eutrophs. Thus, the value of 10.2 kg N ha^{-1} yr^{-1} does not appear in the chapter summarizing the critical loads for all ecoregions (Chapter 19).

comprise up to 47 percent of native lichen communities, due to the warm climate and prevalence of hardwood substrates. The critical load which would prevent elevated NO_3^- leaching and further reductions in fine root biomass of ponderosa pine (Fenn et al. 2008) is estimated at 17 kg N ha^{-1} yr^{-1}. The critical load of 17 kg N ha^{-1} yr^{-1} for reductions in fine root biomass (Table 13.5) is preliminary; data from a greater number of sites are needed to refine the critical load. However, the available information on fine root biomass responses demonstrate that when N deposition is sufficient to increase NO_3^- leaching from soil and in streamwater, undesirable physiological effects are also apparent in plants. The critical load for streamwater NO_3^- is reliable, while for fine root biomass effects a fairly reliable rating is assigned (Table 13.5).

Based on a critical mineral soil pH value of 4.6 (MacDonald et al. 2002), an empirical critical load of 26 kg N ha^{-1} yr^{-1} was also estimated and considered to be fairly reliable (Table 13.5), but the basis of this critical pH value has a tenuous connection to any firm ecosystem-specific biological or ecological effects or responses (Breiner et al. 2007, Wood et al. 2007). The estimated critical loads of 24 to 39 kg N ha^{-1} yr^{-1}, which would maintain forest sustainability and biodiversity in the understory community, are included in Table 13.5 and are only established as expert judgment. These are uncertain, as few data are available from research sites in the case of forest sustainability (Grulke and Balduman 1999, Grulke et al. 1998, Jones et al. 2004) and because of confounding factors in regard to understory biodiversity (Allen et al. 2007). The critical load for effects on ectomycorrhizal communities in California forests cannot be determined from current data because only two sites and a high N treatment level (150 kg ha^{-1} yr^{-1}) were studied (Sirajuddin 2009).

13.5 Critical Loads Comparisons Across Ecosystem Types

The lowest critical load estimated for these California Mediterranean ecosystem types (Table 13.6) was 3.1 kg ha^{-1} yr^{-1} for the mixed-conifer forest. This value is based on the throughfall N deposition input leading to N concentrations in lichen thalli (*Letharia vulpina*) of the Sierra Nevada that exceed that of the low N deposition site threshold (Fenn et al. 2008). At a throughfall N deposition critical load of 3.5 to 5.9 kg ha^{-1} yr^{-1} the lichen community in mixed-conifer forests is predicted to shift from oligotroph dominance to mesotroph/eutroph dominance. The lichen community responses to simulated N deposition resulted in a critical load of 3.1 to 6.4 kg N ha^{-1} yr^{-1} for chaparral, oak woodland, and Central Valley lichen communities. Lichen communities of coastal sage scrub have not been studied with regard to air pollution effects. Thus, lichens are not yet an available bioindicator in coastal sage scrub.

The critical load for invasion of annual grasses in a nutrient-poor serpentine grassland (6 kg N ha^{-1} yr^{-1}) was similar to the high end of the range for the lichen critical load in chaparral and forests (Table 13.6). This grassland critical load is based on a site to the west of the Central Valley and downwind of the San Jose/San Francisco metropolitan area. The serpentine grassland critical load may be a reasonable estimate for California grasslands in more fertile soils of the Central Valley and other regions of California, considering studies suggesting that serpentine grasslands are less responsive to added N than other California grasslands and are also less prone to exotic invasions (Harrison and Viers 2007). The critical load for NO_3^- leaching in chaparral catchments (10 kg ha^{-1} yr^{-1}) is about 60 percent of that for mixed-conifer forest (17 kg ha^{-1} yr^{-1}). The lower critical load in chaparral is believed to be due to the lower biological N demand and N retention capacity of chaparral catchments that are characterized by steep slopes and sandy soils. Another factor for the lower chaparral critical load may be the small size (4.3 ha) of the Chamise Creek catchment (Li et al. 2006) upon which the chaparral critical load of 10 kg ha^{-1} yr^{-1} is based. Smaller catchments are often associated with lower N retention capacity (Meixner and Fenn 2004). Thus, it isn't clear if the critical load value for NO_3^- leaching from Chamise Creek is generally applicable to chaparral catchments.

For all vegetation types, catchment characteristics that increase the contact time of soil solution NO_3^- within the soil profile and with plant roots are expected to increase N uptake and increase the critical load. Stand

Table 13.6—Empirical critical loads of nutrient N for the Mediterranean California ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem	Critical load for N deposition[a] *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Coastal Sage Scrub	7.8-10	#	Exotic invasive grass cover, native forb richness, arbuscular mycorrhizal richness	Modeled and inferential N deposition estimates and published data for mycorrhizae, unpublished data for vegetation survey.	Allen unpublished [b], Egerton-Warburton and Allen 2000, Tonnesen et al. 2007
Chaparral	3.1-14	#	NO_3 leaching; changes in lichen communities	Critical load for NO_3 leaching of 10 kg N ha^{-1} yr^{-1} is based on one year of throughfall data in Chamise Creek and an additional year of throughfall data from adjacent Ash Mountain, both in Sequoia National Park. Lichen critical load of 5.5 kg N ha^{-1} yr^{-1} is from modeled N deposition data and published data for lichens. Lower estimated value for the lichen critical load of 3.1 kg N ha^{-1} yr^{-1} is from application of a model developed in the Pacific NW including the effect of precipitation.	Fenn et al. 2003a; Fenn et al. 2003b; Fenn et al. 2010; Geiser et al. 2010; Jovan 2008; Jovan and McCune 2005; Meixner et al. 2006; Meixner and Fenn 2004; Riggan et al. 1985
Mixed-conifer forest	3-39	##	Lichen chemistry and community changes; NO_3 leaching; soil acidification; reduced fine root biomass	The lowest critical load is based on lichen tissue chemistry above the clean site threshold. NO_3 leaching and fine root biomass critical load is 17 kg N ha^{-1} yr^{-1}, and soil acidification critical load is 26 kg N ha^{-1} yr^{-1}.	Allen et al. 2007; Breiner et al. 2007; Fenn et al. 2008 ; Fenn et al. 2010 ; Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004
Serpentine grassland	6	##	Annual grass invasion, replacing native herbs	Critical load based on a local roadside gradient; Serpentine grassland site is actually west of the Central Valley.	Weiss 1999; Fenn et al. 2010

[a] N deposition in the mixed-conifer sites is reported as throughfall. Critical loads for coastal sage scrub and for lichen communities in chaparral (5.5 kg N ha^{-1} yr^{-1}) are based on CMAQ simulated N deposition.

[b] See footnote 15 on page 144

management is also expected to affect the critical load for a given site. For example, a decrease in the site N capital due to fire or stand thinning operation, followed by vigorous vegetation regrowth and increased N demand, could increase site N retention and thus lead to a higher critical load. The critical load for biological effects in coastal sage scrub is relatively low (10 to 11 kg ha^{-1} yr^{-1}) and may be lower, considering the lack of low N deposition control sites in estimating the critical loads. A major factor contributing to the N sensitivity of coastal sage scrub vegetation is the fact that N accumulates to high concentrations in the surface soils during the long summer dry period and the entire rooting zone is probably only thoroughly leached of NO_3^- in unusually high rainfall years (Wood et al. 2006).

Mediterranean ecosystems exposed to chronic N deposition often cycle between periods of N accumulation and periods of N availability, mobilization, uptake, and loss. This latter period is presumably the season of greatest ecosystem sensitivity to the effects of excess N. Critical loads estimates are needed that protect ecosystems from detrimental effects during these periods of greatest sensitivity. The empirical critical loads in this study are based on the predominant ecological conditions, which include fire suppression, co-occurrence of O_3 and chronic N deposition, and recurring drought. Critical load, by definition, refers to the threshold deposition below which adverse biological effects are not observed. However, some critical loads in this chapter (and others) are tied to ecosystem processes or responses that don't always have a biological link within the terrestrial ecosystem that has yet been well established or defined (e.g., nitrate leaching).

13.6 Comparison to European Critical Loads

Few empirical N critical loads studies for European Mediterranean ecosystems have been published. Based on a European-wide modeling effort, Kuylenstierna et al. (1998) concluded that Mediterranean scrub has low to moderate sensitivity to N deposition, with a lower critical load of 15 kg N ha^{-1} yr^{-1}. A relatively small area of the Mediterranean scrub exceeds this level of deposition (Kuylenstierna et al. 1998). Lorenz et al. (2008) used the simple mass balance approach and reported low nutrient N critical load values for Spain, ranging from 3.5 to 10.5 kg ha^{-1} yr^{-1}, or possibly even lower in some instances. These modeled critical load values appear to be lower than expected based on empirical studies (Fenn et al. 2008, Michopoulos et al. 2008, this chapter). Modeled deposition to coniferous forest for the year 2000 shows N deposition of 10 to 20 kg ha^{-1} yr^{-1} over most of Mediterranean Europe (Simpson et al. 2006), showing the potential for exceedance of the N critical load in many forested sites.

A critical load of 5 kg N ha^{-1} yr^{-1} as bulk deposition in forest clearings can be estimated for Spanish fir (*Abies pinsapo*) forests in southern Spain (Torres-Cañabate et al. 2008). Throughfall N deposition from an earlier study was reportedly 12 kg N ha^{-1} yr^{-1} in these forests (Torres-Cañabate et al. 2008). At the reported level of bulk deposition, N enrichment of soil and foliage were evident, along with increased potential net nitrification and emissions of N_2O from soil compared to a more N-limited site. However, bulk N deposition was higher at the N-limited site than the site showing symptoms of N saturation, making interpretation of these findings difficult (Torres-Cañabate et al. 2008). We estimate a tentative N critical load for incipient NO_3^- leaching at a beech forest in central eastern Greece of 13 kg N ha^{-1} yr^{-1}, based on data reported by Michopoulos et al. (2008), but more data are needed to determine if the critical load is actually higher. Catchments in northern Italy along the Swiss border (Rogora 2007) are strongly N saturated (at level 2-3 of Stoddard's [1994] classification), but these are not typical Mediterranean ecosystems. A notable example of a Mediterranean forest where deposition exceeds the N critical load is an Aleppo pine site in Athens, Greece (Michopoulos et al. 2004). Because this site is presumably well above the critical load, with annual throughfall deposition as high as 38 kg N ha^{-1} yr^{-1}, the critical load cannot be determined.

In summary, few European Mediterranean sites have been reported to be above the N critical loads based on empirical data. On the other hand, broad-scale models of N deposition and nutrient N critical loads predict that critical loads exceedance is not uncommon in the European Mediterranean region (Lorenz et al. 2008, Simpson et al. 2006). Lorenz et al. (2008) calculated low critical load values in Spain because of low plant growth rates, low timber harvest, and low levels of N export in seepage water due to low precipitation, resulting in low net N export from the ecosystems. It was concluded that, in these cases, the critical load can be exceeded by relatively low N deposition. However, modeled deposition and critical loads need to be validated with empirical data, particularly considering the co-occurrence of elevated O_3 levels and the pronounced seasonality in precipitation and N deposition inputs and outputs in these unique Mediterranean ecosystems (Fenn et al. 2008). DeVries et al. (2007) also recommended that for these cases the empirical critical loads for N should be determined.

The N critical loads in European Mediterranean ecosystems appear to be generally similar to those in California, but the lack of reported empirical critical loads for Mediterranean Europe prevent any strong comparisons. It seems safe to assume that in both regions, lichens are the most sensitive terrestrial responders to N deposition, and are impacted in regions of sufficient exposure. Lichen responses to NH_3 have been reported from Italy and Portugal, but critical load estimates are not available due to lack of deposition data (Frati et al. 2008, Pinho et al. 2009). However, recent studies on the responses of epiphytic lichen communities to NH_3 exposure indicate similar dose responses in Europe and the Mediterranean California ecoregion. In an oak woodland in Portugal, also with a Mediterranean climate, the estimated critical level for lichen community diversity impacts was 1.4 to 1.7 $\mu g\ m^{-3}$ (Pinho et al. 2009). The estimated critical level for epiphytic lichen community changes in mixed-conifer forests in the southern Sierra Nevada of California falls within this same range.[20] Recently a critical level of 1.0 $\mu g\ m^{-3}$ as a long-term average concentration was proposed for NH_3 effects on epiphytic lichen communities based on European studies (Cape et al. 2009, Sutton et al. 2009) and a critical level of 3.0 $\mu g\ m^{-3}$ was proposed for effects on herbaceous plant communities (Cape et al. 2009). The California serpentine grassland results presented in this chapter are in general agreement with the herbaceous plant critical level for NH_3. Monthly average NH_3 concentrations were 0.3 to 0.7 $\mu g\ m^{-3}$ at a site where impacts were minimal, compared to NH_3 concentrations of 1 to 3.5 $\mu g\ m^{-3}$ at sites where plant communities were strongly impacted by invasive species.[21]

However, in regard to broader ecosystem effects from excess N, as suggested by Rodà et al. (2002) and in contrast to the conclusions of Lorenz et al. (2008) cited above, the N-limited state of some European Mediterranean ecosystems may be enhanced by the repeated nutrient losses from fire and biomass harvesting over the centuries. Under these N-demanding conditions, the critical loads for soil, vegetative, and hydrologic responses to N deposition may be higher than those reported for California. These effects of land-use history on the critical loads are expected to vary across the landscape. Information on critical loads for all vegetation types in Mediterranean ecosystems has been identified as a major research gap (Bobbink et al. 2003). Because of the dearth of critical load work in European Mediterranean ecosystems, the work summarized herein from California Mediterranean ecosystems may be useful to the European scientific community.

13.7 Future Research Directions and Gaps in Data

To better understand the effects of chronic N deposition in Mediterranean ecosystems, further research is needed on levels of N input and mechanisms and fluxes of N loss and storage, the effects of fire on N pools and processing, and the response of plant, lichen, and mycorrhizal communities to deposition. Gaseous N losses have not been well quantified and may be an important process by which a significant proportion of the excess N accumulation is reduced (Anderson and Poth 1989, Fenn

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[20] Bytnerowicz, A.; Jovan, S. Unpublished data on file with Andrzej Bytnerowicz, research ecologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

[21] Weiss, S.B.; Bytnerowicz, A. Unpublished data on file with Mark Fenn, research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

et al. 1996, Fenn and Poth 2001). A large proportion of trace gas losses are expected to occur in the riparian and near-riparian zones, possibly as degassing of dissolved N_2O from groundwater-fed streams. Further streamwater measurements are needed across N deposition gradients using $\Delta^{17}O$ as a tracer for atmospheric NO_3^- (Michalski et al. 2004) to determine the threshold percent of exported NO_3^- as direct throughput of unassimilated atmospheric NO_3^- associated with N-saturated catchments. As stands with lower air pollution or N fertilization at realistic levels are studied, we may find that lower levels of N deposition also have effects on ecosystem dynamics. Research is needed on the best management practices for improving water quality in chaparral and mixed-conifer forest catchments. Questions remain regarding the level of N deposition reduction necessary to reverse the symptoms of saturation. It would be valuable to characterize the spatial patterns of N deposition throughout catchments, but this is difficult because of the steep terrain in many chaparral and forested catchments.

Research is needed on the effects of fire in Mediterranean ecosystems. Fire is a natural part of Mediterranean ecosystems, and its interactions with N deposition are complex. In coastal sage scrub, fire may interact with increased N deposition to promote the growth of exotic grass fuel and cause rapid degradation in native vegetation (Allen et al. 1998, Minnich and Dezzani 1998, Talluto and Suding 2008). In chaparral and mixed-conifer forests, fire in combination with decreased N deposition may help mitigate N saturation (Gimeno et al. 2009). Studies are needed to test the effectiveness of periodic fire as a management tool in N-saturated catchments, considering that 65 to 85 and 80 to 95 percent of site N capital in forest (Johnson et al. 2009) and chaparral (Rundel and Parsons 1980, Rundel and Vankat 1989) ecosystems is stored in the mineral soil, which is unimpacted by fire disturbance (Meixner et al. 2006). Recurring fire is a normal process in California chaparral and forest ecosystems and prescribed fire can be applied without causing significant alterations in nutrient cycling or plant nutrient status (Murphy et al. 2006).

Little is known about the effects of N deposition on plant biodiversity in chaparral and in the forest understory, including the putative indirect effects on plant communities as a result of the impacts of N deposition on mycorrhizal communities. Nitrogen addition studies at appropriate doses are also needed to determine the N critical load for biodiversity effects in California grasslands. Additional analysis is needed to separate lichen responses due to NH_3 from those caused by other forms of N deposition in the oak woodlands, chaparral, and forest communities, and to account for the influence of precipitation on lichen responses to N deposition over the regional landscape. The original interpretation of lichen community work in the greater Central Valley was limited by available air pollution data. The simulated CMAQ deposition data presented herein has allowed for preliminary estimates of lichen-based critical loads in chaparral and oak woodlands. This should be complemented with empirical deposition data to better define the critical load for lichen community responses.

More work is needed to determine the critical load for acidity in chaparral ecosystems. Evidence strongly suggests that atmospheric deposition has acidified chaparral soils over the past several decades, but N deposition data are not available from enough sites to determine empirical relationships. Modeled estimates of the critical loads for acidity have not yet been made for chaparral ecosystems. Better definition is needed of the N input levels that contribute to decreases in forest sustainability by way of physiological perturbations, greater sensitivity to bark beetles, and increased drought stress and mortality (Grulke et al. 2009). Further comparisons of modeled and empirical critical loads are needed for California ecosystems and for Mediterranean ecosystems in general.

LITERATURE CITED

Aber, J.D.; Nadelhoffer, K.J.; Steudler, P.; Melillo, J.M. 1989. **Nitrogen saturation in northern forest ecosystems.** BioScience. 39: 378-386.

Allen, E.B.; Padgett, P.E.; Bytnerowicz, A.; Minnich, R. 1998. **Nitrogen deposition effects on coastal sage vegetation of southern California.** In: Bytnerowicz, A.; Arbaugh, M.J.; Schilling, S.L., tech. coords. Proceedings of the international symposium on air pollution and climate change effects on forest ecosystems; 1996 February 5-9; Riverside, CA. Gen. Tech. Rep. PSW-166. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 131-140.

Allen, E.B.; Temple, P.J.; Bytnerowicz, A.; Arbaugh, M.J.; Sirulnik, A.G.; Rao, L.E. 2007. **Patterns of understory diversity in mixed coniferous forests of southern California impacted by air pollution.** The Scientific World Journal. 7(S1): 247-263.

Anderson, I.C.; Poth, M.A. 1989. **Semiannual losses of nitrogen as NO and N_2O from unburned and burned chaparral.** Global Biogeochemical Cycles. 3: 121-135.

Arbaugh, M.; Bytnerowicz, A.; Grulke, N.; Fenn, M.; Poth, M.; Temple, P.; Miller, P. 2003. **Photochemical smog effects in mixed conifer forests along a natural gradient of ozone and nitrogen deposition in the San Bernardino Mountains.** Environment International. 29: 401-406.

Arbaugh, M.J.; Johnson, D.W.; Pulliam, W.M. 1999. **Simulated effects of N deposition, ozone injury and climate change on a forest stand in the San Bernardino Mountains.** In: Miller, P.R.; McBride, J.R., eds. Oxidant air pollution impacts in the montane forests of southern California: A case study of the San Bernardino Mountains. Ecological Studies 134. New York, NY: Springer-Verlag: 353-372.

Bobbink, R.; Ashmore, M.R.; Braun, S.; Fluckiger, W.; van der Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R. eds. Empirical critical loads for nitrogen. Environmental Documentation 164. Berne, Switzerland: Swiss Agency for the Environment, Forests and Landscape: 43-170.

Bowden, W.B.; Bormann, F.H. 1986. **Transport and loss of nitrous oxide in soil water after forest clear-cutting.** Science. 233: 867-869.

Breiner, J.; Gimeno, B.S.; Fenn, M. 2007. **Calculation of theoretical and empirical nutrient N critical loads in the mixed-conifer ecosystems of southern California.** The Scientific World Journal. 7(S1): 198-205.

Bytnerowicz, A.; Fenn, M.E. 1996. **Nitrogen deposition to California forests: a review.** Environmental Pollution. 92: 127-146.

Cape, J.N.; van der Eerden, L.J.; Sheppard, L.J.; Leith, I.D.; Sutton, M.A. 2009. **Evidence for changing the critical level for ammonia.** Environmental Pollution. 157: 1033-1037.

CDFFP (California Department of Forestry and Fire Protection). 2007. **FRAP [Fire and resource assessment program] data.** Available at http://frap.cdf.ca.gov/data/frapgisdata/download.asp?rec=fveg02_2 (Accessed March 30, 2011).

CEC (Commission for Environmental Cooperation). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

De Vries, W.; Kros, H.; Reinds, G.J.; Wamelink, W.; Mol, J.; van Dobben, H.; Bobbink, R.; Emmett, B.; Smart, S.; Evans, C.; Schlutow, A.; Kraft, P.; Belyazid, S.; Sverdrup, H.; van Hinsberg, A.; Posch, M.; Hettelingh, J.-P. 2007. **Developments in deriving critical limits and modelling critical loads of nitrogen for terrestrial ecosystems in Europe.** Alterra Report 1382 [Alterra-rapport 1382]. Wageningen, The Netherlands: Wageningen University, Alterra. 206 p.

Egerton-Warburton, L.M.; Allen, E.B. 2000. **Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient.** Ecological Applications. 10: 484-496.

Egerton-Warburton, L.M.; Graham, R.C.; Allen, E.B.; Allen, M.F. 2001. **Reconstruction of the historical changes in mycorrhizal fungal communities under anthropogenic nitrogen deposition.** Proceedings of the Royal Society of London. B268: 2479-2484.

Fenn, M.E. 1991. **Increased site fertility and litter decomposition rate in high-pollution sites in the San Bernardino Mountains.** Forest Science. 37: 1163-1181.

Fenn, M.E.; Allen, E.B.; Weiss, S.B.; Jovan, S.; Geiser, L.; Tonnesen, G.S.; Johnson, R.F.; Rao, L.E.; Gimeno, B.S.; Yuan, F.; Meixner, T.; Bytnerowicz, A. 2010. **Nitrogen critical loads and management alternatives for N-impacted ecosystems in California.** Journal of Environmental Management. 91: 2404-2423.

Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W.; Neitlich, P. 2003a. **Ecological effects of nitrogen deposition in the western United States.** BioScience. 53: 404-420.

Fenn, M.E.; Jovan, S.; Yuan, F.; Geiser, L.; Meixner, T.; Gimeno, B.S. 2008. **Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests.** Environmental Pollution. 155: 492-511.

Fenn, M.E.; Poth, M.A. 1996. **Preliminary evidence of nitrogen saturation in the San Bernardino Mountains in Southern California.** In: Cox, R.; Percy, K.; Jensen, K.; Simpson, C. comps. Proceedings of the IUFRO air pollution and multiple stresses 16th international meeting for specialists in air pollution effects on forest ecosystems; 1994 September 7-9; Fredericton, NB. Fredericton, NB: Natural Resources Canada, Canadian Forest Service, Atlantic Centre: 97-102.

Fenn, M.E.; Poth, M.A. 1999. **Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California.** Journal of Environmental Quality. 28: 822-836.

Fenn, M.E.; Poth, M.A. 2001. **A case study of nitrogen saturation in western U.S. forests.** In: Galloway, J.; Cowling, E.; Erisman, J.W.; Wisniewski, J.; Jordan, C. eds. Optimizing nitrogen management in food and energy production and environmental protection: Proceedings of the 2nd international nitrogen conference; 2001 October 14-18; Potomac, MD. Lisse, The Netherlands: Balkema Publishers: 433-439.

Fenn, M.E.; Poth, M.A. 2004. **Monitoring nitrogen deposition in throughfall using ion exchange resin columns: A field test in the San Bernardino Mountains.** Journal of Environmental Quality. 33: 2007-2014.

Fenn, M.E.; Poth, M.A.; Aber, J.D.; Baron, J.S.; Bormann, B.T.; Johnson, D.W.; Lemly, A.D.; McNulty, S.G.; Ryan, D.F.; Stottlemyer, R. 1998. **Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies.** Ecological Applications. 8(3): 706-733.

Fenn, M.E.; Poth, M.A.; Bytnerowicz, A.; Sickman, J.O.; Takemoto, B.K. 2003b. **Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada.** In: Bytnerowicz, A.; Arbaugh, M.J.; Alonso, R., eds. Developments in environmental science, volume 2: Ozone air pollution in the Sierra Nevada: Distribution and effects on forests. Amsterdam, The Netherlands: Elsevier: 111-155.

Fenn, M.E.; Poth, M.A.; Dunn, P.H.; Barro, S.C. 1993. **Microbial N and biomass, respiration and N-mineralization in soils beneath two chaparral species along a fire-induced age gradient.** Soil Biology and Biochemistry. 25: 457-466.

Fenn, M.E.; Poth, M.A.; Johnson, D.W. 1996. **Evidence for nitrogen saturation in the San Bernardino Mountains in southern California.** Forest Ecology and Management. 82: 211-230.

Fenn, M.E.; Poth, M.A.; Terry, J.D.; Blubaugh, T.J. 2005. **Nitrogen mineralization and nitrification**

in a mixed conifer forest in southern California: Controlling factors, fluxes, and nitrogen fertilization response at a high and low nitrogen deposition site. Canadian Journal of Forest Research. 35: 1464-1486.

Fenn, M.E.; Poth, M.A.; Schilling, S.L.; Grainger, D.B. 2000. **Throughfall and fog deposition of nitrogen and sulfur at an N-limited and N-saturated site in the San Bernardino Mountains, southern California.** Canadian Journal of Forest Research. 30: 1476-1488.

Fenn, M.E.; Sickman, J.O.; Bytnerowicz, A.; Clow, D.W.; Molotch, N.P.; Pleim, J.E.; Tonnesen, G.S.; Weathers, K.C.; Padgett, P.E.; Campbell, D.H. 2009. **Methods for measuring atmospheric nitrogen deposition inputs in arid and montane ecosystems of western North America.** In: Legge, A.H., ed. Developments in environmental science, vol. 9: Air quality and ecological impacts: Relating sources to effects. Amsterdam, The Netherlands: Elsevier: 179-228.

Frati, L.; Brunialti, G.; Loppi, S. 2008. **Effects of reduced nitrogen compounds on epiphytic lichen communities in Mediterranean Italy.** Science of the Total Environment. 407: 630-637.

Geiser, L.H.; Jovan, S.E.; Glavich, D.A.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in western Oregon and Washington forests, USA.** Environmental Pollution. 158: 2412-2421.

Gimeno, B.S.; Yuan, F.; Fenn, M.E.; Meixner, T. 2009. **Management options for mitigating nitrogen (N) losses from N saturated mixed conifer forests in California.** In: Bytnerowicz, A.; Arbaugh, M.J.; Riebau, A.R.; Andersen, C., eds. Wildland fires and air pollution. Developments in environmental science, volume 8. Amsterdam, The Netherlands: Elsevier: 425-455.

Grulke, N.E.; Andersen, C.P.; Fenn, M.E.; and Miller, P.R. 1998. **Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California.** Environmental Pollution. 103: 63-73.

Grulke, N.E.; Balduman, L. 1999. **Deciduous conifers: High N deposition and O_3 exposure effects on growth and biomass allocation in ponderosa pine.** Water, Air and Soil Pollution. 116: 235-248.

Grulke, N.E.; Minnich, R.A.; Paine, T.D.; Seybold, S.J.; Chavez, D.J.; Fenn, M.E.; Riggan, P.J.; Dunn, A. 2009. **Air pollution increases forest susceptibility to wildfires: A case study in the San Bernardino Mountains in southern California.** In: Bytnerowicz, A.; Arbaugh, M.J.; Riebau, A.R.; Andersen, C., eds. Wildland fires and air pollution. Developments in environmental science, volume 8. Amsterdam, The Netherlands: Elsevier: 365-403.

Harrison, S.P.; Viers, J.H. 2007. **Serpentine grasslands.** In: Stromberg, M.R.; Corbin, J.D.; D'Antonio, C.M., eds. California grasslands: Ecology and management. Berkeley, CA: University of California Press: 145-155.

Hasse, H.E. 1913. **The lichen flora of southern California.** Contributions from the United States National Herbarium. 17: 1-132.

Johnson, D.W.; Fenn, M.E.; Miller, W.W.; Hunsaker, C.F. 2009. **Fire effects on carbon and nitrogen cycling in forests of the Sierra Nevada.** In: Bytnerowicz, A.; Arbaugh, M.J.; Riebau, A.R.; Andersen, C., eds. Wildland fires and air pollution. Developments in environmental science, volume 8. Amsterdam, The Netherlands: Elsevier: 405-423.

Jones, M.E.; Paine, T.D.; Fenn, M.E.; Poth, M.A. 2004. **Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions.** Forest Ecology and Management. 200: 67-76.

Jordan, F.L.; Cantera, J.J.L.; Fenn, M.E.; Stein, L.Y. 2005. **Autotrophic ammonia-oxidizing bacteria contribute minimally to nitrification in**

a nitrogen-impacted forested ecosystem. Applied Environmental Microbiology. 71: 197-206.

Jovan, S. 2008. **Lichen bioindication of biodiversity, air quality, and climate: baseline results from monitoring in Washington, Oregon, and California.** Gen. Tech. Rep. PNW-737. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 56 p.

Jovan, S.; McCune, B. 2005. **Air quality bioindication in the greater Central Valley of California with epiphytic macrolichen communities.** Ecological Applications. 15(5): 1712-1726.

Keeley, J.E.; Davis, F.W. 2007. **Chaparral. Chapter 13.** In: Barbour, M.J.; Keeler-Wolf, T.; Schoenherr, A.A., eds. Terrestrial vegetation of California. Berkeley, CA: University of California Press: 339-366.

Kuylenstierna, J.C.I.; Hicks, W.K.; Cinderby, S.; Cambridge, H. 1998. **Critical loads for nitrogen deposition and their exceedance at European scale.** Environmental Pollution. 102: 591-598.

Li, X.; Meixner, T.; Sickman, J.O.; Miller, A.E.; Schimel, J.P.; Melack, J.M. 2006. **Decadal-scale dynamics of water, carbon and nitrogen in a California chaparral ecosystem: DAYCENT modeling results.** Biogeochemistry. 77: 217-245.

Lorenz, M.; Nagel, H.-D.; Granke, O.; Kraft, P. 2008. **Critical loads and their exceedances at intensive forest monitoring sites in Europe.** Environmental Pollution. 155: 426-435.

MacDonald, J.A.; Dise, N.B.; Matzner, E.; Armbruster, M.; Gundersen, P.; Forsius, M. 2002. **Nitrogen input together with ecosystem nitrogen enrichment predict nitrate leaching from European forests.** Global Change Biology. 8: 1028-1033.

McCune, B.; Grenon, J.; Mutch, L.S.; Martin, E.P. 2007. **Lichens in relation to management issues in the Sierra Nevada national parks.** Pacific Northwest Fungi. 2: 1-39.

Meixner, T.; Fenn, M. 2004. **Biogeochemical budgets in a Mediterranean catchment with high rates of atmospheric N deposition—importance of scale and temporal asynchrony.** Biogeochemistry. 70: 331-356.

Meixner, T.; Fenn, M.E.; Wohlgemuth, P.; Oxford, M.; Riggan, P. 2006. **N saturation symptoms in chaparral catchments are not reversed by prescribed fire.** Environmental Science and Technology. 40: 2887-2894.

Michalski, G.; Meixner, T.; Fenn, M.; Hernandez, L.; Sirulnik, A.; Allen, E.; Thiemens, M. 2004. **Tracing atmospheric nitrate deposition in a complex semiarid ecosystem using Δ^{17}O.** Environmental Science and Technology. 38: 2175-2181.

Michopoulos, P.; Baloutsos, G.; Economou, A. 2008. **Nitrogen cycling in a mature mountainous beech forest.** Silva Fennica. 42: 5-17.

Michopoulos, P.; Baloutsos, G.; Economou, A.; Nikolis, N. 2004. **Effects of nitrogen deposition on nitrogen cycling in an Aleppo pine stand in Athens, Greece.** Science of the Total Environment. 323: 211-218.

Minnich, R.A., 1999. **Vegetation, fire regimes, and forest dynamics.** In: Miller, P.R.; McBride, J.R., eds. Oxidant air pollution impacts in the montane forests of southern California: A case study of the San Bernardino Mountains. Ecological Studies 134. New York: Springer-Verlag: 44-78.

Minnich, R.A.; Bahre, C.J. 1995. **Wildland fire and chaparral succession along the California Baja-California Boundary.** International Journal of Wildland Fire. 5: 13-24.

Minnich, R. A.; Dezzani, R.J. 1998. **Historical decline of coastal sage scrub in the Riverside-Perris plain, California.** Western Birds. 29: 366-391.

Munz, P. A. 1973. **A California flora.** Berkeley, CA: University of California Press. 1681 p.

Murphy, J.D.; Johnson, D.W.; Miller, W.W.; Walker, R.F.; Blank, R.R. 2006. **Prescribed fire effects on forest floor and soil nutrients in a Sierra Nevada forest.** Soil Science. 171: 181-199.

Nash III, T.H.; Sigal, L.L. 1999. **Epiphytic lichens in the San Bernardino Mountains in relation to oxidant gradients.** In: Miller, P.R.; McBride, J.R., eds. Oxidant air pollution impacts in the montane forests of southern California: A case study of the San Bernardino Mountains. Ecological Studies 134. New York: Springer-Verlag: 223-234.

Padgett, P.E.; Allen, E.B.; Bytnerowicz, A.; Minnich, R.A. 1999. **Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California.** Atmospheric Environment. 33: 769-781.

Peterson, D.L.; Arbaugh, M.J. 1992. **Mixed conifer forests of the Sierra Nevada.** In: Olson, R.K.; Binkley, D.; Böhm, M., eds. The response of western forests to air pollution. Ecological studies series, volume 97. New York, NY: Springer-Verlag: 433-459.

Pinho, P.; Branquinho, C.; Cruz, C.; Tang, Y.S.; Dias, T.; Rosa, A.P.; Máguas, C.; Martins-Loução, M.-A. 2009. **Assessment of critical levels of atmospheric ammonia for lichen diversity in cork-oak woodland, Portugal.** In: Sutton, M.A.; Reis, S.; Baker, S.M.H., eds. Atmospheric ammonia: Detecting emission changes and environmental impacts. New York, NY: Springer: 109-119.

Rao, L.E.; Allen, E.B.; Meixner, T. 2010. **Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts.** Ecological Applications. 20: 1320-1335.

Riddell, J; Nash, T.H., III; Padgett, P. 2008. **The effect of HNO_3 gas on the lichen *Ramalina menziesii*.** Flora. 203: 47-54

Riggan, P.J.; Lockwood, R.N.; Jacks, P.M.; Colver, C.G.; Weirich, F.; DeBano, L.F.; Brass, J.A. 1994. **Effects of fire severity on nitrate mobilization in watersheds subject to chronic atmospheric deposition.** Environmental Science and Technology. 28: 369-375.

Riggan, P.J.; Lockwood, R.N.; Lopez, E.N. 1985. **Deposition and processing of airborne nitrogen pollutants in Mediterranean-type ecosystems of southern California.** Environmental Science and Technology. 19: 781-789.

Rodà, F.; Avila, A.; Rodrigo, A. 2002. **Nitrogen deposition in Mediterranean forests.** Environmental Pollution. 118: 205-213.

Rogora, M. 2007. **Synchronous trends in N-NO_3 export from N-saturated river catchments in relation to climate.** Biogeochemistry. 86: 251-268.

Ross, L.J. 1982. **Lichens on coastal live oak in relation to ozone.** Tempe, AZ: Arizona State University. M.S. thesis.

Ross, L.J.; Nash, T.H., III. 1983. **Effect of ozone on gross photosynthesis of lichens.** Environmental and Experimental Botany. 23: 71-77.

Rundel, P.W.; Parsons, D.J. 1980. **Nutrient changes in two chaparral shrubs along a fire-induced age gradient.** American Journal of Botany. 67: 51-58.

Rundel, P.W.; Vankat, J.L. 1989. **Chaparral communities and ecosystems.** In: Keely, S.C., ed. The California chaparral: Paradigms reexamined. No. 34 Science Series. Los Angeles, CA: Natural History Museum of Los Angeles County: 127-139.

Sigal, L.L.; Nash III, T.H. 1983. **Lichen communities on conifers in southern California: an ecological survey relative to oxidant air pollution.** Ecology. 64: 1343-1354.

Simpson, D.; Butterbach-Bahl, K.; Fagerli, H.; Kesik, M.; Skiba, U.; Tang, S. 2006. **Deposition and**

emissions of reactive nitrogen over European forests: A modelling study. Atmospheric Environment. 40: 5712-5726.

Sirajuddin, A.T. 2009. **Impact of atmospheric nitrogen pollution on belowground mycorrhizal community structure and composition in the San Bernardino Mountains.** Riverside, CA: University of California. 120 p. Ph.D. dissertation.

Sirulnik, A.G.; Allen, E.B.; Meixner, T.; Fenn, M.E.; Allen, M.F. 2007. **Changes in N cycling and microbial N with elevated N in exotic grasslands of Southern California.** Applied Soil Ecology. 36: 1-9.

Stoddard, J.L. 1994. **Long-term changes in watershed retention of nitrogen: Its causes and aquatic consequences.** In: Baker, L.A., ed. Environmental chemistry of lakes and reservoirs. Advances in chemistry series 237. Washington, DC: American Chemical Society: 223-284.

Stolte, K.W. 1982. **The effects of ozone on chaparral plants in the California south coast air basin.** Riverside, CA: University of California. 108 p. M.S. thesis.

Sutton, M.A.; Wolseley, P.A.; Leith, I.D.; van Dijk, N.; Tang, Y.S.; James, P.W.; Theobald, M.R.; Whitfield, C. 2009. **Estimation of the ammonia critical level for epiphytic lichens based on observations at farm, landscape and national scales.** In: Sutton, M.A.; Reis, S.; Baker, S.M.H., eds. Atmospheric ammonia: Detecting emission changes and environmental impacts. New York, NY: Springer: 71-86.

Talluto, M.V.; Suding, K.N. 2008. **Historical change in coastal sage scrub in southern California in relation to fire frequency and air pollution.** Landscape Ecology. 23: 803-815.

Temple, P.J. 1999. **Effects of ozone on understory vegetation in the mixed conifer forest.** In: Miller, P.R.; McBride, J.R., eds. Oxidant air pollution impacts in the montane forests of southern California: A case study of the San Bernardino Mountains. Ecological Studies 134. New York: Springer-Verlag: 208-222.

Tonnesen, G.; Wang, Z.; Omary, M.; Chien, C.J. 2007. **Assessment of nitrogen deposition: Modeling and habitat assessment.** CEC-500-2005-032. Sacramento, CA: California Energy Commission, PIER Energy-Related Environmental Research. Available at http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF (Accessed May 12, 2010).

Torres-Cañabate, P.; Davidson, E.A.; Bulygina, E.; García-Ruiz, R.; Carreira, J.A. 2008. **Abiotic immobilization of nitrate in two soils of relic *Abies pinsapo*-fir forests under Mediterranean climate.** Biogeochemistry. 91: 1-11.

Vourlitis, G.L.; Pasquini, S.; Zorba, G. 2007a. **Plant and soil N response of southern Californian semi-arid shrublands after 1 year of experimental N deposition.** Ecosystems. 10: 263-279.

Vourlitis, G. L.; Zorba, G. 2007. **Nitrogen and carbon mineralization of semi-arid shrubland soil exposed to long-term atmospheric nitrogen deposition.** Biology and Fertility of Soils. 43: 611-615.

Vourlitis, G.L.; Zorba, G.; Pasquini, S.C.; Mustard, R. 2007b. **Chronic nitrogen deposition enhances nitrogen mineralization potential of semiarid shrubland soils.** Soil Science Society of America Journal. 71: 836-842.

Weiss, S.B. 1999. **Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species.** Conservation Biology. 13: 1476-1486.

Wood, Y.A.; Fenn, M.; Meixner, T.; Shouse, P.J.; Breiner, J.; Allen, E.; Wu, L. 2007. **Smog nitrogen and the rapid acidification of forest soil, San Bernardino Mountains, southern California.** The Scientific World Journal. 7(S1): 175-180.

Wood, Y.A.; Meixner, T.; Shouse, P.J.; Allen, E.B. 2006. **Altered ecohydrologic response drives native shrub loss under conditions of elevated N-deposition.** Journal of Environmental Quality. 35: 76-92.

Wood, H.B.; Olivier, K.L.; Ryan, T.M. 1992. **Surface soil acidification in smog-polluted chaparral ecosystems in the San Gabriel Mountains, California.** Bulletin of the Ecological Society of America. 73: 392.

Yoshida, L.C.; Allen, E.B. 2004. **^{15}N uptake by mycorrhizal *Artemisia californica* and the invasive *Bromus madritensis* of a N-eutrophied shrubland.** Biology and Fertility of Soil. 39:243-248.

14 SOUTHERN SEMI-ARID HIGHLANDS

M.E. Fenn, E.B. Allen

14.1 Ecoregion description

Most of the Southern Semi-Arid Highlands ecoregion occurs in Mexico, but a portion centered on the Chiricahua Mountains of Arizona and New Mexico lies in the United States. The ecoregion description is adapted from CEC (1997). Rainfall is 300 to 600 mm, with biseasonal distribution (winter and summer). The mountains are volcanic in origin, with valleys and plains of alluvial sediments. The area lies at the intersection of the Sonoran and Chihuahuan Deserts, the Rocky Mountains, and the Sierra Madre (CEC 1997, Fig. 2.1). Consequently, this region is high in plant and animal diversity, having components of all four ecosystem types. Vegetation includes desert grassland interspersed with desert scrub (especially mesquite [*Prosopis* spp.] and acacia [*Acacia* spp.]) at low elevations, oak (*Quercus* spp.) and juniper (*Juniperus* spp.) at intermediate elevations, and coniferous forests at high elevations.

14.2 Ecosystem Responses to N Deposition

Potential nitrogen (N) deposition impacts to the southern highlands are likely to be similar to those described for Mediterranean California and North American Deserts ecoregions (Chapters 13 and 12), where similar vegetation types occur. In the lowlands, ecosystem responses to N deposition might include increases in exotic species, an effect which can lead to the accumulation of fire-sustaining fuel loads and thus increased fire frequency and severity. Other potential effects to lowland ecosystems include alteration of mycorrhizal fungal diversity, abundance, and functioning; shifts in lichen communities; and alteration of biotic crust composition as reported for other desert areas (see Chapter 12).

At intermediate elevations, ecosystem responses to N deposition might include alteration of lichen community composition or functional groups. Further increases in N deposition might affect mycorrhizae and herbaceous plant communities.

In the uplands, ecosystem responses to N at current deposition inputs likely include changes in lichen communities. We hypothesize that if N deposition increased two- to threefold (to approximately 12 to 18 kg ha^{-1} yr^{-1}), many effects reported for mixed conifer forests (see Chapter 13) would become apparent within a few years as N accumulates in the ecosystem. These expected effects would include elevated nitrate (NO_3^-) leaching and nitrogenous trace gas emissions from soil, impaired root production, altered mycorrhizal community composition and function, increased susceptibility to pests, and possible effects on understory biodiversity.

14.3 Range of Responses Observed

As we were not able to identify U.S. studies documenting a particular ecosystem response at a given level of N input for this ecoregion, we focus instead on the reported deposition for the U.S. ecoregion and documented ecosystem responses not linked to a specific N level.

The Chiricahua National Monument, a semi-arid site with sparse vegetation cover, is designated a Class I airshed under the Clean Air Act, with management objectives of clear views to 100 miles in any direction (NPS 2006). Threats to air quality include smelting and power plants in Mexico, but especially future plans for power plants within 50 miles of the border. Because both smelting and coal-fired power plants produce sulfur oxides (SO_x), the greater ecological threats in past decades may have come from sulfur (S) rather than N deposition. However, based on temporal trends in the National Atmospheric Deposition Program (NADP) and Clean Air Status and Trends Network (CASTNET) data at the Chiricahua site, N deposition is now greater than S deposition. Sulfur emissions have decreased in this area since around 1999 (US EPA 2008b), when smelters in Playas, New Mexico, and Cananea, Sonora, Mexico, closed. Total S deposition over the past several years as reported by NADP and CASTNET is approximately 1.2 kg ha^{-1} yr^{-1}. Even if the dry deposition of S is underestimated, S deposition levels would still be considered low.

The NADP and CASTNET data report total annual N deposition of 2 to 3 kg ha^{-1} yr^{-1} over the past 15 years at the Chiricahua site (US EPA 2008a). Average annual precipitation at the monitoring site is approximately 400 mm. Reported values of wet N deposition are three times greater than those for dry N deposition, suggesting that the CASTNET modeling approach is underestimating dry deposition and thus total deposition, as has been reported by CASTNET data for other semi-arid sites in the western United States (Fenn et al. 2009). According to NADP data, wet deposition of ammonium (NH_4^+) is similar to wet deposition of NO_3^-. However, dry deposition of ammonia (NH_3) is not measured, and as a result, total N deposition is almost certainly greatly underestimated.

In our judgment, bulk N deposition at the Chiricahua NADP site is likely closer to 4 to 5 kg ha^{-1} yr^{-1}. Depending on leaf area index, deposition to canopies in areas with significant vegetation cover would be even higher. Nitrogen deposition in this region was estimated to be 4 to 7 kg ha^{-1} yr^{-1}, by the Environmental Protection Agency's Models-3/Community Multiscale Air Quality (CMAQ) model (Byun and Schere 2006) and 2002 emissions data (Fenn et al. 2003b). Based on these estimates, we hypothesize that N deposition in the Chiricahua National Monument occurs at levels that can affect sensitive ecosystem components such as lichen community composition. Other possible effects of incipient N enrichment are community shifts of annual plant species (Fenn et al. 2003a). However, lichen communities likely have also been affected by historical S emissions from copper smelters in the region.

In the San Simon Valley, near Portal, Arizona, and adjacent to the Chiricahua National Monument, the winter annual plant community has undergone marked community change associated with the sustained proliferation of stork's bill (*Erodium cicutarium*), the Eurasian invasive winter annual plant (Schutzenhofer and Valone 2006). As a result, winter annual plant diversity has declined drastically and species composition has shifted. Possible factors contributing to these plant community changes are changes in climate, including decreased winter precipitation and more frequent drought, N deposition from agricultural fields and copper smelters (Bytnerowicz 2009[22]), and changes in the rodent community (Ernest et al. 2000). Preliminary atmospheric concentration data for NO_3^- and nitric acid (HNO_3) measured from December 2006 to January 2007 in the San Simon Valley were higher than expected for a remote site.[22]

14.4 Future Research Directions and Gaps in Data

Little is known about the effects of N deposition in the Southern Semi-Arid Highlands, as they have not been studied. N deposition needs to be measured within the major ecosystem types. Ecological effects should be investigated by surveying for sites showing N accumulation and enrichment associated with N deposition. Sulfur deposition levels and effects from past and current S deposition should also be evaluated. Where lichen communities occur, they can be surveyed for community shifts and S and N accumulation as early sentinels of ecosystem change and response to air pollution.

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[22] Bytnerowicz, A. 2009. Personal communication. Ecologist, Pacific Southwest Research Station Forest Fire Laboratory, 4955 Canyon Crest Drive, Riverside, CA 92507.

LITERATURE CITED

Byun, D.; Schere, K.L. 2006. **Review of the governing equations, computational algorithms, and other components of the Models-3 Community Multiscale Air Quality (CMAQ) modeling system.** Applied Mechanics Reviews. 59: 51-77.

CEC (Commission for Environmental Cooperation). 1997. **Ecological regions of North America. Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (May 24, 2010).

Ernest, S.K.M.; Brown, J.H.; Parmenter, R.R. 2000. **Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources.** Oikos. 88: 470-482.

Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W.; and Neitlich, P. 2003a. **Ecological effects of nitrogen deposition in the western United States.** BioScience. 53: 404-420.

Fenn, M.E.; Haeuber, R.; Tonnesen, G.S.; Baron, J.S.; Grossman-Clarke, S.; Hope, D.; Jaffe, D.A.; Copeland, S.; Geiser, L.; Rueth, H.M.; Sickman, J.O. 2003b. **Nitrogen emissions, deposition, and monitoring in the western United States. BioScience.** 53: 391-403.

Fenn, M.E.; Sickman, J.O.; Bytnerowicz, A.; Clow, D.W.; Molotch, N.P.; Pleim, J.E.; Tonnesen, G.S.; Weathers, K.C.; Padgett, P.E.; Campbell.; D.H. 2009. **Methods for measuring atmospheric nitrogen deposition inputs in arid and montane ecosystems of western North America.** In: Legge, A.H., ed. Developments in environmental science. Relating atmospheric source apportionment to vegetation effects: Establishing cause effect relationships. Vol. 9. Amsterdam: Elsevier: 179-228.

NPS (National Park Service). 2006. **Chiricahua National Monument—air quality.** Washington, DC: U.S. Department of Interior, National Park Service, Chiricahua National Monument. Available at http://www.nps.gov/chir/naturescience/airquality.htm (Accessed May 12, 2010).

Schutzenhofer, M.R.; Valone, T.J. 2006. **Positive and negative effects of exotic *Erodium cicutarium* on an arid ecosystem.** Biological Conservation. 132: 376-381.

US EPA (U.S. Environmental Protection Agency). 2008a. **Clean air status and trends network—Chiricahua, total N.** Washington, DC: U.S. Environmental Protection Agency. Available at http://epa.gov/castnet/javaweb/charts/CHA467_totn.png (Accessed March 28, 2011).

US EPA (U.S. Environmental Protection Agency). 2008b. **Clean air status and trends network—Chiricahua, total S.** Washington, DC: U.S. Environmental Protection Agency. Available at http://epa.gov/castnet/javaweb/charts/CHA467_tots.png (Accessed March 28, 2011).

15 TEMPERATE SIERRAS

M.E. Fenn, L.H. Geiser

15.1 Ecoregion Description

Much of the Temperate Sierras ecoregion is located in Mexico, but a northern portion of this ecoregion is found in the southwestern United States (mainly in Arizona and New Mexico) (CEC 1997, Fig. 2.1). The ecoregion description is adapted from CEC (1997). Forested montane regions are typically surrounded at lower elevations by arid and semi-arid deserts, scrublands, or grasslands. Vegetation can be evergreen or deciduous, and is primarily composed of conifers and oaks which grow from 10 to 30 m, sometimes reaching 50 m. This vegetative cover may comprise from one to three tree layers, one or two shrub layers, and an herbaceous stratum. This forest community is characterized by about 3000 vascular plant species, 30 percent of which are endemic to Mexico (CEC 1997).

15.2 Ecosystem Responses to N Deposition

Responses to N deposition in this ecoregion (Fenn et al. 1999, 2002a, 2002b) appear to be similar to those in the mixed conifer forest of the Mediterranean California ecoregion (Chapter 13). These effects include elevated foliar N concentrations, increased soil N cycling rates, increased N export in solution and via trace gas emissions, increased susceptibility to pests, changes in native species composition, enhanced establishment of exotic invasive species, and changes in mycorrhizal and epiphytic lichen communities. Although data on N deposition and effects are scarce for the U.S. portion of the Temperate Sierras ecoregion, under current simulated estimates (3 to 6 kg N ha^{-1} yr^{-1}) of total N deposition (Fenn et al. 2003) and National Atmospheric Deposition Program (NADP) wet deposition data, we expect that the most likely effects occurring in some areas under current deposition levels are likely to be effects on lichen communities and possibly effects on herbaceous or grass understory communities.

15.3 Range of Responses Observed

Little research has been done on N deposition effects in forests of the Temperate Sierras ecoregion in Arizona and New Mexico. However, a combination of modeling and monitoring were used to estimate N deposition fluxes for forests northeast of Phoenix, Arizona, a rapidly expanding metropolis (Fenn et al. 2003). Estimated deposition fluxes to the forested area ranged from 13 to 23 kg ha^{-1} yr^{-1}. Further measurements are needed to confirm these data and to determine the extent of the affected areas, but these estimates suggest that current levels of N deposition are likely to have significant impacts on these forests. The spatial extent of affected areas may be relatively limited.

Because we found no studies relating N inputs to ecosystem responses in the United States, we summarize research conducted in the Mexico City air basin (Fig. 15.1) within this ecoregion, as it may shed some light on the levels at which responses may be observed. Mexico City (Fig. 15.1) is located within the larger Basin of Mexico, sometimes called the valley of Mexico. The 9600 km^2 basin is defined by mountain ranges surrounding the valley floor. The Mexico City air basin refers to the ground-level atmosphere of the basin. In Mexican mountain pine (*Pinus hartwegii*) forests in the Mexico City air basin, the primary documented response to N deposition was nitrate (NO_3^-) leaching (Fenn et al. 1999, Fenn et al. 2002b). Foliar N was sometimes higher in the more polluted sites, but this result was inconsistent. Also, soil N levels did not always correspond with N deposition (Fenn et al. 1999, 2002b, 2006). The inconsistent response of foliar and soil N may be due to the inherent high soil N fertility of the volcanic soils prevalent in the Mexico City air basin (Fenn et al. 2002b, 2006). The role of N deposition in the historical and current deterioration of native lichen communities is unclear, as lichen community impacts in the Mexico City Air Basin began decades ago

Figure 15.1—The Mexico City air basin, showing major mountain ranges, towns, and Mexico City. The high N deposition forested sites studied, Desierto de los Leones and Ajusco, are in the southwestern portion of the basin. The low deposition forest sites are in the southeastern portion of the basin within the Rio Frio and Nevada mountain ranges.

when sulfur (S) emissions and deposition were much greater than current levels and greater than nitrogen oxides (NO_x) emissions. However, it is likely that as S deposition levels have decreased in the Mexico City air basin in the past decade (Fenn et al. 2002a), the relative importance of N deposition on the remaining lichen communities has increased.

In the Mexico City air basin, NO_3^- concentrations in stream and spring water were highly elevated in forested catchments south and southwest of Mexico City. Nitrogen deposition in throughfall at the highly N-saturated Desierto de los Leones National Park was 18.5 kg ha^{-1} yr^{-1} in 1996/1997 (Fenn et al. 1999). Nitrate concentrations in springs and streamwater at this site were frequently 20 to 90 µeq L^{-1} (Fenn et al. 2002b), indicating that this site is strongly N saturated. Elevated NO_3^- concentrations were also found at the Ajusco site, where N deposition is believed to be lower than at the Desierto site (Fenn et al. 2002a), but annual deposition fluxes have not been quantified. Because the Andisols in these study sites are typically high in N, even without elevated N deposition, no clear patterns of increased net N mineralization, nitrification, soil N or foliar N were observed (Fenn et al. 2002b). Nitrogen fertilization sometimes results in little plant growth response (Fenn et al. 2002b, 2006); preliminary evidence suggests a depressive growth effect from added N in the Mexico City air basin in some cases, possibly because added N induces greater phosphorus (P) deficiency (Fenn et al. 2006, 2002b). Widespread P deficiency, presumably because of the high P-fixation capacity of these Andisols (Shoji et al. 1993), and the high inherent N fertility in these study sites, may enhance the tendency of these catchments to leach NO_3^- with increasing atmospheric N deposition.

At the Ajusco Mexican mountain pine site located south and downwind of Mexico City, an unknown soil factor was highly toxic to growth of river redgum (*Eucalyptus camaldulensis)* seedlings and the percentage of short roots colonized by putative symbiotic fungi in association with external mycelium was severely reduced (Fenn et al. 2006, Perea-Estrada et al. 2005). In the absence of fertilization, the percentage of eucalyptus roots that were ecto- and endomycorrhizal was consistently lower in high deposition sites. When eucalpytus seedlings were fertilized with P alone or a combination of N and P, a strong positive plant growth response occurred and the levels of root-associated fungi no longer differed between the polluted and clean sites (Perea-Estrada et al. 2005). Furthermore, at two of the three study sites in the Mexico City air basin, added N caused a significant reduction in the number of short roots of eucalyptus seedlings colonized by symbiotic fungi with external mycelium (Perea-Estrada et al. 2005). Further mechanistic studies are needed before firm conclusions can be reached regarding the role of N deposition in the strongly growth-depressive effects of soil from the Ajusco site. However, the negative effects of added N on symbiotic root fungi and the positive effects of added P on plant growth and root-associated fungi suggest that excess N may exacerbate P deficiency, particularly if symbiotic fungi important for P uptake are inhibited by high N levels in soil.

15.3.1 Lichens

Lichen responses to air pollutants in the Temperate Sierras ecoregion have not been studied, except in the Mexico City air basin. A series of studies contrasted fir and oak forests in Desierto de los Leones and Sierra de las Cruces (both south of Mexico City) to those of El Chico National Park, a relatively unpolluted site about 100 km to the northeast. Epiphytic lichen diversity at Desierto de los Leones is severely impoverished compared to El Chico National Park. Desierto de los Leones may have lost nearly 50 percent of its lichen species and lichen abundance is reduced by 60 percent, presumably as a result of the severe air pollution at this site. Based on historical herbarium collections, the decline in lichen diversity appears to coincide with the period of accelerated industrial and population growth of Mexico City since the 1930s and 1940s (Zambrano et al. 2002). Short-term lichen transplant experiments in Sierra de las Cruces, a montane region just south-southwest and downwind of the urbanized zone, showed 30 percent lower carbon fixation and 15 to 25 percent chlorophyll degradation compared to samples in El Chico National Park (Zambrano and Nash 2000, Zambrano et al. 1999). These results suggested that chronic air pollution (ozone (O_3), N- and S-containing compounds) is a major cause of lichen decline in forests surrounding the city, along with a variety of other anthropogenic disturbance factors (Zambrano et al. 2002). In the most recent study, Valencia-Islas et al. (2007) showed that the composition and location of phenolics in thalli of the sensitive parmotrema lichen (*Parmotrema stuppeum*) and tolerant Asahina's cartilage lichen (*Ramalina asahinae*) was consistent with their contrasting survival in forests stressed by O_3 (oxidative air pollution). Such responses illustrate potential confounding effects to lichen communities by codominant acidifying and oxidative pollutants in contrast to environments dominated solely by nutrient N.

15.4 Critical Loads Estimates

We estimate a N critical load for NO_3^- leaching from pine stands in the Mexico City air basin of 15 kg ha^{-1} yr^{-1} (Table 15.1). This critical load is based on streamwater data from two regions of low N deposition east of Mexico City and two regions south and southwest of Mexico City (Fenn et al. 1999, 2002b). At the Desierto de los Leones site, where throughfall N deposition was 18.5 kg ha^{-1} yr^{-1} in 1996/1997, NO_3^- concentrations in springs and streamwater were frequently 20 to 90 μeq L^{-1} (Fenn et al. 2002b), indicating that this site is strongly N saturated and well above the critical load. Elevated NO_3^- concentrations were also found at the Ajusco site, where N deposition is believed to be lower than at the Desierto site (Fenn et al. 2002a), but annual deposition fluxes have not been quantified. Uncertainty in this estimated critical load is largely due to an insufficient number of study sites spanning a range of deposition fluxes and because deposition data are from only 1 year for throughfall from one high and one low deposition site (Fenn et al. 1999). Also note that high levels of NO_3^- leaching in the Mexico City air basin occur both during

Table 15.1—Empirical critical loads of nutrient N for Temperate Sierras ecoregion forests in the Mexico City air basin[a]. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical Load for N deposition[b] *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
New Mexico and Arizona forests	4-7	(#)	Epiphytic lichens	Assumes 60% eutroph threshold and 30-180 cm precipitation	Based on application of Geiser et al. 2010 model
Las Cruces and Chichinautzin Ranges S/SW of Mexico City	15	#	Elevated NO_3^- in stream and spring waters	Data are from Mexican mountain pine sites in the Desierto de los Leones National Park and Ajusco	Fenn et al. 1999, 2002b

[a] A variety of studies in the Mexico City air basin have demonstrated that air pollution is an important factor contributing to major changes in lichen communities, to the decline of sacred fir, and possible reductions in plant growth, root production and mycorrhizal symbionts. However, because of insufficient data and the co-occurrence of multiple pollutants, the role of N deposition is unclear and critical loads for N deposition cannot be determined without further study.

[b] Nitrogen deposition was measured as throughfall (Fenn et al. 1999).

the rainy summer growing season and during the winter dry season (Fenn et al. 1999, 2002b).

Although lichen species have disappeared and lichen communities have been severely altered in the Mexico City air basin, it is difficult to estimate a N critical load for lichen effects because of the lack of historical pollution exposure and deposition data and the potential effects of multiple pollutants. Emissions of S, N and heavy metals have been historically high; O_3 exposure until recently has been among the highest in the world (Fenn et al. 2002a). Geiser et al. (2010) developed a method for relating N deposition to lichen community response. They select a threshold for the shift in the community composition from oligotroph- to eutroph-dominated. This approach is described in detail in Chapter 4. For U.S. portions of the ecoregion, our best estimate of N critical loads for epiphytic lichens is 4 to 7 kg ha^{-1} yr^{-1}. This estimate assumes a response threshold of about 60 percent eutrophs, mean annual precipitation of 30 to 180 cm, and general applicability of the Geiser et al. (2010) model to temperate forests.

15.5 Comparison to Critical Loads for Other Regions

There are no relevant lichen data from Europe for comparison with this ecoregion; critical loads developed for North American deserts or Northwestern Forested Mountains may have some applications. The lichen data from Mexico, summarized above, demonstrate a response in lichen community structure, but no conclusions can be made regarding a N critical load because trace metals, O_3, and S and N deposition were all at high levels during the decades of rapid industrial and population growth in the Mexico City air basin (Fenn et al. 2002a).

The estimated critical load for NO_3^- leaching in the Mexico City air basin (15 kg ha^{-1} yr^{-1}) is lower than that of mixed conifer forests in Mediterranean California. This difference may be due to the high N fertility and low P availability of the Andisols common in the Mexico City air basin. Because N is not strongly limiting in the Mexico City air basin, presumably, less added N is needed to induce N losses from the ecosystem. The critical load for NO_3^- leaching in the Mexico City air basin is uncertain because it is based on only 1 year of deposition data, but assuming the deposition data approximate longer term inputs, we conclude that the Mexican forests are more prone to NO_3^- leaching than the forests of California (Fenn et al. 2008). In the Mexico City air basin with N deposition of 18.5 kg N ha^{-1} yr^{-1}, NO_3^- concentrations in stream and springwater were commonly at high levels (20 to 90 µeq L^{-1}), even during the growing season (Fenn et al. 2002b). By comparison, a throughfall deposition of 17 kg N ha^{-1} yr^{-1} was determined as the critical load for incipient increases in NO_3^- leaching (peak values above 14 µeq L^{-1}) in California mixed conifer forests during the winter dormant wet season (Fenn et al. 2008).

The critical load for incipient NO_3^- leaching in the Mexico City air basin cannot be determined without streamwater sampling and N deposition measurements from sites at intermediate levels of N deposition. Nitrogen deposition levels leading to NO_3^- leaching in the Mexico City air basin appear to be within the range described from surveys of temperate forest catchments in Europe and North America (Dise and Wright 1995, Gundersen et al. 2006, MacDonald et al. 2002, Stoddard et al. 2001).

15.6 Future Research Directions and Gaps in Knowledge

Future research could be directed at mountain forests outside of Phoenix, Arizona, to determine actual deposition fluxes and ecosystem impacts at different deposition levels. Follow up studies are needed in forests surrounding Mexico City to better understand nutrient cycling responses to N deposition of forests growing on N-rich but P-limited Andisols. Preliminary results indicate the value of developing critical load for N effects on mycorrhizal fungi, root production, and lichen communities, and of further refinement of the estimated critical load for NO_3^- leaching. Emissions of nitrogenous trace gases from soil in response to N deposition should also be investigated, particularly considering the high N concentrations in soil and the role of these gases in smog formation and climate change. The possible role of N deposition in combination with S deposition and elevated O_3 exposure merits further investigation as contributing or causal factors in the severe decline of sacred fir (*Abies religiosa*) in the more polluted regions of the Desierto de los Leones National Park (Alvarado-Rosales and Hernández-Tejeda 2002, Fenn et al. 2002a).

Forest Inventory and Analysis lichen community surveys have been completed for the parts of this ecoregion in Arizona and New Mexico. Analysis of these lichen data along depositional N gradients estimated by NADP and the Environmental Protection Agency's Models-3/Community Multiscale Air Quality (CMAQ) simulation model (Tonnesen et al. 2007) could refine the lichen-based critical load estimate for this ecoregion. More research is also needed to better understand the separate effects of acidifying and oxidizing versus fertilizing N-containing/N-derived pollutants on vegetation and lichens.

LITERATURE CITED

Alvarado-Rosales, D.; Hernández-Tejeda, T. 2002. **Decline of sacred fir in the Desierto de los Leones National Park.** In: Fenn, M.E.; de Bauer, L.I.; Hernández-Tejeda, T., eds. Urban air pollution and forests: Resources at risk in the Mexico City air basin. Ecological Studies Series, volume 156. New York, NY: Springer-Verlag: 243-260.

CEC (Commission for Environmental Cooperation). 1997. **Ecological regions of North America. Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

Dise, N.B.; Wright, R.F. 1995. **Nitrogen leaching from European forests in relation to nitrogen deposition.** Forest Ecology and Management. 71: 153-161.

Fenn, M.E.; de Bauer, L.I.; Hernández-Tejeda, T. 2002a. **Summary of air pollution impacts on forests in the Mexico City air basin.** In: Fenn, M.E.; de Bauer, L.I.; Hernández-Tejeda, T., eds. Urban air pollution and forests: Resources at risk in the Mexico City air basin. Ecological Studies Series, volume 156. New York, NY: Springer-Verlag: 337-355.

Fenn, M.E.; de Bauer, L.I.; Quevedo-Nolasco, A.; Rodriguez-Frausto, C. 1999. **Nitrogen and sulfur deposition and forest nutrient status in the valley of Mexico.** Water, Air, and Soil Pollution. 113: 155-174.

Fenn, M.E.; de Bauer, L.I.; Zeller, K.; Quevedo, A.; Rodríguez, C.; Hernández-Tejeda, T. 2002b. **Nitrogen and sulfur deposition in the Mexico City air basin: Impacts on forest nutrient status and nitrate levels in drainage waters.** In: Fenn, M.E.; de Bauer, L.I.; Hernández-Tejeda, T., eds. Urban air pollution and forests: Resources at risk in the Mexico

City air basin. Ecological Studies Series, volume 156. New York, NY: Springer-Verlag: 298-319.

Fenn, M.E.; Haeuber, R.; Tonnesen, G.S.; Baron, J.S.; Grossman-Clarke, S.; Hope, D.; Jaffe, D.A.; Copeland, S.; Geiser, L.; Rueth, H.M.; Sickman, J.O. 2003. **Nitrogen emissions, deposition, and monitoring in the western United States.** BioScience. 53: 391-403.

Fenn, M.E.; Jovan, S.; Yuan, F.; Geiser, L.; Meixner, T.; Gimeno, B.S. 2008. **Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests.** Environmental Pollution. 155: 492-511.

Fenn, M.E.; Perea-Estrada, V.M.; de Bauer, L.I.; Perez-Suarez, M.; Parker, D.R.; Cetina-Alcalá, V.M. 2006. **Nutrient status and plant growth effects of forest soils in the Basin of Mexico.** Environmental Pollution. 140: 187-199.

Geiser, L.H.; Jovan, S.E.; Glavich, D.A.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in western Oregon and Washington Forests, USA.** Environmental Pollution. 158: 2412-2421.

Gundersen, P.; Schmidt, I.K.; Raulund-Rasmussen, K. 2006. **Leaching of nitrate from temperate forests - effects of air pollution and forest management.** Environmental Reviews. 14: 1-57.

MacDonald, J.A.; Dise, N.B.; Matzner, E.; Armbruster, M.; Gundersen, P.; Forsius, M. 2002. **Nitrogen input together with ecosystem nitrogen enrichment predict nitrate leaching from European forests.** Global Change Biology. 8: 1028-1033.

Perea-Estrada, V.M.; Pérez-Moreno, J.; de Bauer, M.L.I.; Fenn, M.; Trinidad-Santos, A.; Hernández-Tejeda, T. 2005. **Fertilización, tipos de suelos y hongos micorrízicos y endófitos radicales asociados al eucalipto (*Eucalyptus camaldulensis*).** Terra Latinoamericana. 23: 201-212.

Shoji, S.; Nanzyo, M.; Dahlgren, R. 1993. **Productivity and utilization of volcanic ash soils.** In: Shoji, S.; Nanzyo, M.; Dahlgren, R., eds. Volcanic ash soils: Genesis, properties and utilization. Developments in Soil Science, volume 21. Amsterdam: Elsevier: 209-251.

Stoddard, J.L.; Traaen, T.S.; Skjelkvale, B.L. 2001. **Assessment of nitrogen leaching at ICP-Waters sites (Europe and North America).** Water, Air and Soil Pollution. 130: 781-786.

Tonnesen, G.; Wang, Z.; Omary, M.; Chien, C.J. 2007. **Assessment of nitrogen deposition: Modeling and habitat assessment.** CEC-500-2006-032. Sacramento, CA: California Energy Commission, PIER Energy-Related Environmental Research. Available at http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF (Accessed May 12, 2010).

Valencia-Islas, N.; Zambrano, A.; Rojas, J.L. 2007. **Ozone reactivity and free radical scavenging behavior of phenolic secondary metabolites in lichens exposed to chronic oxidant air pollution from Mexico City.** Journal of Chemical Ecology. 33: 1619-1634.

Zambrano, A.; Nash, T.H., III. 2000. **Lichen response to short-term transplantation in Desierto de los Leones, Mexico City.** Environmental Pollution. 107: 407-412.

Zambrano, A.; Nash, T.H., III; Gries, C. 1999. **Physiological effects of the Mexico City atmosphere on lichen transplants on oaks.** Journal of Environmental Quality. 28: 1548-1555.

Zambrano, A.; Nash, T.H., III; Herrera-Campos, M.A. 2002. **Lichens and air pollution in the forests surrounding Mexico City.** In: Fenn, M.E.; de Bauer, L.I.; Hernández-Tejeda, T., eds. Urban air pollution and forests: Resources at risk in the Mexico City air basin. Ecological Studies Series, volume 156. New York, NY: Springer-Verlag: 283-297.

16 TROPICAL AND SUBTROPICAL HUMID FORESTS

S.J. Hall

16.1 Ecoregion Description

Tropical humid forests of the United States are located below 1000 m in elevation and experience average year-round temperatures between 20 °C to 26 °C, receive more than 1500 mm of precipitation annually, and experience fewer than three dry months per year (CEC 1997; Fig. 2.2). In addition to tropical humid forests, we include in this chapter lower montane and low elevation tropical and subtropical humid forests with precipitation >1000 mm and mean annual temperatures >16 to 20 °C. Regions within the United States that contain forests of this type include coastal, low elevation, and lower montane regions: (1) on the windward slopes of the Hawaiian Islands, and (2) across Puerto Rico. Additionally, included in this chapter are (3) forests of the coastal plains of southern Florida within the greater Everglades wetland ecosystem, although mangrove and other saturated or seasonally saturated ecosystems are biogeochemically quite distinct and thus may respond differently than other, upland tropical forests discussed in this chapter. Tropical and subtropical humid forests occur in warm climates with plentiful rainfall and are thus well suited for agriculture. Consequently, many of the remaining forests of this type in the United States are in various stages of recovery following agricultural abandonment and are composed of a mix of native and exotic species. Native or primary forests in this class are highly fragmented and threatened by anthropogenic changes in land use and hydrology, and by invasive species. However, protected areas that contain forest communities less impacted by human activity compared to surrounding areas occur within each of the three regions. Some of the largest protected areas of tropical and subtropical forests in the United States include Hawai'i Volcanoes and Haleakala National Parks and a suite of forest reserves in the Hawaiian Islands; El Yunque National Forest in Puerto Rico; mangroves, tropical hammocks, and other tree islands within the Everglades and Biscayne National Parks; and protected pineland preserves in Dade and Monroe Counties, southern Florida.

16.1.1 Subtropical Humid Forests of Hawaii: Ecosystem Description

Subtropical humid forests in Hawaii are diverse, varying with rainfall and elevation, time since disturbance, degree of invasion, topography, and soil age. Native forest communities include the common dominant trees ohi'a lehua (*Metrosideros polymorpha*) and koa (*Acacia koa*), tree ferns, other common wet forest tree species (e.g., ʻōlapa [*Cheirodendron* spp.]) and Hawaiian holly (*Ilex anomala*), and a diverse understory of epiphytes and shrubs. Rates of endemism in the Hawaiian Islands are among the highest in the world, in part due to their isolated geography. Notable among these communities is a diversity of endemic birds and lobelioids, which are a special group of flowering plants in the Campanulaceae (bellflower) family. Few, purely native Hawaiian wet forest communities exist at low elevations but instead consist of a mix of native and exotic species (Zimmerman et al. 2008). However, at higher elevations, tracts of intact humid forest remain in protected areas on most islands (Ricketts et al. 1999).

16.1.2 Subtropical Humid Forests of Puerto Rico: Ecosystem Description

Subtropical humid forests of Puerto Rico are also diverse biologically and geographically, occurring primarily as secondary growth in former agricultural or pasture lands or as primary or successional growth within remnant, protected forest reserves. These ecosystems are composed of various plant communities that are associated with gradients in tidal inundation, rainfall, elevation, soil characteristics determined by geology, and time since disturbance (e.g., human, landslides, hurricanes) (Ewel and Whitmore 1973). Subtropical wet forests on volcanic soils include tabonuco forest at lower elevations in various stages of succession, dominated by abundant epiphytes and the tabonuco tree (*Dacryodes excelsa*) among others. Colorado and dwarf cloud forests grow at higher elevations, associated with trees such as palo colorado (*Cyrilla racemiflora*) and nemoca cimarrona (*Ocotea spathulata*), respectively. Forests on serpentine or limestone-derived soils are more xerophytic, supporting sclerophyllous, evergreen vegetation (Ewel and Whitmore 1973). Subtropical forests on the humid northern and southern coasts of Puerto Rico contain mixed stands of red, black, and white mangroves (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*) (Tomlinson 1986).

16.1.3 Tropical Forests of Southern Florida: Ecosystem Description

Tropical forests in southern Florida include pine rocklands and hardwood hammocks in the uplands, various 'tree islands' that are surrounded by occasional or persistent water, and coastal mangrove communities. Florida pine rocklands and tropical hardwood hammocks are located on shallow soils of limestone outcroppings in higher elevations of the Everglades (Lodge 2004). Pineland ecosystems are fire-maintained, dominated by Florida slash pine (*Pinus elliottii*) and saw palmetto (*Serenoa repens*). Tropical hardwood hammocks develop in the absence of fire, and are composed of numerous species characteristic of the Caribbean such as gumbo limbo (*Bursera simarouba*) and mahogany (*Swietenia mahogani*). Pinelands and hardwood hammocks are highly threatened by urbanization and land-use change, composing 2 percent of their former range (Ricketts et al. 1999). Mangroves are extensive along the southern Florida coastline, providing habitat for a variety of marine, estuarine, and terrestrial species of mammals, birds, reptiles, invertebrates, and fish. These forests are dominated by red, black, and white mangroves, and buttonwood (*Conocarpus erectus*). Various other tree islands exist in the Everglades ecosystem, maintained by seasonal hydroperiods and serving as biogeochemical and floral hotspots on the flooded landscape (Sklar and van der Walk 2002). Common species within tree islands in the Everglades include the strangler fig (*Ficus aurea*) and coco plum (*Chrysobalanus icaco)*, among others (Wetzel et al. 2008).

16.2 Ecosystem Responses to N Deposition

Few studies have explored the impacts of nitrogen (N) enrichment on ecological processes in tropical and subtropical humid forests worldwide, and none have explicitly assessed the consequences of atmospheric N deposition in the three tropical ecoregions of the United States. However, exceptional, long-term N addition experiments within native ecosystems of Florida and Hawaii have contributed greatly to our understanding of tropical forest functioning (Table 16.1; Feller et al. 2007, 2009; Vitousek 2004). Existing studies used high rates of fertilizer addition primarily to assess nutrient limitation of vegetation and thus are not useful in identifying thresholds of response to N inputs. Nonetheless, these fertilization experiments and others do suggest that plant growth and ecosystem processes in some humid tropical and subtropical forests may be susceptible to N enrichment while others may be less susceptible, depending on numerous factors that alter forest nutrient status.

In the following sections we summarize the types and range of ecosystem responses to N fertilization observed in native U.S. tropical and subtropical forests. However, because the consequences of N deposition have not been well studied in these regions, evidence is also included from fertilization studies in other tropical forests that may operate similarly to those in Hawaii, Puerto Rico, and southern Florida. Data from non-U.S. forests are used only as supporting evidence; thus, information in this chapter is not intended to be a thorough review of ecosystem responses to N deposition or fertilization in tropical/subtropical forests worldwide. Information from non-U.S. regions is noted where included.

Nutrient limitation of primary production cannot be assessed using indirect measures of ecosystem N availability or cycling (Tanner et al. 1998). However, without abundant data, we broadly characterize tropical forests as relatively 'N-rich' or 'N-poor' and summarize the responses observed in these systems following N fertilization or those expected following N deposition.

In N-rich tropical and subtropical forests where primary production or nutrient cycling may be limited by factors other than N, N enrichment is not expected to change plant growth or species composition, although some evidence suggests that tissue chemistry, decomposition, and herbivory may be altered in some ecosystems (Benner and Vitousek 2007, Feller et al. 2007, Ostertag

Table 16.1—Responses to long-term N-fertilization of native tropical and subtropical humid forests of the United States and related ecosystems.[a]

Site Location		Hawaii, Lower montane forests		Florida and Belize, Coastal mangrove forests	
Forest Type		N-limited, *M. polymorpha* (ohi'a lehua)	P-limited, *M. polymorpha* (ohi'a lehua)	N-limited, Florida	P-limited, Belize
Type of N Deposition		Wet, dry, fog	Wet	Wet	Wet + dry
N Deposition kg ha^{-1} yr^{-1}		17	< 1	4	2
N Fert. Rate kg ha^{-1} yr^{-1}		100	100	>100	>100
Form of N Fertilizer		Urea/NH_4NO_3	Urea/NH_4NO_3	Urea	Urea
Start year		1985	1991	1997	1997
Duration (years)		11-13	5-7	2-4	2-4
--Response relative to Control [b]--	Tree growth	+	0	+	0
	Foliar %N	+/0	+	+	0
	Herbivory	ND	ND	+	-
	Plant community composition	+	0	ND	ND
	Epiphyte abundance	ND	0	ND	ND
	Decomposition	0	+	ND	ND
	Soil C:N	0	0	ND	ND
	N mineralization	+	+	ND	ND
	Nitrification	+	+	ND	ND
	Microbial biomass N	0	0	ND	ND
	N-oxide emissions	+	+	ND	ND
	NO_3^- leaching	+	+	ND	ND
	Soil pH	0	0	0	0
References		1-7	1-8	9-11	11,12

[a] Studies from Belize included to illustrate differences in ecosystem response to N fertilization in N-limited (Florida) vs. P-limited mangrove ecosystems.

[b] Responses are indicated as increase (+), decrease (–), or no response (0) in fertilized relative to control plots, or no data (ND) in indicated references.

References: 1) Vitousek et al. 1993; 2) Harrington et al. 2001; 3) Ostertag and Hobbie 1999; 4) Lohse and Matson 2005; 5) Hall and Matson 2003; 6) Ostertag and Verville 2002; 7) Cordell et al. 2001; 8) Benner et al. 2007; 9) Caccia and Boyer 2007; 10) Feller et al. 2003a; 11) Feller et al. 2007; 12) Howarth et al. 1996.

and Hobbie 1999, Ostertag and Verville 2002). On the other hand, N addition to N-rich tropical forests may immediately increase N losses as gases (NO_x, N_2O, or N_2) or in drainage, but this response depends in large part on soil properties, redox conditions, and hydrological pathways (Hall and Matson 2003, Herbert and Fownes 1995, Lohse and Matson 2005, Templer et al. 2008). Rivers that drain N deposition-affected tropical forests may experience increases in nitrate (NO_3^-) relative to dissolved organic N, which is the form of N that typically dominates export of undisturbed tropical catchments (Downing et al. 1999, Lewis et al. 1999; reviewing tropical forests in the Americas and worldwide).

In tropical and subtropical forests where N availability is relatively low, ecosystem responses to atmospheric N deposition are expected to be similar to temperate forests and include increased plant growth, elevated rates of soil N cycling, increased foliar N concentration

Table 16.2—Empirical critical loads of nutrient N for the Tropical and Subtropical Humid Forests ecoregion. Reliability rating: (#) – expert judgment; no data are available for this ecosystem category. The critical load is based on expert judgment and knowledge of ecosystems which may function similarly.

Ecosystem component	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
N-poor tropical and subtropical forests	5-10	(#)	Changes in community composition; NO_3^- leaching, N trace gas emissions	Critical load for N-poor forests based on estimates for Southeastern Coastal Plain forests	ND
N-rich tropical and subtropical forests	<5-10	(#)	NO_3^- leaching, N trace gas emissions	Critical load for N-rich forests should be lower than for N-poor forests based on possibility of N losses	ND

and herbivory of some plant species, possible changes in community composition, and eventually elevated N losses as NO_3^- or as gases as ecosystems become N saturated (Erickson et al. 2001, Feller et al. 2007, Hall and Matson 2003, Lohse and Matson 2005, Ostertag and Verville 2002, Vitousek and Farrington 1997). However, unlike in some temperate forests, atmospheric N deposition may be retained first in the canopy rather than the forest floor (Wanek et al. 2007), for example, stimulating nutrient cycling and growth within epiphyte communities that intercept cloud and rainwater (Clark et al. 2005, Reich et al. 2003; both in Costa Rica).

Alkaline soils in Puerto Rico and southern Florida can be expected to have high acid neutralizing capacity that may buffer acidity derived from N deposition. In contrast, highly weathered, poorly buffered volcanic soils in Puerto Rico and Hawaii or peat soils in Florida may be more susceptible to the negative effects of acidity, including elevated aluminum mobility and phosphorus (P) fixation in soils that can further limit primary production (Asner et al. 2001; Matson et al. 1999, 2002; all review tropical forests worldwide). Alkaline sea salt aerosols and dust likely enter coastal tropical forests but it is unclear whether these inputs will mitigate the impacts of acidity generated from deposition and microbial N cycling in soils (Evans et al. 2004 for Florida; Vogt et al. 2007 for a review of tropical forests worldwide).

16.3 Range of Responses Observed

Although small in their geographical extent within the United States, tropical and subtropical humid forests harbor an extraordinary diversity of soil types, species, plant assemblages, landscape characteristics, and landscape histories that will likely vary in their sensitivity to N enrichment (Nardoto et al. 2008 in Brazil; Townsend et al. 2008 for tropical forests worldwide). Furthermore, few studies have tested nutrient limitation of plant growth in tropical or subtropical forests or have explored soil and microbial responses to N additions in these regions, further compounding the uncertainty about how these forests will respond to N deposition.

16.3.1 N-Rich Tropical and Subtropical Forests

Worldwide, many tropical and subtropical forests are rich in N relative to other limiting factors, such as P, and are thus expected to respond to N deposition differently than N-limited forests in the temperate zone. For example, some tropical forests grow on geomorphically stable, highly weathered soils that contain few remaining primary minerals, leading to low available pools of rock-derived nutrients such as potassium (K), calcium (Ca), magnesium (Mg), or P relative to N (Chadwick et al. 1999, Walker and Syers 1976). Other tropical forests, such as those in south Florida, are low in available P relative to N due in part to their growth on geologic substrates that lack P-bearing minerals or are subject to abiotic conditions that restrict P solubility (Noe et al. 2001, Troxler Gann et al. 2005). Additionally, many tropical forests support an abundance of legumes and other N-fixing plant species that can lead to large available N pools in soil (Vitousek et al. 2002), including both mature forests and successional plant communities that are recovering from agricultural abandonment (Erickson et al. 2001).

In these cases, plant growth can be limited by elements or factors other than N, which may limit the ability of these forests to retain atmospheric N deposition within plant reservoirs. Because N cycles in relative excess compared to other nutrients in these systems, these humid tropical forests exhibit naturally high rates of NO_3^- leaching and N trace gas emissions compared to temperate forests (Davidson et al. 2007, Lewis et al. 1999, Matson and Vitousek 1990, Martinelli et al. 1999; all in tropical forests worldwide). Thus, it has been hypothesized that N-rich, P-limited wet tropical forests are 'naturally N saturated' and will have little ability to retain additional N in biotic pools, possibly leading to elevated N losses to aquatic systems and the atmosphere (Hall and Matson 1999).

Few studies have tested this hypothesis at low levels of N inputs that simulate expected rates of atmospheric deposition in humid tropical forests of the United States and abroad. In a dose-response experiment in lower montane forests of Hawaii, Hall and Matson (1999) found immediate and elevated nitrous oxide (N_2O) and nitric oxide (NO) emissions from soils after first-time application of 15 kg N ha^{-1} as ammonium nitrate (NH_4NO_3) in a P-limited forest on the island of Kaua'i that received <1 kg N ha^{-1} yr^{-1} in ambient wet deposition (Carillo et al. 2002, Hall and Matson 1999). However, N-oxide emissions from this forest were not elevated following application of 5 kg N ha^{-1}. Similar patterns were found after a dose-response experiment in an N-rich, P-poor lowland tropical rain forest in southeast Asia that experienced higher rates of soil N-oxide emissions compared to unfertilized controls after application of 15 kg N ha^{-1} (Hall et al. 2004).

If excess N is not effectively retained in biotic reservoirs, N-rich tropical forests might also be expected to respond to N deposition with elevated NO_3^- losses. However, acidic, highly weathered soils often contain variably charged, subsurface, clayey horizons that can impede water infiltration and retain anions such as NO_3^- on clay particles. For example, in the same Hawaiian lower montane forests described earlier, Lohse and Matson (2005) found that NO_3^- leaching was restricted by clay layers in the P-limited forest after both first-time and long-term N fertilization with 50 kg N ha^{-1}, despite lack of retention by biota, whereas NO_3^- was readily leached after similar rates of fertilization in an N-limited forest that was well drained (Lohse and Matson 2005). Other factors associated with humid tropical forests may also favor NO_3^- retention, even when N cycles in relative excess. For example, forests in Puerto Rico support high rates of dissimilatory nitrate reduction to ammonia (NH_3) (DNRA), an anaerobic microbial process that consumes NO_3^- anions (Silver et al. 2001). DNRA was once thought to occur primarily in aquatic sediments but now appears to be a NO_3^- retention pathway favored by variable redox conditions characteristic of upland tropical forest soils (Pett-Ridge et al. 2006, Templer et al. 2008).

In N-rich humid tropical forests, it is expected that atmospheric N deposition will have relatively small direct effects on plant growth or community composition. For example, long-term N fertilization with 100 kg N ha^{-1} yr^{-1} had no effect on epiphytic cyanolichen abundance, diversity, or N-fixation capacity in P-limited and N+P co-limited lower montane rain forests in Hawaii (ambient N deposition < 1 kg N ha^{-1} yr^{-1} and ≤ 17 kg N ha^{-1} yr^{-1}, respectively) (Benner et al. 2007, Benner and Vitousek 2007, Carillo et al. 2002). Similarly, in an N-rich Hawaiian lower montane forest, N additions had no effect on plant growth or species richness and composition (Harrington et al. 2001, Ostertag and Verville 2002). Some responses to N deposition in upland tropical forests hold for mangrove ecosystems as well: fertilization with >100 kg N ha^{-1} yr^{-1} in a P-limited, dwarf black mangrove ecosystem in Belize had no impact on plant growth or morphology (Feller et al. 2007). Although N deposition may not alter plant growth in forests that are not limited by N, chronic N inputs to acidic, poorly buffered humid tropical forest soils may affect soil properties such as pH, aluminum mobility, and P fixation that may indirectly decrease tropical forest growth over the long term (Asner et al. 2001, Matson et al. 1999; both describing tropical forests worldwide). However, few studies have tested these hypotheses in the field.

While plant growth or community composition in relatively N-rich tropical and subtropical forests may not be affected by N deposition, tissue chemistry of some plant species may be more sensitive to changes in N supply. For example, N additions increased foliar N concentrations and the decomposability of leaf and fine roots in P-limited Hawaiian lower montane forests (Ostertag and Hobbie 1999), and they increased litter N concentrations in lowland Panamanian forests that were not limited by N or P (Kaspari et al. 2008). However, based on the few studies that have measured these responses, this effect is not consistent across ecosystem types. For instance, N additions to a P-limited red mangrove stand in Belize and an N+P-limited red mangrove stand in Panama had no effect on foliar N or N:P ratios, or the amount of leaf area damaged by herbivores (Feller and Chamberlain 2007, Lovelock et al. 2004).

16.3.2 N-Poor Tropical and Subtropical Forests

While many humid tropical forests are relatively N rich, numerous processes can replenish rock-derived nutrients or increase N losses relative to other elements, thus promoting N limitation or conservative N cycling (LeBauer and Treseder 2008). These processes include deposition of transported dust or sea salt aerosols, erosion, fire, and other disturbances such as forest clearing that increase N losses or N sinks in vegetation (Chadwick et al. 1999, Davidson et al. 2007, Porder et al. 2005, Scatena and Lugo 1995; in Amazon forests). For example, much of the forested land area in Puerto Rico is successional, as >75 percent of the landscape is affected by hurricanes or landslides each century (Lugo and Scatena 1996, Walker et al. 1996). These disturbances can cause N losses to the atmosphere and water that may remain elevated for years until biological sinks are re-established (Erickson and Ayala 2004, McDowell et al. 1996, Schaefer et al. 2000). Combined, these spatially and temporally heterogeneous factors will likely cause variation in the extent of N retention in humid tropical and subtropical forests in response to atmospheric N deposition.

Measures of nutrient availability are often correlated with the responsiveness of plant growth to fertilization but are not sufficient to establish nutrient limitation (Tanner et al. 1998). However, evidence in the literature suggests that many tropical forests in the United States with low N availability will respond to N deposition in ways similar to temperate forests, with increased rates of primary production and foliar N concentrations, and potentially increased soil N cycling and N gas emissions over time. For example, emissions of N_2O and NO were elevated after 6 years of complete nutrient additions (300 kg N ha^{-1} yr^{-1} and 100 kg P ha^{-1} yr^{-1} plus cations; ambient deposition of 4 to 9 kg N ha^{-1} yr^{-1}) in a >60-yr-old tropical forest in Puerto Rico that cycled N conservatively (Erickson et al. 2001, Ortiz-Zayas et al. 2006). In a strongly N-limited, lower montane forest on the island of Hawai'i, NO_x emissions were elevated, but relatively low after application of ≥25 to 50 kg N ha^{-1}, but long-term N additions of 100 kg N ha^{-1} yr^{-1} increased rates of net N mineralization and nitrification in soils (ambient deposition of 17 kg N ha^{-1} yr^{-1}, primarily as fog from active volcanic sources) (Carillo et al. 2002, Hall and Matson 2003). Long-term N additions to this N-limited Hawaiian lower montane forest also altered species composition and decreased species richness, moss cover, and native seedling abundance (Ostertag and Verville 2002). However, decomposition rates were not affected by N additions, suggesting that carbon (C) mineralization rates were limited more strongly by C quality than nutrient availability (Hobbie 2000).

Growth of mangrove forests in Florida is limited by N in some regions and P in others, varying across small scales within mangrove stands (Feller et al. 2003b, 2007) and across landscape gradients of tidal inundation that restrict availability of nutrients under saline conditions (Boyer 2006, McKee 1995). In an N-limited black mangrove ecosystem in Florida (ambient deposition ~ 4.1 kg N ha^{-1} yr^{-1}) (Caccia and Boyer 2007), N additions of >100 kg N ha^{-1} yr^{-1} increased growth (wood allocation and shoot elongation), altered foliar chemistry (increased N and P resorption efficiency and foliar N concentrations; decreased C:N ratios of green and senescent tissue), and increased herbivory by some species (Feller et al. 2007). Plants are known to decrease N resorption from senescing tissue with increasing N availability, although the strength of this process varies widely across species (Norris and Reich 2009). In N-limited lagoons in Florida, increased N resorption in N fertilized mangrove stands may have resulted from simultaneous changes in P dynamics (Feller et al. 2007). In contrast, N fertilization had no effect on leaf area ratio, specific leaf area, photosynthetic rates, or hydraulic traits of N-limited black mangrove stands (Lovelock et al. 2006). Other work shows that the impact of N enrichment may also depend on species composition. For example, Feller et al. (2003b) and Lovelock et al. (2004) found that N fertilization had no impact on N resorption efficiencies in N+P-limited red mangroves in Panama or N-limited (seaward fringe), N+P-limited (transition zone), or P-limited (forest interior) red mangroves in Belize. Also, unlike in N-limited black mangroves, N fertilization in N+P limited red mangroves in Panama had no effect on the fraction of leaf area damaged by herbivores (Lovelock et al. 2004).

Although N may be retained in some N-poor tropical forests as in temperate systems, the mechanisms of N retention may differ depending on the structure of tropical plant communities. For example, high year-round leaf area of tropical forests may act to retain N in canopies, intercepting N deposition before it reaches microbial and plant communities of the soil and forest floor (Bakwin et al. 1990, Sparks et al. 2001). In a study of cloud forests in Costa Rica, epiphytes within the canopy retained 50 percent of the N applied experimentally in the laboratory and field, leading to higher foliar N concentrations in bryophyte species (Clark et al. 2005). In mangrove ecosystems of Belize, ammonium (NH_4^+) in bulk precipitation was retained in the canopy in an N-limited stand, but not in a P-limited stand, decreasing throughfall fluxes of N compared to rainwater (Wanek et al. 2007). These data suggest that change in composition or chemistry of foliage or canopy epiphyte communities may indicate initial stages of N saturation of tropical forest ecosystems.

Finally, recent work suggests that after disturbance in some tropical forests, N limitation may be short-lived. For example, tropical forests in the Amazon supported low rates of N cycling early in succession following agricultural abandonment, but returned to ‘leaky’ N cycling similar to N-rich, mature tropical forests within decades (Davidson et al. 2007).

16.4 Critical Loads Estimates

Estimates of critical loads of N in the U.S. Tropical and Subtropical Humid Forests ecoregion are uncertain due to lack of data across N deposition gradients or from low-level N addition studies. Furthermore, critical loads will depend on the form of N inputs and numerous ecosystem characteristics that influence N retention, most of which vary considerably across tropical and subtropical forests. These factors include, among others, the form of N deposition (NH_4^+ vs. NO_3^-), the extent of N limitation of primary production; spatial and temporal heterogeneity in soil organic matter, water-holding capacity, and moisture that can influence microbial N cycling processes (e.g., nitrification and dentrification); subsurface soil properties that may alter N leaching (e.g., retention or loss of NH_4^+ or NO_3^- from deposition will depend on soil texture and cation vs. anion exchange capacity); and composition of heterogeneous and diverse plant communities. However, in the absence of data, we estimate critical loads of 5 to 10 kg N ha^{-1} yr^{-1} for N-poor tropical and subtropical forests (e.g., some mangrove ecosystems in Florida, early successional forests or forests growing on pedogenically young substrates), within the same range as forests in the Southeastern Coastal Plain that may have similarly weathered soil types and experience warm year-round temperatures. Critical loads for N-rich tropical and subtropical forests may be lower than this level if N deposition rapidly stimulates pathways for N loss. Thus, we estimate critical loads of <5 to 10 kg N ha^{-1} yr^{-1} for N-rich tropical and subtropical forests.

16.5 Comparison to Critical Loads for Other Regions

Few estimates exist for N critical loads in tropical and subtropical forests. Studies in south China recommend high critical loads of 50 to >150 kg N ha^{-1} yr^{-1} to prevent departure from current conditions based on fertilization experiments across a range of ecosystem types (reviewed in Duan 2009). However, N deposition to Chinese subtropical forests ranges from at least 8 to 50 kg N ha^{-1} yr^{-1} (Chen and Mulder 2007a, Chen and Mulder 2007b). Thus, it is impossible to determine whether current conditions represent a change from conditions prior to elevated N deposition. Furthermore, species composition within Chinese subtropical forests varies considerably from tropical and subtropical forests in the United States. As a result, it is unclear whether critical load estimates developed for China are applicable to forests reviewed in this chapter.

16.6 Future Research, Gaps in Data, Gaps in Knowledge

Currently, tropical and subtropical forests in the United States are highly fragmented and are threatened primarily by land-use change, invasive species, and nutrient pollution from agricultural runoff. Consequently, to date no studies have evaluated the ecological consequences of atmospheric N deposition in these regions. Refined estimates of N critical loads for this ecoregion will require studies that explore ecological processes across N deposition gradients or following low-level N additions.

LITERATURE CITED

Asner, G.P.; Townsend, A.R.; Riley, W.J.; Matson, P.A.; Neff, J.C.; Cleveland, C.C. 2001. **Physical and biogeochemical controls over terrestrial ecosystem responses to nitrogen deposition.** Biogeochemistry. 54(1): 1-39.

Bakwin, P.S.; Wofsy, S.C.; Fan, S. 1990. **Measurements of reactive nitrogen oxides (NO_y) within and above a tropical forest canopy in the wet season.** Journal of Geophysical Research. 95(D10): 16765-16772.

Benner, J.W.; Conroy, S.; Lunch, C.K.; Toyoda, N.; Vitousek, P.M. 2007. **Phosphorus fertilization increases the abundance and nitrogenase activity of the cyanolichen *Pseudocyphellaria crocata* in Hawaiian montane forests.** Biotropica. 39(3): 400-405.

Benner, J.W.; Vitousek, P.M. 2007. **Development of a diverse epiphyte community in response to phosphorus fertilization.** Ecology Letters. 10(7): 628-636.

Boyer, J.N. 2006. **Shifting N and P limitation along a north-south gradient of mangrove estuaries in south Florida.** Hydrobiologia. 569: 167-177.

Caccia, V.G.; Boyer, J.N. 2007. **A nutrient loading budget for Biscayne Bay, Florida.** Marine Pollution Bulletin. 54(7): 994-1008.

Carillo, J.; Hastings, M.G.; Sigman, S.M.; Huebert, B.J. 2002. Atmospheric deposition of inorganic and organic nitrogen and base cations in Hawaii. Global Biogeochemical Cycles. 16(4): 1076.

CEC (Commission for Environmental Cooperation.) 1997. **Ecological regions of North America. Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

Chadwick, O.A.; Derry, L.A.; Vitousek, P.M.; Huebert, B.J.; Hedin, L.O. 1999. **Changing sources of nutrients during four million years of ecosystem development.** Nature. 397(6719): 491-497.

Chen, X.Y.; Mulder, J. 2007a. **Atmospheric deposition of nitrogen at five subtropical forested sites in South China.** Science of the Total Environment. 378: 317-330.

Chen, X.Y.; Mulder, J. 2007b. **Indicators for nitrogen status and leaching in subtropical forest ecosystems, South China.** Biogeochemistry. 82 (2): 165-180.

Clark, K.L.; Nadkarni, N.M.; Gholz, H.L. 2005. **Retention of inorganic nitrogen by epiphytic bryophytes in a tropical montane forest.** Biotropica. 37(3): 328-336.

Cordell, S.; Goldstein, G.; Meinzer, F.C.; Vitousek, P.M. 2001. **Morphological and physiological adjustment to N and P fertilization in nutrient-limited *Metrosideros polymorpha* canopy trees in Hawaii.** Tree Physiology. 21(1): 43-50.

Davidson, E.A.; de Carvalho, C.J.R.; Figueira, A.M.; Ishida, F.Y.; Ometto, J.; Nardoto, G.B.; Saba, R.T.; Hayashi, S.N.; Leal, E.C.; Vieira, I.C.G.; Martinelli, L.A. 2007. **Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment.** Nature. 447(7147): 995-998.

Downing, J.A.; McClain, M.; Twilley, R.; Melack, J.M.; Elser, J.; Rabalais, N.N.; Lewis, W.M.; Turner, R.E.; Corredor, J.; Soto, D.; Yanez-Arancibia, A.; Kopaska, J.A.; Howarth, R.W. 1999. **The impact of accelerating land-use change on the N-cycle of tropical aquatic ecosystems: Current conditions and projected changes.** Biogeochemistry. 46(1-3): 109-148.

Duan, L. 2009. **Empirical critical loads of nitrogen in China.** In: Proceedings from a workshop on nitrogen deposition, critical loads, and biodiversity; 2009 November 16-18; Edinburgh, Scotland. Available at http://www.rivm.nl/thema/images/Poster_lei_duan_icpmm_2010_tcm61-48704.pdf [Poster] (Accessed April 21, 2011).

Erickson, H.; Ayala, G. 2004. **Hurricane-induced nitrous oxide fluxes from a wet tropical forest.** Global Change Biology. 10: 1155-1162.

Erickson, H.; Keller, M.; Davidson, E.A. 2001. **Nitrogen oxide fluxes and nitrogen cycling during postagricultural succession and forest fertilization in the humid tropics.** Ecosystems. 4(1): 67-84.

Evans, M.S.C.; Campbell, S.W.; Bhethanabotla, V.; Poor, N.D. 2004. **Effect of sea salt and calcium carbonate interactions with nitric acid on the direct dry deposition of nitrogen to Tampa Bay, Florida.** Atmospheric Environment. 38(29): 4847-4858.

Ewel, J.J.; Whitmore, J.L. 1973. **The ecological life zones of Puerto Rico and the US Virgin Islands.** Res. Pap. IITF-018. Rio Pedras, PR: U.S. Department of Agriculture, Forest Service, Institute of Tropical Forestry. 72 p.

Feller, I.C.; Chamberlain, A. 2007. **Herbivore responses to nutrient enrichment and landscape heterogeneity in a mangrove ecosystem.** Oecologia. 153(3): 607-616.

Feller, I.C.; Lovelock, C.E.; McKee, K.L. 2007. **Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus phosphorus limited mangrove ecosystems.** Ecosystems. 10(3): 347-359.

Feller, I.C.; Lovelock, C.E.; Piou, C. 2009. **Growth and nutrient conservation in *Rhizophora mangle* in response to fertilization along latitudinal and tidal gradients.** Smithsonian Contributions to the Marine Sciences. 38: 345-358.

Feller, I.C.; McKee, K.L.; Whigham, D.F.; O'Neill, J.P. 2003b. **Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest.** Biogeochemistry. 62(2): 145-175.

Feller, I.C.; Whigham; D.F., McKee, K.L.; Lovelock, C.E. 2003a. **Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida.** Oecologia. 134(3): 405-414.

Hall, S.J.; Asner, G.P.; Kitayama, K. 2004. **Land use, climate, and substrate controls over soil N dynamics and N-oxide emissions in Borneo.** Biogeochemistry. 70: 27-58.

Hall, S.J.; Matson, P.A. 1999. **Nitrogen oxide emissions after nitrogen additions in tropical forests.** Nature. 400(6740): 152-155.

Hall, S.J.; Matson, P.A. 2003. **Nutrient status of tropical rain forests influences soil N dynamics after N additions.** Ecological Monographs. 73(1): 107-129.

Harrington, R.A.; Fownes, J.H.; Vitousek, P.M. 2001. **Production and resource use efficiencies in N- and P-limited tropical forests: A comparison of**

responses to long-term fertilization. Ecosystems. 4(7): 646-657.

Herbert, D.A.; Fownes, J.H. 1995. **Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil.** Biogeochemistry. 29: 223-235.

Hobbie, S.E. 2000. **Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest.** Ecosystems. 3(5): 484-494.

Howarth, R.W.; Billen, G.; Swaney, D.; Townsend, A.; Jaworski, N.; Lajtha, K.; Downing, J.A.; Elmgren, R.; Caraco, N.; Jordan, T.; Berendse, F.; Freney, J.; Kudeyarov, V.; Murdoch, P.; Zhu, Z.L. 1996. **Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: Natural and human influences.** Biogeochemistry. 35(1): 75-139.

Kaspari, M.; Garcia, M.N.; Harms, K.E.; Santana, M.; Wright, S.J.; Yavitt, J.B.; 2008. **Multiple nutrients limit litterfall and decomposition in a tropical forest.** Ecology Letters. 11(1): 35-43.

LeBauer, D.S.; Treseder, K.K. 2008. **Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed.** Ecology. 89(2): 371-379.

Lewis, W.M.; Melack, J.M.; McDowell, W.H.; McClain, M.; Richey, J.E. 1999. **Nitrogen yields from undisturbed watersheds in the Americas.** Biogeochemistry. 46(1-3): 149-162.

Lodge, T.E. 2004. T**he Everglades handbook: Understanding the ecosystem.** Boca Raton, FL: CRC Press. 303 p.

Lohse, K.A.; Matson, P.A. 2005. **Consequences of nitrogen additions for soil losses from wet tropical forests.** Ecological Applications. 15(5): 1629-1648.

Lovelock, C.E.; Feller, I.C.; Ball, M.C.; Engelbrecht, B.M.J.; Ewe, M.L. 2006. **Differences in plant function in phosphorus- and nitrogen-limited mangrove ecosystems.** New Phytologist. 172: 514-522.

Lovelock, C.E.; Feller, I.C.; McKee, K.L.; Engelbrecht, B.M.J.; Ball, M.C. 2004. **The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panamá.** Functional Ecology. 18: 25-33.

Lugo, A.E.; Scatena, F.N. 1996. **Background and catastrophic tree mortality in tropical moist, wet and rain forests.** Biotropica. 28: 585-599.

Martinelli, L.A.; Piccolo, M.C.; Townsend, A.R.; Vitousek, P.M.; Cuevas, E.; McDowell, W.; Robertson, G.P.; Santos, O.C.; Treseder, K. 1999. **Nitrogen stable isotope composition in leaves and soils: tropical versus temperate forests.** Biogeochemistry. 46(1): 45-65.

Matson, P.A.; Lohse, K.; Hall, S.J. 2002. **The globalization of nitrogen: consequences for terrestrial ecosystems.** Ambio. 31(2): 113-119.

Matson, P.A.; McDowell, W.H.; Townsend, A.R.; Vitousek, P.M., 1999. **The globalization of N deposition: ecosystem consequences in tropical environments.** Biogeochemistry. 46(1): 152-155.

Matson, P.A.; Vitousek, P.M. 1990. **Ecosystem approach to the global nitrous oxide budget.** BioScience. 40(9): 667-672.

McDowell, W.H.; McSwiney, C.P.; Bowden, W.B. 1996. **Effects of hurricane disturbance on groundwater chemistry and riparian function in a tropical rain forest.** Biotropica. 28 4a: 577-584.

McKee, K.L. 1995. **Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors.** Oecologia 101: 448-460.

Nardoto, G.B.; Ometto, J.; Ehleringer, J.R.; Higuchi, N.; Bustamante, M.M.D.; Martinelli, L.A. 2008. **Understanding the influences of spatial patterns on N availability within the Brazilian Amazon Forest.** Ecosystems. 11(8):1234-1246.

Noe, G.B.; Childers, D.L.; Jones, R.D. 2001. **Phosphorus biogeochemistry and the impact of phosphorus enrichment: Why is the Everglades so unique?** Ecosystems. 4(7): 603-624.

Norris, M.D.; Reich, P.B. 2009. **Modest enhancement of nitrogen conservation via retranslocation in response to gradients in N supply and leaf N status.** Plant and Soil. 316(1-2): 193-204.

Ortiz-Zayas, J.R.; Cuevas, E.; Mayol-Bracero, O.L.; Donoso, L.; Trebs, I.; Figueroa-Nieves, D.; McDowell, W.H. 2006. **Urban influences on the nitrogen cycle in Puerto Rico.** Biogeochemistry. 79(3): 109-133.

Ostertag, R.; Hobbie, S.E. 1999. **Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability.** Oecologia. 121(4): 564-573.

Ostertag, R.; Verville, J.H. 2002. **Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests.** Plant Ecology. 162(1): 77-90.

Pett-Ridge, J.; Silver, W.L.; Firestone, M.K. 2006. **Redox fluctuations frame microbial community impacts on N-cycling rates in a humid tropical forest soil.** Biogeochemistry. 81(1): 95-110.

Porder, S.; Paytan, A.; Vitousek, P.M. 2005. **Erosion and landscape development affect plant nutrient status in the Hawaiian Islands.** Oecologia. 142(3): 440-449.

Reich, A.; Ewel, J.J.; Nadkarni, N.M.; Dawson, T.; Evans, R.D. 2003. **Nitrogen isotope ratios shift with plant size in tropical bromeliads.** Oecologia. 137(4): 587-590.

Ricketts, T.H.; Dinerstein, E.; Olson, D.M.; Loucks, C.J. 1999. **Terrestrial ecoregions of North America: A conservation assessment.** Washington, DC: Island Press. 452 p.

Scatena, F.N.; Lugo, A.E. 1995. **Geomorphology, disturbance, and the soil and vegetation of 2 subtropical wet steepland watersheds of Puerto Rico.** Geomorphology. 13(1-4): 199-213.

Schaefer, D.A.; McDowell, W.H.; Scatena, F.N.; Asbury, C.E. 2000. **Effects of hurricane disturbance on stream water concentrations and fluxes in eight tropical forest watersheds of the Luquillo Experimental Forest, Puerto Rico.** Journal of Tropical Ecology. 16:189-207.

Silver, W.L.; Herman, D.J.; Firestone, M.K. 2001. **Dissimilatory nitrate reduction to ammonium in upland tropical forest soils.** Ecology. 82(9): 2410-2416.

Sklar, F.; van der Walk, A., eds. 2002. **Tree islands of the Everglades.** Dordrecht, Netherlands: Kluwer Academic Publishers. 552 p.

Sparks, J.P.; Monson, R.K.; Sparks, K.L.; Lerdau, M. 2001. **Leaf uptake of nitrogen dioxide (NO_2) in a tropical wet forest: implications for tropospheric chemistry.** Oecologia. 127(2): 214-221.

Tanner, E.V.J.; Vitousek, P.M.; Cuevas, E. 1998. **Experimental investigation of nutrient limitation of forest growth on wet tropical mountains.** Ecology. 79(1): 10-22.

Templer, P.H.; Silver, W.L.; Pett-Ridge, J.; DeAngelis, K.M.; Firestone, M.K. 2008. **Plant and microbial controls on nitrogen retention and loss in a humid tropical forest.** Ecology. 89(11): 3030-3040.

Tomlinson, P.B. 1986. **The botany of mangroves.** New York, NY: Cambridge University Press. 413 p.

Townsend, A.R.; Asner, G.P.; Cleveland, C.C. 2008. **The biogeochemical heterogeneity of tropical forests.** Trends in Ecology and Evolution. 23(8): 424-431.

Troxler Gann, T.G.; Childers, D.L.; Rondeau, D.N. 2005. **Ecosystem structure, nutrient dynamics, and hydrologic relationships in tree islands of the southern Everglades, Florida, USA.** Forest Ecology and Management. 214(1-3): 11-27.

Vitousek, P.M. 2004. **Nutrient cycling and limitation: Hawai'i as a model system.** Princeton, NJ: Princeton University Press. 232 p.

Vitousek, P.M.; Cassman, K.; Cleveland, C.; Crews, T.; Field, C.B.; Grimm, N.B.; Howarth, R.W.; Marino, R.; Martinelli, L.; Rastetter, E.B.; Sprent, J.I. 2002. **Towards an ecological understanding of biological nitrogen fixation.** Biogeochemistry. 57(1): 1-45.

Vitousek, P.M.; Farrington, H. 1997. **Nutrient limitation and soil development: Experimental test of a biogeochemical theory.** Biogeochemistry. 37: 63-75.

Vitousek, P.M.; Walker, L.R.; L.Whiteaker; Matson, P. 1993. **Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park.** Biogeochemistry. 23: 197-215.

Vogt, R.D.; Guo, J.H.; Luo, J.H.; Peng, X.Y.; Xiang, R.J.; Xiao, J.S.; Zhang, X.S.; Zhao, D.W.; Zhao, Y. 2007. **Water chemistry in forested acid sensitive sites in sub-tropical Asia receiving acid rain and alkaline dust.** Applied Geochemistry. 22(6): 1140-1148.

Walker, T.W.; Syers, J.K. 1976. **The fate of phosphorus during pedogenesis.** Geoderma. 15: 1-19.

Walker, L.R.; Zarin, D.J.; Fetcher, N.; Myster, R.W.; Johnson, A.H. 1996. **Ecosystem development and plant succession on landslides in the Caribbean.** Biotropica. 28: 566-576.

Wanek, W.; Hofmann, J.; Feller, I.C. 2007. **Canopy interactions of rainfall in an off-shore mangrove ecosystem dominated by *Rhizophora mangle* (Belize).** Journal of Hydrology. 345(1-2): 70-79.

Wetzel, P.R.; Pinion, T.; Towles, D.T.; Heisler, L. 2008. **Landscape analysis of tree island head vegetation in Water Conservation Area 3, Florida Everglades.** Wetlands. 28(2): 276-289.

Zimmerman, N.; Hughes, R.F.; Cordell, S.; Hart, P.; Chang, H.K.; Perez, D.; Like, R.K.; Ostertag, R. 2008. **Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai'i.** Biotropica. 40(3): 277-284.

17 WETLANDS

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17.1 Ecosystem Description

The U.S. Clean Water Act defines wetlands as "those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions". Frequent water saturation of the soil creates anaerobic conditions and results in slow decomposition of organic matter. Wetlands in the United States support more than 4200 native plant species, of which 121 are federally threatened or endangered (NRCS 2009). Wetlands also offer key ecosystem services, such as sequestering carbon (C), providing habitat, regulating flood, maintaining water quality, and stabilizing coastal slope (US EPA 1993). About 107.7 million acres of wetlands are widely distributed in the conterminous United States (Fig. 17.1), 95 percent of which are freshwater wetlands and 5 percent are estuarine or marine wetlands (FWS 2005).

Depending on geology, position in the watershed, and climate, very different types of wetland ecosystems may develop. Wetlands have numerous classifications in North America. In general, marshes (dominated by herbaceous species) and swamps (dominated by woody species) occur on mineral soils or shallow peats. Peatlands, including ombrotrophic (raised) bogs, minerotrophic (true) fens, and transition (poor fens), are true peat-accumulating communities (Vitt 1994). Wetlands can be divided into three hydrology-based categories that are useful for discussing nitrogen (N) sources and cycling: bogs; fens, marshes, swamps, and riparian wetlands; and intertidal wetlands.

Ombrotrophic bogs are acidic, moss-dominated freshwater wetlands that receive water inputs primarily via precipitation. They develop where precipitation exceeds evapotranspiration and where there is some impediment to drainage of surplus water (Mitsch and Gosselink 2000). Bogs are especially common in the cool boreal zones of North America.

Fens, freshwater marshes, freshwater swamps, and riparian wetlands are characterized by ground and surface water inputs that are often on the same order of magnitude as precipitation (Koerselman 1989). Fens generally receive some drainage from surrounding mineral soils and, in many ecological aspects, are transitional between bogs and freshwater marshes. Freshwater marshes are characterized by tall graminoids, while freshwater swamps are forested wetlands dominated by various species (e.g., bald cypress [*Taxodium distichum*], pond cypress [*Taxodium ascendens*], white-cedar [*Chamaecyparis thyoides*], or red maple, [*Acer rubrum*]). Riparian wetlands are linear systems along rivers and streams and formed by the flooding of these streams or rivers.

Intertidal wetlands (e.g., salt marshes and mangrove swamps) develop on sheltered coasts or in estuaries where they are inundated by water with a periodicity that reflects the combination of tidal cycles and freshwater inputs (e.g., precipitation and ground water). Marine water input depends on the proximity to the coast; wetlands that occur nearest to the coast are the most saline and those towards the inland are primarily freshwater habitats (Archibold 1995, Mitsch and Gosselink 2000).

17.2 Ecosystem Responses to N Deposition

Known responses to N enrichment are generally derived from nutrient-addition studies in the field and observations along gradients of N deposition. A variety of ecological endpoints are evaluated, such as altered soil biogeochemistry, increased peat accumulation, elevated primary production, changes in plant morphology, changes in plant population dynamics, and altered plant species composition (US EPA 2008). Morris (1991) suggested the effect of N deposition on wetland ecosystems depends on the fraction of rainfall (a proxy for atmospheric N deposition) in its total water budget; the sensitivity to N deposition was suggested as bogs >

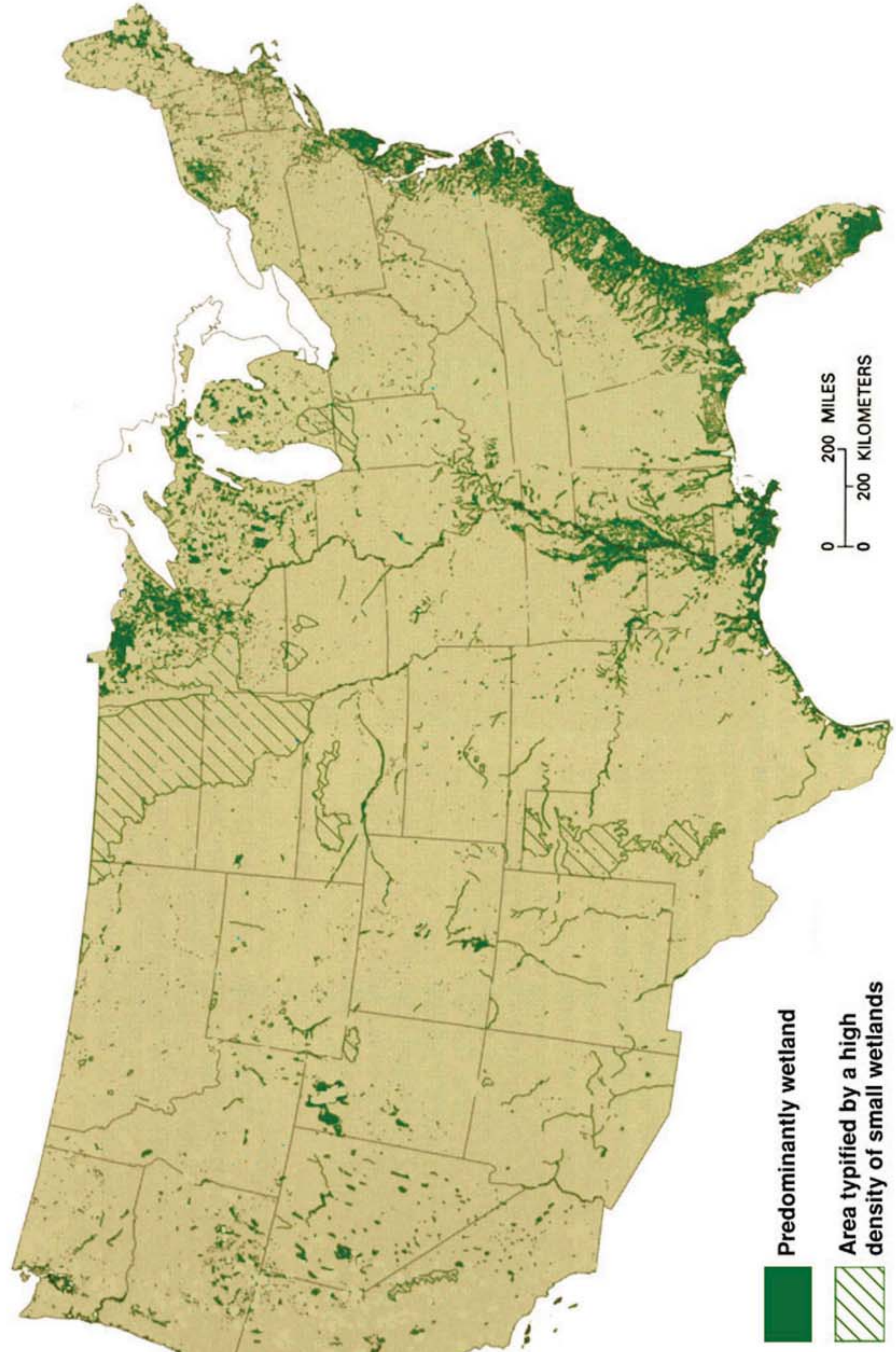

Fig 17.1—Distribution of wetlands in the United States. Source: Dahl and Allord 1997.

fens, marshes, swamps > intertidal wetlands. At the most sensitive end of the spectrum, ombrotrophic bogs receive exogenous nutrients (from external sources) primarily from precipitation, and the species in these ecosystems are adapted to low levels of N (Bridgham et al. 1995, 1996; Shaver and Melillo 1984). Intertidal wetlands are at the other end of this spectrum; in these ecosystems, N loading from marine/estuarine water sources exceed that from atmospheric inputs by one or two orders of magnitude (Morris 1991). Building on these early observations by Morris (1991), it is now generally accepted that nutrient budgets in wetland ecosystems are tightly linked with local hydrology (Bobbink et al. 2003). In general, N deposition is expected to have a larger effect on ecosystems with more closed N cycles, such as bogs, than on those with open N cycles, such as intertidal wetlands. Most data for U.S. wetlands indicates nutrient-related effects, unlike Europe, where acidification effects in wetlands are well documented.

17.3 Range of Responses Observed

Both freshwater and estuarine wetlands tend to be N-limited ecosystems (LeBauer and Tresseder 2008, US EPA 1993). Most studies evaluate short-term fertilization with high N loading that typically exceeds atmospheric deposition. Therefore, it is difficult to assess how long-term N deposition will affect N limitation, especially considering that the degree of N limitation varies among wetlands across the United States (Bedford 1999).

17.3.1 Freshwater Wetlands

Freshwater wetlands harbor large numbers of plant species that have evolved under N-limited conditions. These include quillworts (*Isoetes* spp.)*,* of which three species are federally endangered; insectivorous plants such as the endangered green pitcher (*Sarracenia oreophila);* and the genus *Sphagnum*, of which there are 15 species listed as endangered by some eastern states*.* An extensive literature survey on temperate North American wetlands found that, in general, plant communities under high nutrient supply had low species richness when compared among different wetland types (Bedford et al. 1999).

Sphagnum moss. The genus *Sphagnum* dominates ombrotrophic bogs and some nutrient poor fens in the northern United States and Canada. The species composition of bogs in both countries is similar, therefore, the Canadian data are included in the following discussion. These mosses efficiently capture atmospheric N deposition with retention rates between 50 and 90 percent; much of the variation is due to the depth of the water table (Aldous 2002a, 2002b). Studies conducted on four species of *Sphagnum* in Maine (2 to 4 kg N ha^{-1} yr^{-1} wet deposition) and New York (10 to 13 kg N ha^{-1} yr^{-1} wet deposition) document that higher wet deposition of N resulted in higher tissue N concentrations and greater net primary productivity (NPP), but lower bulk density (Aldous 2002a; Table 17.1). Note that these results are for wet deposition and not total deposition of N.

A study of *Sphagnum fuscum* in six Canadian peatlands showed a weak, although significant, negative correlation between NPP and modeled total N deposition when deposition levels were greater than 3 kg N ha^{-1} yr^{-1} (Vitt et al. 2003; Table 17.1). A study of 23 ombrotrophic peatlands in Canada with total modeled N deposition ranging from 2.7 to 8.1 kg N ha^{-1} yr^{-1} showed that peat accumulation increases linearly with N deposition. However, in recent years this rate has begun to slow, indicating a limited capacity for N to stimulate accumulation (Moore et al. 2004; Table 17.1).

In summary, documented responses to N deposition by *Sphagnum* mosses in the United States and Canada are limited to changes in N tissue concentration, bulk density, and NPP. There is additional information from European ecosystems that prolonged N deposition may ultimately lead to N saturation, leaching of excess N, and ultimately a shift in community composition. For example, N additions to a boreal bog in Europe resulted in a collapse of the *Sphagnum* mat followed by increased growth of ericaceous shrubs and the sedge, tussock cottongrass (*Eriophorum vaginatum*) (Wiedermann et al. 2007). In more southerly bogs in Europe, excess N permitted an invasion of vascular plants normally held at bay due to low N concentration because of the N-filtering capacity of mosses (Lamers et al. 2000).

Table 17.1—Response to N inputs of biological and chemical indicators for freshwater wetlands

Site	N Input *kg N ha^{-1} yr^{-1}*	Indicator	Responses	Reference
Peatlands:				
23 ombrotrophic peatlands in Canada	2.7 to 8.1	Peat accumulation	Peat accumulation increases linearly with N deposition: $y = 2.84x + 0.67$, $r^2 = 0.32$, $P<0.001$, where x is wet atmospheric N deposition from 1990-1996 (g m^{-2} yr^{-1}), y is 50-year peat N accumulation (g m^{-2} yr^{-1}). However, in recent years this rate has begun to slow, indicating limited capacity for N to stimulate accumulation	Moore et al. 2004
Six Canadian peatlands	3	*Sphagnum fuscum*	At sites with deposition levels ranging from 0.7 to 152 kg N ha^{-1} yr^{-1}, a weak, although significant, negative correlation between NPP and N deposition when deposition levels were greater than 3 kg N ha^{-1} yr^{-1}: $y = 150 - 3.4x$, $R^2=0.01$, $P=0.04$, where x is N deposition rate (kg N ha^{-1} yr^{-1}), y is NPP (g m^{-2} yr^{-1}).	Vitt et al. 2003
Poor fen in NW Ontario, Canada	4.6	*Sphagnum magellanicum*	Growth was stimulated by 4.6 kg N ha^{-1} yr^{-1} as NO_3^--N. However, additional N loading (18 kg N ha^{-1} yr^{-1} as NO_3^--N and 18 kg N ha^{-1} yr^{-1} as NH_4^+-N) did not further stimulate growth	Rochefort et al. 1990
Two bogs, Adirondacks (NY)	10 to 13 wet deposition	*Sphagnum* spp. *Polytrichum commune*	Comparison of low (2 to 4 kg N ha^{-1} yr^{-1}) and high N deposition level (10 to 13 kg N ha^{-1} yr^{-1}) showed elevated tissue N concentrations, greater NPP and lower bulk density under the higher level of deposition	Aldous 2002a
Lindsey Brook Bog, Vanceboro Bog (ME)	2 to 4 wet deposition			
Two bogs, Adirondacks (NY)	10 to 13 wet deposition	*Sphagnum* spp.	Main findings of the ^{15}N tracer experiments are 1) the two Adirondack sites had a greater N% translocation of N to the growing capitula than the Maine sites; 2) 11% of the tracer was retained in Maine and 80% in the Adirondacks; 3) atmospheric deposition is a portion of the *Sphagnum* N budget, the remaining N likely comes from N mineralization	Aldous 2002b
Lindsey Brook Bog, Vanceboro Bog (ME)	2 to 4 wet deposition			
Pitcher plant:				
Hawley Bog (MA) Molly Bog (VT)	6.8	Pitcher plant *(Sarracenia purpurea)*	Based on empirical demographics, an increase above 6.8 kg N ha^{-1} yr^{-1} would cause substantial increase in the extinction risk	Gotelli and Ellison 2002
26 bogs in Massachusetts and Vermont, US	9.76 to 16.42	Pitcher plant; [NH_4] of soil pore water	Relative keel size of *S. purpurea* increased from 0.4 to 0.7 with soil pore water NH_4 concentration increase from 0.1 to 0.5 mg L^{-1}	Ellison and Gotelli 2002
Hawley Bog (MA) Molly Bog (VT)	10 to 14	Pitcher plant	When populations occurring under low deposition (0-1.4 kg N ha^{-1} yr^{-1}) are compared to those at higher deposition (10 to 14 kg N ha^{-1} yr^{-1}), negative population growth rate is observed under higher deposition	Gotelli and Ellison 2006
Molly Bog (VT)	35	Pitcher plant	Relative keel size of *S. purpurea* was compared in two nitrogen addition treatments (0 and 35 kg N ha^{-1} yr^{-1}). Keel size increased from 0.2 to 0.8 under the higher loading	Ellison and Gotelli 2002
Prairie wetland:				
Controlled mesocoms at the University of Minnesota Horticultural Research Center (MN)	0,120, and 480	11 species in sedge meadow community common to prairies	N addition as nitrate-N 1) increased community biomass; 2) decreased the root:shoot ratio from 0.82 at 0 addition to 0.48 at 120 kg N ha^{-1} yr^{-1}, no further reduction was observed at the highest N addition level; 3) decreased community diversity and evenness between the control and highest N addition.	Green and Galatowitsch 2002

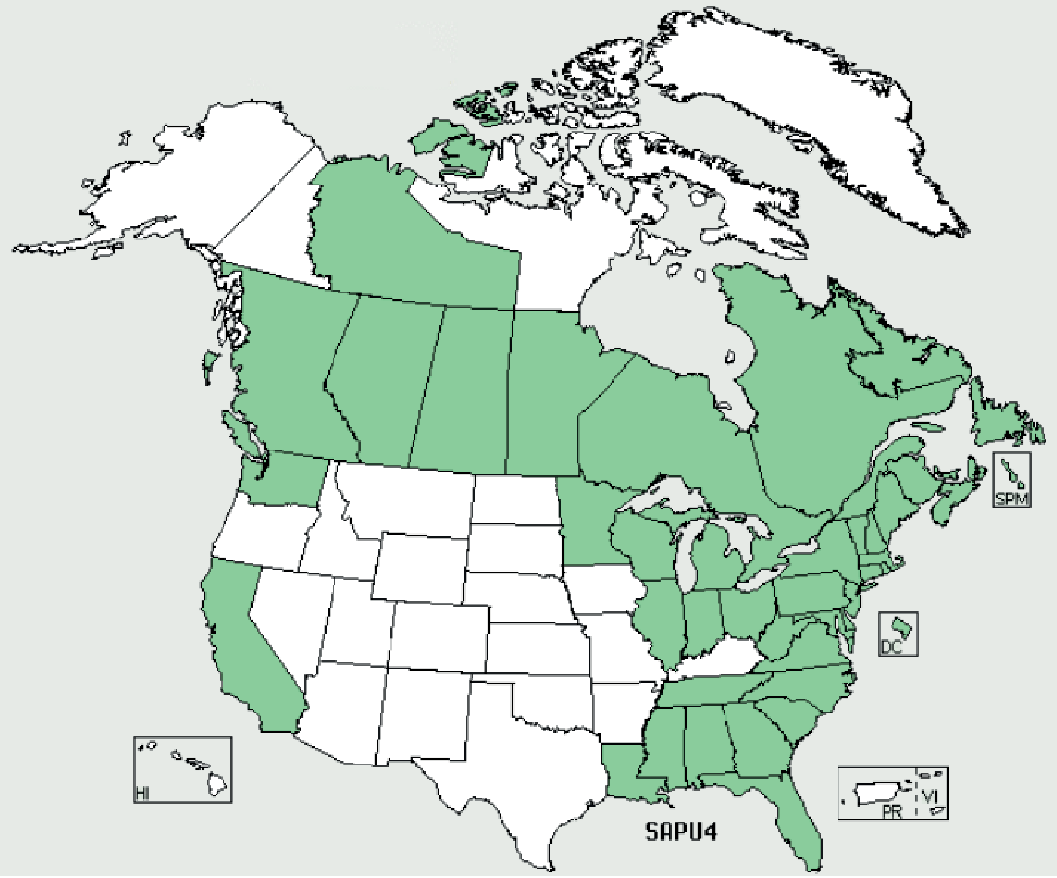

Figure 17.2—Distribution of purple pitcher plant in North America. Green denotes areas where purple pitcher plant is known to occur. Sources: USDA 2009.

Purple pitcher plant. Purple pitcher plant (*Sarracenia purpurea*), also known as northern pitcher plant, is long lived (30 to 50 years) and widely distributed in bogs, fens, and swamps across Canada and the eastern United States (Fig. 17.2; Ellison and Gotelli 2002). Purple pitcher plant has adapted to nutrient poor environments and is very sensitive to increasing N input. Purple pitcher plant was listed as vulnerable in New York, threatened in Florida, Maryland, and Michigan, and endangered in Illinois (USDA 2009). In a study of purple pitcher plant in Vermont and Massachusetts, Ellison and Gotelli (2002) conducted a series of N addition experiments by augmenting N availability to leaves with solution of 0, 0.1, and 1 mg L^{-1} nitrogen as ammonium chloride (NH_4Cl) for one growing season. Population growth rates, estimated by demographic survey, were positive for 0 and 0.1 mg N L^{-1} additions (equal to atmospheric deposition of 0 to 1.4 kg N ha^{-1} yr^{-1})[23] and negative for 1 mg N L^{-1} additions (equivalent to 14 kg N ha^{-1} yr^{-1})[23] (Gotelli and Ellison 2006; Table 17.1). Based on the annual demographic information, a nonstationary matrix model forecasted that the extinction risk within the next 100 years was small if N deposition rate was maintained at 4.5 to 6.8 kg N ha^{-1} yr^{-1}.[23] However, a small annual increase (1 to 4.7 percent) in N deposition rates would substantially increase the extinction risk (Gotelli and Ellison 2002).

Increasing N availability not only reduced population growth of purple pitcher plant, but also dramatically altered plant morphology. Purple pitcher plant produces carnivorous leaves (pitcher) and photosynthesis efficient

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[23] N treatments were selected to represent annual N deposition measured at the nearest monitoring sites of National Atmospheric Deposition Program (NADP). The unit of N treatments reported in the publication was precipitation-weighted mean concentrations (mg N L^{-1}), from which we calculated the level of deposition (kg N ha^{-1} yr^{-1}) using the equation: *deposition= precipitation-weighted mean concentrations* × *annual precipitation*. More detailed information on N deposition is available on the NADP website: http://nadp.sws.uiuc.edu/sites/ntnmap.asp

leaves (phyllodia). Nitrogen enrichment was shown to stimulate the photosynthesis rate and increase the production of phyllodia relative to pitcher (Ellison and Gotelli 2002). The field N deposition simulation experiment (treatments ranged from 0 to 35 kg N ha^{-1} yr^{-1})[23] revealed a positive linear relationship between N deposition level and relative keel size (keel width/total width, an indication of the relative size of the pitcher tube, in which prey are digested). This correlation was supported by the field surveys of 26 sites across Massachusetts and Vermont (Ellison and Gotelli 2002), and 39 sites across Canada and the eastern United States (Ellison et al. 2004). The relative keel size of northern pitcher plant increased with increasing ammonium (NH_4^+) concentration in soil water, and may be used as a bioindicator (log [NH_4^+] = -1.57 + 1.78x relative keel size).

Greenhouse Gas Flux. A recent meta-analysis evaluated the effects of N enrichment on biogenic greenhouse gas (GHG) flux from terrestrial ecosystems (Liu and Greaver 2009). In wetlands, N enrichment increased methane (CH_4) emission and nitrous oxide (N_2O) emission, but had no effect on net ecosystem exchange of C or CH_4 uptake. These results are the average response for N addition experiments on wetlands located around the world. Data is limited for the United States; there are just four field addition experiments on freshwater wetlands. Of these, three studies demonstrated a response to N addition. These are summarized in Table 17.2. In the first study, N addition of 20 and 60 kg ha^{-1} yr^{-1} in combination with 6.7 and 20 kg ha^{-1} yr^{-1} phosphorus (P) had no effect on carbon dioxide (CO_2) or CH_4 emissions from a Minnesota peatland fen (Keller et al. 2005). There is evidence that N addition increases N_2O flux from swamp forest in Louisiana and mangrove forest in Florida. However, the lowest N addition level was 100 kg ha^{-1} yr^{-1}, making it difficult to determine if N deposition would also increase N_2O flux (Lindau et al. 1994, Delaune et al. 1998, Whigham et al. 2009). A 5-year addition study indicated that net ecosystem exchange of CO_2 with the atmosphere of bogs in Ottawa, Ontario, was reduced by 45 percent with an addition of 64 kg N ha^{-1} yr^{-1} (Bubier et al. 2007).

17.3.2 Intertidal Wetlands

Nitrogen loading to intertidal wetlands tends to be much higher than loading to freshwater wetlands because, in addition to atmospheric deposition, N sources may include land runoff, ground water, marine water, and waste-water effluent. Nitrogen load to one salt marsh in Narragansett Bay, Rhode Island, was calculated to be 10,253 kg N ha^{-1} yr^{-1} (Wigand et al. 2003), an extremely high value. Compared to N brought in by tidal water and ground water (typically 565 to 668 kg N ha^{-1} yr^{-1}), the N deposited directly to the surface of coastal marshes (~ up to 30 kg N ha^{-1} yr^{-1}) is a small proportion of the total N budget (Morris 1991). However, atmospheric deposition can be the primary N source in some regions. For example, in southern New England estuaries, where N loading (mean =167 kg N ha^{-1} yr^{-1}) was much lower than other U.S. estuaries (mean =893 kg N ha^{-1} yr^{-1}), direct atmospheric deposition to the estuary surface was the largest N source, accounting for 37 percent of the total N loading (Latimer and Charpentier 2010). This information suggests that the impact of direct atmospheric deposition of N may vary among regions. Indirect atmospheric deposition—N deposited to the watershed and transported via surface or ground water—could be another major source of the total N load to coastal marshes. For example, the modeled contribution from the atmosphere (36 million kg N yr^{-1}) was about 21 to 30 percent of the total N loading of 170 million kg N yr^{-1} (Castro et al. 2003, Driscoll et al. 2003) for Chesapeake Bay waters, and 16 percent of the total N loading of 0.029 million kg N yr^{-1} for southern New England estuaries (Latimer and Charpentier 2010) Future studies are needed to determine the role of direct and indirect atmospheric N deposition on the nutrient budget of intertidal wetlands.

Regardless of its source, N enrichment is shown to alter the structure and function of intertidal wetland ecosystems (Table 17.3) by causing increased primary production (Darby and Turner 2008a, Mendelssohn 1979, Tyler et al. 2007, Wigand et al. 2003); invasion of nonnative species (Tyler et al. 2007); altered competition between native species (Crain 2007, Mendelssohn 1979, Wigand et al. 2003); loss of

Table 17.2—Greenhouse gas flux in response to N enrichment for freshwater wetlands.

Site	N Input *kg N ha^{-1} yr^{-1}*	Indicator	Responses	Reference
Mer Bleue Bog, Ottawa, ON	64 +PK	NEE (net ecosystem exchange of carbon)	After 5 years nutrient treatment, the rate of maximum NEE was significantly reduced (45%) under the highest levels of nutrient addition (64 kg N ha^{-1} yr^{-1} +5.0 kg P ha^{-1} yr^{-1} + 63 kg K ha^{-1} yr^{-1}), but was not changed under other nutrient levels, compared to control	Bubier et al. 2007
Swamp forest, St. James Parish, LA	100	N_2O emission	Addition of NO_3 and NH_4 to the columns increased N_2O production 56% and 15% over the control, respectively	Delaune et al. 1998
Swamp forest, Spring Bayou Wildlife Management Area, LA	100, 300 NH^{4+} - N; 100, 300 NO^{3-} -N	N_2O emission	N_2O emission was largely stimulated by NO_3^-addition but not NH_4^+; Total N_2O evolution was estimated to be 0.44,0.36,2.83 and 10.45 kg ha^{-1} yr^{-1} for the 100 NH_4^+, 300 NH4+, 100 NO_3- and 300 kg NO_3-N ha $^{-1}$ yr^{-1} treatments, respectively	Lindau et al. 1994
Mangroves forest, Indian River Lagoon, FL	100	N_2O emission	Averaged across the three experimental years (2001 -2003), N_2O emission was almost six times higher in fertilized plots (0.028 mg N_2O-N m^2 hr^{-1}), compared to that in control plots (0.005 mg N_2O- N m^2 hr^{-1})	Whigham et al. 2009

sensitive species (Latimer and Rego 2010); increased herbivore damage to plants (Bertness et al. 2008); stimulated evapotranspiration (Howes et al. 1986); altered microbial community and pore water chemistry (Caffrey et al. 2007); and altered carbon allocation between roots and shoots (Darby and Turner 2008b). It is unclear if these effects could occur in response to current levels of deposition alone because most studies apply N additions that are several orders of magnitude greater than atmospheric deposition.

Spartina. *Spartina* is an aggressive perennial cordgrass native to the coasts of the Atlantic Ocean. The dense root mats of *Spartina* trap sediment, elevating the substrate, and creating new shoreline. Nitrogen enrichment has been shown to alter the ecophysiological processes and community composition of *Spartina* salt marshes. This work is based on N addition levels that simulate total loading, not deposition alone. Evidence from Mendelssohn et al. (1979) indicates 280 kg N ha^{-1} yr $^{-1}$ alters growth and biomass of *Spartina*. Howes et al. (1986) found N addition (416 kg N ha^{-1} yr $^{-1}$) increased live aboveground biomass, leaf area coverage, and evapotranspiration of smooth cordgrass (*S. alterniflora).* Under N-enriched condition, saltmeadow cordgrass (*S. patens)* is often out-competed and replaced by smooth cordgrass (Emery et al. 2001). Wigand et al. (2003) examined plant community structure of 10 salt marshes over a 2-year period, with N ranging from 2 to 10,253 kg N ha^{-1} yr $^{-1}$, in Narragansett Bay. Several dose response curves based on their findings are given in Figure 17.3. Species richness decreased linearly with increasing N loading. With N loading higher than 63 to 400 kg N ha^{-1} yr $^{-1}$, the density of saltmeadow cordgrass and short smooth cordgrass rapidly decreased and the density of tall smooth cordgrass increased.

Eelgrass. Eelgrass, genus *Zostera*, is submerged aquatic vegetation that provides important habitat for many wildlife species, such as fish, shellfish, sea turtles, and waterfowl. Eelgrass beds are also important for sediment deposition and substrate stabilization. The massive decline of eelgrass has been widely documented in estuaries across Atlantic and Pacific coast (Latimer and Rego 2010, Ward et al. 2003). Excess N loading is one of the primary disturbances causing the rapid loss of eelgrass habitat. Latimer and Rego (2010) estimated the relationship between eelgrass extent and predicted watershed-derived N loading for 62 shallow estuaries along the coasts of Connecticut, Rhode Island, and Massachusetts. They found that N loading greater than 50 kg N ha^{-1} yr^{-1} lead to a significant decline of eelgrass coverage, and almost all eelgrass habitats were lost at loading levels higher than 100 kg N ha^{-1} yr^{-1}.

Table 17.3—Responses of coastal marsh ecosystems to N fertilization. Note an asterisk (*) indicates that N addition units were converted to kg N ha^{-1} yr^{-1} when different units were given in the publication.

Site	N Input	Indicator	Responses	Reference
Walden Creek, NC	0, 280, 560, and 1120 kg N ha^{-1} yr^{-1}	Smooth cordgrass (*Spartina alterniflora*) (short and tall)	1) increased the growth of short smooth cordgrass, but had no effect on tall smooth cordgrass; 2) NH_4^+ showed higher growth stimulation on short smooth cordgrass than NO_3^- 3) biomass production of short smooth cordgrass increased linearly with N addition	Mendelssohn et al. 1979
Great Sippewissett Marsh, MA	26 and 76 kg N ha^{-1}wk^{-1} from June to Sept (~416 and 1216 kg N ha^{-1} yr^{-1}*)	Smooth cordgrass	N addition 1)increased live aboveground biomass 100 and 270% in the low and high addition, respectively; 2) increased leaf area coverage; 3) doubled the rate of evapotranspiration	Howes et al. 1986
San Diego Bay, CA	15 g N m^{-2}·wk^{-1} from March to Aug 1995 and 1996 (~3600 kg N ha^{-1} yr^{-1}*)		N addition 1) increased plant tissue N concentration; 2) did not increase soil N concentration	Boyer et al. 2000
Narragansett Bay, RI	N gradient from 2 to 10,253 kg N ha^{-1} yr^{-1}	Saltmeadow cordgrass (*Spartina patens*); smooth cordgrass (short and tall)	N addition 1) reduced species richness; 2) decreased the density and extent of saltmeadow cordgrass; 3) increased the density and extent of tall smooth cordgrass	Wigand et al. 2003
Tomales Bay, CA	N addition of 15 g N m^{-2} urea fertilizer every two weeks from March 2000-July 2001 (~2100 to 3000 kg N ha^{-1} yr^{-1}*)	Saltgrass (*Distichlis spicata*), Virginia glasswort (*Salicornia virginica*), marsh rosemary (*Limonium californicum*), Canadian sandspurry (*Spergularia caadensis*), arrowgrass (*Triglochin sp*).	N addition 1) increased soil nitrogen; 2)increased height, plant tissue N concentration in all species; 3)increased biomass *of* saltgrass, marsh rosemary, Canadian sandspurry, arrowgrass; 4) increased percent cover of all species at one or more times during the experiment	Traut 2005

San Francisco Bay (CA); Willapa Bay (WA)	Added 800 kg N ha^{-1} yr^{-1}	Smooth cordgrass; Hybrid *Spartina* (*S. alterniflora* x *S. foliosa*); Virginia glasswort	1) increased biomass, stem density and the rate of habitat invasion; 2) promoted the spread of invaded species (hybrid *Spartina*); 3) decreased the density of native species (Virginia glasswort)	Tyler et al. 2007
Nags Creek (RI)	2 g N m^{-2} added once per month from May-Aug for 3 years (~80 kg N ha^{-1} yr^{-1}*)	Saltmeadow cordgrass	N addition 1) increased bacterial production; 2) increased pore water NH_4^+ and NO_3^- concentrations; 3) increased the uptake of dissolved inorganic phosphorous; 4) inconclusive effects on mineralization and denitrification rates	Caffrey et al. 2007
Cocodrie (LA)	N additions made once per month from April- Aug 2004 (~0, 230, 465, 930, 1860 and 3720 kg N ha^{-1} yr^{-1}*)	Smooth cordgrass	N addition 1) increased the aboveground biomass and stem density; 2) did not change live belowground biomass	Darby and Turner 2008b
York River (ME); Nonesuch River (ME)	N addition of 1630 kg N ha^{-1} yr^{-1} for 3 years	Salt, brackish and oligohaline marshes	N addition 1) increased the productivity of all three types of marshes by 100% after 3 years; 2) lowered C:N and increased N:P in plant tissue in all marsh-types; 3) had no significant effect on species composition of salt and brackish marshes, however a combination of N and P fertilization changed the species composition of oligohaline marshes	Crain 2007
Narragansett Bay (RI)	Added 30% N by weight of 60 g m^{-2} per month from May to August 2005 and 2006 (~720 kg N ha^{-1} yr^{-1}*)	Smooth cordgrass	N was added with phosphorous and potassium. The herbivore consumption of primary production was small in pristine marshes, but increased to 50-75% in eutrophic marshes	Bertness et al. 2008
62 New England estuaries	N gradient from 24.2 to 928 kg N ha^{-1} yr^{-1}	Eelgrass	N loading greater than 50 kg N ha^{-1} yr^{-1} led to a significant decline of eelgrass coverage, and almost all eelgrass habitats were lost at loading levels higher than 100 kg N ha^{-1} yr^{-1}.	Latimer and Rego 2010

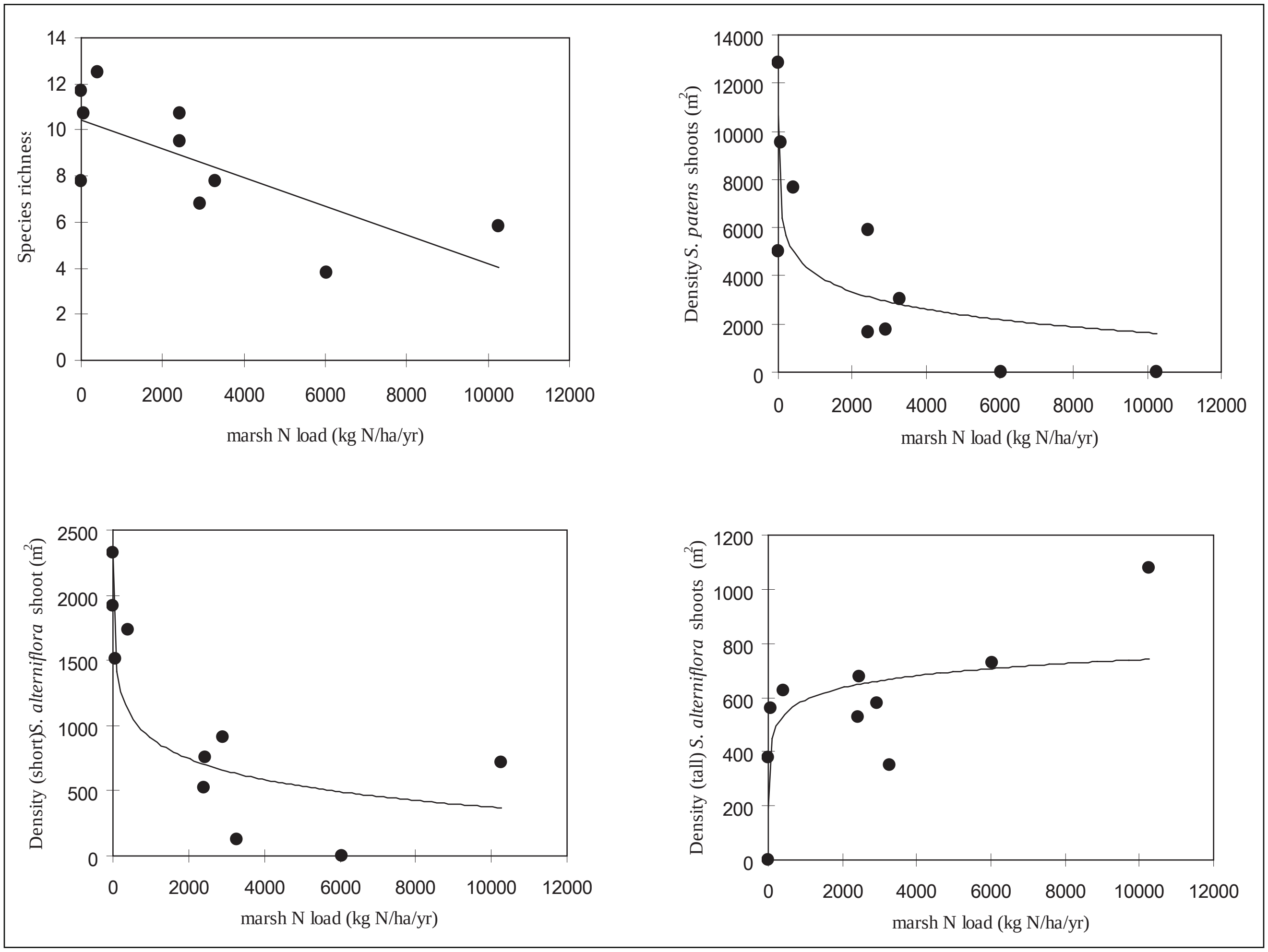

Figure 17.3—The effect of N loading on plant community structure of 10 salt marshes in Narragansett Bay (graphs plotted from data presented in Wigand et al. 2003)

17.4 Critical load estimates

17.4.1 Freshwater Wetlands

There is correlative evidence that *Sphagnum*-dominated freshwater wetlands in the United States are altered by N deposition. The critical load for altered peat accumulation and NPP is between 2.7 and 13 kg N ha^{-1} yr^{-1}, based on observations from Aldous (2002a), Moore et al. (2004), Rochefort et al. (1990) and Vitt et al. (2003). The upper end of this critical load range is based on measurements of wet deposition only (10 to 13 kg N ha^{-1} yr^{-1}) (Aldous 2002a, 2002b) and therefore does not reflect total N loading. There is evidence showing that N deposition alters both the morphology and population dynamics of purple pitcher plant. The empirical evidence suggests a critical load to protect the population of purple pitchers of 10 to 14 kg N ha^{-1} yr^{-1} (Gotelli and Ellison 2006), while matrix modeling to forecast long-term population sustainability based on observations of population demographics suggests a lower value of 6.8 kg N ha^{-1} yr^{-1} (Gotelli and Ellison 2002).

17.4.2 Intertidal Wetlands

The critical load range for atmospheric deposition is difficult to establish for intertidal wetlands because they have open nutrient cycles which are often strongly affected by N loading sources other than atmospheric deposition. Typically, the amount of N added in experimental treatments simulates total N input and therefore far exceeds the amount that U.S. intertidal wetlands would receive by atmospheric deposition. Only two studies (Table 17.3) have addition levels below 100 kg N ha^{-1} yr^{-1}. Based on the results of Wigand et al. (2003), a critical load to protect the community structure of salt marshes is likely to be 63 to 400 kg

Table 17.4—European empirical critical loads of nutrient N for mire, bog and fen habitats (EUNIS class D). Reliability rating: ## reliable, # quite reliable and (#) expert judgment.

Ecosystem type	kg N ha^{-1} yr^{-1}	Reliability	Indication of exceedance
Raised bogs and blanket fens	5-10	##	Increased vascular plants, decrease bryophytes, altered growth and species composition of mosses, increased N in peat and peat water
Poor fens	10-20	#	Increases in sedges and vascular plants, negative effects on peat mosses
Rich fens	15-35	(#)	Increases on tall graminoids, decrease diversity
Montane rich fens	15-25	(#)	Increase vascular plants, decrease bryophytes

From Bobbink et al. 2003; Table 6.1

N ha^{-1} yr^{-1}. Caffrey et al. (2007) provide additional evidence that 80 kg N ha^{-1} yr^{-1} alters microbial activity and biogeochemistry. Latimer and Rego (2010) found that eelgrass coverage started to decrease rapidly at N loading higher than 50 kg N ha^{-1} yr^{-1}, with no eelgrass at loading levels higher than 100 kg N ha^{-1} yr^{-1}. Note that these values are the total N loading to salt marshes, including N deposition directly to the marsh surface, as well as N deposited indirectly to the watershed, surface or ground water, and runoff from agriculture, urban areas, and other sources. Additional experimental evidence on ecosystem response to N loads that are similar to the amount of loading due to N deposition is needed to improve the critical load calculation for intertidal wetlands in the United States.

17.5 Comparison to Critical Loads from Europe

The 2003 assessment of N critical loads in Europe designated critical loads for multiple types of wetlands, including raised and blanket bogs, poor fens, rich fens, mountain rich fens, and intertidal wetlands (Bobbink et al. 2003). There are numerous publications on N effects to wetlands in Europe compared to the United States. In general, documented responses include effects on growth and species composition, competition between species, peat and peat water chemistry, decomposition, and nutrient cycling. A brief summary of the European critical loads for wetlands is presented here and summarized in Table 17.4.

Bobbink et al. (2003) assigned a critical load of 5 to 10 kg N ha^{-1} yr^{-1} for bog ecosystems, based on plant community and species responses to N deposition, and indicated that precipitation and P limitation should be used to assign critical loads to individual sites. The observed changes in the plant communities of ombrotrophic bogs included the replacement of *Sphagnum*-forming species with nitrophilous moss species (20 to 40 kg N ha^{-1} yr^{-1} in Dutch bogs) (Greven 1992); the absence of characteristic *Sphagnum* species in British bogs (30 kg N ha^{-1} yr^{-1}) (Lee and Studholme 1992); and reduction in the growth survivorship of characteristic bog species roundleaf sundew (*Drosera rotundifolia*) (10 kg N ha^{-1} yr^{-1} in Swedish bogs) (Bobbink et al 2003, Redbo-Torstensson 1994). The European critical load is similar to the range of critical loads suggested for freshwater wetlands in the United States (Table 17.5).

It is unclear how European critical loads for poor fens, rich fens, and mountain rich fens relate to the critical loads for similar wetlands in North America because the impacts of N loads have not been studied in the United States. European poor fens have a critical load of 10 to 20 kg N ha^{-1} yr^{-1} based on increased sedge and vascular plants and negative effects on peat mosses. The critical load for rich fens in Europe is 15 to 35 kg N ha^{-1} yr^{-1} based on increased tall graminoids and decreased diversity. The critical load for montane rich fens in Europe was 15 to 25 kg N ha^{-1} yr^{-1} based on increased vascular plants and decreased bryophytes. Note that changes in the vegetation composition and structure likely affect fauna species assemblages, such as spiders and beetles living in the originally open bog vegetation, and ground-breeding birds. Increased nutrient

Table 17.5—Empirical critical loads of nutrient N for wetlands. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem	Critical loads for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Study
Freshwater wetlands	2.7-13	#	Peat accumulation and NPP	Aldous 2002a, Moore et al. 2004, Rochefort et al. 1990, Vitt et al 2003
Freshwater wetlands	6.8-14	(#)	Pitcher plant community change	Gotelli and Ellison 2002, 2006
Intertidal salt marsh	63-400	(#)	Salt marsh community structure, microbial activity and biogeochemistry	Caffrey et al. 2007, Wigand et al. 2003
Intertidal wetlands	50-100	##	Loss of eelgrass	Latimer and Rego 2010

availability results in an increase of the nutrient content of plant material (Limpens et al. 2003a, Tomassen et al. 2003) and algal growth (Gulati and DeMott 1997, Limpens et al. 2003b), and affects herbivorous, detritivorous, and carnivorous invertebrates (Van Duinen et al. 2004).

The European critical load for salt marshes, based on expert judgment, is 30 to 40 kg N ha^{-1} yr^{-1} (Bobbink et al. 2003), but studies of European salt marshes are limited. High levels of N input (65 to 70 kg N ha^{-1} yr^{-1}) significantly increased biomass production in the Netherlands (Van Wijnen and Bakker 1999); no changes in species composition and in diversity have been observed for the current deposition of 15 to 25 kg N ha^{-1} yr^{-1} at sites in the Netherlands and Germany (Bobbink et al. 2003). The critical load for North American intertidal ecosystems may be closer to these values than to the high levels of N input previously studied (section 17.3.2).

17.6 Future Research Directions and Gaps in Data

An great diversity of wetlands ecosystems are found across Northern America, but experimental studies on the impacts of N enrichment in these wetland systems are scarce. Some data are present for bog systems and intertidal wetland (salt marshes), but even in these ecosystems field additions studies with realistic N loads are rare. Realistic levels of long-term (5 to 10 years) experimental N addition in low background regions, with a high resolution of treatments, are needed to refine and establish reliable critical loads for wetlands. In addition, these studies should be done across a range of wetlands types in the United States, especially in oligotrophic to mesotrophic wetland habitat.

LITERATURE CITED

Aldous, A.R. 2002a. **Nitrogen retention by *Sphagnum* mosses: responses to atmospheric nitrogen deposition and drought.** Canadian Journal of Botany. 80: 721-731.

Aldous, A.R. 2002b. **Nitrogen translocation in *Sphagnum* mosses: effects of atmospheric nitrogen deposition.** New Phytologist. 156: 241-253

Archibold, O.W. 1995. **Ecology of world vegetation.** London: Chapmann and Hall. 528 p.

Bedford, B.L.; Walbridge, M.R.; Aldous, A.R. 1999. **Patterns in nutrient availability and plant diversity of temperate North American wetlands.** Ecology. 80: 2151-2169.

Bertness, M.D.; Crain, C.; Holdredge, C.; Sala, N. 2008. **Eutrophication and consumer control of New England salt marsh primary productivity.** Conservation Biology. 22: 131-139.

Bobbink, R.; Ashmore, M.R.; Braun, S.; Fluckiger, W.; van der Wyngaert, I.J.J. 2003. **Empirical**

nitrogen critical loads for natural and semi-natural ecosystems: 2002 update. In: Achermann, B.; Bobbink, R., eds. Empirical critical loads for nitrogen. Environmental Documentation 164. Berne, Switzerland: Swiss Agency for the Environment, Forests and Landscape: 143-170.

Boyer, K.E.; Callway, J.C.; Zedler, J.B. 2000. **Evaluating the progress of restored cordgrass (*Spartina foliosa*) marshes: Belowground biomass and tissue nitrogen.** Estuaries. 23: 711-721.

Bridgham, S.D.; Pastor, J.; McClaugherty, C.A.; Richardson, C.J. 1995. **Nutrient-use efficiency: a litterfall index, a model, and a test along a nutrient-availability gradient in North Carolina peatlands.** American Naturalist. 145: 1-21.

Bridgham, S.D.; Pastor, J.; Janssens, J.; Chapin, C.; Malterer, T. 1996. **Multiple limiting gradients in peatlands: a call for a new paradigm.** Wetlands. 16: 45-65.

Bubier, J.L.; Moore, T.R.; Bledzki, L.A. 2007. **Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog.** Global Change Biology. 13: 1168-1186.

Caffrey, J.M.; Murrell, M.C.; Wigand, C.; McKinney, R. 2007. **Effect of nutrient loading on biogeochemical and microbial processes in a New England salt marsh.** Biogeochemistry. 82: 251-264.

Castro, M.S.; Driscoll, C.T.; Jordan, T.E.; Reay, W.G.; Boynton, W.R. 2003. **Sources of nitrogen to estuaries in the United States.** Estuaries. 25: 803-814.

Crain, C.M. 2007. **Shifting nutrient limitation and eutrophication effects in marsh vegetation across estuarine salinity gradients.** Estuaries and Coasts. 30(1): 26-34.

Dahl, T.E.; Allord, G.J. 1997. **Technical aspects of wetlands, history of wetlands in the conterminous United States.** Water Supply Pap. 2425. Washington, DC: U.S. Department of the Interior, Geological Survey. Available at http://usgs.gov/nwsum/history.html (Accessed August 30, 2010).

Darby, F.A.; Turner, R.E. 2008a. **Below- and aboveground *Spartina alterniflora* production in a Louisiana salt marsh.** Estuaries and Coasts. 31: 223-231.

Darby, F.A.; Turner, R.E. 2008b. **Below- and aboveground biomass of *Spartina alterniflora*: Response to Nutrient Addition in a Louisiana Salt Marsh.** Estuaries and Coasts. 31: 326-334.

Delaune R.D.; Lindau C.W.; Sulaeman E.; Jugsujinda A. 1998. **Nitrification and denitrification estimates in a Louisiana swamp forest soil as assessed by N-15 isotope dilution and direct gaseous measurements.** Water Air and Soil Pollution. 106: 149-161.

Driscoll, C.; Whitall, D.; Aber, J.; Boyer, E.; Castro, M.; Cronan, C.; Goodale, C.; Groffman, P.; Hopkinson, C.; Lambert, K.; Lawrence, G.; Ollinger, S. 2003. **Nitrogen pollution in the northeastern United States: Sources, effects and management options.** BioScience. 53: 357-374.

Ellison, A.M.; Gotelli, N.J. 2002. **Nitrogen availability alters the expression of carnivory in the northern pitcher plant, *Sarracenia purpurea*.** Proceedings of the National Academy of Sciences of the United States of America. 99: 4409-4412.

Ellison, A.M.; Buckley, H.L.; Miller,T.E.; Gotelli, N.J. 2004. **Morphological variation in *Sarracenia purpurea Sarraceniaceae*: Geographic, environmental, and taxonomic correlates.** American Journal of Botany. 91: 1930-1935.

Emery, N.C.; Ewanchuk, P.J.; Bertness, M.D. 2001. **Competition and salt-marsh plant zonation: Stress tolerators may be dominant competitors.** Ecology. 82: 2471-2485.

FWS (U.S. Fish and Wildlife Service). 2005. **Status and trends of wetlands in the conterminous United States 1998 to 2004.** Washington, DC: U.S. Department of Interior, Fish and Wildlife Service. 112 p.

Green, E.K.; Galatowitsch, S.M. 2002. **Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities.** Journal of Applied Ecology. 39: 134-144.

Greven, H.C. 1992. **Changes in the moss flora of the Netherlands.** Biological Conservation. 59: 133-137.

Gotelli, N.J.; Ellison, A.M. 2002. **Nitrogen deposition and extinction risk in the northern pitcher plant, *Sarracenia purpurea*.** Ecology. 83: 2758-2765.

Gotelli, N.J.; Ellison, A.M. 2006. **Forecasting extinction risk with nonstationary matrix models.** Ecological Applications. 16: 51-61.

Gulati, R.D.; DeMott, W.R. 1997. **The role of food quality for zooplankton: remarks on the state-of-the-art, perspectives and priorities.** Freshwater Biology. 38: 753-768.

Howes, B.L.; Dacey, W.H.; Goehringer, D.D. 1986. **Factors controlling the growth form of *Spartina Alterniflora*: Feedbacks between above-ground production, sediment oxidation, nitrogen and salinity.** Journal of Ecology. 74: 881-898.

Keller, J.K.; Bridgham, S.D.; Chapin, C.T.; Iversen, C.M. 2005. **Limited effects of six years of fertilization on carbon mineralization dynamics in a Minnesota fen.** Soil Biology and Biochemistry. 37: 1197-1204.

Koerselman, W. 1989. **Groundwater and surface water hydrology of a small groundwater-fed fen.** Wetlands Ecology and Management. 1: 31-43.

Lamers, L.P.M.; Bobbink, R.; Roelofs, J.G.M. 2000. **Natural nitrogen filter fails in polluted raised bogs.** Global Change Biology. 6: 583-586.

LeBauer, D.S.; Treseder, K.K. 2008. **Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed.** Ecology. 89(2): 371-379.

Latimer, J.S.; Charpentier, M.A. 2010. **Nitrogen inputs to seventy-four southern New England estuaries: Application of a watershed nitrogen loading model.** Estuarine, Coastal and Shelf Science. 89(2): 125-136.

Latimer J.S.; Rego, S.A. 2010. **Empirical relationship between eelgrass extent and predicted watershed-derived nitrogen loading for shallow New England estuaries.** Estuarine, Coastal and Shelf Science. 90: 231-240.

Lee, J.A.; Studholme, C.J. 1992. **Responses of *Sphagnum* species to polluted environments.** In: Bates, J.W.; Farmer, A.M., eds. Bryophytes and lichens in a changing environment. New York, NY: Oxford University Press: 314-322.

Limpens, J.; Berendse, F.; Klees, H. 2003a. **N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation.** New Phytologist. 157(2): 339-347.

Limpens, J.; Raymakers, J.T.A.G.; Baar, J.; Berendse, F.; Zijlstra, J.D. 2003b. **The interaction between epiphytic algae, a parasitic fungus and *Sphagnum* as affected by N and P.** Oikos. 103: 59-68.

Lindau, C.W.; Delaune, R.D.; Pardue, J.H. 1994. **Inorganic nitrogen processing and assimilation in a forested wetland.** Hydrobiologia. 277: 171-178.

Liu, L.; Greaver, T.L. 2009. **A review of nitrogen enrichment effects on three biogenic GHGs: The CO_2 sink may be largely offset by stimulated N_2O and CH_4 emission.** Ecology Letters. 12: 1103-1117.

Mendelssohn, I.A. 1979. **The influence of nitrogen level, form, and application method on the**

growth response of *Spartina alterniflora* in North Carolina. Estuaries. 2:106-118.

Mitsch, W.J.; Gosselink, J.G. 2000. **Wetlands.** 3rd ed. New York, NY: John Wiley & Sons. 936 p.

Morris, J.T. 1991. **Effects of nitrogen loading on wetland ecosystems with particular reference to atmospheric deposition.** Annual Review of Ecology and Systematics. 22: 257-279.

Moore, T.; Blodau, C.; Turunen, J.; Roulet, N.; Richard, P.J.H. 2004. **Patterns of nitrogen and sulfur accumulation and retention in ombrotrophic bogs, eastern Canada.** Global Change Biology. 11(2): 256-367.

NRCS (Natural Resources Conservation Service). 2011. **The PLANTS database.** Baton Rouge, LA: U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Center. Available at http://plants.usda.gov. (Accessed Feb. 9, 2011).

Redbo-Torstensson, P. 1994. **The demographic consequences of nitrogen fertilization of a population of sundew, *Drosera rotundifolia*.** Acta Botanica Neerlandica. 43: 175-188.

Rochefort, L; Vitt,D.H.; Bayley, S.E. 1990. **Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions.** Ecology. 71(5):1986-2000.

Shaver, G.R.; Melillo, J.M. 1984. **Nutrient budgets of marsh plants - efficiency concepts and relation to availability.** Ecology. 655: 1491-1510

Tomassen, H.B.M.; Smolders, A.J.P.; Lamers, L.P.M.; Roelofs, J.G.M. 2003. **Stimulated growth of *Betula pubescens* and *Molinia caerulea* on ombrotrophic bogs: role of high levels of atmospheric nitrogen deposition.** Journal of Ecology. 91(3): 357-370.

Traut, B.H. 2005. **Effects of nitrogen addition and salt grass *Distichlis spicata*. upon high salt marsh vegetation in Northern California, USA.** Estuaries. 282: 286-295.

Tyler, A.C.; Lambrinos, J.G.; Grosholz, E.D. 2007. **Nitrogen inputs promote the spread of an invasive marsh grass.** Ecological Applications. 17: 1886-1898.

US EPA (U.S. Environmental Protection Agency). 1993. **Air quality criteria for oxides of nitrogen.** Rep. No. EPA/600/8-91/049aF-cF.Research Triangle Park, NC: Office of Health and Environmental Assessment, Environmental Criteria and Assessment Office; 3v. Available from: NTIS, Springfield, VA; PB95-124533, PB95-124525, and PB95-124517.

US EPA (U.S. Environmental Protection Agency). 2008. **Integrated science assessment of oxides of nitrogen and sulfur- ecological criteria.** Rep. No. EPA/600/R-08/082F. Research Triangle Park, NC: U.S. Environmental Protection Agency, National Center for Environmental Assessment, Environmental Media Assessment Group.

Van Duinen, G.A.; Brock, A.M.T.; Kuper, J.T.; Peeters, T.M.J.; Esselink, H. 2004. **Do raised bog restoration measures rehabilitate aquatic fauna diversity? A comparative study between pristine, degraded, and rewetted raised bogs.** In: Päivänen, J., ed. Wise use of peatlands. Proceedings of the 12th International Peat Congress; 2004 June 6-11; Tampere, Finland. Jyväskylä, Finland: International Peat Society.

Van Wijnen, H.J.; Bakker, J.P. 1999. **Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession.** Journal of Ecology. 87: 265-272.

Vitt, D.H. 1994. **An overview of factors that influence the development of canadian peatlands.** Memoirs of the Entomological Society of Canada. 169: 7-20.

Vitt, D.H.; Wieder, K.; Halsey, L.A.; Turetsky, M. 2003. **Response of *Sphagnum fuscum* to nitrogen deposition: A case study of ombrogenous peatlands in Alberta, Canada.** The Bryologist. 1062: 235-245.

Ward, D.H.; Morton, A.; Tibbitts, T.L.; Douglas, D.C.; Carrera-Gonzalez, E. 2003. **Long-term change in eelgrass distribution at Bahia San Quintin, Baja California, Mexico, using satellite imagery.** Estuaries and Coasts. 26(6): 1529-1539.

Weidermann, M.M,; Nordina, A.; Gunnarsson, U.; Nilsson, M.B.; Ericson, L. 2007. **Global change shifts vegetation and plant-parasite interactions in a boreal mire.** Ecology. 88: 454-464.

Whigham, D.F.; Verhoeven, J.T.A.; Samarkin, V.; Megonigal, P.J. 2009. **Responses of *Avicennia germinans* (black mangrove) and the soil microbial community to nitrogen addition in a hypersaline wetland.** Estuaries and Coasts. 32: 926-936.

Wigand, C.; McKinney, R.A.; Charpentier, M.A.; Chintala, M.M.; Thursby, G.B. 2003. **Relationships of nitrogen loadings, residential development, and physical characteristics with plant structure in New England salt marshes.** Estuaries. 26: 1494-1504.

18 INLAND SURFACE WATERS

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18.1 Ecosystems Description

Freshwater aquatic ecosystems include rivers and streams, large and small lakes, reservoirs, and ephemeral ponds. Wetlands are defined and discussed in Chapter 17 of this report. It is estimated that there are 123,400 lakes with a surface area greater than 4 ha in the United States. Most lakes, however, are smaller than 4 ha; small lakes account for the majority of lake surface area both globally and in the United States (Table 18.1; Downing et al. 2006). The density of lakes varies greatly by region of the country, from 8.4 lakes per 100 km^2 in the upper Midwest and 7.8 lakes per 100 km^2 in Florida, to much lower values in other areas of the country (e.g., mid-Atlantic, Southeast, and West <1.0 lakes per 100 km^2) (Eilers and Selle 1991). The cumulative surface area of these lakes is approximately 9.5 million ha. The U.S. Geologic Survey's National Hydrographic Dataset (NHD) estimates that there are approximately 1.1 million km of perennial flowing streams in the United States. Of these about 91 percent are first through fourth order (“wadeable”) (US EPA 2006).

Table 18.1—Number and distribution of lakes (>4 ha in surface area) in the United States (after US EPA 2010)

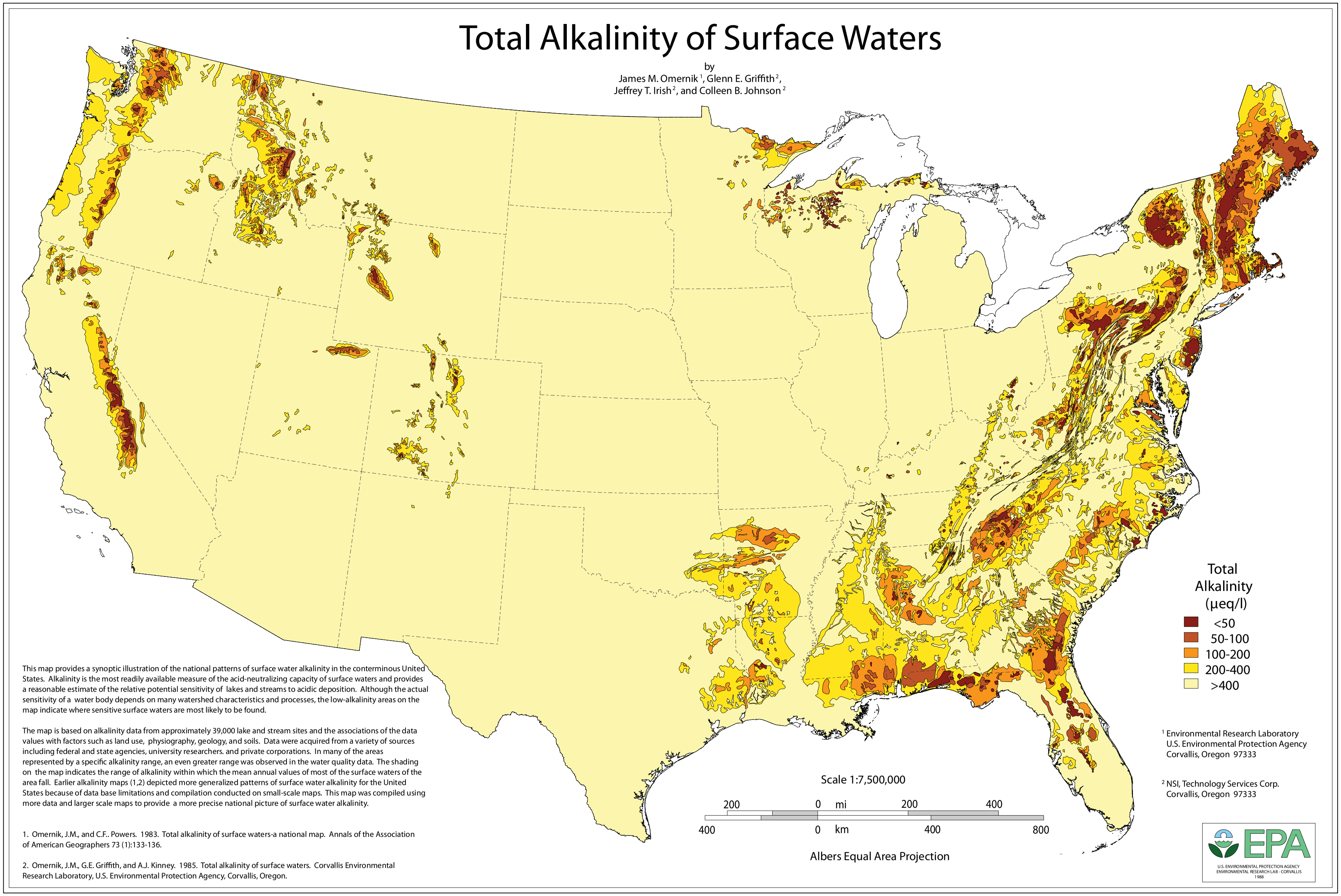
Lake size category *ha*	Total number of lakes in the U.S.	Cumulative Surface Area *ha*
1-4	155,201	310,402
4-10	68,559	433,605
10-20	24,902	352,167
20-50	16,488	521,396
50-100	6,134	433,739
>100	7,356	7,356,000
Total	278,640	9,407,310

18.2 Ecosystem Responses to N Deposition

A cascade of environmental effects occurs in response to elevated inputs of reactive N (Chapter 1; Galloway et al. 2003), but in freshwater ecosystems effects can be grouped under the categories of eutrophication (excess nutrient N) and acidification. Reactive N from anthropogenic activities enters lakes and streams from a number of sources, including wastewater treatment point sources, agricultural and other nonpoint sources, and atmospheric deposition (Driscoll et al. 2003b). The relative importance of these reactive N sources varies by the position of lakes and streams on the landscape. In protected headwater areas (such as national or state forests or parks), atmospheric deposition is the only source of anthropogenic reactive N. Surface waters with drainage from agricultural, industrial, or urban areas may receive proportionally less reactive N from atmospheric deposition and more from point and other nonpoint sources. The focus of this chapter is on surface waters that primarily receive N inputs from atmospheric deposition directly or indirectly through the watershed.

Freshwater aquatic ecosystems in which N has been observed to influence ecological processes either receive chronic or seasonally high inputs. Chemical responses range from long-term or temporary acidification (Dumont et al. 2005), to measurable N concentrations in the water column (Stoddard 1994). Nitrogen-limited waters respond rapidly to inputs of N with increased productivity, or eutrophication (Baron et al. 2000, Bergström and Jansson 2006).

The number of surface waters that are sensitive to or impacted by acidic deposition is relatively small compared to the total number of surface waters in the United States (Charles 1991). The areas of the United States with low values of acid neutralizing capacity (ANC <400 μeq/L) are shown in Figure 18.1. Of the areas shown, only those with ANC values <100 μeq/L would be considered sensitive to acidification by N deposition. These areas include the northern, central, and southern Appalachian Mountain regions, portions of southern New England, the Pine Barrens of New Jersey, portions of Georgia and Florida, portions of the upper Midwest, portions of the Rockies, the Cascades and the Sierra Nevada Mountains of the West. Note



This map provides a synoptic illustration of the national patterns of surface water alkalinity in the conterminous United States. Alkalinity is the most readily available measure of the acid-neutralizing capacity of surface waters and provides a reasonable estimate of the relative potential sensitivity of lakes and streams to acidic deposition. Although the actual sensitivity of a water body depends on many watershed characteristics and processes, the low-alkalinity areas on the map indicate where sensitive surface waters are most likely to be found.

The map is based on alkalinity data from approximately 39,000 lake and stream sites and the associations of the data values with factors such as land use, physiography, geology, and soils. Data were acquired from a variety of sources including federal and state agencies, university researchers. and private corporations. In many of the areas represented by a specific alkalinity range, an even greater range was observed in the water quality data. The shading on the map indicates the range of alkalinity within which the mean annual values of most of the surface waters of the area fall. Earlier alkalinity maps (1,2) depicted more generalized patterns of surface water alkalinity for the United States because of data base limitations and compilation conducted on small-scale maps. This map was compiled using more data and larger scale maps to provide a more precise national picture of surface water alkalinity.

1. Omernik, J.M., and C.F.. Powers. 1983. Total alkalinity of surface waters-a national map. Annals of the Association of American Geographers 73 (1):133-136.

2. Omernik, J.M., G.E. Griffith, and A.J. Kinney. 1985. Total alkalinity of surface waters. Corvallis Environmental Research Laboratory, U.S. Environmental Protection Agency, Corvallis, Oregon.

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[2] NSI, Technology Services Corp.
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Figure 18.1—Map of surface water values of acid neutralizing capacity (ANC) across the U.S. Note that ANC values less than 100 μeq L^{-1} are more sensitive to the effects of acidic deposition (Omernik and Powers 1982).

that surface water acidification mostly results from the combined effects of atmospheric sulfur (S) and N deposition.

Episodic acidification from atmospheric N deposition has been reported mostly from snow-dominated environments where winter N deposition accumulates in the snowpack. Snowmelt triggers a pulse of reactive N to streams and lakes (Sickman and Melack 1998, Sickman et al. 2001, Stoddard 1994, Williams and Tonnessen 2000). Both preferential elution of solutes, including N, from the snowpack, and N-rich soil solutions produced by N mineralization and nitrification during the winter season of vegetation dormancy, are sources of spring nitrate (NO_3^-) pulses to streams and lakes (Brooks et al. 1998, Stoddard 1994). Episodic acidification associated with nitrate leaching can also occur during summer and fall rain events (Wigington et al. 1996).

The extent of lakes and streams affected by the eutrophication effects from atmospheric N deposition is much greater than those impacted by acidification (see below).

In the United States, atmospheric N deposition effects on surface waters have received less attention than effects from atmospheric S deposition. A number of factors have combined to draw the scientific and policy focus away from N. First, efforts to study the effects of atmospheric deposition had been largely directed toward surface water acidification, where the focus has been on chronic acidification, and particularly on the effects of S deposition on chronic acidification (Stoddard et al. 2003). The acidification response to N deposition is largely associated with episodic acidification, which has received less attention. Sulfur emissions and deposition have been declining since 1973, and with substantial decreases since 1995 following the 1990 amendments of the Clean Air Act (Dennis et al. 2007). In contrast, changes in atmospheric N deposition have been variable (Lehmann et al. 2005). Atmospheric NO_3^- deposition has generally decreased in the East following controls on emissions from electric utilities, but has increased in the west and central United States. Increases in ammonium (NH_4^+) deposition have been relatively widespread, particularly in the central and northern Midwest (Lehmann et al. 2005, 2007). The relative importance of N deposition has increased in recent years as S deposition has decreased, creating an opportunity to re-examine the role of N deposition in surface water acidification (Lehmann et al. 2005).

Second, aquatic biologists have been focused on the role of phosphorus (P) in eutrophication of freshwaters for the past 40 years, largely due to the demonstrated effect of P increasing algal productivity worldwide (Schindler 1977, 1978). The prevailing wisdom is that P, an essential nutrient, is often the limiting nutrient to aquatic organisms, while N is tightly cycled in terrestrial systems, and that little N leaching occurs in undisturbed environments (Vitousek and Howarth 1991). Only within the past 20 years have there been studies questioning the established science and showing N limitation in some freshwaters, N leaching in some forest and alpine ecosystems, and N-induced acidification in lakes and streams with low ANC. A global meta-analysis of 990 freshwater field experiments found that N limitation of stream benthos, lake benthos, and phytoplankton was as common as P limitation from sites in all biomes worldwide (Elser et al. 2007); experimental additions of N to these ecosystems stimulated primary production. While P-amendment experiments in some lakes and mesocosms have shown an increase in compensatory N fixation, giving rise to the paradigm that P, not N, limits eutrophication (Schindler 1977, Schindler et al. 2008), many studies show N and P co-limitation (Elser et al. 1990, Elser et al. 2007). There presently is no evidence for a consistently significant contribution of planktonic N fixation to oligotrophic and mesotrophic lakes (Lewis and Wurtsbaugh 2008). Oligotrophic (nutrient poor) and ultra-oligotrophic waters are inherently sensitive to even low inputs of atmospheric N deposition (Bergström et al. 2005, Bergstrom and Jansson 2006, Elser et al. 2009, Lewis and Wurtsbaugh 2008).

The current extent of N limitation can be estimated from nutrient data collected as part of regional lake surveys in the eastern (Linthurst et al. 1986) and western (Landers et al. 1987) United States. Table 18.2 presents ratios of dissolved inorganic nitrogen (DIN; sum of NO_3^- and NH_4^+) to total phosphorus (TP)

Table 18.2—Proportion of lakes in three nutrient limitation classes (N limited, P limited, and N and P co-limited) based on ratios of dissolved inorganic nitrogen (DIN; $NO_3^- + NH_4^+$) to total phosphorus (TP). Data are from the Eastern Lake Survey (Linthurst et al. 1986), conducted in the fall of 1984, and the Western Lake Survey (Landers et al. 1987), conducted in the fall of 1985.

Region	Number of Lakes[a]	Number of N limited lakes (%)[b]	Number of P limited lakes (%)[c]	Number of lakes with co-limited N:P (%)[d]
Adirondacks	1,290	208 (16%)	777 (60%)	3.5 (23%)
New England	4,361	1,470 (34%)	1,363 (31%)	1,529 (35%)
Poconos/Catskills	1,506	607 (40%)	559 (37%)	341 (22%)
Southeast	2,424	735 (30%)	1,148 (47%)	541 (22%)
Upper Midwest	8,755	3,142 (37%)	2,787 (32%)	2,646 (31%)
Rockies	6,666	2,998 (45%)	2,259 (34%)	1,409 (21%)
Sierra/Cascades	4,155	1,468 (35%)	1,958 (47%)	729 (18%)
Total	28,976	10,627 (36%)	10,851 (37%)	7,499 (26%)

[a] The eastern and western Lake surveys were stratified random samples of lakes; estimates of the number of lakes in each region are based on the target population sizes for each survey.

[b] Lakes with DIN:TP ratios (by weight) less than four were characterized as N limited, based on the work of Morris and Lewis (1988).

[c] Lakes with DIN:TP ratios (by weight) greater than 12 were characterized as P limited, based on the work of Morris and Lewis (1988).

[d] Lakes with DIN:TP ratios (by weight) between 4 and 12 could not be assigned to nutrient limitation class, and are characterized as either co-limited, or limited by something other than N or P.

as an indicator of nutrient status of lakes. These are based on water column analyses from the regional lake surveys. In Colorado lakes, Morris and Lewis (1988) found DIN:TP to be the most reliable predictor of nutrient limitation when compared against nutrient algal bioassays; they suggested using DIN:TP thresholds to identify probable N limitation (DIN:TP <4 by mass), P limitation (DIN:TP >12) and co-limitation (intermediate ratios). Percentages of N limited lakes vary from about 16 percent in the Adirondack Mountains, to 45 percent in the Rocky Mountains (Table 18.2). In general, N limitation is more common in regions with low N deposition (e.g., Sierra Nevada and Rocky Mountain ranges) and P limitation is more common in regions with higher N deposition (Adirondacks, New England, the Southeastern United States).

While the results in Table 18.2 suggest that N limitation is more widespread than is commonly understood, these values may actually underestimate historical rates of N limitation. Surveys of the literature report that oligotrophic waters are commonly N limited, especially undisturbed northern temperate or boreal lakes that receive low levels of atmospheric N deposition (Bergström et al. 2005, Elser et al. 1990, Elser et al. 2007, Elser et al. 2009). A comprehensive study of available data from the northern hemisphere found unequivocal evidence of N limitation in lakes with low inputs of N, and increased N concentrations in lakes receiving N solely from atmospheric N deposition (Bergström and Jansson 2006). Studies of the response of phytoplankton to N or P amendments similarly found strong growth responses to N in lakes with low atmospheric N deposition, but no response to N in lakes with high N deposition (Elser et al. 2009). These authors suggested that the majority of lakes in the northern hemisphere may have originally been N limited, and that long-term atmospheric N deposition has changed the balance of N and P in lakes such that P limitation is observed today.

18.2.1 Abiotic Responses to N Deposition

The primary abiotic effect of excess N deposition for inland surface waters is acidification. Acidification occurs when acidic deposition (primarily sulfuric (H_2SO_4) and nitric (HNO_3) acids) exceeds the ability of watershed soils, vegetation, and surface waters to neutralize these inputs. Catchment sensitivity to acidification is largely governed by bedrock and surficial geology, and much of the United States is insensitive to acidic deposition (Charles 1991). The regions of most concern for acidification are areas underlain by intrusive igneous rocks, typical of the western mountains, upper Midwest and parts of the Northeast, and base-poor sandstones typical of the Northeast, the mid-Atlantic, and the central and southern Appalachian Mountains (Figure 18.1; Charles 1991). Catchment sensitivity is also influenced by past acidic deposition, which can diminish the ability of soil to neutralize ongoing acidic deposition, due to long-term declines in exchangeable base cations (Driscoll et al. 2001, Huntington et al. 2000).

Surface water sensitivity to acidification is commonly measured in terms of pH and ANC. These indicators decline as lakes and streams acidify, and waters are classified as acidic when ANC values decrease to less than 0 µeq L^{-1}. Acidification can be further subdivided into chronic acidification (when lakes and streams are acidic year-round) and episodic acidification (short-term decreases in pH and ANC, lasting on the order of hours to weeks). In water bodies with low ANC, strong hydrologic events can temporarily decrease ANC. While N deposition can influence both chronic and episodic acidity, it has the most marked effect on episodic acidification (Murdoch and Stoddard 1992, Schaefer et al. 1990, Wigington et al. 1996).

Severe episodes can produce conditions that are as deleterious to biota as chronic acidification (Baker et al. 1996). The mechanisms that produce acidic episodes include dilution, and flushing of NO_3^-, sulfate (SO_4^{2-}), and/or organic acids from forest soils or snowpack (Baker et al. 1996, Kahl et al. 1992, Lawrence 2002, Wigington et al. 1996, Williams and Tonnessen 2000). Acidic deposition may contribute to episodic acidification by supplying N to sensitive watersheds (producing pulses of NO_3^- during high flow events), producing hydrologically mobile SO_4^{2-}, and by lowering baseline pH and ANC so that even modest episodes are sufficient to produce acidic (i.e., ANC <0 µeq L^{-1}) or near-acidic conditions (i.e., low but positive values of ANC). A generally accepted conceptual model of episodic acidification is that hydrologic events dilute base cation concentrations and trigger a pulsed increase in NO_3^-, causing short-term decreases in ANC (Figure 18.2). In low ANC waters, hydrologic events can result in decreases in ANC to near or below 0 µeq L^{-1}, causing adverse ecological effects (Baker et al. 1996). The deposition and associated leaching of SO_4^{2-} lowers the ANC of surface waters during baseflow, so that short-term pulses of NO_3^- (and, to a lesser extent, pulses of stored SO_4^{2-} and naturally produced organic acids)

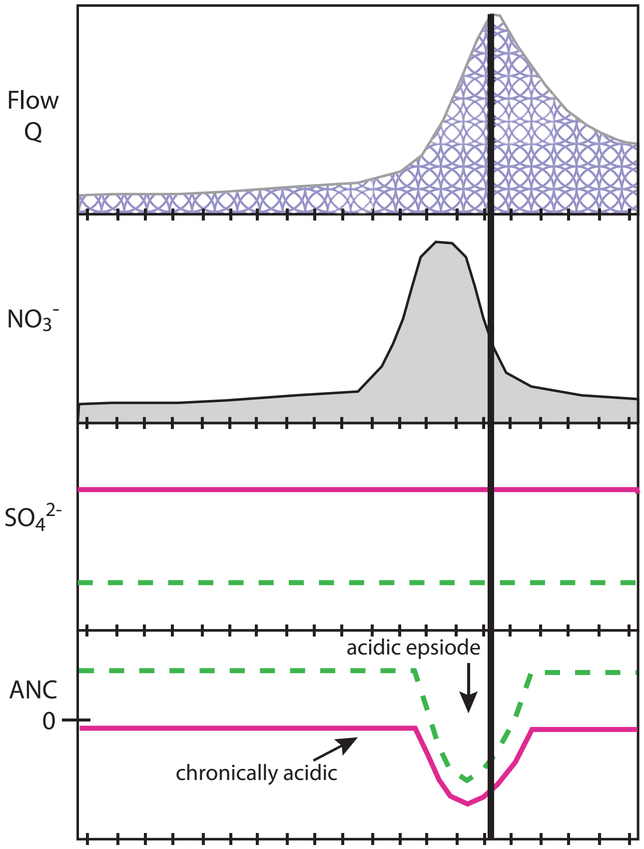


Figure 18.2—Conceptual diagram of changes in surface water chemistry of two contrasting upland streams impacted by atmospheric deposition in response to a hydrologic event. The upper two panels are discharge (Q) and nitrate (NO_3^-) during the stream event; the pattern is identical for both streams. The two streams have two different concentrations of SO_4^{2-} in the third panel; the solid line represents a stream with high SO_4^{2-} and the dashed line is a stream with low SO_4^{2-}. The fourth panel is acid neutralizing capacity (ANC). The stream with the higher SO_4^{2-} (solid line) has a lower ANC during baseflow, and is chronically acidic. During the episodic event, ANC values decrease somewhat from low baseflow values, due to the pulsed input of NO_3^-. The low SO_4^{2-} stream (dashed line) has low, but positive ANC during baseflow. At this site the pulse of NO_3^- during the event causes a short-term decrease in ANC to acidic conditions (ANC < 0 µeq/L).

increase the severity of episodic or seasonal acidification (Driscoll et al. 2001, Stoddard et al. 2003, Wigington et al. 1996).

18.2.2 Biotic Responses to N Deposition

The biotic effects of excess N deposition for inland surface waters can be caused by both acidification and eutrophication. Acidification can have toxic effects on animals (zooplankton, macroinvertebrates, and fish), often as a result of the mobilization of aluminum and low pH conditions (Driscoll et al. 2001). Nutrient N primarily affects lower trophic levels (phytoplankton, periphyton) by increasing productivity in N limited systems (Wetzel 2001). Increased productivity can lead to secondary effects, including changes in the species composition or biodiversity of algae. Whether low or modest N enrichment influences animal populations is poorly understood.

Although chronically high acid levels stress aquatic life, acidic episodes are particularly harmful because abrupt, large changes in water chemistry allow fish and other organisms few areas of refuge (Baker et al. 1996). High concentrations of dissolved inorganic aluminum (Al) are directly toxic to fish, and pulses of Al during acidic episodes are a primary cause of fish mortality (Baker et al. 1996, MacAvoy and Bulger 1995, Van Sickle et al. 1996). Lethal effects are brought about by a combination of high acidity and Al concentrations, which disrupt the salt and water balance of blood in a fish (Driscoll et al. 2001), and respiratory stress caused by gill damage and mucous clogging of gills (Baker and Schofield 1982).

For the analysis of nutrient N effects, we relied on papers and studies that linked aquatic biological and ecological response to atmospheric deposition, but the results are consistent with laboratory or *in situ* dose-response studies and even land-use change studies. Essentially, the productivity of minimally disturbed aquatic ecosystems is often limited by the availability of N, and slight increases in available N trigger a rapid biological response that increases productivity and rearranges algal species assemblages (Lafrancois et al. 2004, Michel et al. 2006, Nydick et al. 2004, Saros et al. 2005). The mechanism for change is alteration of N:P ratios, which can increase productivity of some species at the expense of others (Elser et al. 2009). Higher trophic levels (zooplankton, macroinvertebrates) may be secondarily affected by N, but further increases in primary, or autotrophic, production will be limited by other nutrients such as P or silica (Si).

18.3 Range of Responses Observed

18.3.1 Observed Abiotic Responses to N Deposition

Episodic acidification is more widespread than chronic acidification and can be important in acid-sensitive regions. For example, roughly 10 percent of Adirondack lakes were chronically acidified in the early 1990s, but more than three times that number (31 percent) underwent episodic acidification (Lawrence 2002). In a study of episodic acidification in the northeastern United States, Wigington et al. (1996) ranked the importance of various mechanisms in producing short-term acidity. Pulses of NO_3^- were ranked as the second most important process in the Adirondack and Catskill mountains; only dilution of base cations, which occurs in virtually all surface waters under increased flow, ranked higher.

In the western United States, there are no lakes that are chronically acidic, but episodic acidity has been observed in both the Colorado Front Range and Sierra Nevada Mountains, where episodic NO_3^- leaching during snowmelt decreases ANC to 0 μeq L^{-1} or below (Leydecker et al. 1999, Stoddard 1995, Williams and Tonnessen 2000).

18.3.2 Observed Biotic Responses to N Deposition

Algae are the aquatic biota most likely to show rapid eutrophication effects from N deposition. Eutrophication effects are most likely to occur in fresh waters that historically received low nutrient inputs. Especially in the western United States, these ecosystems are mainly located at high elevations. Studies have shown an increase in phytoplankton biomass in lakes with increasing N deposition in the Snowy Range in Wyoming, the Colorado Front Range, Sierra Nevada, Sweden, and across Europe (Table 18.3; Bergström et al. 2005, Bergström and Jansson 2006, Elser et al. 2009, Lafrancois et al. 2004, Nydick et al. 2004,

Table 18.3—Nitrate concentrations at which phytoplankton response has been observed

Site	N concentration *mg* NO_3^{-}*-N* L^{-1}	Response	Study
Colorado Front Range	1.1	Diatom spp. growth stimulation	Lafrancois et al. 2004
Snowy Range, WY	1.0	Shift in species composition	Nydick et al. 2004
Beartooth Mountains WY	0.9	Stimulation of *A. formosa, F. crotonensis*	Saros et al. 2005
Sweden	0.9	Increasing biomass	Bergström et al. 2005
Europe and No. Amer. Lakes	0.9	Increasing biomass	Bergström and Jansson 2006

Table 18.4—Biological response observed in paleolimnological studies

Site	Year(s)	Response (method)	Study
Colorado Rocky Mountains	1950	Increased microbial activity, greater primary production, change in species composition (isotopic analysis)	Enders et al. 2008
	1950	Greater primary production, stimulation of *A. formosa, F. crotonensis*, shift in species assemblages (pigment analysis).	Das et al. 2005
	1950	Greater primary production, Stimulation of *A. formosa, F. crotonensis,* shift in species assemblages (taxonomy and cell counts)	Wolfe et al. 2001, 2003
	1950-1964	Threshold modeled at 1.5 kg N ha^{-1} yr^{-1}	Baron 2006
Beartooth Mountain Range, WY	1990	Greater primary production, stimulation of *A. formosa, F. crotonensis*, shift in species assemblages	Saros et al. 2003

Sickman et al. 2003). Paleolimnological reconstructions show a stronger eutrophication response in lakes where N deposition is higher than in lakes with lower N deposition (Das et al. 2005; Enders et al. 2008; Saros et al. 2003; Wolfe et al. 2001, 2003; Table 18.4).

Community shifts in phytoplankton were observed in the Snowy Range, with chrysophytes (golden algae) favored in lakes having lower N and cyanophytes (photosynthetic bacteria, also called blue-green algae) and chlorophytes (green algae) favored in lakes having higher N (Lafrancois et al. 2004). Sediment cores from lakes in the Colorado Front Range showed increasing representation of mesotrophic diatoms in recent times, as compared with predevelopment conditions (Enders et al. 2008; Wolfe et al. 2001, 2003). In Lake Tahoe, California, there has been a sharp increase in the ratio of araphidinate pennate (characteristic of nutrient rich conditions) to centric (characteristics of nutrient poor conditions) diatoms since about 1950 (largely due increases in *Fragilaria crotenensis),* associated with increased N loading to the lake. Jassby et al. (1994) found that atmospheric deposition supplies most of the N to Lake Tahoe. While runoff from catchment streams supplies organic N to Lake Tahoe (Coats and Goldman 2001), a recent meta-analysis finds little relation between DON runoff and atmospheric N deposition (Pellerin et al. 2006).

Two species of diatom, *Asterionella formosa* and *Fragilaria crotonensis*, now dominate the flora of at least several alpine and montane Rocky Mountain lakes (Baron et al. 2000; Interlandi and Kilham 1998; Saros et al. 2003, 2005; Wolfe et al. 2001, 2003). The growth of *A. formosa* has been stimulated with N amendments during *in situ* incubations, using bioassays and mesocosms (6.4 to 1616.0 μmol L^{-1} N, McKnight et al. 1990; 76.0 μmol L^{-1}, Lafrancois et al. 2004; 18.0 μmol L^{-1}, Saros et al. 2005). *In situ* incubations in large lakes of Yellowstone National Park also stimulated *F. crotonensis* (Michel et al. 2006). The N requirements for *A. formosa* and *F. crotonensis* were determined to be 0.041 μmol L^{-1} and 0.006 μmol L^{-1}, respectively; higher concentrations stimulated growth (Michel et al. 2006). Other species, including *Tetracyclus glans*, and *Staurosirella pinnata*, have shown negative growth responses to increased N (Michel et al. 2006). In studies of lake sediment diatom remains, typical oligotrophic species such as *Aulacoseria perglabra*, *Cyclotella steligera*, and *Achnanthes spp*. declined coincident with the rise in dominance of *A. formosa* and *F. crotonensis* (Wolfe et al. 2003)

Interlandi and Kilham (1998) demonstrated that maximum species diversity was maintained when N concentrations were low (<3.0 µmol L^{-1}) in lakes in the Yellowstone National Park (Wyoming, Montana) region. The implication is that species diversity declines with increasing availability of N. This finding complements the results of terrestrial studies that also showed a negative relationship between species diversity and N availability (Gilliam 2006, Suding et al. 2005).

Studies of Lake Erie found N to be seasonally, but only moderately, limiting to phytoplankton growth. Phytoplankton were far more responsive to additions of P, iron (Fe), or Si than N during different seasons (Moon and Carrick 2007, North et al. 2007). Studies of Lake Superior have documented a century-long increase in lake NO_3^- concentrations, which has produced a stoichiometric imbalance and strong P limitation (Finlay et al. 2007, Sterner et al. 2007).

There have been few studies on the effects of nutrient enrichment from N deposition on aquatic animals. Nydick et al. (2004) found that zooplankton density and biomass were altered by changes in nutrients in enclosure experiments, probably as a result of poor food quality. A whole-ecosystem experiment at the Bear Brook watershed, Maine simulated the effects of N and S deposition by means of experimental ammonium sulfate ($(NH_4)_2SO_4$) addition over a 10-year period. Researchers found that elevated N inputs had minimal effect on stream detritus processing (Chadwick and Huryn 2005). They also found that N additions had no significant effect on stream macroinvertebrate secondary production or varying production by functional feeding groups. They concluded that climate-related variables, such as flow duration and litter inputs, controlled secondary production when N was not limiting.

Nitrogen deposition appears to have stimulated productivity and altered algal species assemblages at deposition rates of 1.5 to 2.5 kg N $ha^{-1}yr^{-1}$ (Baron 2006, Bergström and Jansson 2006). A meta-analysis of lakes from 42 regions of Europe and North America concluded that atmospheric N deposition was responsible for increased concentrations of N in lake water, and elevated phytoplankton biomass (Bergström and Jansson 2006). Bergström and Jansson (2006) found a consistent pattern of nutrient limitation, showing N limitation for deposition below approximately 2.5 kg N $ha^{-1}yr^{-1}$, co-limitation of N and P for deposition between ~2.5 and 5.0 kg N $ha^{-1}yr^{-1}$, and P limitation in areas with N deposition greater than 5.0 kg N $ha^{-1}yr^{-1}$.

18.4 Critical Loads Estimates

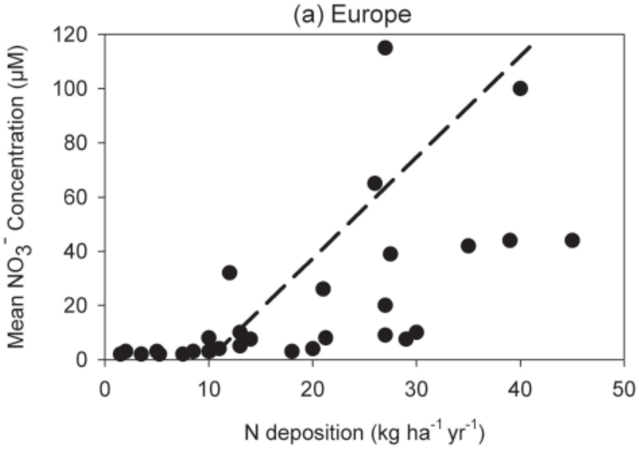
18.4.1 Critical Loads for Abiotic Responses to N Deposition

Despite the difficulty of predicting current and future N behavior in lakes and streams, as discussed below (see section 18.6), both mechanistic (Aber and Driscoll 1997) and conceptual (Stoddard 1994) models of N saturation predict that elevated rates of N deposition will eventually produce elevated runoff concentrations of NO_3^- in relatively undisturbed catchments. Empirical cross-site watershed studies show the relationship between watershed N concentrations or loss as a function of atmospheric N deposition (Aber et al. 2003, Baron et al. 2000, Elser et al. 2009, Fenn et al. 2003, Sickman et al. 2002).

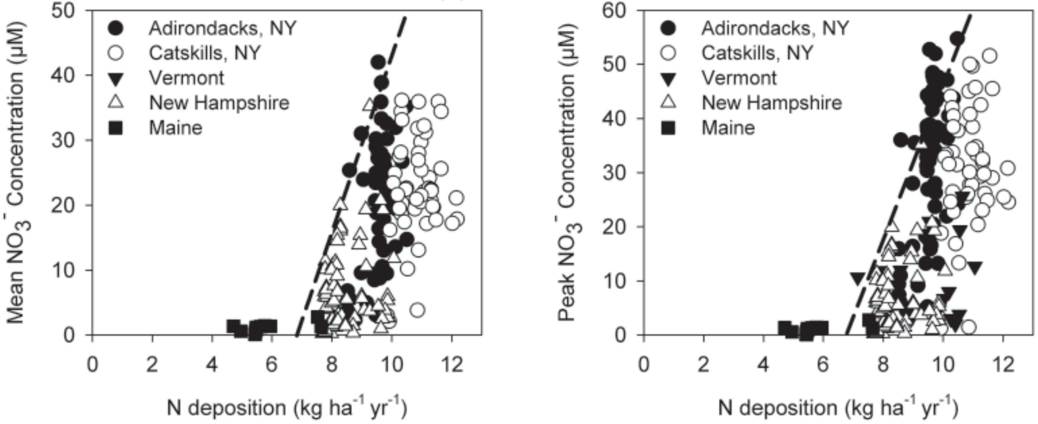
Such cross-site analyses were originally conducted for Europe (Dise and Wright 1995, Wright et al. 2001), and typically show a "dog-leg" pattern—low surface water NO_3^- concentrations or leaching with low levels of N deposition, and elevated leaching losses and concentrations above a "threshold" of deposition. For the European data, the threshold is roughly 10 kg N $ha^{-1}yr^{-1}$ (Wright et al. 2001).

We examined watershed NO_3^- concentrations as a function of total atmospheric N deposition for the eastern (Aber et al. 2003) and western United States (Sickman et al. 2002). Relationships are presented for annual average NO_3^- and peak springtime NO_3^-

(a) Europe



(b) Northeastern U.S.



(c) Western U.S., High Elevation

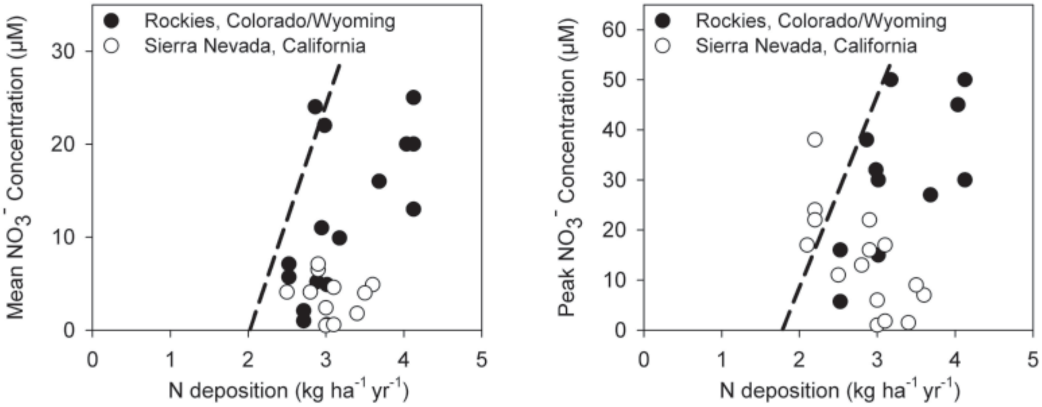


Figure 18.3—Relationship between mean and peak annual nitrate concentration (µM) and nitrogen deposition (kg N ha^{-1} yr^{-1}) in (a) forested catchments in Europe; (b) forested catchments in the northeastern United States; and (c) high elevation catchments in the western United States. European data from (Wright et al. 2001). Northeastern United States data are from Aber et al. (2003). Western NO_3^- data are from Sickman et al. (2002) and Burns (2004). Western deposition was estimated from modeled NO_3 deposition (Nanus et al. 2003) and NH_4^+ deposition from the nearest NADP station. Lines are drawn by eye to estimate the x- intercept, the value of N deposition at which significant NO_3^- leaching begins to occur.

in Figure 18.3. We consider the development of relationships between lake and stream NO_3^- and atmospheric N deposition to be the first step toward empirical critical loads for N in these aquatic ecosystems. Because both abiotic and biotic responses to N deposition in surface water begin only when excess NO_3^- begins to leach from catchments, the thresholds suggested in Figure 18.3 imply the lower limits for N

Table 18.5—Summary of critical loads of N for eutrophication and acidification for Eastern and Western high elevation lakes. Reliability rating: ## reliable; # fairly reliable; (#) expert judgement

	Western lakes *kg N ha^{-1} yr^{-1}*	Reliability for Western lakes	Eastern lakes *kg N ha^{-1} yr^{-1}*	Reliability for Eastern lakes
Critical load of N for eutrophication	2	##	8	#
Critical load of N for acidity	4-8	#	9	(##)

deposition below which effects are unlikely. The data suggest preliminary N critical loads of about 2 kg N ha^{-1}yr^{-1} for the western mountains, and 8 kg N ha^{-1}yr^{-1} for forested catchments in the East based on NO_3^- leaching (Table 18.5). This value for the Western lakes can be considered a critical load of N for eutrophication. Note that there is some uncertainty in these estimates due to inherent difficulty in quantifying dry N deposition (see Chapter 3 this report). In addition, deposition varies by elevation within watersheds, adding additional uncertainty (Weathers et al. 2006).

We anticipate that the critical loads of N for acidity would be higher than the threshold values for eutrophication. Note that it is essential to establish the values of watershed ANC and SO_4^{2-} and other major solutes in order to determine the critical load for acidity (Leydecker et al. 1999, Meixner et al. 2004). This is most effectively done with steady-state or dynamic acidification models that consider all major solutes simultaneously. We estimated critical loads of N for acidity using the literature and expert judgment. For Eastern lakes, we used TIME lake data (US EPA 2006) to identify lakes with low ANC values where a 10 µeq L^{-1} decrease in ANC, might increase the proportion of lakes exhibiting episodic acidification (ANC < 0 µeq L^{-1}). This change could result from an increase of approximately 20 µeq L^{-1} in NO_3^- during snowmelt based on the stoichiometric response of changes in ANC with additions in strong acid anions during snowmelt (Schaefer et al. 1990). Comparing average NO_3^- concentrations with snowmelt values for Eastern lakes (Figure 18.3), suggests an N critical load for acidity of approximately 9 kg N ha^{-1}yr^{-1}. This analysis assumes that SO_4^{2-} concentrations remain constant and are not changing. This value is similar to that derived for Northern Forests (Chapter 7; Aber et al. 2003), as well as that derived for European forested streams (Dise and Wright 1995), thus we consider it to be reliable.

Williams and Tonnessen (2000) reported episodic acidification in a Colorado Front Range lake during spring snowmelt with annual wet N deposition rates of 4 kg N ha^{-1}yr^{-1} (Table 18.6). An ecosystem modeling effort with MAGIC (Model of Acidification of Groundwater in Catchments) proposed an acidification critical load for the Colorado Front Range of 8 kg N ha^{-1} yr^{-1} (Table 18.6; Sullivan et al. 2005). Because the empirical value came from a high elevation lake that was highly responsive to changes in deposition values, while the modeled value was for a stream with at least some surrounding vegetation, we consider the measured value of 4 kg N ha^{-1}yr^{-1} to be fairly reliable, although more observations from additional lakes would lend strength to the critical load. Note these measurements are extremely difficult to obtain.

18.4.2 Critical Loads for Biotic Responses to N Deposition

Our estimate for N critical loads for eutrophication in the mountain West (i.e., 2 kg N ha^{-1} yr^{-1}) is similar to other estimates of aquatic critical loads for the region (Baron 2006, Fenn et al. 2003a). The estimated aquatic critical N load is lower than for terrestrial ecosystems, which is suggested to be 4 kg N ha^{-1} yr^{-1} for tundra based on experimental studies (Bowman et al. 2006), 3 to 4 kg N ha^{-1} yr^{-1} for tundra based on modeled studies (Baron et al. 1994), and 4 kg N ha^{-1} yr^{-1} for subalpine forest based on regional surveys (Rueth and Baron 2002). Nitrogen deposition appears to have stimulated productivity and altered algal species assemblages at deposition rates of 1.5 to 2.5 kg N ha^{-1} yr^{-1} (Table 18.7). A hindcasting exercise determined that the changes in algal communities in Rocky Mountain National Park

Table 18.6—Critical load for N for acidity for surface water in the Rocky Mountains. RMNP=Rocky Mountain National Park

Ecosystem	Site	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Response	Comments	Study
Alpine lake	Southern Rockies/Niwot	4.0	Episodic freshwater acidification	Observed	Williams and Tonnesson 2000
Alpine stream	Southern Rockies/Loch Vale RMNP	5	Episodic freshwater acidification	Modeled	Baron and Hartman 2004
Alpine stream	Southern Rockies/Loch Vale RMNP	7.3	Chronic freshwater acidification	Modeled	Baron and Hartman 2004
Alpine stream	Southern Rockies/Loch Vale RMNP	8	Freshwater acidification; ANC = 20 µeq L^{-1}	Modeled	Sullivan et al. 2005
Subalpine stream/lake	Southern Rockies/Loch Vale RMNP	12	Freshwater acidification; ANC = 20 µeq L^{-1}	Modeled	Sullivan et al. 2005
Alpine stream	Southern Rockies/Loch Vale RMNP	14	Freshwater acidification; ANC = 0 µeq L^{-1}	Modeled	Sullivan et al. 2005
Subalpine stream/lake	Southern Rockies/Loch Vale RMNP	21	Freshwater acidification; ANC = 0 µeq L^{-1}	Modeled	Sullivan et al. 2005

Table 18.7—Critical load for N for eutrophication for surface water in the Rocky Mountains. RMNP=Rocky Mountain National Park

Ecosystem	Site	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Response	Comments	Study
Alpine lake	Southern Rockies/ Loch Vale RMNP	1.5	Eutrophication	Paleolimnological	Baron 2006
Alpine lake	Northern Rockies/ Beartooth Mountains, WY	1.5	Eutrophication	Paleolimnological	Saros et al. 2003
Alpine stream	Southern Rockies/ Loch Vale RMNP	2	Freshwater eutrophication	Modeled	Baron et al. 1994
Alpine lakes	Rocky Mountains	2.5	Eutrophication, N and P co-limitation	Surveys and references therein	Bergström and Jansson 2006

that occurred between 1850 and 1964 were associated with an increase in wet N deposition that was 1.5 kg N ha^{-1} yr^{-1} (Baron 2006; Table 18.7). Similar changes inferred from lake sediment cores of the Beartooth Mountains of Wyoming also occurred at about 1.5 kg N ha^{-1} yr^{-1} deposition (Table 18.7). Pre-industrial inorganic N deposition is estimated to have been 0.1 to 0.7 kg N ha^{-1} yr^{-1}, based on measurements from remote parts of the world (Galloway et al. 2004, Holland et al. 1999). In the western United States, pre-industrial, or background, inorganic N deposition was estimated by Holland et al. (1999) to range from 0.4 to 0.7 kg N ha^{-1} yr^{-1}.

The determination of N critical loads for eutrophication of eastern lakes and the Great Lakes is problematic. Our analysis of N-limited lakes in lake districts of the United States suggests that, surprisingly, there are relatively large numbers of N-limited lakes in the East (Table 18.2). For those lakes, inputs of N associated with elevated atmospheric deposition are possibly stimulating plant productivity and altering algal communities, although mesotrophic lakes are often limited by P, and large lakes may be limited by Fe (Moon and Carrick 2007, Schindler et al. 2008, Sterner et al. 2007, Wetzel 2001). In a study of hundreds of Swedish lakes along an N deposition gradient, lakes receiving greater than 4 kg N ha^{-1} yr^{-1} had greater ratios of chlorophyll *a*:total P, signifying a eutrophication response (Bergström et al. 2005). In the eastern United States, it is unknown whether a reduction in atmospheric N emissions and deposition would affect productivity in the N-limited lakes. Because these ecosystems are currently receiving elevated N deposition and have been receiving elevated deposition for decades, it is difficult to determine a value for critical loads of N. Moreover, evaluating the benefits associated with control on NO_3^- or NH_4^+ inputs in these N limited lakes is not straightforward. Inputs of NO_3^- and NH_4^+ are partially removed by in-lake processing (Kelly et al. 1987), which alters ANC. This process will influence the change in ANC associated with acidic deposition to eastern lakes.

18.5 Comparison to Critical Loads for Other Regions

The threshold of atmospheric N deposition at which elevated NO_3^- leaching may occur is highest in Europe, intermediate in eastern North America and lowest in the West (Figure 18.3). Note that elevated leaching losses do not necessarily occur at deposition levels above these thresholds. These thresholds only represent conditions of deposition above which elevated leaching has been noted at some sites and below which leaching rarely occurs. The mechanism(s) responsible for regional differences in the thresholds is not clear. Possible factors may include differences in the relative deposition of NH_4^+ and NO_3^-; more intensive forest and land management practices in Europe (Dise and Wright 1995), and differences in climate and hydrology. For a given region, even under elevated atmospheric N deposition, there is also considerable variability across sites. This variability may be due to several factors, the most important of which are likely land disturbance history (e.g., past forest cutting and agricultural practices) and climatic factors.

18.6 Future Research Directions and Limitations in Understanding

Adverse direct effects of N deposition on most fauna due to nutrient enrichment are probably minimal. Nitrogen concentrations alone are not high enough to influence animal metabolism, and the extent of eutrophication is insufficient (due to induced P limitation in oligotrophic waters) to cause oxygen depletion. Effects of N on invertebrates that are essential parts of aquatic food webs, however, are not well understood. Individual algal taxa are stimulated at low N concentrations, and several, including *Asterionella formosa* and *Fragilaria crotonensis*, have come to dominate some lakes that have received elevated N deposition (Saros et al. 2005, Wolfe et al. 2003). Other species have declined commensurate with increased available N, but we found only one study that addressed the question of effects of N deposition on freshwater aquatic diversity. Clearly, more work is needed to clarify these effects.

Research is needed to address two other questions. First, how do freshwater ecosystems respond to decreases in inputs of N? Alternative responses, which are not mutually exclusive, include decreases in productivity, reversion of species assemblages to former compositions, or irreversible alterations that develop into novel ecosystems (Hobbs et al. 2006, Schindler et al. 2008). Second, how does climate change interact with N deposition to influence aquatic productivity and assemblages?

One manifestation of limited understanding of ecosystem response to atmospheric N deposition is our inability to effectively explain the long-term temporal patterns of surface water N concentrations and loss in watershed ecosystems. Nitrate concentrations have been increasing in Lake Superior since at least the 1930s, but the cause remains unknown, and examination of stable N isotopes shows a more complex N-cycling story than can be explained by atmospheric N deposition alone (Finlay et al. 2007). In the mountain West, a few monitoring sites have shown increases in surface water NO_3^- attributable to increases in atmospheric N emissions and deposition (Jassby et al. 1994, Williams et al. 1996). Other sites have reported measurably high N concentrations since monitoring began in the 1980s (Baron et al. 2000, Fenn et al. 2003a). In the Northeast, however, investigators have reported declines in surface water concentrations and loss of NO_3^- in watersheds (Driscoll et al. 2003a, 2007; Goodale et al. 2003; Stoddard et al. 2003), with little change in atmospheric N deposition. The mechanism(s) contributing to this decline in surface water NO_3^- in the Northeast is not clear but may be influenced by carbon dioxide-fertilization of forest vegetation, shifts in the composition of tree species, increases in in-stream N retention and/or changes in climate (Bernhardt et al. 2005, Driscoll et al. 2003b, Goodale et al. 2003, Thomas et al. 2010).

Ecosystem models, as mentioned above, are useful for augmenting empirical studies for deriving critical loads. This is especially true for addressing acidification critical loads, but ecosystem models have value for aiding in selection of critical loads for eutrophication where measurements are scarce. Ecosystem models, while widely used to represent N-cycling and effects, are still unable to represent some responses, reflecting an inadequate understanding of ecosystem processes and drivers. Although there are many ecosystem N-cycling models, there are flaws in all of them. For example, PnET-CN was developed to simulate N dynamics in forest ecosystems (Aber et al. 1997). While PnET-CN depicts many N-cycling processes, it over-predicts recent surface water NO_3^- in eastern forest watersheds and fails to capture the recent declines in NO_3^- concentrations (e.g., Aber et al. 2002). DayCent-Chem is another promising nutrient-cycling and geochemical model, but it also is not able to reproduce New England stream NO_3^- trends (Hartman et al. 2007, Hartman et al. 2009). Hydrochemical models such as the Alpine Hydrochemical Model (AHM) suffer from similar problems in reproducing chemical weathering or specific events (Meixner et al. 2004). As with many active ecosystem and hydrochemical models, however, AHM is constantly undergoing revisions and improvements (Molotch et al. 2008). Without effective simulation models, it will be difficult to develop critical loads for N and conduct comprehensive critical loads for acidity.

LITERATURE CITED

Aber, J.D.; Driscoll, C.T. 1997. **Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests.** Global Biogeochemical Cycles. 11: 639-648.

Aber, J.D.; Goodale,C.L.; Ollinger, S.V.; Smith, M-L.; Magill, A.H.; Martin, M.E.; Hallett, R.A.; Stoddard, J.L. 2003. **Is nitrogen deposition altering the nitrogen status of Northeastern forests?** BioScience. 53: 375-389.

Aber, J.D.; Ollinger, S.V.; Driscoll, C.T. 1997. **Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition.** Ecological Modeling. 101: 61-78.

Aber, J.D., Ollinger, S.V.; Driscoll, C.T.; Likens, G.E.; Holmes, R.T.; Freuder, R.J.; Goodale,C.L. 2002. **Inorganic nitrogen losses from a forested ecosystem in response to physical, chemical, biotic, and climatic perturbations.** Ecosystems. 5: 648-658.

Baker, J.P.; Schofield, C.W. 1982. **Aluminum toxicity to fish in acidic waters.** Water, Air, and Soil Pollution. 18: 289-309.

Baker, J.P.; Van Sickle, J.; Gagen, C.J.; Baldigo, B.P.; Bath, D.W.; Carline, R.F.; DeWalle, D.R.; Kretser, W.A.; Murdoch, P.S.; Sharpe, W.E.; Simonin, H.A.; Wigington, P.J. 1996. **Episodic acidification of small streams in the northeastern United States: Effects on fish populations.** Ecological Applications. 6: 422-437.

Baron, J.S. 2006. **Hindcasting nitrogen deposition to determine ecological critical load.** Ecological Applications. 16(2): 433-439

Baron, J.S.; Ojima, D.S; Holland, E.A.; Parton, W.J. 1994. **Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: Implications for aquatic systems.** Biogeochemistry. 27: 61-82.

Baron, J.S.; Rueth, H.M.; Wolfe, A.M.; Nydick, K.R.; Allstott, E.J.; Minear, J.T.; Moraska, B. 2000. **Ecosystem responses to nitrogen deposition in the Colorado Front Range.** Ecosystems. 3: 352-368.

Bergström, A.; Blomqvist, P.; Jansson, M. 2005. **Effects of atmospheric nitrogen deposition on**

nutrient limitation and phytoplankton biomass in unproductive Swedish lakes. Limnology and Oceanography. 50: 987-994.

Bergström, A.; Jansson, M. 2006. **Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere.** Global Change Biology. 12: 635-643.

Bernhardt, E.S.; Likens, G.E.; Hall, R.O.; Buso, D.C.; Fisher, S.G.; Burton, T.M.; Meyer, J.L.; McDowell, W.H.; Mayer, M.S.; Bowden, W.B.; Findlay, S.E.G.; Macneale, K.H.; Stelzer, R.S.; Lowe, W.H. 2005. **Can't see the forest for the stream? - In-stream processing and terrestrial nitrogen exports.** BioScience. 55: 219-230.

Bowman, W.D.; Larson, J.R.; Holland, K.; Wiedermann, M.; Nieves, J. 2006. **Nitrogen critical loads for alpine vegetations and ecosystem response- are we there yet?** Ecological Applications. 16(3): 1183-1193.

Brooks, P.D.; Williams, M.W.; Schmidt, S.K. 1998. **Inorganic nitrogen and microbial biomass dynamics before and during snowmelt.** Biogeochemistry. 43: 1-15.

Burns, D.A. 2004. **The effects of atmospheric nitrogen deposition in the Rocky Mountains of Colorado and southern Wyoming, USA—a critical review.** Environmental Pollution. 127: 257-269.

Chadwick, M. A.; Huryn, A.D. 2005. **Response of stream macroinvertebrate production to atmospheric nitrogen deposition and channel drying.** Limnology and Oceanography. 50: 228-236.

Charles, D.R., ed. 1991. **Acidic deposition and aquatic ecosystems. Regional case studies.** New York: Springer-Verlag. 747 p.

Coats, R.N.; Goldman, C.R. 2001. **Patterns of nitrogen transport in streams of the Lake Tahoe basin, California-Nevada.** Water Resources Research. 37: 405-415.

Das, B.; Vinebrooke, R.D.; Sanchez-Azofeifa, A.; Rivard, B.; Wolfe, A.P. 2005. **Inferring sedimentary chlorophyll concentrations with reflectance spectroscopy: a novel approach to reconstructing historical changes in the trophic status of mountain lakes.** Canadian Journal of Fisheries and Aquatic Science. 62: 1067-1078.

Dennis, R.; Haeuber, R.; Blett, T.; Cosby, B.J.; Driscoll, C.T.; Sickles, J.; Johnston, J.M. 2007. **Sulfur and nitrogen deposition on ecosystems in the United States.** EM: Air and Waste Management Associations Magazine for Environmental Managers. December 2007: 12-17.

Dise, N.B.; Wright, R.F. 1995. **Nitrogen leaching from European forests in relation to nitrogen deposition.** Forest Ecology and Management. 71: 153-161.

Downing, J.A.; Prairie, Y.T.; Cole, J.J.; Duarte, C.M.; Tranvik, L.J.; Striegl, R.G.; McDowell, W.H.; Kortelainen, P.; Caraco, N.F.; Melack, J.M.; Middleburg, J. 2006. **The global abundance and size distribution of lakes, ponds, and impoundments.** Limnology and Oceanography. 51: 2388-2397.

Driscoll, C.T.; Driscoll, K.M.; Roy, K.M.; Dukett, J. 2007. **Changes in the chemistry of lakes in the Adirondack region of New York following declines in acidic deposition.** Applied Geochemistry. 22: 1181-1188.

Driscoll, C.T.; Driscoll, K.M.; Roy, K.M.; Mitchell, M.J. 2003a. **Chemical response of lakes in the Adirondack region of New York to declines in acidic deposition.** Environmental Science and Technology. 37: 2036-2042.

Driscoll, C.T.; Lawrence, G.B.; Bulger, A.J.; Butler, T.J.; Cronan, C.S.; Eager, C.; Lambert, K.F.; Likens, G.E.; Stoddard, J.L.; Weathers, K.C. 2001.

Acidic deposition in the northeastern United States: Sources and inputs, ecosystem effects and management strategies. BioScience. 51: 180-198.

Driscoll, C.T.; Whitall, D.; Aber, J.D.; Boyer, E.W.; Castro, M.S.; Cronan, C.; Goodale, C.L.; Groffman, P.M.; Hopkinson, C.; Lambert, K.; Lawrence, G.; Ollinger, S.V. 2003b. **Nitrogen pollution in the northeastern United States: Sources, effects, and management options.** BioScience. 53: 357-374.

Dumont, E.; Harrison, J.A.; Kroeze, C.; Bakker, E.J.; Seitzinger, S.P. 2005. **Global distribution and sources of dissolved inorganic nitrogen export to the coastal zone: Results from a spatially explicit, global model.** Global Biogeochemical Cycles. 19: GB4S02.

Eilers, J.M.; Selle, A.R. 1991. **Geographic overview of the regional case study areas.** In: Charles, D.F., ed. Acidic deposition and aquatic ecosystems. New York: Springer-Verlag: 107-125.

Elser, J.J.; Anderson, T.; Baron, J.S.; Bergström, A-K; Kyle, M.; Nydick, K.R.; Steger, L.; Hessen, D.O. 2009. **Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition.** Science. 326: 835-837.

Elser, J.J.; Bracken, M.E.S.; Cleland, E.E.; Gruner, D.S.; Harpole, W.S.; Hellebrand, H.; Ngai, J.T.; Seabloom, E.W.; Shurin, J.B.; Smith, J.E. 2007. **Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems.** Ecology Letters. 10: 1135-1142.

Elser, J.J.; Marzolf, E.R.; Goldman, C.R. 1990. **Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments.** Canadian Journal of Fisheries and Aquatic Science. 47: 1468-1477.

Enders, S.K.; Pagani, M.; Pantoja, S.; Baron, J.S.; Wolfe, A.P.; Pedentchouk, N.; Nuñez, L. 2008. **Compound-specific stable isotopes of organic compounds from lake sediments track recent environmental changes in an alpine ecosystem, Rocky Mountain National Park (United States of America).** Limnology and Oceanography. 53(4): 1468-1478.

Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W. 2003. **Ecological effects of nitrogen deposition in the Western United States.** BioScience. 53: 404-420.

Finlay, J.C.; Sterner, R.W.; Kumar, S. 2007. **Isotopic evidence for in-lake production of accumulating nitrate in Lake Superior.** Ecological Applications. 17: 2323-2332.

Galloway, J.N.; Aber, J.D.; Erisman, J.W.; Seitzinger, S.P.; Howarth, R.W.; Cowling, E.B.; Cosby, B.J. 2003. **The nitrogen cascade.** BioScience. 53: 341-356.

Galloway, J.N.; Dentener, F.J.; Capone, D.G.; Boyer, E.W.; Howarth, R.W.; Seitzinger, S.P.; Asner, G.P.; Cleveland, C.C.; Green, P.A.; Holland, E.A.; Karl, D.M.; Michaels, A.F.; Porter, J.H.; Townsend, A.R.; Vorosmarty, C.J. 2004. **Nitrogen cycles: past, present, and future.** Biogeochemistry. 70: 153-226.

Gilliam, F.S. 2006. **Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition.** Journal of Ecology. 94: 1176-1191.

Goodale, C.L.; Aber, J.D.; Vitousek, P.M. 2003. **An unexpected nitrate decline in New Hampshire streams.** Ecosystems. 6: 75-86.

Hartman, M.D.; Baron, J.S. 2004. **Modeling the timeline for lake and stream acidification from excess nitrogen deposition for Rocky Mountain National Park.** In: Proceedings, Ecological Society of America annual meeting; 2004 August 1-6; Portland, OR. Washington, DC: Ecological Society of America. [Abstract.].

Hartman, M.D., Baron, J.S.; Clow, D.W.; Creed, I.S.; Driscoll, C.T.; Ewing, H.; Haines, B.D.; Lajtha, K.; Knoepp, J.; van Migroet, H.; Ojima, D.S.; Parton, W.J.; Renfro, J.; Robinson, B.; Weathers, K.; Williams, M.W. 2009. **DayCent-Chem simulations of ecological and biogeochemical processes of eight mountain ecosystems in the United States.** USGS Scientific Investigations Report SIR 2009-5150. Ft. Collins, CO; U.S. Geological survey. 174 p. Available at http://pubs.usgs.gov/sir/2009/5150/

Hartman, M.D.; Baron, J.S.; Ojima, D.S. 2007. **Application of a coupled ecosystem-chemical equilibrium model, DayCent-Chem, to stream and soil chemistry in an alpine watershed.** Ecological Modeling. 200: 493-510.

Hobbs, R.J.; Arico, S.; Aronson, J.; Baron, J.S.; Bridgewater, P.; Cramer, V.A.; Epstein, P.R.; Ewel, J.J.; Klink, C.A.; Lugo, A.E.; Norton, D.; Ojima, D.; Richardson, D.M.; Sanderson, E.W.; Valladares, F.; Vilà, M.; Zamora, R.; Zobel, M. 2006. **Novel ecosystems: theoretical and management aspects of the new ecological world order.** Global Ecology and Biogeography. 15: 1-7.

Holland, E.A.; Dentener, F.J.; Braswell, B.H.; Sulzman, J.M. 1999. **Contemporary and pre-industrial global reactive nitrogen budgets.** Biogeochemistry. 46: 7-43.

Huntington, T.G.; Hooper, R.P.; Johnson, C.E.; Aulenbach, B.T.; Cappellato, R.; Blum, A.E. 2000. **Calcium depletion in a southeastern United States forest ecosystem.** Soil Science Society of America Journal. 64: 1845-1858.

Interlandi, S.J.; Kilham, S.S. 1998. **Assessing the effects of nitrogen deposition on mountain waters: A study of phytoplankton community dynamics.** Water Science and Technology. 38: 139-146.

Jassby, A.D.; Reuter, J.E.; Axler, R.P.; Goldman, C.R.; Hackley, S.H. 1994. **Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California-Nevada).** Water Resources Research. 30: 2207-2216.

Kahl, J.S.; Norton, S.A.; Haines, T.A.; Rochette, E.A.; Heath, R.H.; Nodvin, S.C. 1992. **Mechanisms of episodic acidification in low-order streams in Maine, USA.** Environmental Pollution. 78: 37-44.

Kelly, C.A.; Rudd, J.W.M.; Hesslein, R.H.; Driscoll, C.T.; Gherini, S.A.; Hecky, R.E. 1987. **Prediction of biological acid neutralization in acid-sensitive lakes.** Biogeochemistry. 3: 129-140.

Lafrancois, B.M.; Nydick, K.R.; Johnson, B.M.; Baron, J.S. 2004. **Cumulative effects of nutrients and pH on the plankton of two mountain lakes.** Canadian Journal of Fisheries and Aquatic Science. 61: 1153-1165.

Landers, D.H.; Eilers, J.M.; Brakke, D.F.; Overton, W.S.; Kellar, P.E.; Silverstein, W.E.; Schonbrod, R.D.; Crowe, R.E.; Linthurst, R.A.; Omernik, J.M.; Teague, S.A.; Meier, E.P. 1987. **Characteristics of lakes in the western United States - Volume I: population descriptions and physico-chemical relationships.** EPA/600/3-86/054a. Washington, DC: U.S. Environmental Protection Agency. 176 p.

Lawrence, G.B. 2002. **Persistent episodic acidification of streams linked to acid rain effects on soil.** Atmospheric Environment. 36: 1589-1598.

Lehmann, C.M.B.; Bowersox, V.C.; Larson, S.M. 2005. **Spatial and temporal trends of precipitation chemistry in the United States, 1985-2002.** Environmental Pollution. 135: 347-361.

Lehmann, C.; Bowersox, V.; Larson, R.S.; Larson, S.M. 2007. **Monitoring Long-term Trends in Sulfate and Ammonium in US Precipitation: Results from the National Atmospheric Deposition Program/National Trends Network.** Water, Air, and Soil Pollution. 7(1): 59-66.

Lewis Jr., W.M.; Wurtsbaugh, W.A. 2008. **Control of lacustrine phytoplankton by nutrients: erosion of**

the phosphorus paradigm. International Review of Hydrobiology. 93: 446-465.

Leydecker, A.; Sickman, J.O.; Melack, J.M. 1999. **Episodic lake acidification in the Sierra Nevada, California.** Water Resources Research. 35: 2793-2804.

Linthurst, R.A.; Landers, D.H.; Eilers, J.M.; Brakke, D.F.; Overton, W.S.; Meier, E.P.; Crowe, R.E. 1986. **Characteristics of lakes in the eastern United States - Volume I: Population descriptions, and physico-chemical relationships.** EPA/600/4-86/007a. Washington, DC: U.S. Environmental Protection Agency. 136 p.

MacAvoy, S.E.; Bulger, A.J. 1995. **Survival of brook trout (*Salvelinus fontinalis*) embryos and fry in streams of different acid sensitivity in Shenandoah National Park, USA.** Water, Air, and Soil Pollution. 85: 445-450.

McKnight, D.M.; Smith, R.L.; Bradbury, J.P.; Baron, J.S.; Spaulding, S. 1990. **Phytoplankton dynamics in 3 Rocky Mountain lakes, Colorado, USA.** Arctic and Alpine Research. 22: 264-274.

Meixner, T.; Gutmann, C.; Bales, R.; Leydecker, A.; Sickman, J.; Melack, J.; McConnell, J. 2004. **Multidecadal hydrochemical response of Sierra Nevada watershed: sensitivity to weathering rate and changes in deposition.** Journal of Hydrology. 285: 272-285.

Michel, T.J.; Saros, J.E.; Interlandi, S.J.; Wolfe, A.P. 2006. **Resource requirements of four freshwater diatom taxa determined by in situ growth bioassays using natural populations from alpine lakes.** Hydrobiologia. 568: 235-243.

Molotch, N.P.; Meixner, T.; Williams, M.W. 2008. **Estimating stream chemistry during the snowmelt pulse using a spatially distributed, coupled snowmelt and hydrochemical modeling approach.** Water Resources Research. 44: W11429.

Moon, J.B.; Carrick, H.J. 2007. **Seasonal variation of phytoplankton nutrient limitation in Lake Erie.** Aquatic Microbial Ecology. 48: 61-71.

Morris, D.P.; Lewis, Jr., W.M. 1988. **Phytoplankton nutrient limitation in Colorado mountain lakes.** Freshwater Biology. 20: 315-327.

Murdoch, P.S.; Stoddard, J.L. 1992. **The role of nitrate in the acidification of streams in the Catskill Mountain of New York.** Water Resources Research. 28: 2707-2720.

Nanus, L.; Campbell, D.H.; Ingersoll, G.P.; Clow, D.W.; Mast, M.A. 2003. **Atmospheric deposition maps for the Rocky Mountains.** Atmospheric Environment. 37: 4881-4892.

North, R.L.; Guidford, S.J.; Smith, R.E.H.; Havens, S.M.; Twiss, M.R. 2007. **Evidence for phosphorus, nitrogen, and iron colimitation of phytoplankton communities in Lake Erie.** Limnology and Oceanography. 52: 315-328.

Nydick, K.R.; Lafrancois, B.M.; Baron, J.S.; Johnson, B.M. 2004. **Nitrogen regulation of algal biomass, productivity, and composition in shallow mountain lakes, Snowy Range, Wyoming, USA.** Canadian Journal of Fisheries and Aquatic Science. 61: 1256-1268.

Omernik, J.M.; Powers, C.F. 1982. **Total alkalinity of surface waters—a national map.** Rep. No. EPA-600/D-82-333. Corvallis, OR: Corvallis Environmental Research Laboratory, U.S. EPA.

Pellerin, B.A.; Kaushal, S.S.; McDowell, W.H. 2006. **Does anthropogenic nitrogen enrichment increase organic nitrogen concentrations in runoff from forested and human-dominated watershed?** Ecosystems. 9: 852-864.

Rueth, H.M.; Baron, J.S. 2002. **Differences in Engelmann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA.** Ecosystems. 5: 45-57.

Saros, J.E.; Interlandi, S.J.; Wolfe, A.P.; Engstrom, D.R. 2003. **Recent changes in the diatom community structure of lakes in the Beartooth Mountain Range, USA.** Arctic Antarctic and Alpine Research. 35: 18-23.

Saros, J.E.; Michel, T.J.; Interlandi, S.J; Wolfe, A.P. 2005. **Resource requirements of *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations.** Canadian Journal of Fisheries and Aquatic Science. 62: 1681-1689.

Schaefer, D.A.; Driscoll, C.T.; Van Dreason, R.S.; Yatsko, C.P. 1990. **The episodic acidification of Adirondack Lakes during snowmelt.** Water Resources Research. 26: 1639-2099.

Schindler, D.W. 1977. **Evolution of phosphorus limitation in lakes: natural mechanisms compensate for deficiencies of nitrogen and carbon in eutrophied lakes. Science.** 195: 260-262.

Schindler, D.W. 1978. **Factors regulating phytoplankton production and standing crop in the world's freshwaters.** Limnology and Oceanography. 23: 478-486.

Schindler, D.W.; Hecky, R.E.; Findlay, D.L.; Stainton, M.P.; Parker, B.R.; Paterson, M.J.; Beaty, K.G.; Lyng, M.; Kasian, S.E.M. 2008. **Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment.** Proceedings of the National Academy of Sciences of the United States of America. 105: 11254-11258.

Sickman, J.O.; Clow, D.; Melack, J.M. 2003. **Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California.** Limnology and Oceanography. 48(5): 1885-1892.

Sickman, J.O.; Leydecker, A.; Melack, J.M. 2001. **Nitrogen mass balances and abiotic controls on N retention and yield in high-elevation ecosystems of the Sierra Nevada, California, USA.** Water Resources Research. 37: 1445-1461.

Sickman, J.O.; Melack, J.M. 1998. **Nitrogen and sulfate export from high elevation catchments of the Sierra Nevada.** Water, Air, and Soil Pollution. 105: 217-226.

Sickman, J.O.; Melack, J.M.; Stoddard, J.L. 2002. **Regional analysis of inorganic nitrogen yield and retention in high-elevation ecosystems of the Sierra Nevada and Rocky Mountains.** Biogeochemistry. 57: 341-374.

Sterner, R.W.; Anagnostou, E.; Brovold, S.; Bullerjahn, G.S.; Finlay, J.C.; Kumar, S.; McKay, R.M.L.; Sherrell, R.M. 2007. **Increasing stoichiometric imbalance in North America's largest lake: Nitrification in Lake Superior.** Geophysical Research Letters. 34: L10406.

Stoddard, J.L. 1994. **Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences.** In: Baker, L.A., ed. Environmental chemistry of lakes and reservoirs. Washington, DC: American Chemical Society: 223-284.

Stoddard, J.L. 1995. **Episodic acidification during snowmelt of high elevation lakes in the Sierra Nevada Mountains of California.** Water, Air, and Soil Pollution. 85: 353-358.

Stoddard, J.L.; Kahl, J.S.; Deviney, F.A.; DeWalle, D.R.; Driscoll, C.T.; Herlihy, A.T.; Kellogg, J.H; Murdoch, P.S.; Webb, J.R.; Webster, K.E. 2003. **Response of surface water chemistry to the Clean Air Act Amendments of 1990.** EPA/620/R-03/001. Washington, DC: U.S. Environmental Protection Agency.

Suding, K.N.; Collins, S.L.; Gough, L.; Clark, C.; Cleland, E.E.; Gross, K.L.; Milchunas, D.G.; Pennings, S. 2005. **Functional- and abundance-based mechanisms explain diversity loss due to N**

fertilization. Proceedings of the National Academy of Sciences of the United States of America. 102: 4387-4392.

Sullivan, T.J.; Cosby, B.J.; Tonnessen, K.A.; Clow, D.W. 2005. **Surface water acidification responses and critical loads of sulfur and nitrogen deposition in Loch Vale watershed, Colorado.** Water Resources Research. 41: WO1021.

Thomas, R.Q.; Canham, C.D.; Weathers, K.C.; Goodale, C.L. 2010. **Increased tree carbon storage in response to nitrogen deposition in the US.** Nature Geoscience. 3: 13-17.

US EPA. (U.S. Environmental Protection Agency). 2006. **Wadeable streams assessment. A collaborative survey of the nation's streams.** EPA 841-B-06-002. Washington, DC: U.S. EPA, Office of Research and Development/Office of Water.

US EPA. (U.S. Environmental Protection Agency). 2010. **National lakes assessment.** Washington, DC: U.S. Environmental Protection Agency. Available at http://www.epa.gov/owow/lakes/lakessurvey/ (Accessed September 10, 2010).

Van Sickle, J.; Baker, J.P.; Simonin, H.A.; Baldigo, B.P.; Kretser, W.A.; Sharpe, W.E. 1996. **Episodic acidification of small streams in the northeastern United States: Fish mortality in field bioassays.** Ecological Applications. 6: 408-421.

Vitousek, P.M.; Howarth, R.W. 1991. **Nitrogen limitation on land and in the sea: How can it occur?** Biogeochemistry. 13: 87-115.

Weathers, K.C.; Simkin, S.M.; Lovett, G.M.; Lindberg, S.E. 2006. **Empirical modeling of atmospheric deposition in mountainous landscapes.** Ecological Applications. 16: 1590-1607.

Wetzel, R.G. 2001. **Limnology, Third Edition.** Academic Press. New York, NY: 1006 p.

Wigington, P.J.; Baker, J.B.; DeWalle, D.R.; Kretser, W.A.; Murdoch, P.S.; Simonin, H.A.; Van Sickle, J.; McDowell, M.K.; Peck, D.V.; Barchet, W.R. 1996. **Episodic acidification of small streams in the northeastern United States: Episodic response project.** Ecological Applications. 6: 374-388.

Williams, M.W.; Baron, J.; Caine, N.; Sommerfeld, R.; Sanford, R. 1996. **Nitrogen saturation in the Colorado Front Range.** Environmental Science and Technology. 30: 640-646.

Williams, M.W.; Tonnessen, K.A. 2000. **Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA.** Ecological Applications. 10: 1648-1665.

Wolfe, A.P.; Baron, J.S.; Cornett, R.J. 2001. **Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA).** Journal of Paleolimnology. 25: 1-7.

Wolfe, A.P.; Van Gorp, A.C.; Baron, J.S. 2003. **Recent ecological and biogeochemical changes in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to anthropogenic nitrogen deposition.** Geobiology. 1: 153-168.

Wright, R.F.; Alewell, C.; Cullen, J.M.; Evans, C.D.; Marchetto, A.; Moldan, F.; Prechtel, A.; Rogora, M. 2001. **Trends in nitrogen deposition and leaching in acid-sensitive streams in Europe.** Hydrology and Earth System Sciences. 5: 299-310.

19 SYNTHESIS

L.H. Pardo, L.H. Geiser, M.E. Fenn, C.T. Driscoll, C.L. Goodale, E.B. Allen, J.S. Baron, R. Bobbink, W.D. Bowman, C.M. Clark, B. Emmett, F.S. Gilliam, T. Greaver, S.J. Hall, E.A. Lilleskov, L. Liu, J.A. Lynch, K. Nadelhoffer, S.S. Perakis, M.J. Robin-Abbott, J.L. Stoddard, K.C. Weathers

19.1 Background

19.1.1 Effects of Nitrogen Deposition on Ecosystems

Human activity in the last century has led to a substantial increase in nitrogen (N) emissions and deposition (Galloway et al. 2003). Because of past, and, in some regions, continuing increases in emissions (Lehmann et al. 2005, Nilles and Conley 2001), this N deposition has reached a level that has caused or is likely to cause alterations and damage in many ecosystems across the United States. In some ecoregions, the impact of N deposition has been severe and has changed the biotic community structure and composition of ecosystems. In the Mediterranean California ecoregion, for example (see Chapter 13), replacement of native by exotic invasive vegetation is accelerated because exotic species are often more productive under elevated N deposition than native species in some California grasslands, coastal sage scrub, and desert scrub (Fenn et al. 2010, Rao and Allen 2010, Rao et al. 2010, Weiss 1999, Yoshida and Allen 2004). Such shifts in plant community composition and species richness can have consequences beyond changes in ecosystem structure: shifts may lead to overall losses in biodiversity and further impair particular threatened or endangered species (Stevens et al. 2004). The extirpation of the endangered checkerspot butterfly (*Euphydryas editha bayensis*), because the host plant for the larval stage disappears in N-enriched ecosystems (Fenn et al. 2010, Weiss 1999), is just one example of the detrimental impacts of elevated N deposition.

In addition to altering ecosystem structure, N deposition can also affect ecosystem function, affecting N-cycle processes such as N mineralization, nitrification rates, and nitrate (NO_3^-) leaching rates, as well as plant tissue N concentration. These changes indicate early stages of N saturation. Nitrogen saturation is the series of ecosystem changes that occur as available N exceeds plant and microbial demand (Aber et al. 1989, 1998). In some cases, these early responses may lead to a cascade of alterations in the N cycle that ultimately affect the function or structure of the ecosystem (Galloway et al. 2003). For example, elevated N inputs may lead to plant nutrient imbalances, which then increase plant susceptibility to inciting stressors such as cold, drought, or pests (Bobbink et al. 1998, Schaberg et al. 2002). This series of responses was observed in a southern Vermont montane red spruce (*Picea rubens*) stand, where increased foliar N concentration was associated with reductions in foliar membrane-associated calcium (Ca) and decreased cold tolerance, which resulted in increased winter injury (Schaberg et al. 2002). Another example of the N cascade (Galloway et al. 2003) is increased soil NO_3^- leaching, which can result in episodic acidification of surface waters, harming fish species (Baker et al. 1996). Other responses to low levels of elevated N deposition, such as increased plant growth and increased carbon (C) sequestration by trees (Thomas et al. 2010), may be perceived as beneficial where forests are managed for tree growth. In other instances, it is not known whether the early indicators of N saturation will be followed by other effects. In these cases, the perceived extent of harm caused by N deposition depends, in part, on which ecosystem service is of particular value for different stakeholders. For example, the level or type of change or harm that is unacceptable may vary according to resource management goals. In a conservation area, for example, any alteration in N cycling may be considered unacceptable, whereas for other land areas, changes of a certain magnitude or scope may be acceptable or even desirable based on resource use (such as timber harvesting) or other factors. Land and resources may be valued for a wide range of purposes, including biodiversity, food and wood production, clean water, and recreation. Quantification and then valuation of these ecosystem services for each land area of interest is required to fully account for impacts of N deposition.

19.1.2 Critical Loads Definition and Previous Uses

One method for evaluating the potential impacts of air pollution on ecosystems is the critical loads approach. The critical load is defined as *the level of a pollutant below which no detrimental ecological effect occurs over the long term according to present knowledge* (UBA 2004). Critical loads have been used most broadly in Europe (Posch et al. 1995, 2001) as a tool in the process of negotiating decreases in air pollution. Critical loads have been more widely applied in Canada than in the United States; critical loads have been published for upland forests (Ouimet et al. 2006) and lakes (Dupont et al. 2005) in eastern Canada and included in European assessments (Hettelingh et al. 2008). In the United States, critical loads have been calculated for specific regions such as the northeastern United States (Dupont et al. 2005, NEG/ECP 2003), California (Fenn et al. 2008, 2010), and Colorado (Baron 2006, Bowman et al. 2006, Williams and Tonnessen 2000), and, at a coarse scale, the conterminous United States (McNulty et al. 2007). Critical loads are of interest to policy makers for assessing emission control programs and to natural resource managers as a tool to evaluate the potential impact of new pollution sources (Burns et al. 2008, Environment Canada 2008, Lovett and Tear 2008, Lovett et al. 2009, Porter et al. 2005, US EPA 2007, US EPA 2008). Critical loads are also used by policy makers and resource managers to establish benchmarks for resource protection and to communicate the impacts of deposition on natural resource conditions. The development and use of critical loads provides a framework in which the research community collaborates with natural resource managers to quantify the effects of air pollution on ecosystems and help guide emission control programs. As a result, scientific progress, international collaboration, and interactions between researchers and policy makers are enhanced. Likewise, as a result of this focus on developing critical loads, the results of scientific studies are more broadly applied toward ecosystem protection by land managers, policy makers, and regulators.

Critical loads have been determined most frequently in the United States for effects of acidity (NEG/ECP 2003, Sullivan et al. 2005), but are also being increasingly used in evaluating impacts of excess N deposition on ecosystems (Fenn et al. 2008, 2010). Empirical critical loads are determined from observations of detrimental responses of an ecosystem or ecosystem component to a given, observed N deposition input (Pardo 2010). This level of N deposition is set as the critical load and extrapolated to similar ecosystems. Empirical critical loads for N, which are set based on field evidence, have been used in Europe since the 1990s (Bobbink et al. 1992, 2003, 2010). Empirical critical loads are particularly valuable because they are based on actual observations of detrimental effects to ecosystems by N deposition. Other approaches include the steady-state mass balance method (UBA 2004) and dynamic modeling (de Vries et al. 2010, Slootweg et al. 2007), both of which have been used broadly in Europe. Steady-state mass balance modeling is based on estimating the net loss or accumulation of N inputs and outputs over the long term under the assumption that the ecosystem is at steady-state with respect to N inputs. Dynamic models also use a mass balance approach, but consider time-dependent processes and require detailed data sets for parameterization and testing (Belyazid et al. 2006, de Vries et al. 2007).

Exceedance of the critical load is defined as the current deposition minus critical load; when exceedance is greater than zero, the ecosystem is susceptible to harmful ecological effects. The exceedance is useful in communicating the extent of risk to ecosystems under current and future deposition scenarios. The target load is a level of deposition set by policy makers to protect sensitive ecosystem components. The target load can be set below the critical load in order to eliminate exceedance within a given time period.

19.1.3 Objectives

The objective of this project is to synthesize current research relating atmospheric N deposition to effects on terrestrial and aquatic ecosystems in the United States and to identify empirical critical loads for atmospheric N deposition where possible. In this final chapter, we summarize the critical loads reported for all the ecoregions of the United States, discuss the abiotic and biotic factors that affect the critical load for N within each ecoregion, compare critical loads by life form or ecosystem compartment (mycorrhizal fungi, lichens, herbaceous species, and trees/forest ecosystems) across all ecoregions, and compare critical loads in the United States to those for similar ecoregions or ecosystems in Europe. Finally, we discuss the significance of these findings and the highest priorities for future research.

19.2 Approach

For this assessment, we report responses to N inputs for ecoregions that occur in the United States based on the Commission for Environmental Cooperation (CEC) for North America Level I map of ecoregions for North America (CEC 1997; Figures 2.1 and 2.2; see Chapter 2). The approach we used was to identify the receptor of concern (organism or ecosystem compartment), the response of concern, the critical threshold value for that response, which studies could be utilized, and the criteria for setting the critical load and extrapolating it to other sites or regions. These methods are described in detail in Chapter 4.

The receptors that we evaluated included freshwater diatoms, mycorrhizal fungi and other soil microbes, lichens, bryophytes, herbaceous plants, shrubs, and trees. We also considered biogeochemical processes within the ecosystem. The main responses reported fell into two categories: (1) biogeochemical; and (2) individual species, population, and community responses. Biogeochemical responses included increased N mineralization and nitrification (and N availability for plant and microbial uptake), increased gaseous N losses (ammonia (NH_3)) volatilization, nitric oxide (NO) and nitrous oxide (N_2O) from nitrification and denitrification), and increased N leaching. Individual species, population, and community responses included increased tissue N concentration, physiological and nutrient imbalances, altered growth, altered root:shoot ratios, increased susceptibility to secondary stresses, altered fire regimes, changes in species abundance, shifts in competitive interactions and community composition, and changes in species richness and other measures of biodiversity, and increases in invasive species.

We considered experimental N-addition studies, N-deposition gradient studies, and long-term monitoring studies in order to evaluate ecosystem response to N-deposition inputs. Most of these studies were not designed to quantify critical loads, which presented some challenges. We afforded greater weight to long-term fertilization studies (5 to 10 years) than to short-term studies, although short-term studies were also considered when other observations were scarce. Single-dose forest fertilization studies exceeding 50 kg N ha^{-1} were generally not considered. When studies were designed to determine critical loads, the addition levels generally depicted modest increases above ambient deposition, and were more likely to have smaller increments between the treatment levels, multiple (three or more) treatment levels, and, ideally, treatments spanning the critical load. In such cases, our estimates of the critical load are made with greater certainty than with other approaches. Nitrogen gradient studies implicitly include long-term exposure to pollutants and therefore are more likely than N manipulation studies to depict conditions that are near steady-state with respect to ambient N inputs. Long-term monitoring studies sometimes offer the opportunity to observe changes over time in response to increasing or elevated N-deposition inputs. We estimated critical loads based on data from >3200 sites (Figure 3.1).

The critical threshold of the response parameter is the threshold value at which an acceptable response is still observed. For example, when lichens are the receptors of concern and the response variable is thallus N concentration, the critical threshold is the highest value of thallus N concentration that represents a desirable condition: the critical threshold is reported as 1 percent for a recent study (Fenn et al. in 2008). The critical threshold is also referred to as the critical limit (UBA 2004). The critical threshold is different from the critical load; in this case, the critical load is the deposition at which the lichen thallus N concentration has reached or exceeded the critical threshold of 1 percent.

In general, we determined the critical load based on the observed response pattern. In some cases, there was a clear dose-response relationship where the response changed above a certain threshold. In other cases, when response to increasing N was more linear, we estimated the "pristine" state and the deposition level that corresponded to a departure from that state. The criteria for setting critical loads are discussed in detail in Chapter 4.

19.3 Deposition

Total N emissions have increased substantially since the 1950s (Galloway 1998, Galloway et al. 2003). As S deposition has declined in response to U.S. Federal emission control programs, the magnitude of N relative to S deposition has increased since the 1980s (Driscoll et al. 2003). More recently, the relative proportion of NH_x (ammonium (NH_4^+) and ammonia (NH_3)) to NO_x (nitric oxide (NO) and nitrogen dioxide (NO_2)) emissions has also increased for many areas of the United States (Kelly et al. 2005, Lehmann et al. 2005).

In order to quantify the critical load, we generally used the deposition reported in the publication or, when that was not available, we used modeled deposition (e.g., Community Multiscale Air Quality [CMAQ] model, ClimCalc [Ollinger et al. 1993], National Atmospheric Deposition Program [NADP; NADP 2009] maps). The different forms of N deposition included in this assessment for estimating critical loads are: wet, bulk, wet plus dry, throughfall, and total (wet plus dry plus cloud/fog) inorganic N deposition. Total N deposition is considered the most appropriate value to use in evaluating ecosystem responses, however, in many studies this information is not available. Throughfall N is generally considered a good surrogate for total N deposition, because it typically does not underestimate total N inputs as much as wet or bulk deposition and it is a good estimate of N delivered to the forest floor (Weathers et al. 2006). However, because of the potential for canopy uptake and transformation of N, throughfall is usually considered as a lower-bound estimate of total N deposition. None of the studies include reported inputs of organic N, so this report focuses on responses to inputs of inorganic N. Deposition used to calculate exceedance at sites included in this analysis (Chapter 3) was quantified by the CMAQ model v.4.3 (hereafter CMAQ 2001 model, which uses 2001 reported data) (Byun and Ching 1999, Byun and Schere 2006) simulations of wet plus dry deposition of N species (Figure 3.1).

We rarely had sufficient data to distinguish plant or ecosystem response to reduced forms (NH_x) versus oxidized forms (NO_y: NO, NO_2, nitric acid (HNO_3), organic and inorganic nitrates) of N. There is some evidence that for some species, reduced forms of N may have more substantial impacts than oxidized N (Bobbink et al. 2003, Kleijn et al. 2008). This differential response may be due to direct toxicity of gaseous NH_3 (Krupa 2003) or the toxicity to some plant species (or their mycorrhizal fungi) of high levels of NH_4^+ in soil, but can also be a result of soil acidification (van den Berg et al. 2005). Lichens in California's Central Valley (Jovan and McCune 2005) have been shown to be particularly sensitive to total reduced N (i.e. NH_4^+ plus NH_3). Across Europe, lichen responded to NH_3 and to a lesser extent NH_4^+ (Cape et al. 2009, Sutton et al. 2009). Much of the research on NH_3 effects evaluates the response to concentration of NH_3, which would be used for determining the critical level of NH_3 rather than the critical load. This is an important distinction: the critical level is the atmospheric concentration above which adverse effects to sensitive vegetation may occur (UBA 2004). Differences in uptake rates and preference for NH_4^+ versus NO_3^- across different plant taxa (Falkengren-Grerup 1995, McKane et al. 2002, Miller and Bowman 2002, Nordin et al. 2006) lead to differences in sensitivity to NH_x (Krupa 2003) and NO_y. Importantly, not all species are more sensitive to NH_x than NO_y: these responses vary by species and functional type. Some species are more sensitive to increases in NO_y, as was demonstrated for boreal forests by Nordin et al. (2006).

The accuracy of the atmospheric N-deposition values used directly influences the accuracy of critical load and exceedance estimates. Several factors contribute to uncertainty in N-deposition estimates, including sparse data for many ecosystem types, including arid, high elevation sites, and for sites with high inputs from snow or cloudwater/fog deposition, where N deposition tends to be underestimated. In addition, models of deposition often assume homogenous canopies or terrain, or the output (e.g., CMAQ) is at a spatial scale (grid size) too coarse to capture complex topography and other local influences on deposition (Weathers et al. 2006). These issues are discussed in detail in Chapter 3. When more accurate and precise N-deposition estimates become available, the data presented in this study may be re-evaluated to refine the critical loads estimates.

Note that CMAQ deposition data at a 36 km x 36 km grid were used to calculate exceedances (current deposition—critical load) for this analysis. CMAQ deposition includes dry deposition of NH_3 and trace NO_y species which are not included in many estimates of deposition (including those used to estimate many of the N critical loads in this assessment). Although these N constituents generally make up a small fraction of total estimated N deposition, the use of CMAQ data has the potential to overestimate the area of exceedance. However, some studies suggest CMAQ actually underestimates N deposition (Fenn et al. 2010). The discrepancy between CMAQ estimates and actual deposition would be of greatest concern at sites where NH_3, NO, and NO_2 dry deposition or fog represent a high fraction of inputs. Their inclusion would be most significant where the critical load is lowest. Fortunately, most of the lichen critical loads, which are typically the lowest reported within a given ecoregions (i.e., the most likely to be affected by the slightly higher CMAQ deposition), were determined based on CMAQ inputs. In other instances, for example in the arid West when emissions are high, CMAQ may underestimate total deposition (Fenn et al. 2010).

19.4 Sources of Uncertainty in Empirical Critical Loads Estimates

There are several other sources of uncertainty in our assessment of empirical critical loads, beyond those associated with the measurement of atmospheric deposition. In general, there is a dearth of observations on ecosystem response to inputs near the critical load. To addesss these data gaps, we suggest priorities for future research below. In some ecoregions, a single study or very few studies are available. If the variability of ecosystem response to N deposition across an ecoregion is not depicted by the studies available, the estimated critical load for N may be relevant for only a single ecosystem type or a single sub-region within the ecoregion. Without extensive data, it is not possible to know whether a study site is more or less sensitive than other sites in the ecoregion. It is most effective to have a large number of studies which demonstrate the range of responses observed to better define the threshold value (or constrain the deposition range over which the response occurs).

Other sources of uncertainty include time lags in the response to N deposition and the effects of multiple stressors, both of which are artifacts of the empirical approach, and, as such, are difficult to address. However, with more long-term studies and more response data, confidence in these empirical critical load estimates will improve, as has been demonstrated in Europe (Bobbink et al. 1992, 2010). Because ecosystems do not respond instantaneously to changes in N inputs, there are inherent time lags associated especially with N addition studies. These time lags become more important with increasing lifespan or size of organism; a tree will respond more slowly than an herbaceous annual, for example. Time lags also depend on the rate of N input, with lower rates of input typically leading to longer time lags before an initial response (Clark and Tilman 2008). Some species adapted to low nutrient supply also tend to respond slowly to N additions (Theodose and Bowman 1997). (Note that, although the time lag may be longer for these low-N-adapted species, they may still be amongst the most sensitive to small N additions). There may be large differences in responses among species within the same ecosystem, with many species being relatively nonresponsive and a few opportunistic species transforming community structure and function. Ecosystems with inherently large N pools or capacity to absorb N will exhibit longer time lags with respect to changes in N inputs than ecosystems with smaller N storage pools. Thus, it can be difficult to extrapolate the response at a higher dose over a short study to a lower input over the long term (Clark and Tilman 2008). The absence of low N addition studies further complicates interpolation because often N additions are far greater than the critical load. For both N addition and gradient studies, the reference plot or low end of the deposition gradient may already have been altered from a "pristine" condition. Even for gradient studies, the time lag in response to N deposition must be considered. As the ecosystems in gradient studies are typically still being exposed to elevated N inputs, they are continuously responding to those N inputs, although they have had more time to approach steady-state with the N inputs compared with N addition studies. For N gradient studies, it can also be difficult to sort out the effects of other factors that may also vary along the deposition gradient, such as climate, interannual variation in weather, soils, vegetation, disturbances, and other pollutants. On the other hand, because these variations represent "real-world" conditions—in most locations, multiple stressors co-occur—the critical loads estimated in the presence of these stressors may better protect the ecosystems under the current conditions (Fenn et al. 2008).

Another source of uncertainty in empirical relationships is that they are simply field observations of responses to N inputs, and are often lacking mechanistic explanations. They also can only reflect research done to date, and with the exception of N addition studies, only conditions (N deposition rates) observed to date. Because these factors affect the accuracy of the critical load, we indicate the level of uncertainty in our critical loads tables.

19.5 Advantages of the Empirical Critical Loads Approach

In spite of some of the challenges discussed above, an important advantage of empirical critical loads is that they are based on measurable, physical evidence of ecosystem responses to N inputs. Conceptually, steady-state mass balance models have an advantage over empirical critical loads in terms of estimating long-term sustainability, because they are calculated over the long term. This means that steady-state models are less likely to overestimate the critical load, which can happen with empirical critical loads determined based on a rapidly occurring ecosystem response at a given deposition, although lower levels of atmospheric deposition over a longer time period will actually generate the same response. Currently in the United States, the uncertainty associated with the steady-state mass balance method is high because data are not available to refine the terms in the equations. In fact, the data assembled for empirical critical loads may be useful in defining the acceptable critical thresholds used in steady-state mass balance critical loads calculations. For example, provisional descriptions of the relationships between soil solution NO_3^- concentration and changes in species composition in The Netherlands (Posch et al. 1993, de Vries et al. 2007), have allowed determination of the critical NO_3^- concentration term used in steady-state calculations of critical loads. Dynamic models for critical loads of N in the United States have been applied on a limited basis (Fenn et al. 2008, Wu and Driscoll 2010). For dynamic modeling of nutrient N critical loads, empirical critical loads and other response data are essential: the current understanding of ecosystem response to N deposition in the United States has not been sufficient to develop dynamic models that characterize the range of effects (for example, changes in biodiversity) such as those utilized in Europe (de Vries et al. 2010, Emmett and Reynolds 2003). Dynamic models must be based on a systematic understanding of the responses and mechanisms for those responses. Dynamic models are necessary to adequately characterize the complexity of N cycling at the ecosystem scale, but the models can only be as good as the data upon which they are based. Thus, empirical critical loads currently provide a uniquely valuable approach for assessing the risk of harm to ecosystems in the United States. This report represents a first step toward that understanding by indicating which data are available for key ecosystems and where dynamic modeling could most profitably be applied in the United States after further data collection.

19.6 Overview of Critical Loads across U.S. Ecoregions

The range of critical loads for nutrient N reported for the U.S. ecoregions, inland surface waters, and freshwater wetlands is 1 to 39 kg N ha^{-1} yr^{-1}, while coastal wetlands are between 50 to 400 kg N ha^{-1} yr^{-1} (Table 19.1). This range, excluding coastal wetlands, spans N deposition observed over most of the country (see Chapter 3). Because N deposition varies considerably by region and the critical load varies both by region and receptor, we present the critical loads and likely risk of exceedance by receptor in section 19.8. The locations for which ecosystem response data were available (Figure 3.1) also vary in density of spatial distribution, which impacts the level of certainty of the empirical critical loads estimates. The basis for the critical loads values (Table 19.1) is discussed in detail in the preceding chapters.

The empirical critical loads for N tend to increase in the following sequence for different life forms: freshwater diatoms, lichens and bryophytes, mycorrhizal fungi, herbaceous plants and shrubs, and trees (see section 19.8). Low biomass ecosystem types (e.g., grasslands, coastal sage scrub, desert) are more sensitive to N-enhanced growth of invasive species (if invasive pressure occurs), leading to vegetation-type change. These vegetation types sometimes occur because of warm and dry climatic conditions. As warmer temperatures often correspond to greater metabolic rates, longer periods of biological activity, greater biomass, and more rapid N cycling, one might expect that the critical load would increase with increasing temperature as has been suggested in Europe (Bobbink et al. 2003). We do not observe such a pattern across U.S. ecoregions in the critical loads reported in this study, but Europe does not have warm and dry deserts with low critical loads as in the United States. Note, however, that the reliability of the critical load estimates varies and is often fairly low, which may make it difficult to discern patterns in critical load values across regions. Moreover, a temperature pattern may be confounded by gradients in deposition form and quantity, moisture, and elevation. Critical loads seem to vary more by receptor and response type than by region. The western portion of the United States has generally similar critical loads values to the eastern United States for the same response for a given receptor. The apparent exception is that in forests the critical load for NO_3^- leaching is approximately twice as high in Mediterranean California mixed conifers compared to northeastern forests (see section 19.8 and Figure 19.7). In contrast, the critical load for NO_3^- leaching in high elevation catchments in the Colorado Front Range is lower than anywhere else in the United States, likely attributable to low biological N retention and storage capacity in these steep, rocky catchments (Baron et al. 2000, Fenn et al. 2003a, Sickman et al. 2002, Williams and Tonnessen 2000).

In this synthesis, we found that higher N critical loads were often reported for regions with higher ambient N deposition, as has been observed outside the United States. One explanation for this pattern is that for ecosystems experiencing elevated N deposition, the current condition already represents a change from the condition prior to elevated N deposition (i.e., a pristine or near-pristine state). This pattern would explain why the empirical critical load is often above the ambient deposition even as that deposition increases in the same ecosystem type across a region. Empirical critical loads for N in Europe (see section 19.9) tend to be higher than those for the United States; in China, they are higher still (Duan 2009). This pattern suggests that sometimes the initial change in the ecosystem was not captured in ecosystem measurements, thus the critical load only prevents further change from the current state. This is even more likely to have occurred at sites in Europe where deposition has been very high. For example, European critical loads for lichens were influenced by a study in Scotland based on a deposition gradient from 10 to 22 kg N ha^{-1} yr^{-1} which set critical loads at 11 to 18 kg N ha^{-1} yr^{-1} (Mitchell et al. 2005). However, the species composition at all sites across the deposition gradient did not include any oligotrophic species, which were presumably present prior to elevated N deposition inputs. This critical load, which is higher than critical loads for lichens in the United States, may simply prevent further change from an already altered state. Similarly, in the Great Plains (see Chapter 11), it is not possible to determine whether the current condition of sites where deposition is lowest differs from the pristine condition (Clark and Tilman 2008). This further emphasizes the need to include "pristine" sites in gradient studies and for research experiments that remove N deposition in order to more accurately define the baseline condition, which helps describe the ecosystem state prior to elevated N deposition.

Table 19.1—Summary of empirical critical loads of nutrient N for U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Chapter	Ecoregion	Ecosystem Component	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
5	Tundra	Prostrate dwarf shrubs	1-3	##	Changes in CO_2 exchange, cover, foliar N, and community composition of vascular plants	N addition study, Greenland high arctic, P enhanced N effects.	Arens et al. 2008[a]
5	Tundra	Lichens	1-3	(#)	Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover	N addition studies, high and low arctic, P enhanced or moderated N effects.	Arens et al. 2008[a], Hyvärinen et al. 2003[b], Makonen et al. 2007[b]
6	Taiga	Lichen, moss, and algae	1-3	#	Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates.	Application of western OR and WA model for lichens	Berryman et al. 2004[c], Berryman and Straker 2008[c], Geiser et al. 2010, Moore et al. 2004[c], Poikolainen et al. 1998[b], Strengbom et al. 2003[d], Vitt et al. 2003[c]
6	Taiga	Mycorrhizal fungi, spruce-fir forests	5-7	(#)	Ectomycorrhizal fungi, change in community structure	Expert judgment extrapolated from Marine West coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
6	Taiga	Shrublands	6	##	Shrub and grass cover, increased parasitism of shrubs	Long term, low N addition study: shrub cover decreased, grass cover increased	Nordin et al. 2005[d], Strengbom et al. 2003[d]
7	Northern Forests	Hardwood and coniferous forests	>3	#	Tree growth and mortality	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood	Thomas et al. 2010
7	Northern Forests	Lichens	4-6	(#)	Epiphytic lichen community change	Loss of oligotrophic species. Synergistic/confounding effects of acidic deposition not considered; assumes response threshold similar to Marine West Coast Forests	Geiser et al. 2010
7	Northern Forests	Ectomycorhizzal fungi	5-7	#	Change in fungal community structure		Lilleskov et al. 2008
7	Northern Forests	Herbaceous cover species	>7 and <21	#	Loss of prominent species	Response observed in low-level fertilization experiment	Hurd et al. 1998
7	Northern Forests	Hardwood and coniferous forests	8	##	Increased surface water NO_3^- leaching		Aber et al. 2003

7	Northern Forests	Old-growth montane red spruce	>10 and <26	#	Decreased growth and/or induced mortality	Response observed in low-level fertilization experiment	McNulty et al. 2005
7	Northern Forests	Arbuscular mycorrhizal fungi	<12	(#)	Biomass decline and community composition change		van Diepen 2008, van Diepen et al. 2007
8	Northwestern Forested Mountains	Alpine lakes	1.5	##	Diatom assemblages	As wet deposition only	Baron 2006
8	Northwestern Forested Mountains	Lichens	1.2-3.7	(#)	Epiphytic lichen community change in mixed-conifer forests, Alaska	Application of western Oregon and Washington model	Geiser et al. 2010
8	Northwestern Forested Mountains	Lichens	2.5-7.1	##	Epiphytic lichen community change, thallus N enrichment in mixed-conifer forests, non-Alaska		Fenn et al. 2008, Geiser et al. 2010
8	Northwestern Forested Mountains	Subalpine forest	4	##	Increase in organic horizon N, foliar N, potential net N mineralization, and soil solution N, initial increases in N leaching below the organic layer		Rueth and Baron 2002, Baron et al. 1994
8	Northwestern Forested Mountains	Alpine lakes	4.0	#	Episodic freshwater acidification		Williams and Tonnesson 2000
8	Northwestern Forested Mountains	Alpine grassland	4-10	##	Plant species composition		Bowman et al. 2006
8	Northwestern Forested Mountains	Ectomycorrhizal fungi	5-10	(#)	Ectomycorrhizal fungi community structure in white, black, and Engelmann spruce forests	Expert judgment extrapolated from Marine West Coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
8	Northwestern Forested Mountains	Mixed conifer forest	17	## #	NO_3^- leaching, reduced fine root biomass	Fine root biomass in ponderosa pine is reduced by both ozone and elevated soil nitrogen	Fenn et al. 2008
9	Marine West Coast Forests	Western OR and WA forests	2.7-9.2	##	Epiphytic lichen community change	Loss of oligotrophic species, enhancement of eutrophic species. Critical load increases with regional range in mean annual precipitation from 45-450 cm	Geiser et al. 2010

continued

Table 19.1—continued

Chapter	Ecoregion	Ecosystem Component	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
9	Marine West Coast Forests	SE Alaska forests	5	(#)	Fungal community change; declines in ectomycorrhizal fungal diversity		Lilleskov 1999; Lilleskov et al. 2001, 2002; Whytemare et al. 1997
10	Eastern Temperate Forests	Eastern hardwood forest	>3	#	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		Thomas et al. 2010
10	Eastern Temperate Forests	Lichens	4-8	(#)	Epiphytic lichen community change	Loss of oligotrophic species. Synergistic/confounding effects of acidic deposition not considered. Application of western OR and WA model	Geiser et al. 2010
10	Eastern Temperate Forests	Southeastern coastal plain	5-10	(#)	Ectomycorrhizal fungi community response		Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008
10	Eastern Temperate Forests	Eastern hardwood forests	8	##	Increased surface water loading of NO_3^-		Aber et al. 2003
10	Eastern Temperate Forests	Michigan deposition gradient	<12	(#)	Arbuscular mycorrhizal fungal biomass decline and community composition change		van Diepen 2008, van Diepen et al. 2007
10	Eastern Temperate Forests	Herbaceous species	<17.5	(#)	Increases in nitrophilic species, declines in species-rich genera (e.g., Viola)		Gilliam 2006,2007; Gilliam et al. 2006
11	Great Plains	Tallgrass prairie	5-15	#	Biogeochemical N cycling, plant and insect community shifts		Clark et al. 2009, Clark and Tilman 2008; Tilman 1993, 1987; Wedin and Tilman 1996
11	Great Plains	Mixed-grass prairie	10-25	#	Soil NO_3^- pools, leaching, plant community shifts		Clark et al. 2003, 2005; Jorgenson et al. 2005
11	Great Plains	Shortgrass prairie	10-25	(#)		Inferred from mixed-grass prairie	Epstein 2001, Barret and Burke 2002
11	Great Plains	Mycorrhizal fungi	12	(#)	Decline in arbuscular mycorrhizal fungal activity		Egerton-Warburton[e]

12	North American Deserts	Lichens	3	(#)	Lichen community shifts, thallus N concentration	Uncertainty regarding modeled estimates	Geiser et al. 2008, Porter 2007
12	North American Deserts	Shrubland, woodland, desert grassland	3-8.4	#	Vegetation response, vascular plant community change		Allen et al. 2009; Inouye 2006; Rao et al. 2010
13	Mediterranean California	Coastal sage scrub	7.8-10	#	Invasive grass cover, native forb richness, arbuscular mycorrhizal fungi richness	Modeled and inferential N deposition estimates and published data for mycorrhizae, unpublished data for vegetation survey	Allen[f], Egerton-Warburton and Allen 2000, Fenn et al. 2010, Tonnesen et al. 2007
13	Mediterranean California	Chaparral; lichens	3-6	#	Epiphytic lichen community change	Lichen critical load is from modeled N deposition data and published data for lichens	Fenn et al. 2010, Geiser et al. 2010, Jovan 2008, Jovan and McCune 2005
13	Mediterranean California	Chaparral, oak woodlands, Central Valley	10-14	#	NO_3^- leaching; stimulated N cycling	Critical load for NO_3^-leaching of 10 kg N ha^{-1} yr^{-1} is based on one year of throughfall data in Chamise Creek and an additional year of throughfall data from adjacent Ash Mountain, both in Sequoia National Park	Fenn et al. 2003a, 2003b, 2003c; Fenn and Poth 1999; Meixner and Fenn 2004
13	Mediterranean California	Mixed conifer forest; lichens	3.1-5.2	##	Lichen chemistry and community changes	The lowest critical load is based on lichen tissue chemistry above the clean site threshold	Fenn et al. 2008, 2010
13	Mediterranean California	Mixed conifer forest; plant physiology	17	#	Reduced fine root biomass	Fine root biomass in ponderosa pine is reduced by both ozone and elevated soil nitrogen	Fenn et al. 2008, 2010; Grulke et al. 1998
13	Mediterranean California	Mixed conifer forest; soil processes	17-25.9	#	NO_3^- leaching; soil acidification	Fine root biomass in ponderosa pine is reduced by both ozone and elevated soil nitrogen	Breiner et al. 2007; Fenn et al. 2008, 2010
13	Mediterranean California	Mixed conifer forest; forest sustainability	24-39	(#)	Understory biodiversity; forest sustainability	N deposition from Fenn et al. 2008	Allen et al. 2007; Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004
13	Mediterranean California	Serpentine grassland	6	##	Annual grass invasion, replacing native herbs	Critical load based on a local roadside gradient; serpentine grassland site is actually west of the Central Valley	Fenn et al. 2010, Weiss 1999

continued

Table 19.1—continued

Chapter	Ecoregion	Ecosystem Component	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
15	Temperate Sierras	Lichens	4-7	(#)	Epiphytic lichen community change	Increase in proportion of eutrophic species. Application of western OR and WA model, response threshold allows ~60% eutrophs due to dry, hot climate, hardwood influence	Geiser et al. 2010
15	Temperate Sierras	Las Cruces and Chichinautzin Ranges S/SW of Mexico City	15	#	Elevated NO_3^- in stream and spring waters	Data are from Mexican mountain pine (*Pinus hartwegii*) sites in the Desierto de los Leones National Park and Ajusco, Mexico	Fenn et al. 1999, 2002
16	Tropical and Subtropical Humid Forests	N-rich forests	<5-10	(#)	NO_3^- leaching, N trace gas emissions	Critical load for N-rich forests should be lower than for N-poor forests based on possibility of N losses	No direct studies[g]
16	Tropical and Subtropical Humid Forests	N-poor forests	5-10	(#)	Changes in community composition; NO_3^- leaching, N trace gas emissions	Critical load for N-poor forests based on estimates for Southeastern Coastal Plain forests	No direct studies[g]
17	Wetlands	Freshwater wetlands	2.7-13	#	Peat accumulation and net primary productivity (NPP)	Critical load for wetlands in the northeastern U.S. and southeastern Canada	Aldous 2002[c], Moore et al. 2004[c], Rochefort et al. 1990[c], Vitt et al. 2003[c]
17	Wetlands	Freshwater wetlands	6.8-14	(#)	Pitcher plant community change	Critical load based on northeastern populations	Gotelli and Ellison 2002, 2006
17	Wetlands	Intertidal wetlands	50-100	##	Loss of eelgrass		Latimer and Rego 2010
17	Wetlands	Intertidal salt marshes	63-400	(#)	Salt marsh community structure, microbial activity and biogeochemistry		Caffrey et al. 2007, Wigand et al. 2003
18	Freshwaters	Western Lakes	2	##	Freshwater eutrophication		Baron 2006
18	Freshwaters	Eastern Lakes	8	#	NO_3^- leaching		Aber et al. 2003

[a] based on data from Greenland; [b] based on data from Finland; [c] based on data from Canada; [d] based on data from Sweden, [e] see footnote 25 on page 19-11; [f] Allen, E.B. Unpublished data. Professor and Natural Resources Extension Specialist, Department of Botany and Plant Sciences and Center for Conservation Biology, University of California, Riverside, CA 92521; [g] The critical load is based on expert judgment and knowledge of ecosystems which may function similarly.

One would expect that for an ecosystem that is nearer N saturation than another, it would take less additional N to reach a “tipping point”. However, it is important not to confuse that issue with the actual level of deposition—an ecosystem may be near N saturation when the ambient N deposition is low or when it is high. Thus, while prior exposure to elevated N deposition does push an ecosystem toward N saturation, high ambient deposition does not indicate the ecosystems most sensitive to further inputs—that status is a function of the ecosystem and the receptor.

19.7 Factors that Affect the Critical Load

One of the objectives of this assessment was to lay the groundwork for further refining and improving estimates of N critical loads. To that end, in this section, we discuss some of the factors that affect where the value of the critical load falls within the reported range (Table 19.2). We present the factors that were reported in the studies included in this report. These factors may be useful in setting empirical critical loads for specific sites as well as in the development of more complex models to assess ecosystem response to N inputs.

Abiotic factors that may affect the N critical load include elevation, latitude, topographic location, climate (temperature, precipitation, extent and rate of climate change), catchment size, soil type, extent of soil cover in high elevation systems, parent material, and hydrologic flowpaths and processes. Disturbance may also play a substantial role, for example, the type of fire regime or historical forest cutting can impact the critical load. A geographical region within the ecoregion may be more sensitive. Biological factors also likely contribute to lower N critical loads, including particularly sensitive species (diatoms, lichens, mycorrhizal fungi, certain plants), single species versus community responses, low biomass and low productivity ecosystems, short lifespan of receptor of concern, presence of invasive grasses, and presence of ozone-sensitive species.

The factors discussed above may provide some guidance in applying critical loads. To set a critical load for a given site using this report, one would first determine whether the site was similar to the site/or sites on which the critical load for that ecosystem type is based (found in the tables presented in each ecoregion chapter). If the site differs from the sites in the ecoregions tables, one would then refer to Table 19.2 to determine how to adjust the N critical load for a given site based on the range reported for the ecoregion. Finally, one would consider the general factors discussed above and adjust the critical load within the range reported for the ecoregion based on these factors.

With better identification of factors that affect the N critical load, we will move toward a mechanistic understanding of the responses and improve our ability to extrapolate observations across ecoregions or across different ecosystems within an ecoregion. In some cases, it may be possible to develop simple relationships as a function of one or several variables that would allow refinement of critical load estimates. For example, for lichens, Geiser et al. (2010) developed simple regression relationships that included precipitation volume that explain much of the variability in lichen community composition in response to N deposition. These regression models can be used to estimate N critical loads in other regions and also can provide an estimate of the uncertainty associated with the critical load.

Future research could evaluate which of these factors are most important in affecting where the critical load lies within the range for an ecoregion and determining how the critical load varies as the key parameters change across the ecoregions.

19.8 Comparison of Critical Load by Receptor across Ecoregions

Because much of the variation in critical loads occurs as a function of the receptor of concern, we compare the critical loads for the key receptors across ecoregions.

19.8.1 Mycorrhizal fungi

Background. Mycorrhizal fungi reside at the interface between host plants and soils, exchanging soil resources, especially nutrients, with host plants in exchange for photosynthates (carbon compounds). Due to this important and unique ecological niche, mycorrhizal

Table 19.2—Assessment and interpretation of empirical critical loads of nutrient N for U.S. ecoregions

Chapter	Ecoregion	Factors affecting the range of critical loads[a]	Comparison within Ecoregion[b]
5	Tundra	moisture competition between vascular plants and cryptogams P-limitation temperature pH	The critical load is higher in wet and P-limited tundra; acidic tundra may be more sensitive to N deposition than non-acidic tundra. Increased N deposition may be more detrimental to lichens in the presence of graminoids and shrubs in the low and mid arctic than to lichens with less competition in the high arctic. Response time increases with latitude due to colder temperatures, less light, and poorer N and P mobilization.
6	Taiga	soil depth vegetation type and species composition latitude	Morphological damage to lichens has been observed at a lower deposition in forests and woodlands than in shrublands or bogs and fens; cryptogam dominated mats on thin soils become N saturated faster than forest islands.
7	Northern Forests	receptor tree species stand age site history pre-existing N status	Critical loads for lichens are generally lowest, followed by critical loads for ectomycorrhizal fungi and NO_3^- leaching. Critical loads for herbaceous species and forests are generally higher than for other responses.
8	Northwestern Forested Mountains	biotic receptor accumulated load of N ecosystem region	In alpine regions, diatom changes in lakes are seen at the lowest critical load. Changes in individual plants are seen next, followed by vegetation community change, then soil responses. In subalpine forests, the critical load of 4 kg ha^{-1} yr^{-1} for foliar and soil chemistry changes is similar to the lichen critical load of 3.1 - 5.2 for lichen community change.
9	Marine West Coast Forests	background N status soil type species composition fire history climate	The midrange of responses reported for lichens (2.7 - 9.2 kg ha^{-1} yr^{-1}) is broadly comparable to that for plant, soil, and mycorrhizal responses (5 kg ha^{-1} yr^{-1}), despite limited studies for non-lichen responses.
10	Eastern Forests	precipitation soil cation fertility and weathering biotic receptors	The critical load for NO_3^- leaching, lichen community change, and ectomycorrhizal fungal response are within the same range. Arbuscular mycorrhizal fungal and herbaceous critical loads are higher.
11	Great Plains	N status receptor precipitation	Critical loads are lower in the tall grass prairie than in the mixed- and short-grass prairies. Critical loads in tall- and mixed-grass prairie is lower on N poor sites and sites with very N responsive plant species. Critical loads in the short-grass prairie is likely lower in wet years than in dry years.

12	North American Deserts	receptor interaction of annual grasses with native forb cover precipitation	The lichen critical load is lowest, at 3 kg N ha^{-1} yr^{-1}; vegetation critical load varies from 3 to 8.4 kg N ha^{-1} yr^{-1}
13	Mediterranean California	presence of invasive exotic annual grasses interacting with a highly diverse native forb community N-sensitivity of mycorrhizal fungi N-sensitivity of lichens N retention capacity of catchments, catchment size co-occurrence of ozone and ozone-sensitive tree species.	The lowest critical loads in Mediterranean California are for sensitive lichen in chaparral and oak woodlands and mixed conifer forests. The critical load for plant and mycorrhizal fungal community change in coastal sage scrub is higher, at 7.8 to 10 kg ha^{-1} yr^{-1}. Critical load for NO_3^- leaching is lower in chaparral and oak woodlands (10 t0 14 kg ha^{-1} yr^{-1}) than in mixed conifer forests (17 kg ha^{-1} yr^{-1}). Critical loads are highest for mixed conifer forest plant community change and sustainability.
17	Wetlands	vegetation species fraction of rainfall in the total water budget degree of openness of N cycling	Critical load is much higher for intertidal wetlands (50 to 400 kg ha^{-1} y^{-1}) than for freshwater wetlands (2.7 to 14 kg ha^{-1} y^{-1}), which have relatively closed water and N cycles.

[a] This explains what factors cause the critical load (CL) to be at the low or high end of the range reported.

[b] Comparison of values and causes for differences if multiple critical loads are reported for an ecoregion.

fungi are at particular risk due to changes in either the soil environment or host carbon allocation.

Response to N inputs. Nitrogen deposition adversely affects mycorrhizal fungi primarily in two ways: (1) by causing decreased belowground C allocation by hosts and increased N uptake and associated metabolic costs (Wallander 1995); and (2) via soil chemical changes associated with eutrophication and acidification. There are two major groups of mycorrhizal fungi that are evolutionarily and ecologically distinct: arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF). Under sufficiently high N inputs, the progressive effect of elevated N is an early decline of sporocarp (reproductive structure) production for EMF and spore production for AMF, and subsequent decline in biological diversity and loss of taxa adapted to N-poor environments or that are sensitive to acidification (Lilleskov 2005). Sporocarp and spore production appears to be especially sensitive to N deposition, often declining before the communities on root tips have been substantially altered, presumably because sporocarps and spores are at the end of the carbon flux pathway from hosts.

Of the two plant-fungal symbioses examined in this report, mycorrhizal fungi appear to be less sensitive to N deposition than lichens (Tables 19.3 and 19.4), presumably because the soil environment buffers these soil fungi from some of the immediate impacts of N deposition, whereas lichens are directly exposed to atmospheric N pollution. (Lichens have an advantage as indicators when compared with mycorrhizal fungi because they can be relatively easily inventoried.) However, the essential role of mycorrhizal fungi as root symbionts central to plant nutrition and belowground production, as repositories of a large part of the eukaryote diversity in forests, as major components of forest food webs, and as nontimber forest products of high economic value (edible sporocarps) (Amaranthus 1998) provides sufficient justification to improve our understanding of their response to N deposition.

Critical loads of N for mycorrhizal fungi. We reviewed empirical studies on mycorrhizal fungal response to N inputs as the basis for determining empirical critical loads for the United States (Table 19.3, Figure 19.1). Despite the sparse data, it is clear that N deposition sufficient to elevate inorganic N, and especially NO_3^-, availability in soils can have measurable effects on mycorrhizal fungi. The data for EMF indicate that N deposition to N-limited conifer forests in the range of 5 to10 kg ha^{-1} yr^{-1} can significantly alter community structure and composition and decrease species richness (Dighton et al. 2004; Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008). Similarly, the data for AMF suggest N deposition levels of 7.8 to12 kg ha^{-1} yr^{-1} can lead to community changes, declines in spore abundance and root colonization, and changes in community function, based on reanalysis of data from Egerton-Warburton et al. (2000) combined with N deposition data and decreases in fungal abundance (van Diepen et al. 2007, Van Diepen 2008) and declines in fungal activity.[24] The actual threshold for N effects on AMF could be even lower because high background deposition precludes consideration of sites receiving deposition at or near pre-industrial levels. Therefore, our provisional expert judgment is that critical loads for mycorrhizal diversity for sensitive ecosystem types are 5 to10 kg ha^{-1} yr^{-1}. There is high uncertainty in this estimate because few studies have been conducted at low N deposition to further refine the critical load.

The critical load of N for mycorrhizal fungi, when community change occurs, is often on the order of current N deposition and thus is exceeded across much of the Eastern Temperate and Northern Forests ecoregions. Exceedance of N critical loads is more variable in the western United States. The critical load is exceeded in regions downwind of agricultural and urban emissions in the West (Figure 19.2). In the Northwestern Forested Mountains and Marine West Coast Forests, N deposition is generally below the critical load, although the lower end of the critical load range is exceeded in the Cascade Mountains. A similar pattern can be seen in Mediterranean California; the N critical load for mycorrhizal fungi is exceeded in the vicinity of the Sierra Nevada and in the

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[24] Egerton-Warburton, L.M. Unpublished data. Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL, 60022

Table 19.3—Empirical critical loads of nutrient N for mycorrhizal fungi in U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	Critical load for N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Taiga	Spruce forests	5-7	(#)	Ectomycorrhizal fungi, change in community structure	Expert judgment extrapolated from Marine West Coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
Northern Forests	Spruce-fir forest (Northeastern U.S. deposition gradient)	5-7	#	Ectomycorrhizal fungi, change in community structure	Wet deposition estimated from Ollinger et al. (1993) model	Lilleskov et al. 2008
Northern Forests	Northern hardwood forests; sugar maple dominated (Michigan gradient)	<12	(#)	Arbuscular mycorrhizal fungi, decrease in abundance in roots, soil, community change	N fertilization experiment	van Diepen et al. 2007, van Diepen 2008
Northwestern Forested Mountains	Engelmann spruce forests	5-10	(#)	Ectomycorrhizal fungi, change in community structure	Expert judgment extrapolated from Marine West coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
Marine West Coast Forests	White spruce forest (Kenai Peninsula, Alaska)	5	(#)	Ectomycorrhizal fungi, change in community structure, decrease in species richness	Bulk deposition. Historic N deposition was higher but not quantified. Critical load estimated from regression	Lilleskov 1999, Lilleskov et al. 2001, 2002, Whytemare et al. 1997
Eastern Temperate Forests	Southeastern Coastal Plain	5-10	(#)	Ectomycorrhizal fungi, change in community structure	From one study in pine barrens plus extrapolation from other oligotrophic conifer forests	Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008
Eastern Temperate Forests	Pine Barrens (New Jersey; Southeastern Coastal Plain)	<8	(#)	Ectomycorrhizal fungal morphotype community change	Bulk deposition. Gradient study with three sample points	Dighton et al. 2004
Eastern Temperate Forests	Eastern hardwoods; sugar maple dominated (Michigan gradient)	<12	(#)	Arbuscular mycorrhizal fungi; decrease in abundance in roots, soil, community change	Long-term (12 yr) N fertilization experiment in sugar maple	van Diepen et al. 2007, van Diepen 2008
Great Plains	Chicago grassland	12	(#)	Arbuscular mycorrhizal fungi; decrease in % colonization, spore density	Critical load estimated from logarithmic curve of soil N vs. arbuscular mycorrhizal fungal activity. No low N baseline, so critical load may be lower	Egerton-Warburton[a]
Mediterranean California	Coastal sage scrub (southern California)	7.8-9.2	#	Arbuscular mycorrhizal fungi, decrease in % colonization, spore density, spore richness	Critical load estimated from logarithmic curve fitted to data from this study compared to modeled and inferential N deposition data	Egerton-Warburton and Allen 2000, Fenn et al. 2010, Tonnesen et al. 2007

[a] see footnote 24 on page 244

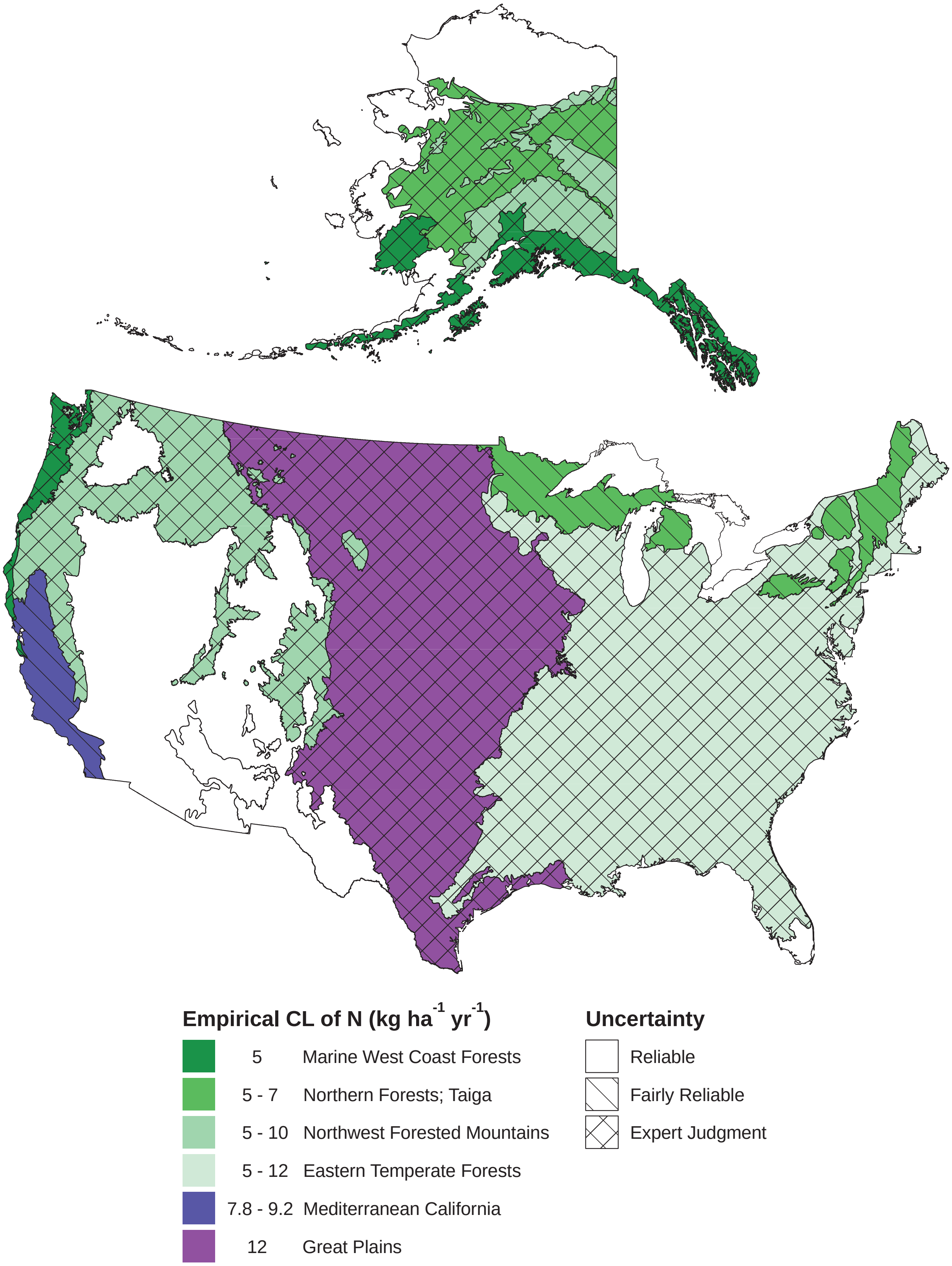

Figure 19.1—Map of critical loads (CL) for mycorrhizal fungi by ecoregion in the United States. The range of critical loads reported for mycorrhizal fungi is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain “reliable” category, single hatching for the “fairly reliable” category, and double hatching for the “expert judgment” category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases. White areas lack data for critical loads determination for mycorrhizal fungi.

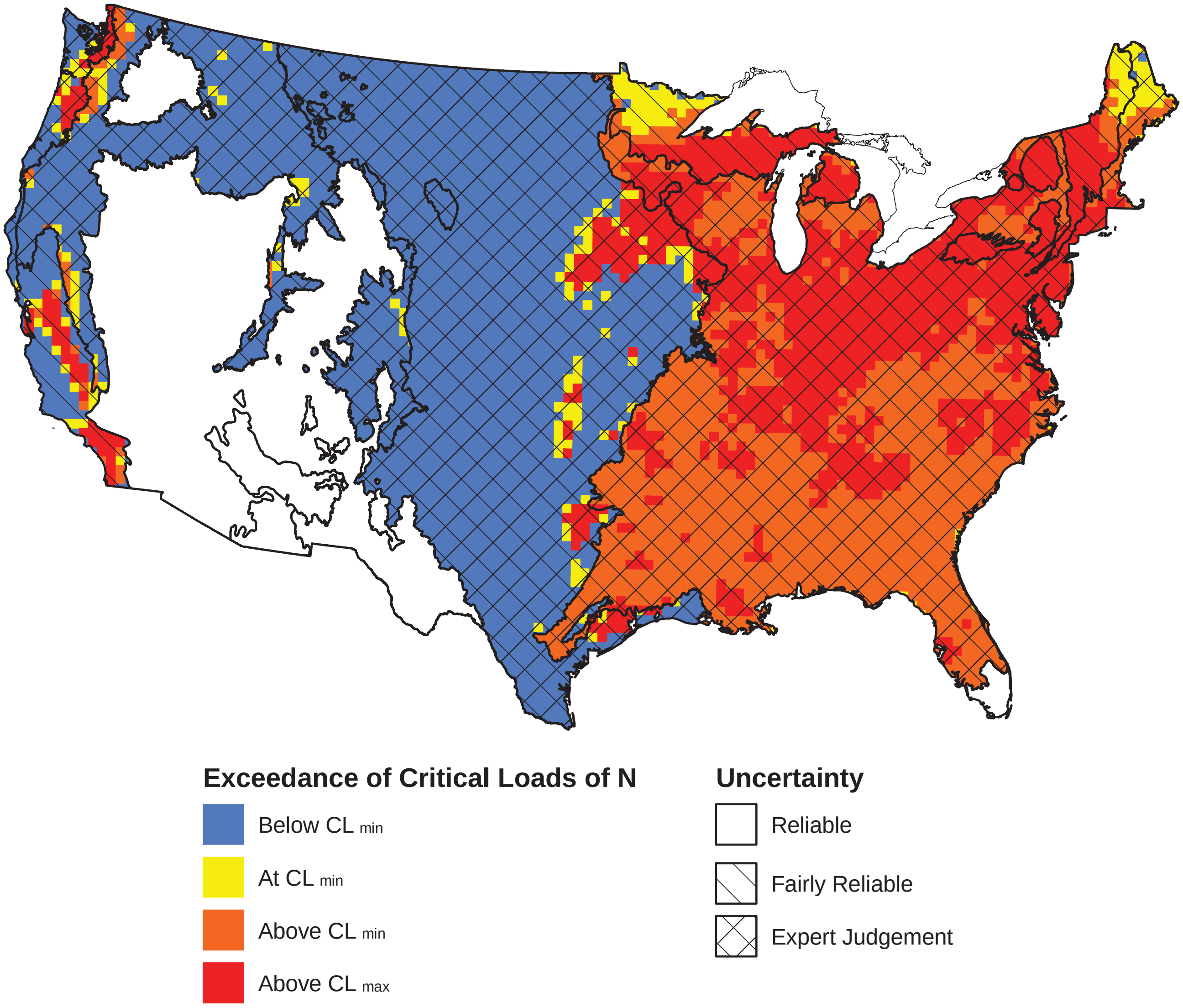

Figure 19.2—Map of exceedance of critical loads (CL) for mycorrhizal fungi by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load - deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for mycorrhizal fungi.

Transverse Mountain ranges of southern California. The uncertainty associated with the exceedance, like that for the critical load, is high.

19.8.2 Lichens and Bryophytes

Background. Lichens and bryophytes make substantial contributions to biodiversity. About 4100 lichen and 2300 bryophyte species are known from North America north of Mexico—as about one-fourth of vascular plant diversity, which is about 26,600 species (NRCS 2009). Therefore, N critical loads protective of the sensitive lichens and bryophytes help protect biological diversity. Lichens are symbiotic organisms consisting of a fungus, for which the organism is named, and a green algal and/or a blue-green bacterial partner. Bryophytes are small, thin-leaved, nonvascular plants encompassing the mosses, liverworts, and hornworts. Neither lichens nor bryophytes have true roots or other specialized conductive tissues. Individual species are adapted to specific nutrient availability regimes, therefore oligotrophic environments will be characterized by different species than eutrophic environments.

Responses to N inputs. Lichens and bryophytes are among the most sensitive bioindicators of N in terrestrial ecosystems (Blett et al. 2003, Bobbink et al. 2003, Fenn et al. 2003a, Glavich and Geiser 2008). Unlike vascular plants, lichens and bryophytes lack specialized tissues to mediate the entry or loss of water and gases (e.g., waxy epidermis, guard cells, root steele). Thus, they rapidly hydrate and absorb gases, water, and dissolved nutrients during high humidity or precipitation events. However, they quickly dehydrate to a metabolically inactive state as well, making them slow-growing and vulnerable to contaminant accumulation. Consequently, the implementation of lichen or bryophyte-derived critical loads may prevent undesired impacts to much of the broader forest ecosystem (McCune et al. 2007). In some cases, alteration of lichen community composition may signal the beginning of a cascade of changes in ecosystem N cycling, which may markedly alter the structure or function of the ecosystem as a whole. In many cases, changes in lichens may have implications in portions of the ecosystem beyond the lichen community. In other cases, alterations in the lichen community may have little impact on the overall structure and function of the ecosystem. It can be difficult to know at the outset whether the ultimate consequences of changes indicated by alterations to the lichen community will be large or small for the overall ecosystem over the long term.

Lichens and bryophytes can play important roles in ecosystems. Species of epiphytic lichens in wet and mesic forests that are most sensitive to N (i.e., the large pendant and foliose species) play important ecological roles that are not duplicated by the eutrophic (i.e., nitrogen tolerant) species that may replace them. Dominant regional oligotrophs (e.g., *Alectoria*, *Bryoria*, *Lobaria*, *Ramalina, Usnea*) comprise the bulk of lichen biomass in old-growth forests, contribute to nutrient cycling through N_2 fixation, and are used for nesting material, essential winter forage for rodents and ungulates, and invertebrate habitat (McCune and Geiser 2009). Storage of water and atmospheric nutrients by these lichen genera and epiphytic bryophytes moderates humidity and provides a slow release system of essential plant nutrients to the soil (Boonpragob et al. 1989, Cornelissen et al. 2007, Knops et al. 1991, Pypker 2004). In the tundra, lichens and bryophytes represent a significant portion of the biomass, and reindeer lichens are a vital link in the short arctic food chain (Kytöviita and Crittenden 2007). Mosses comprise the bulk of the biomass of the extensive boreal peatlands. In the desert, lichens and bryophytes, together with other microbiota, form cryptogamic mats important to soil stabilization and fertility.

A hypothetical example of sensitive species diminishing to the extent where they cannot fulfill their ecological roles for the northern flying squirrel of Pacific Northwest forests follows. Over 90 percent of the squirrel's diet consists of hypogeous and epipgeous mycorrhizal fungi in summer and the N-sensitive horsehair lichen (*Bryoria fremontii*) in winter. The squirrel is both an important dispersal agent for mycorrhizal fungi (obligate symbionts with the roots of conifer trees) and a primary prey of the northern spotted owl (*Strix occidentalis*), a threatened and endangered species (Maser et al. 1985). If N deposition extirpated the horsehair lichen, as it nearly has in the Netherlands (van Herk et al. 2003), all dependent species would presumably decline regardless of whether they are themselves sensitive to N deposition.

Critical loads of N for lichens. The N critical loads estimated in this report for lichens range from 1 to 9 kg N ha^{-1} yr^{-1} (Table 19.4, Figure 19.3). Although the reported range of N critical loads is not as large as the ranges for forests or herbs, the certainty associated with these estimates varies considerably. This is partially because of differences in sampling scheme and intensity. For example in the Pacific Northwest and California, lichen communities were assessed intensively across wide environmental gradients spanning low to high N deposition on a fine grid over time (Geiser and Neitlich 2007, Jovan 2008), yielding highly reliable critical N load estimates. Assessments in the eastern United States are more problematic, due to historical and contemporary S emissions and acid deposition. In such cases, where historical information necessary to identify a "pristine" or "clean" state is lacking, it is more difficult to determine the N critical load, and the resulting confidence associated with the critical load is low. The critical load of N for lichens, based on the shift in community composition when eutrophs dominate at the expense of oligotrophs, is on the order of current N deposition and thus is exceeded across much of the Eastern Temperate and Northern Forest ecoregions and in many areas (e.g., high deposition) in the West (Figure 19.4). The uncertainty associated with the exceedance, like that for the critical load, is low for the Marine West Coast and Northwestern Forested Mountains ecoregions and Mediterranean California forests, but high elsewhere.

Studies in the Pacific Northwest demonstrate that increasing precipitation allows lichens to tolerate higher N deposition (Geiser and Neitlich 2007, Geiser et al. 2010, Chapter 4). The importance of precipitation volume in the N critical load for lichens is likely due to the direct influence of N concentration on lichens, that is, the concentrations of N compounds to which lichens are exposed are more important than total N loading (Geiser et al. 2010). If such simple models could be tested and confirmed in other regions of the country, the confidence in the critical loads in those regions would improve.

19.8.3 Herbaceous Species and Shrubs

Background. Herbaceous species and shrubs (Table 19.5, Figure 19.5) are found in grasslands, shrublands, forests, deserts, and wetlands, and comprise the majority of the roughly 26,600 vascular plant species found in North America north of Mexico (NRCS 2009).

Response to N inputs. Herbaceous species and some shrubs appear intermediate between cryptogram and tree species in their sensitivity to N deposition, due to specialized tissues that mediate the entry or loss of water and gases compared with cryptograms, and rapid growth rates, shallow rooting systems, and often shorter lifespan compared with trees. Thus, herbaceous species in a forest understory will likely respond more rapidly to changes in N deposition and to a greater degree than the trees with which they coexist. Herbaceous species in alpine or tundra environments will respond later and to a lesser degree than the cryptograms with which they coexist. Herbaceous plants obviously play an important role in those ecosystems in which they are the dominant primary producers (e.g., grasslands, shrublands). In forests, however, the role of the herbaceous community in ecosystem function has an importance that is disproportionate to its relatively low biomass. For example, although they represent only approximately 0.2 percent of standing aboveground biomass, herbaceous understory species produce more than15 percent of forest litter biomass and comprise up to 90 percent of forest plant biodiversity, including endangered or threatened species (Gilliam 2007).

Critical loads of N for herbaceous vegetation. The range of critical loads for N for herbaceous species and shrubs across all ecoregions is 3 to 33 kg N ha^{-1} yr^{-1} (Table 19.5, Figure 19.5). Although this range is broader than those for lichens or mycorrhizal fungi, many of the critical loads for herbaceous species fall into the range of 5 to15 kg N ha^{-1} yr^{-1}. There is moderate uncertainty in these estimates. The shorter lifespan of some herbaceous species results in a more rapid response to N addition. This pattern is especially relevant for annuals and perennials with little N storage. In grasslands, for example, elevated N deposition often leads to a rapid (1 to 10 years) increase in herbaceous production and a shift in biomass allocation towards more aboveground tissue. This often decreases light levels at ground surface and decreases the numbers of plant species, primarily of perennials, legumes, and natives (Clark and Tilman 2008, Suding et al. 2004, Tilman 1993). Experimental studies of moderate to long duration (3 to10 years) allow determination of the N critical load with reasonable certainty. Longer studies (>10 years) would decrease the uncertainty further. In some cases, it can be difficult to determine whether the condition in reference plots or at the low end of a deposition gradient represents a “pristine” condition or whether a site has already been altered by N deposition prior to or at the time of the study. For example, the watershed acidification study at Fernow Experimental Forest, West Virginia, Adams et al. (2006) added 35 kg N ha^{-1} yr^{-1} via aerial N application in addition to ambient deposition of 15 to 20 kg N ha^{-1} yr^{-1}, which has led to changes in understory species composition. Recently, similar changes in understory species composition have occurred on the adjacent reference watershed receiving

Table 19.4—Empirical critical loads of nutrient N for lichens in U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	Critical load for N deposition *kg* ha^{-1} yr^{-1}	Reliability	Response of	Comments	Study
Tundra	Tundra	1-3	(#)	Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover	N addition studies, high and low Arctic, P enhanced or moderated N effects	Arens et al. 2008[a], Hyvärinen et al. 2003[b], Makkonen et al. 2007[b]
Taiga	Taiga	1-3	#	Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates		Berryman et al. 2004[c], Berryman and Straker 2008[c], Geiser et al. 2010, Moore et al. 2004[c], Poikolainen et al. 1998[b], Strengbom et al. 2003[d], Vitt et al. 2003[c]
Northern Forests	Northern Forests	4-6	(#)	Changes in lichen physiology and community structure	Application of western OR and WA model	Geiser et al. 2010
Northwest Forested Mountains	Coniferous forests, Alaska	1.2-3.7	(#)	Lichen community composition change	Application of western OR and WA model	Geiser et al. 2010
Northwest Forested Mountains	Coniferous Forests, non- Alaska	2.5-7.1	##	Lichen community composition change	Application of western OR and WA model	Geiser et al. 2010
Northwest Forested Mountains	Central Southern Sierras	3.1-5.2	##	Shifts in epiphytic lichen communities favoring eutrophs	Critical load based on exceedance of a N concentration threshold in the lichen *Letharia vulpina*	Fenn et al. 2008, 2010
Marine West Coast Forests	Western OR and WA forests	2.7-9.2	##	Shifts in epiphytic lichen communities favoring eutrophs	Critical load increases with increasing mean annual precipitation from 40 to 240 cm	Geiser et al. 2010
Eastern Forests	Eastern hardwoods and Southeast Coastal Plain	4-8 4-6	(#) (#)	Shifts in epiphytic lichen communities favoring eutrophs	Application of western OR and WA model	Geiser et al. 2010
North American Deserts	Cold desert (Hells Canyon National Resource Area)	3	(#)	Increased cover and abundance of nitrophilous lichens on tall shrubs, increased parasitism of lichens	Critical load estimated from overlay of course grid (36 km) CMAQ N; local N deposition from NH_3 was likely higher	Geiser et al. 2008, Porter 2007

Mediterranean California	Oak woodlands and chaparral (Central Valley: Sacramento Valley, Coast Ranges and Sierra foothills)	3-6	#	Shifts in epiphytic lichen communities favoring eutrophs	Forest Health Monitoring (FHM) lichen survey of 118 forested sites. Eutrophs dominated communities when CMAQ 4 km N deposition estimates were >5.5 kg ha^{-1} yr^{-1}	Fenn et al. 2010, Geiser et al. 2010, Jovan 2008, Jovan and McCune 2005
Mediterranean California	Mixed Conifer forest (Sierra Nevada)	3.1-5.2	##	Shifts in epiphytic lichen communities favoring eutrophs	Extrapolated from Northwestern Forested Mountains Sierra Nevada study	Fenn et al. 2008, 2010
Temperate Sierras	Lichens	4-7	(#)	Shifts in epiphytic lichen communities favoring eutrophs	Application of western OR and WA model	Geiser et al. 2010

[a] based on data from Greenland; [b] based on data from Finland; [c] based on data from Canada; [d] based on data from Sweden

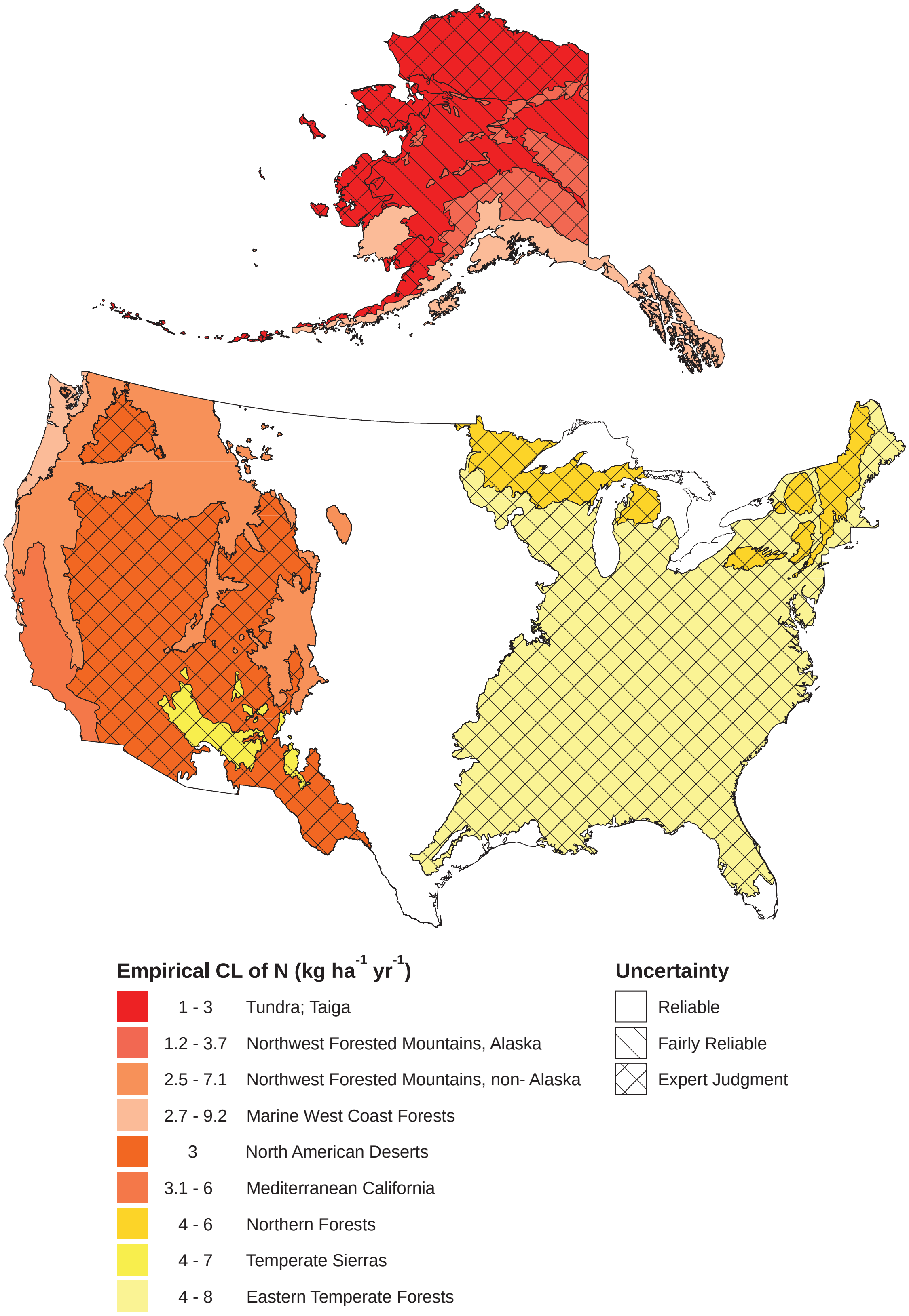

Figure 19.3—Map of critical loads (CL) for lichens by ecoregion in the United States. The range of critical loads reported for lichens is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain “reliable” category, single hatching for the “fairly reliable” category, and double hatching for the “expert judgment” category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases. White areas lack data for critical loads determination for lichens.

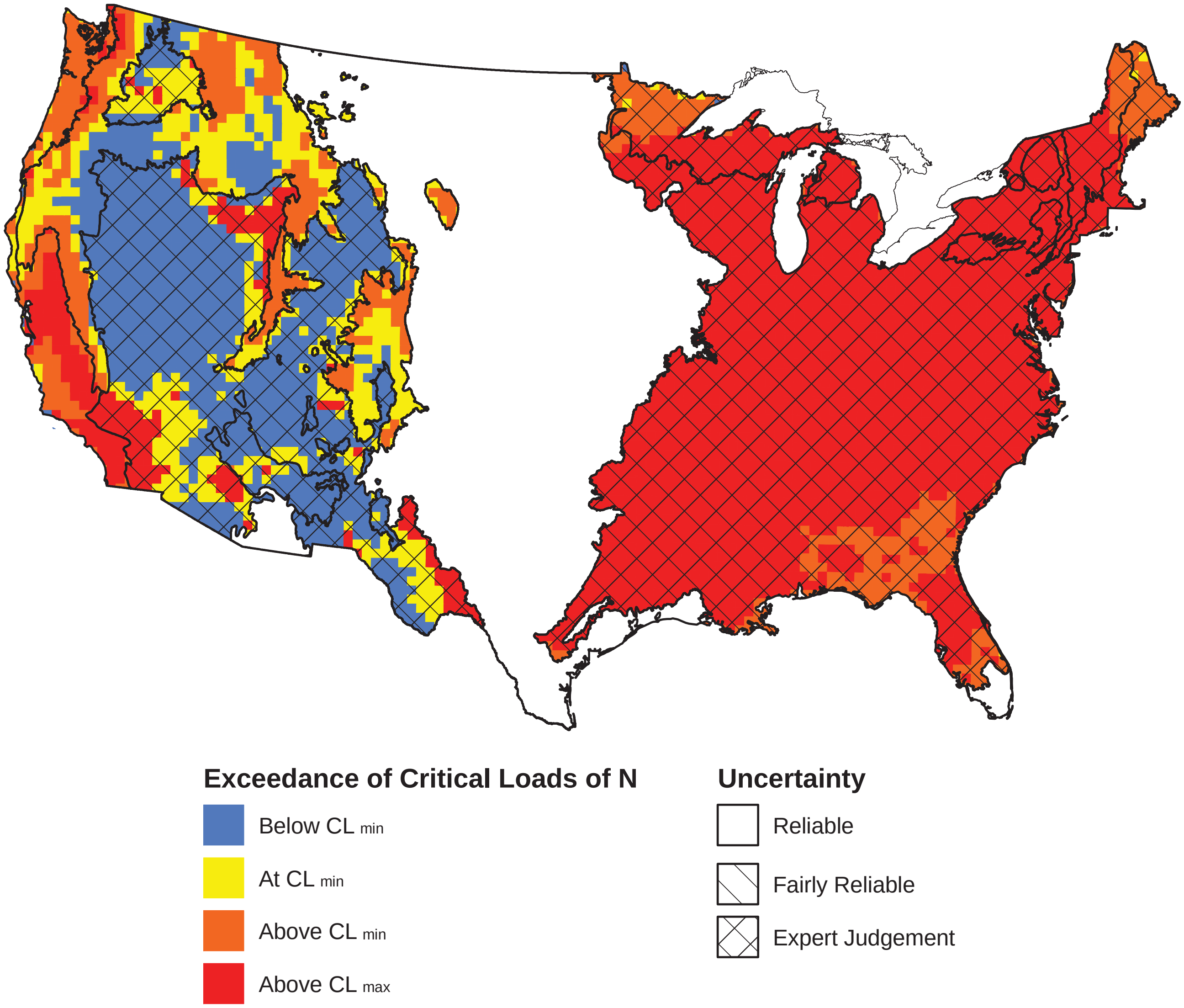

Figure 19.4—Map of exceedance of critical loads (CL) for lichen by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load - deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for lichens.

only ambient atmospheric deposition (Gilliam et al.1996).[25] This pattern suggests that N deposition to the reference watershed currently exceeds the critical load. It is difficult to determine the empirical N critical load at sites where ambient deposition exceeds the critical load. Where deposition rates exceed the critical load, empirical measurement of the rate of change of an ecological metric (e.g., plant abundance, diversity, or community composition) over a range of N inputs provides an approach to estimate the N level at which that metric begins to change (Bowman et al. 2006).

The critical load of N for herbaceous species and herbs, when community change occurs (in some cases with exotic invasives replacing native species), is exceeded across much of the Great Plains ecoregion, in portions of the Southwest, and in high elevation and high deposition areas of the other ecoregions (Figure 19.6). The uncertainty associated with the exceedance, like that for the critical load, varies.

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[25] Gilliam, F.S. Unpublished data. Professor, Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510.

Table 19.5—Empirical critical loads of nutrient N for herbaceous plants and shrubs in U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	Critical load for N *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Tundra	Prostrate dwarf shrub	1-3	##	Changes in CO_2 exchange, cover, foliar N, and community composition of vascular plants	N addition study, Greenland high arctic, P enhanced N effects	Arens et al. 2008[a]
Taiga	Shrublands	6	##	Change in shrub and grass cover, increased parasitism of shrubs	Long-term, low N addition study: shrub cover decreased, grass cover increased	Nordin et al. 2005[b], Strengbom et al 2003[b]
Northern Forests	Northern hardwood forests (Adirondacks)	>7 and <21	#	Alteration of herbaceous understory		Hurd et al. 1998
Northwestern Forested Mountains	Alpine grasslands	4-10	##	Plant species composition change	Based on long-term experiment	Bowman et al. 2006
Eastern Forests	Eastern hardwood forests (Fernow Experimental Forest, WV)	<17.5	(#)	Increases in nitrophilic species, declines in species-rich genera (e.g., Viola)		Gilliam 2006, Gilliam 2007, Gilliam et al. 2006
Great Plains	Tallgrass prairie	5-15	#	Biogeochemical N cycling, plant and insect community shifts	Long-term, low N addition study that also added other nutrients.	Clark et al. 2009; Clark and Tilman 2008; Tilman 1993, 1987; Wedin and Tilman 1996
Great Plains	Mixed-grass prairie	10-25	#	Soil NO_3^- pools, leaching, plant community shifts	Short-term, low N addition study	Jorgenson et al. 2005, Clark et al 2003, 2005
Great Plains	Shortgrass prairie	10-25	(#)		Inferred from mixed-grass prairie	Epstein 2001, Barrett and Burke 2002
North American Desert	Warm desert (Joshua Tree National Park, Mojave Desert)	3-8.4	#	Increased biomass of invasive grasses; decrease of native forbs		Allen et al. 2009; Inouye 2006; Rao et al. 2009, 2010

Mediterranean California	Serpentine grassland	6	##	Annual grass invasion, replacing native herbs	Critical load based on a local roadside gradient; serpentine grassland site is actually west of the Central Valley	Fenn et al. 2010, Weiss 1999
Mediterranean California	Coastal sage scrub	7.8-10	#	Invasive grass cover, native forb richness	Modeled and inferential N deposition estimates and unpublished data for vegetation survey	Allen unpublished[c], Egerton-Warburton et al. 2001, Fenn et al. 2010, Tonnesen et al. 2007
Mediterranean California	Mixed conifer forests (San Bernardino Mountains)	24-33	(#)	Biodiversity of understory: percent cover and no. of species/3 ha	Based on plant surveys in 1970s and 2003	Allen et al. 2007 N deposition data: Fenn et al. 2008 and Fenn[d]
Wetlands	Freshwater wetlands	6.8-14	(#)	Pitcher plant community change	Critical load based on northeastern populations	Gotelli and Ellison 2002, 2006
Wetlands	Intertidal wetlands	50-100	##	Loss of eelgrass		Latimer and Rego 2010
Wetlands	Intertidal salt marsh	63-400	(#)	Salt marsh community structure, microbial activity and biogeochemistry		Caffrey et al. 2007, Wigand et al. 2003

[a] based on data from Greenland; [b] based on data from Sweden; [c] Allen, E.B. Unpublished data. Professor and Natural Resources Extension Specialist, Department of Botany and Plant Sciences and Center for Conservation Biology, University of California, Riverside, CA 92521; [d] Fenn, M.E. Unpublished data. Research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

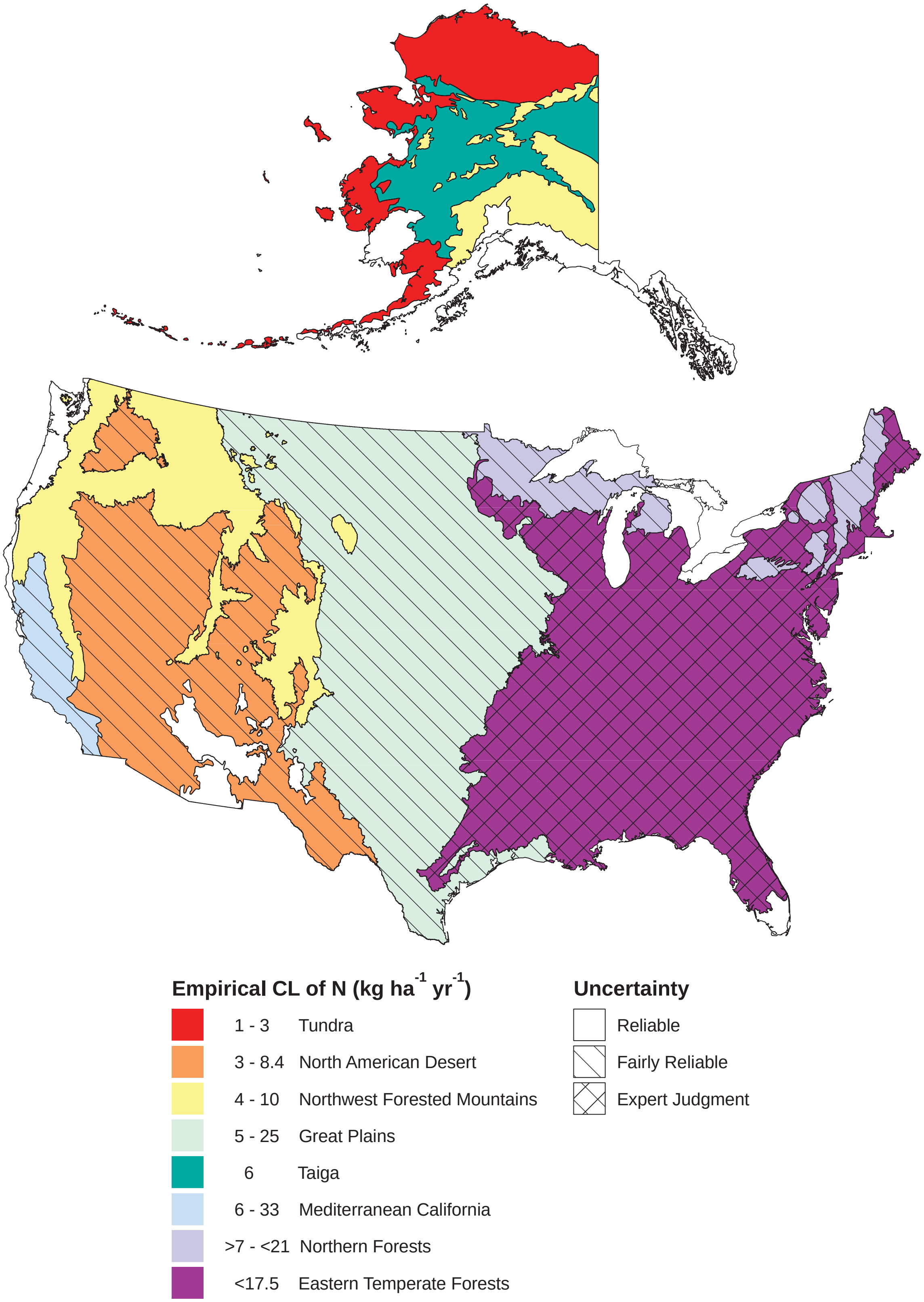

Figure 19.5—Map of critical loads (CL) for herbaceous plants and shrubs by ecoregion in the United States. The range of critical loads reported for herbaceous plants and shrubs is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable" category, single hatching for the "fairly reliable" category, and double hatching for the "expert judgment" category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases. White areas lack data for critical loads determination for herbaceous species and shrubs.

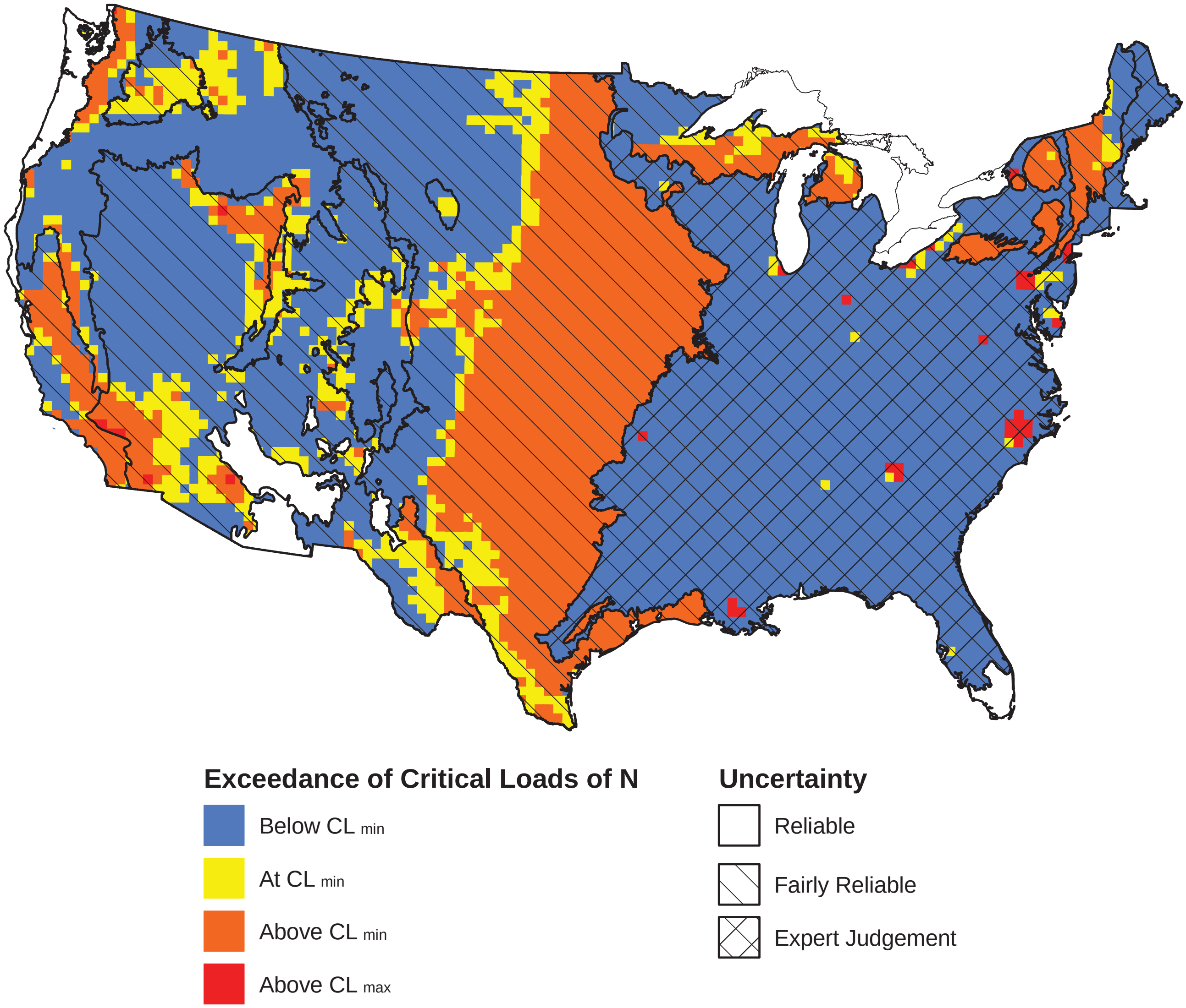

Figure 19.6—Map of exceedance of critical loads (CL) for herbaceous plants and shrubs by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load - deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL$_{min}$, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL$_{max}$, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for herbaceous species and shrubs.

Comparisons of N critical load with current deposition indicates that the low end of the critical load range for herbaceous species is exceeded for most of the Great Plains and Mediterranean California ecoregions (Figure 19.6). The low end of the critical load range is also exceeded in portions of the Eastern Temperate Forests, Northern Forests, Northeastern Forested Mountains, and North American Deserts ecoregions; uncertainty for exceedance varies. Portions of the Cascade Mountain range, the Rocky Mountains, the Adirondacks, and the Green and White Mountain ranges exceed the low end of the critical load range.

19.8.4 Trees/Forest Ecosystems

Background. In this section we discuss the responses of trees and the biogeochemical responses of forest ecosystems to N inputs (Table 19.6), excluding the specific responses of mycorrhizal fungi, lichens, or understory herbaceous plants. Forest ecosystems represent a third of landcover in the United States

(USFS 2001) and are significant in the Northern, Eastern Temperate, Tropical and Subtropical Humid, and Marine West Coast Forests; Northwestern Forest Mountains; and Mediterranean California ecoregions.

Response to N inputs. In northeastern forests, gradient studies demonstrate that N deposition enhances growth in some fast-growing tree species, including the hardwoods studied with arbuscular mycorrhizal associations, whereas it slows growth in some species (red spruce, red maple [*Acer rubrum*]), and has no detectable effect on still other species (Thomas et al. 2010). Similarly, N deposition enhances survivorship in a few species (black cherry [*Prunus serotina*], red maple, paper birch [*Betula papyrifera*]) and decreases survivorship in others (Thomas et al. 2010). Survivorship under chronic N deposition, and possibly other co-occurring pollutants such as ozone, is often dependent on interactions with other stressors such as pests, pathogens, climate change, or drought (Grulke et al. 2009, McNulty and Boggs 2010). Over the long term, these differential effects of N deposition on tree growth and survivorship are likely to shift species composition, possibly to more nitrophilic species, similar to patterns seen for organisms with shorter lifespans.

We have few data that show a major structural or functional shift in forest ecosystems because of the long response time of trees and forest soils to changes in N inputs and N availability (Table 19.6). The relatively large pools of organic N in the forest floor, mineral soil, tree biomass, and detritus contribute to the relatively long lag time in forest ecosystem response to N inputs. Because of the long lag time in response to N treatments, it can be difficult to determine the actual critical N load for forest ecosystems based on short-term fertilization studies. If a response is observed over a relatively short period of time (i.e., years), it is nearly certain that the critical load is below the total N input at the treatment site and it can be difficult to further constrain the critical load.

It is expected that the more complex and interconnected processes in forests will result in a higher N critical load, in part because large N storage pools give forest ecosystems a greater capacity to buffer N inputs. In herbaceous plants, too, responses in individual species tend to be observed at lower N inputs than changes in community composition, which are more complex and interconnected (Bowman et al. 2006).

Critical loads of N in forests. The range of critical loads reported for forest ecosystems is 4 to 39 kg N ha^{-1} yr^{-1} (Table 19.6, Figure 19.7). The threshold N deposition value which caused increased NO_3^- leaching from forest ecosystems into surface water was 8 to 17 kg N ha^{-1} yr^{-1}; the lower end of the range represents Northern and Eastern Temperate Forests, the upper end represents Mediterranean California mixed conifers (Table 19.6, Figure 19.7). At 4 kg N ha^{-1} yr^{-1}, increasing $[NO_3^-]$ was reported in the organic horizon in the Colorado Front Range, which suggests incipient N saturation (Rueth and Baron 2002).The highest critical loads were reported for Mediterranean California mixed-conifer forests for soil acidification caused by increased N deposition and for forest sustainability. These sites experience some of the highest N deposition reported in the United States, up to approximately 70 kg N ha^{-1} yr^{-1} (Fenn et al. 2008).

The N critical load is exceeded across much of the eastern forests (Eastern Temperate and Northern Forest ecoregions). The lower end of the N critical load range is exceeded for the remaining portions of the eastern forests, as well as portions of the Marine West Coast, Northwestern Forested Mountains, and Tropical and Subtropical Humid Forest ecoregions (Figure 19.8). The N critical load for forest ecosystems was not exceeded for much of area of the Mediterranean California ecoregion, in part because the critical load was very high and, in part, because the CMAQ 2001 deposition that we used was at a coarse resolution that underestimates deposition compared to the finer scale (4 km x 4 km grid) used by Fenn et al. (2010). The critical load for nitrate leaching (Figure 19.9) is exceeded in portions of the Mediterranean California and the lower end of the critical load range is exceeded for most eastern forest and part of the Great Plains (Figure 19.10).

19.8.5 Inland Surface Waters and Wetland Ecosystems

Background. Freshwater lakes and streams, and wetlands (freshwater and estuarine intertidal) are ecosystem

Table 19.6—Empirical critical loads of nutrient N for forest ecosystems in U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	CL for N *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Northern Forests	Northeastern gradient	>3	#	Decline in survivorship of sensitive species	Based on study of gradient of N deposition from 3-11 kg N ha^{-1} yr^{-1}	Thomas et al. 2010
Northern Forests	Hardwood and coniferous forests	8	##	Increased surface water and NO_3^- leaching		Aber et al. 2003
Northern Forests	Montane spruce fir (Mt. Ascutney, VT)	>10 and <26	#	Declines in growth and increased mortality		McNulty et al. 2005
Northwestern Forested Mountains	Subalpine forest	4	##	soil organic horizon and foliar N enrichment and higher potential net N mineralization rates		Baron et al. 1994, Rueth and Baron 2002
Northwestern Forested Mountains	Mixed conifer forest	17	## #	NO_3^- leaching, reduced fine root biomass	Co-occurring ozone also affects fine root biomassi in ponderosa pine	Fenn et al. 2008
Marine West Coast Forests	Coastal white spruce forest (South-Central Alaska)	5	(#)	Declines in tree health; changes in understory composition; foliar nutritient imbalances; elevated NO_3^- in forest floor and mineral soil		Lilleskov 1999, Lilleskov et al. 2001, 2002; Whytemare et al. 1997
Eastern Forests	Eastern hardwood forests	>3	#	Decline in survivorship of sensitive species	Based on study of gradient of N deposition from 3-11 kg N ha^{-1} yr^{-1}	Thomas et al. 2010
Eastern Forests	Eastern Hardwood Forests	8	##	Increased surface water loading of NO_3^-		Aber et al. 2003
Mediterranean California	Mixed conifer forests (San Bernardino Mountains and southern Sierra Nevada range)	17	##	Streamwater $[NO_3^-] > 14$ µM	Based on regression of throughfall vs. peak streamwater NO_3^- concentrations. Daycent simulations gave similar results	Fenn et al. 2008, 2010
Mediterranean California	Mixed conifer forests (San Bernardino Mountains)	17	#	Reduced fine root biomass	Based on regression of throughfall N deposition and fine root biomass in ponderosa pine (also affected by co-occurring ozone)	Fenn et al. 2008; Grulke et al., 1998

continued

Table 19.6—continued

Ecoregion	Ecosystem (Site)	CL for N *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Mediterranean California	Mixed conifer forests (San Bernardino Mountains)	25.9	#	Soil acidification; pH ≤ 4.6	Based on regression of throughfall N deposition and mineral soil H^+	Breiner et al. 2007
Mediterranean California	Mixed conifer forests (San Bernardino mountains)	39	(#)	Forest sustainability	Based on shifts in plant phenology and C allocation. Caused by combined effects of ozone and N deposition. Leads to increased bark beetle mortality and wildfire risk	Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004 N deposition data from Fenn et al. 2008.
Tropical and Subtropical Humid Forests	N-poor tropical and subtropical forests	5-10	(#)	Changes in community composition; NO_3^- leaching, N trace gas emissions	Critical load for N-poor forests based on estimates for Southeastern Coastal Plain forests	No direct studies[a]
Tropical and Subtropical Humid Forests	N-rich tropical and subtropical forests	<5-10	(#)	NO_3^- leaching, N trace gas emissions	Critical load for N-rich forests should be lower than for N-poor forests based on possibility of N losses	No direct studies[a]

[a] The critical load is based on expert judgment and knowledge of ecosystems which may function similarly.

types that occur in most ecoregions in North America. In freshwater lakes and streams, phytoplankton, or algae that live in the water column, are sensitive to the chemical environment in which they reside. Many species can be used as indicators of the levels of nutrients or acidity because of individual species' preference for specific chemical conditions. Diatoms, unicellular plants that form the base of freshwater food webs, are used in this discussion because there has been more work published on these algae than others, but other types of algae also respond to N deposition (Lafrancois et al. 2004, Michel et al. 2006). Of the wetlands which occur in the conterminous United States, 95 percent are freshwater wetlands and 5 percent are estuarine or marine wetlands (FWS 2005). The species composition tends to differ between freshwater and intertidal wetlands, although together they support more than 4200 native plant species. Despite the high biodiversity, the effects of N loading are studied in just a few plant species.

Response to N inputs. For the analysis of nutrient N effects to freshwater lakes and streams, we relied on papers and studies that linked aquatic biological and ecological response to atmospheric deposition, but the results are consistent with laboratory or *in situ* dose-response studies and even land-use change studies. The productivity of minimally disturbed aquatic ecosystems is often limited by the availability of N, and slight increases in available N trigger a rapid biological response that increases productivity and rearranges algal species assemblages (Nydick et al. 2004, Saros et al. 2005). The mechanism for change is alteration of nitrogen:phosphorus (N:P) ratios, which can increase productivity of some species at the expense of others (Elser et al. 2009). As with the terrestrial ecosystems described above, freshwater nutrient responses are most evident where land use change and acidic deposition have been limited, thus most evidence of exceedance of N critical loads comes from the western United States (Chapter 18). As with terrestrial plants, some diatoms respond rapidly to an increase in available N. An example is dominance of two diatoms (*Asterionella formosa* and *Fragilaria crotonensis*) in numerous Rocky Mountain lakes with higher N, in contrast with lakes with lower N deposition, where there is a more even distribution, thus high biodiversity, of diatoms. Higher trophic levels (zooplankton, macroinvertebrates) may be secondarily affected by N, but further increases in primary, or autotrophic, production will be limited by other nutrients such as P or silica (Si).

Both freshwater and estuarine intertidal wetlands tend to be N-limited ecosystems (LeBauer and Tresseder 2008, US EPA 1993). Known responses to N enrichment are generally derived from nutrient-addition studies in the field and observations along gradients of N deposition. A variety of ecological endpoints are evaluated, such as altered soil biogeochemistry, increased peat accumulation, elevated primary production, changes in plant morphology, changes in plant population dynamics, and altered plant species composition (US EPA 2008). In general, the sensitivity of wetland ecosystems to N is related to the fraction of rainfall (a proxy for atmospheric N deposition) in its total water budget. Most freshwater wetlands, such as bogs, fens, marshes and swamps, have relatively closed water and N cycles, thus are more sensitive to N deposition than intertidal wetlands, such as salt marshes, and eelgrass (*Zostera* sp.) beds (Chapter 17).

Critical loads of N for freshwater ecosystems. In general, critical loads for freshwater lakes and streams tend to be low because the target organisms are unicellular algae that respond rapidly to changes in their chemical environment. The range of critical loads for eutrophication and acidity is 2 to 9 kg N ha^{-1} yr^{-1} (Chapter 18); the range reported for terrestrial and wetland ecosystems is much broader (Table 19.1). Critical loads for NO_3^- leaching from terrestrial ecosystems ranged from 4 to 17 kg N ha^{-1} yr^{-1} (Figure 19.9), but many sensitive freshwaters at high altitudes are found above the tree line where watershed N retention is limited due to little vegetation, poorly developed soils, short hydraulic residence time, and steep topography. Many hydrological factors including hydraulic residence time, N pool size, and conditions of water saturation affect N loss. These factors influence how rapidly a system exhibits elevated N leaching in response to increased N deposition, and how this increased N availability subsequently influences biota. In general, lakes have relatively rapid N turnover times

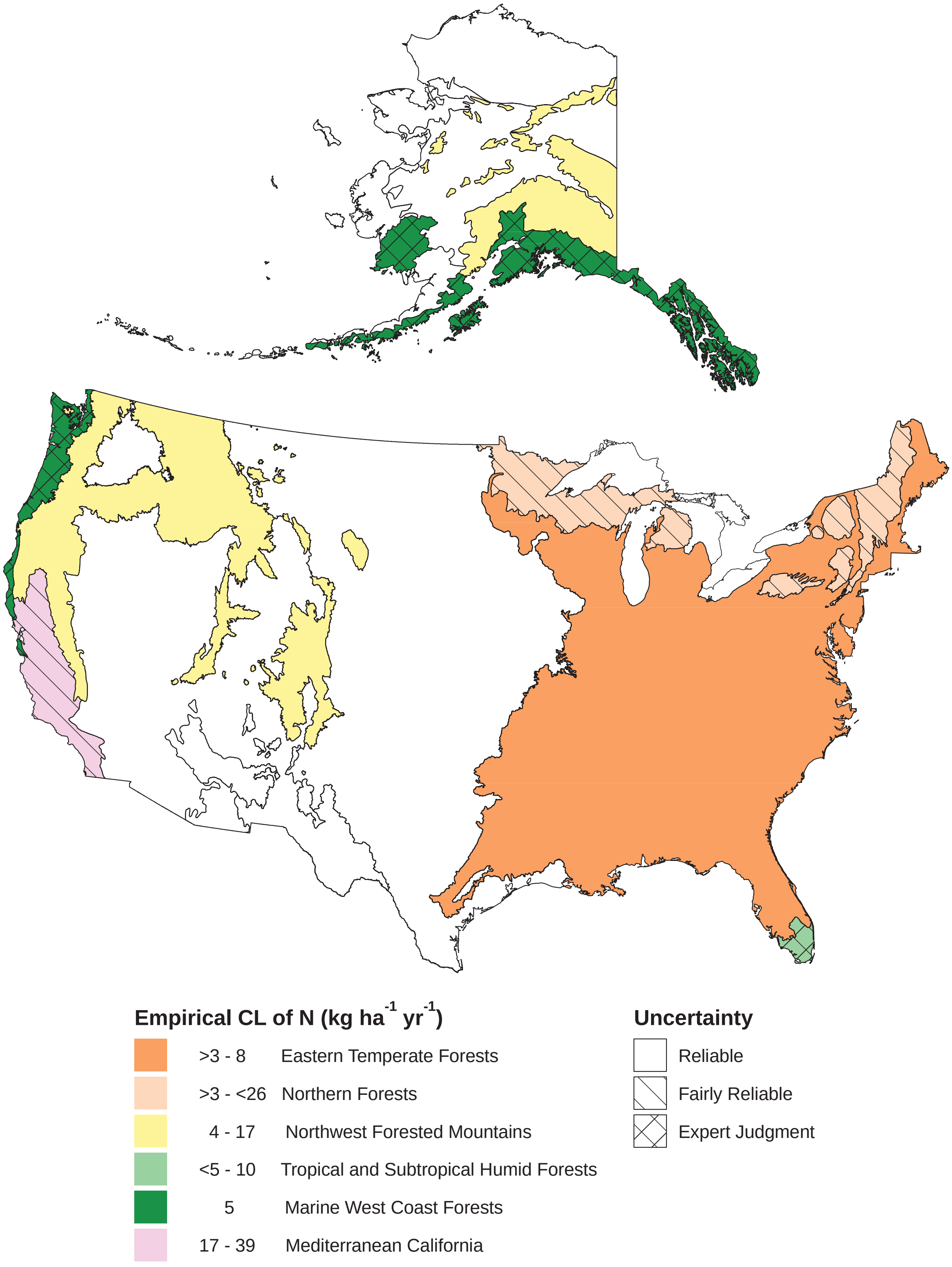

Figure 19.7—Map of critical loads (CL) for forest ecosystems by ecoregion in the United States. The range of critical loads reported for forest ecosystems is shown for each ecoregion; this map does not include the responses of mycorrhizal fungi, lichens, or understory herbaceous plants already represented. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable" category, single hatching for the "fairly reliable" category, and double hatching for the "expert judgment" category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases. White areas lack data for critical loads determination for forest ecosystems.

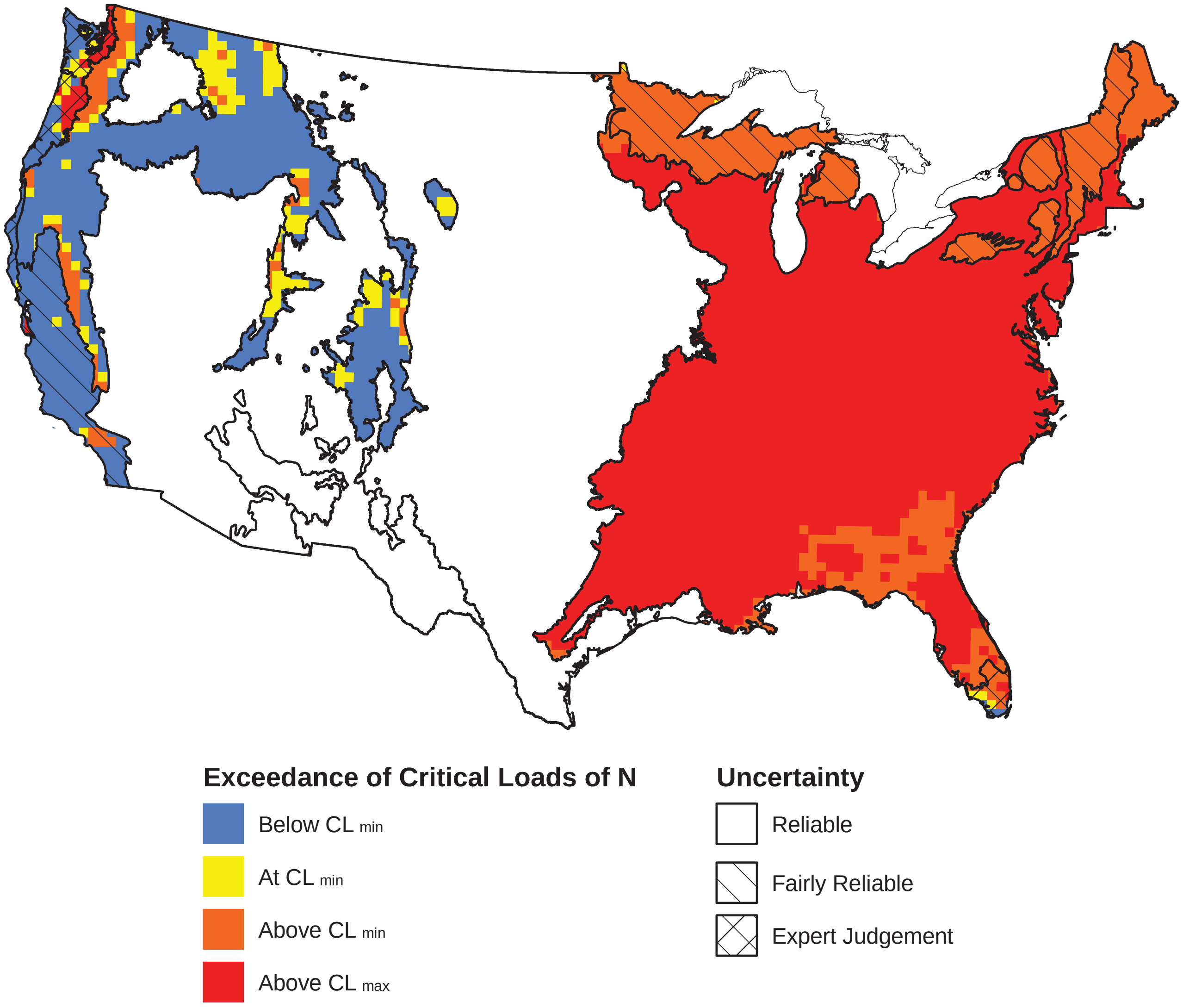

Figure 19.8—Map of exceedance of critical loads (CL) for forest ecosystems by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for forest ecosystems.

compared to soil N pools and are at least seasonally well mixed. They would, thus, be expected to have lower critical loads. Turnover times for N in mineral soil pools can be very long, and, as a result, buffer changes in soil solution that would affect terrestrial plants. Thus responses by terrestrial plants would not be expected to be as rapid as those of freshwater organisms.

Generally the most sensitive type of wetland to N deposition are freshwater wetlands, with critical loads that range from 2.7 to14 kg N ha^{-1} yr^{-1} (Chapter 17). The nonvascular plant genus, *Sphagnum,* and the carnivorous pitcher plant (*Sarracenia* sp.) are the two species most commonly studied. The critical loads reported for freshwater wetlands (Chapter 17) fall between those reported for inland surface waters (Chapter 18) and those reported for terrestrial ecosystems. The critical load tends to be higher for intertidal wetlands than other types of ecosystems because they have open nutrient cycles which are often strongly affected by N loading sources other than atmospheric deposition. Based on field observations of

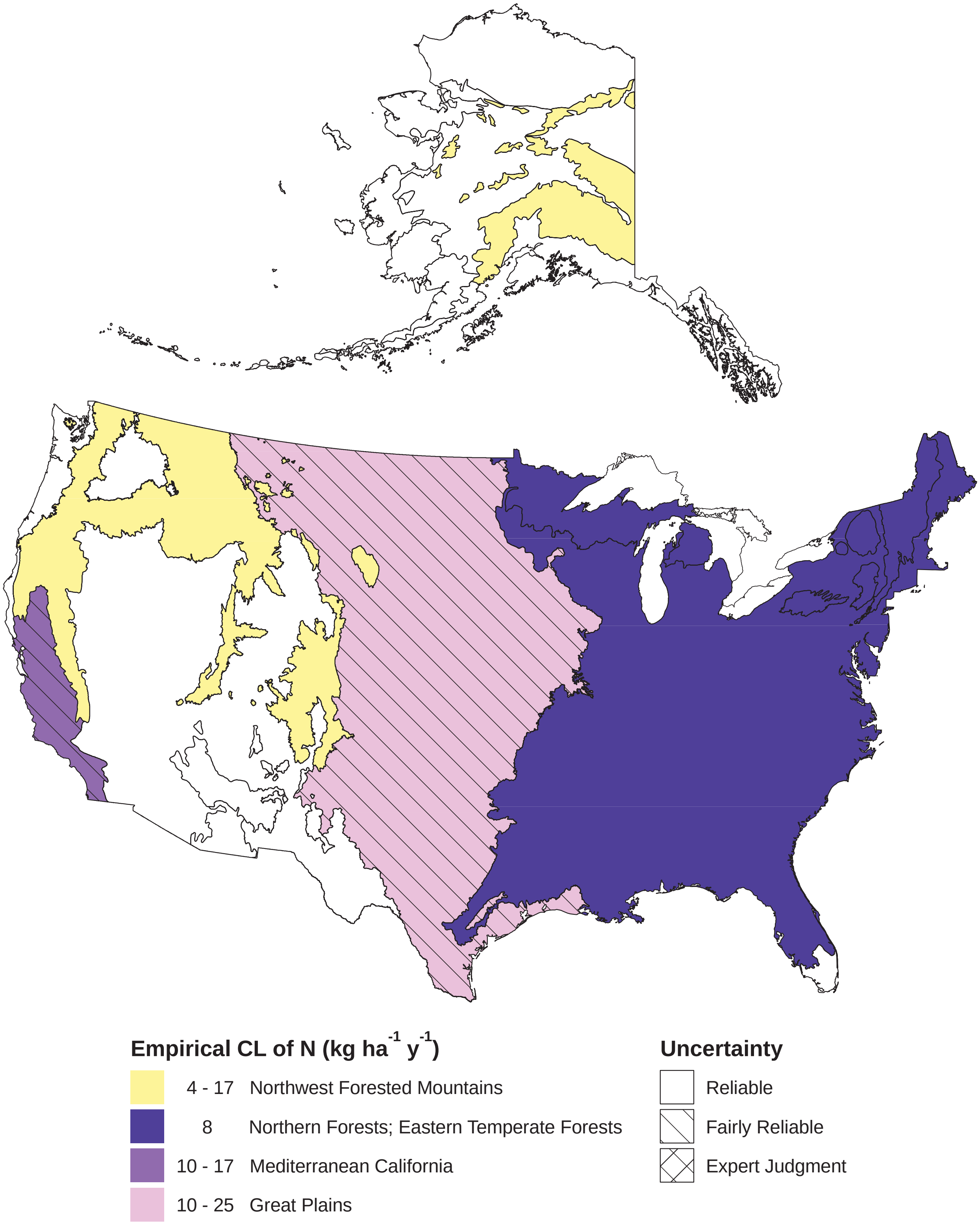

Figure 19.9—Map of critical loads (CL) for NO3- leaching by ecoregion in the United States. The range of critical loads based on increased nitrate leaching for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain “reliable” category, single hatching for the “fairly reliable” category, and double hatching for the “expert judgment” category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases. White areas lack data for critical loads determination for nitrate leaching.

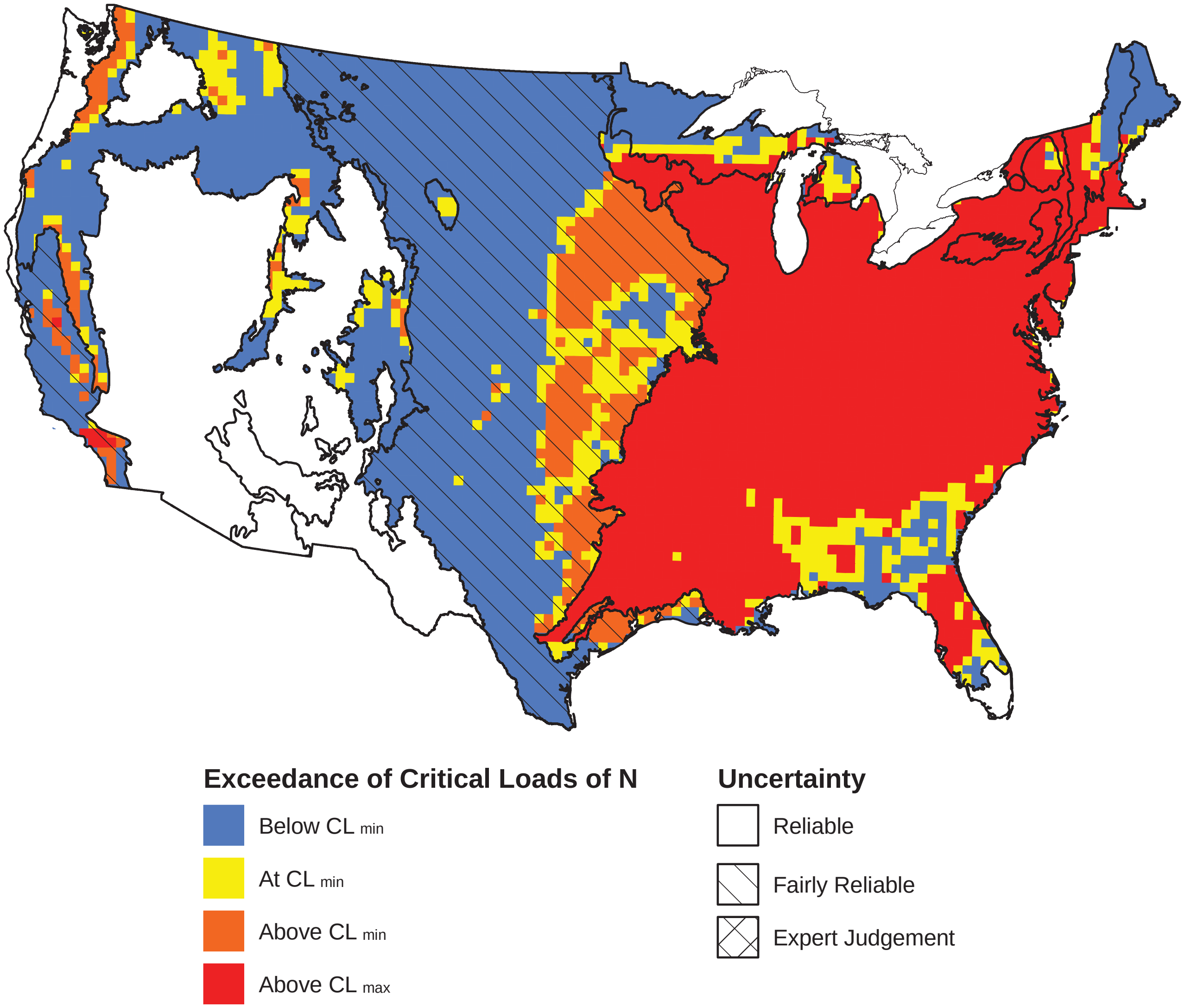

Figure 19.10—Map of exceedance of critical loads (CL) for NO_3^- leaching by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load - deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for nitrate leaching.

N loading to plant growth and species composition on salt marsh and eelgrass habitat, the critical load ranges between 50 and 400 kg N ha^{-1} yr^{-1}.

19.9 Comparison to Critical Loads in Europe

The critical loads for N deposition we report are consistently lower than those reported for Europe, with a few exceptions (Table 19.7). It is difficult to make the comparison between the United States and Europe because the ecosystem classification systems used are not parallel. Empirical N critical loads for Europe (Bobbink et al. 2003) were reported at different scales using the European University Information Systems (EUNIS) than the U.S. critical loads: coarser for forests, for example, and finer for nonforests. Furthermore, the response variables and thresholds values of those variables are not always the same.

There are several reasons that N critical loads in Europe may be higher than in the United States. First, as discussed earlier, because N deposition in Europe has

Table 19.7—Comparison of critical loads for Europe and the United States. Reliability rating: ## reliable; # fairly reliable; (#) expert. judgment. European data from Bobbink et al. 2003.

North American ecoregion	Ecosystem component	Response	Critical Load *kg N ha^{-1} yr^{-1}*	Reliability	European EUNIS code[a]	European ecosystem type or component	European indication of exceedance	European critical load *kg N ha^{-1} yr^{-1}*	Reliability
Tundra	Prostrate dwarf shrub	Changes in CO_2 exchange, cover, foliar N, and community composition of vascular plants	1-3	##	F1	Tundra	Changes in biomass, physiological effects, changes in species composition in moss layer, and decrease in lichens	5-10	#
Tundra	Lichens	Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover	1-3	(#)	F1	Tundra	Changes in biomass, physiological effects, changes in species composition in moss layer, and decrease in lichens	5-10	#
Taiga	Lichens, algae, and bryophytes	Changes community composition, abundance, physiology, or ultrastructure.	1-3	#	G	Temperate and boreal forests: lichens and algae	Increase of algae, decrease of lichens	10-15	(#)
Taiga	Mycorrhizal fungi	Ectomycorrhizal fungal change in community structure	5-7	(#)	G	Temperate and boreal forests: mycorrhiza	Reduced sporocarp production, changed/reduced belowground species composition	10-20	(#)
Taiga	Shrublands	Change in shrub and grass cover, increased parasitism of shrubs	6	##	F2	Arctic, alpine and subalpine scrub habitats	Decline in lichens, mosses, and evergreen shrubs	5-15	(#)
Northern Forests	Lichens	Change in lichen community composition	4-6	(#)	G	Temperate and boreal forests: lichens and algae	Increase of algae, decrease of lichens	10-15	(#)
Northern Forests	Mycorrhizal fungi	Ectomycorrhizal fungal change in community structure	5-7	#	G	Temperate and boreal forests: mycorrhiza	Reduced sporocarp production, changed/reduced belowground species composition	10-20	(#)
Northern Forests	Herbaceous species	Loss of prominent species	>7 and <21	#	G	Temperate and boreal forests: ground vegetation	Changed species composition, increase of nitrophilous species, increased susceptibility to parasites	10-15	#
Northern Forests	Coniferous forests	Increased surface water NO3- leaching	8	##	G	Coniferous forests	Increased NO_3^- leaching	10-15	##
Northern Forests	Hardwood forests	Increased surface water NO3- leaching	8	##	G	Deciduous forests	Increased NO_3^- leaching	10-15	(#)
Northwestern Forested Mountains	Coniferous forests, Alaska: lichens	Lichen community change	1.2-3.7	(#)	G	Temperate and boreal forests: lichens and algae	Increase of algae, decrease of lichens	10-15	(#)
Northwestern Forested Mountains	Coniferous forests, non-Alaska: lichens	Lichen community change	2.5-7.1	##	G	Temperate and boreal forests: lichens and algae	Increase of algae, decrease of lichens	10-15	(#)
Northwestern Forested Mountains	Subalpine forest	Increase in organic horizon N; higher potential net N mineralization rates	4	##	G	Deciduous and coniferous forests	Increased N mineralization and nitrification	10-15	#

Northwestern Forested Mountains	Alpine vegetation: dry meadow tundra	Change in species composition	4-10	##	E4.3	Alpine or subalpine grasslands	Increase in tall graminoids, biodiversity change	10-15	(#)
Northwestern Forested Mountains	Mycorrhizal fungi	Ectomycorrhizal fungal change in community structure	5-10	(#)	G	Temperate and boreal forests: mycorrhiza	Reduced sporocarp production, changed/reduced belowground species composition	10-20	(#)
Marine West Coast Forests	Lichens	Epiphytic lichen community change	2.7-9.2	##	G	Temperate and boreal forests: lichens and algae	Increase of algae, decrease of lichens	10-15	(#)
Eastern Forests	Lichens	Epiphytic lichen community change	4-8	(#)	G	Temperate and boreal forests: lichens and algae	Increase of algae, decrease of lichens	10-15	(#)
Eastern Forests	Southeastern Coastal Plain: mycorrhizal fungi	Ectomycorrhizal fungal community response	5-10	(#)	G	Temperate and boreal forests: mycorrhiza	Reduced sporocarp production, changed/reduced belowground species composition	10-20	(#)
Eastern Forests	Eastern hardwood forests	Increased surface water loading of NO_3^-	8	##	G	Deciduous forests	Increased NO_3^- leaching	10-15	(#)
Eastern Forests	Eastern hardwood forest	Increased foliar percent N	>9[b]		G	Deciduous and coniferous forests	Changed N/macro nutrient ratios, decreased P, K, Mg; increased N concentration in foliar tissue	15-20	#
Eastern Forests	Herbaceous species	Herb layer changes	<17.5	(#)	G	Temperate and boreal forests: ground vegetation	Changed species composition, increase of nitrophilous species, increased susceptibility to parasites	10-15	#
Great Plains	Tallgrass prairie	Biogeochemical N cycling, plant and insect community shifts	5-15	#	E1.7	Non-Mediterranean dry acid and neutral closed grassland	Increase in graminoids, decline typical species	10-20	#
Great Plains	Mixed-grass prairie	Soil NO_3^- pools, leaching, plant community shifts	10-25	#	E1.26	Sub-Atlantic semi-dry calcareous grassland	Increased tall grasses, decline in diversity; increased mineralisation and N leaching	15-25	##
Wetlands	Bogs, fens, and swamps	Alterations in sphagnum accumulation and net primary productivity; alteration in pitcher plant community	2.7-14	#	D1	Raised and blanket bogs	Increase vascular plants, decrease bryophytes, altered growth and species composition of mosses, increased N in peat and peat water	5-10	##
Wetlands	Intertidal salt marsh	Salt marsh community structure, microbial activity and biogeochemistry	63-400	(#)	A2.64 and A2.65	Pioneer and low-mid salt marshes	Increase late-successional species, increase productivity	30-40	(#)
Aquatic	Western high elevation lakes	Eutrophication	2	##	C1.1	Soft-water lakes	Isoetid species negatively affected	5-10	##
Aquatic	Eastern high elevation lakes	Eutrophication	8	#	C1.1	Soft-water lakes	Isoetid species negatively affected	5-10	##

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[a] EUNIS categories: A—Marine habitats; C—Inland surface water habitats; D—Mire, bog, and fen habitats; E—Grasslands and tall forb habitats; F—Heathland, scrub, and tundra habitats; G—Forest habitats

[b] This value, from Boggs et al. (2005) is discussed in Chapter 10 as a response to N deposition. We did not include this value as a critical load in other tables, as the response threshold for detrimental ecological effects was not clear.

been considerably higher than that in the United States over many decades, it is difficult to find background or unimpacted sites as a basis of comparison. This means that, in some cases, the observed change in species composition does not reflect the initial response of a community to increased N inputs, but rather the response of a previously impacted community to further increases in N deposition. In addition, NH_4^+ inputs tend to be higher and represent a greater proportion of total N inputs in Europe. Note also that when dry deposition is underestimated in the United States, the N critical loads will also be underestimated, which would contribute to them being lower than those in Europe. Finally, since a greater proportion of the landscape in Europe, especially forested land, is managed, this may contribute to European N critical loads being higher, as N removal in harvesting results in greater N demand and storage during re-establishment of the forest stand.

Another possible explanation is that the response thresholds utilized in Europe are sometimes higher. A key example is lichen community responses: when a shift in community composition is considered the threshold of change, the N critical loads will be low. Some earlier work in Europe, in contrast, used a different biological threshold—the near extirpation of lichen species—leading to a higher N critical load (Bobbink et al. 2003). Another example of higher response thresholds used for setting critical loads in Europe relates to responses at the forest ecosystem level. Using a more sensitive endpoint, such as changes in N biogeochemistry interpreted as incipient responses of N saturation, led to a critical load <4 kg N ha^{-1} yr^{-1} in the Colorado Front Range (Rueth et al. 2003). This input is a subtle initial N enrichment response when compared to the magnitude of change for the critical loads thresholds in Europe (10 to 15 kg ha^{-1} yr^{-1}).

19.10 Selecting Critical Loads for Natural Resource Decisions

Empirical critical loads may be determined for multiple receptors, responses, and response thresholds within an ecosystem. Thus, several critical loads may be determined for a given ecosystem type (various ecosystem components) when data are available. The determination of these critical loads should be based on the best available scientific information. In section 19.7, we presented some of the factors that affect where the N critical load will fall within the reported range, which could be used to refine the critical load estimate for a given ecosystem. Several other issues need to be addressed in order to select empirical critical loads based on the values reported in this document. The objectives of different policy makers and resource managers will drive the decisions in selecting the N critical load most appropriate for a given area. First, the receptor of concern needs to be defined. The receptor may be a keystone species, the dominant species, the most sensitive species, or a threatened or endangered species. Next the response and response threshold must be set. In some cases, the response itself may be a significant change in the ecosystem (e.g., change in species composition) and in some cases, it may be an earlier stage response (e.g., increase in foliar N concentration). One challenge in determining the critical threshold for the response is that it can be difficult to define a pristine or unimpacted condition when much, or all, of the ecosystem has already experienced elevated N deposition. At this point, the policy makers or resource managers may also consider the degree of harm caused by a particular response; the determination of what level of harm is considered unacceptable is ultimately a policy decision.

Policy and resource management goals will determine the geographic extent and level of response that are considered unacceptable. In a conservation (e.g., wilderness) area, for example, any alteration in N cycling may be considered unacceptable—in these cases, when a range of N critical load values for a suite of resources and responses is presented, the lowest value is usually selected. Federal land managers responsible for Class I areas are required to “err of the side of protecting” these areas in determining the level of pollution these lands can tolerate. Other resource managers may choose to protect certain keystone species, threatened or endangered species, or species of economic or cultural significance. Finally, in some cases, the level of certainty about the critical load may determine which critical load is used.

Another approach for presenting maps of critical loads, which is used in Europe, is to map the critical load that would protect 95 percent of the habitat or ecosystem area (Hettelingh et al. 2008).

19.11 Use of Critical loads in the United States

In the United States, the critical loads approach has not been widely used as an approach for ecosystem protection. For example, the Clean Air Act does not specifically require development and use of critical loads in implementing and assessing environmental and natural resource management programs. Nevertheless, the critical loads approach is being explored at Federal, state, and international levels as an ecosystem assessment tool with great potential to simplify complex scientific information and effectively communicate with the policy community and the public. The critical loads approach can provide a useful lens through which to assess the results of current policies and programs and to evaluate the potential ecosystem-protection value of proposed policy options.

Recent developments in the United States indicate that critical loads might be emerging as a useful ecosystem protection and program assessment tool. In 2004, the National Research Council recommended that critical loads be examined as a tool for ecosystem protection (NRC 2004). Between 2002 and 2006, several Federal agencies convened conferences and workshops to review the experience with critical loads in other countries, discuss science and modeling efforts related to critical loads, and explore the possible future role of a critical loads approach as an air pollution control policy tool in the United States. A growing number of scientists are conducting research related to critical loads and are using various approaches to estimate critical loads in the United States.

Federal and state agencies are now exploring critical loads approaches to protect and manage sensitive ecosystems on Federal lands (Burns et al. 2008, Porter et al. 2005). In 2005, the U.S. Environmental Protection Agency (EPA) included a provision in its Nitrogen Dioxide Increment Rule enabling states to propose the use of critical loads information as part of their air quality management approach, to satisfy requirements under Clean Air Act provisions regarding "prevention of significant deterioration." The National Park Service is working with the Colorado Department of Public Health and Environment and EPA to address harmful impacts to air quality and other natural resources occurring in Rocky Mountain National Park in Colorado, and to reverse a trend of increasing N deposition. The National Park Service has established a resource management goal, linked to a critical load for wet N deposition of 1.5 kg ha^{-1} yr^{-1} for high elevation aquatic ecosystems. Resource managers within the U.S. Forest Service use critical loads to serve as a practical guideline when considering the potential impacts from new sources of emissions on resources in Class I areas. Forest Service resource managers are also using critical loads in the national watershed condition assessment process to identify potential areas on national forests for mitigation of ecosystem impairment. Several states have developed Total Maximum Daily Load (TMDL) estimates for acidic deposition to alleviate surface waters that are impaired due to elevated acidity (i.e., low pH, low ANC).

The critical loads approach recently has been utilized for ecosystem assessments within the broader environmental policy context as well. In 2005, for example, the Clean Air Act Advisory Committee recommended that the EPA use critical loads as a means to evaluate progress in reducing ecological impacts of air pollution. As a result, EPA's 2007 and 2008 Annual Acid Rain Program progress reports utilized critical loads as a means of assessing the extent to which implementation of Title IV of the 1990 Clean Air Act Amendments has decreased S and N sufficiently to protect acid-sensitive ecosystems in the Adirondack Mountain and Central Appalachian regions. The critical loads approach also has entered the realm of bilateral environmental policy. In 2008, the ninth biennial progress report completed under the 1991 United States-Canada Air Quality Agreement included estimates of critical loads in acid-sensitive lakes in the northeastern United States. While the Canadian government routinely reports critical load data, this was the first time critical load data for the United States were reported in a progress report prepared by the bilateral U.S.-Canada Air Quality Committee (Environment Canada 2008).

19.12 Summary

In an analysis of the nine major environmental challenges facing humanity, only three have clearly exceeded safe operating boundaries: biodiversity loss, increased N, and climate change (Rockström et al. 2009). Because most terrestrial and many aquatic ecosystems are N limited under unpolluted conditions, increases in N input to ecosystems are likely to have an impact. Increased N deposition can cause a shift in the processing and movement of N (function) and to the physical composition (structure) of the ecosystem as evidenced by the examples below.

Large parts of the eastern United States, as well as localized areas in the West, are experiencing N deposition that exceeds the critical load for sensitive ecosystem components. The resources most threatened by elevated N deposition include freshwater diatoms, lichens, bryophytes, and herbaceous plants. The most significant changes that we are currently observing in the United States in response to elevated N deposition are changes in species composition: losses of N-sensitive species, shifts in dominance, and losses of native species in favor of exotic, invasive species. Shifts in diatom and lichen community composition away from N-intolerant (oligotrophic) species are observed across the country. Alterations in herbaceous species are broadly observed, but are not always clearly documentable because of the long-term pollution inputs and other disturbances (including land-use change) that caused changes prior to most current studies.

Numerous examples illustrate the significance of these species- and community-level effects. In serpentine grasslands in California, it was clearly demonstrated that unless N inputs are decreased or N is removed in biomass, a larval host plant and numerous nectar source plants utilized by a threatened and endangered butterfly will decrease to levels unable to sustain the butterfly population (Fenn et al. 2010, Weiss 1999). In Joshua Tree National Park and adjacent deserts in southern California, elevated N deposition favors the production of sufficient invasive grass biomass to sustain fires that threaten the survival of the namesake species (Fenn et al. 2010, Rao et al. 2010). Other sensitive ecosystems include alpine meadows, where relatively low levels of N deposition have already changed species composition in this fragile community (Bowman et al. 2006). Changes in historical diatom community composition from N-limited to N-tolerant species have been observed in lake sediment cores at many locations in the western United States, providing early evidence of eutrophication of freshwater ecosystems (Saros et al. 2010; Wolfe et al. 2001, 2003).

Changes in ecosystem structure are linked to changes in ecosystem function. For example, extirpation of lichens can alter food webs by reducing the availability of nesting material for birds, invertebrate habitat, and critical winter forage for mammals, and can also affect nutrient cycling (Cornelissen et al. 2007). In California, where elevated N deposition and arid low-biomass ecosystems coincide (e.g., coastal sage scrub, grassland, desert), N-enhanced growth of invasive species resulting in major alterations of plant communities, conversion of vegetation type, and increased fire risk, even in areas where fire is normally infrequent (Allen et al. 2009, Fenn et al. 2010, Rao et al. 2010).

There is also evidence that N deposition contributes to multiple stress complexes and has decreased forest sustainability in California (Grulke et al. 2009) and in North Carolina (McNulty and Boggs 2010). In North Carolina, elevated N deposition predisposed a pine ecosystem to a pest outbreak following a drought (McNulty and Boggs 2010). Another example of N deposition interactions with other forest stressors is the observation that increased NO_3^- leaching and nitrification contribute to soil acidification and depletion of available nutrient cations which have negative effects on tree growth, vigor, and cold tolerance in some forests. Elevated NO_3^- concentrations in surface water and groundwater may diminish drinking water quality, although the drinking water standard is often only exceeded for brief periods, for example when N saturated watersheds are disturbed (e.g., fire or harvesting). These types of complex interactions may be difficult to predict, but may intensify the impact of elevated N deposition in concert with other stressors including consequences of climate change.

Further examples of changes in ecosystem structure and function are observed in coastal areas, where increased N export has led to toxic algal blooms (Rabalais 2002). As an example of N deposition effects on trace gas chemistry and climate change, N loading to ecosystems results in increased emissions of N trace gases, such as nitric oxide (NO), an ozone (O_3) precursor; nitrous oxide (N_2O), a long-lived greenhouse gas; as well as declines in soil uptake of methane (CH_4), another long-lived greenhouse gas (Liu and Greaver 2009).

The above examples provide compelling evidence for significant alteration of ecosystem structure and function in ecoregions across the United States due to elevated N deposition. To protect ecosystems from harm caused by N deposition, it is necessary to identify the level of N deposition which would lead to detrimental ecological effects. Empirical critical loads for N provide a valuable approach for evaluating the risk of harm to ecosystems. This approach has been used broadly in Europe (Bobbink et al. 2003, UBA 2004) and has the advantage of being scientifically based on observed responses. This link to actual ecosystem responses is especially beneficial in resource management and policy contexts.

This report provides the first comprehensive assessment of empirical critical loads of N for ecoregions across the United States. It represents an important step toward providing policy makers and resource managers with a tool for ecosystem protection as suggested by the National Research Council (NRC 2004).

19.13 Future Research Priorities

The principal knowledge gaps that limit our understanding of N impacts on ecosystems include poor quantification of total N deposition (especially in deposition hotspots) and the paucity of long-term, low N-fertilization studies and adequate deposition gradient studies. A higher density of long-term, low N fertilization studies, as well as long-term and larger scale gradient studies across both a greater diversity of ecosystem types and regions of low N deposition, are necessary to develop dose response curves that would better define critical loads and the associated uncertainty. In the United States, observations of ecosystem response to N inputs are particularly limited in the Tundra, Taiga, and North American Desert ecoregions.

Other important issues include:

- The differential response to reduced (NH_x) versus oxidized (NO_y) N inputs. Because some plants are particularly sensitive to NH_x inputs (Krupa 2003) while others are more sensitive to NO_y (Nordin et al. 2006), assembling more comprehensive data about these species-specific responses would allow more accurate assessment of potential risks to ecosystems in relation to the major N emissions sources. Oxidized and reduced N forms also result in different levels of acidification.
- Impacts on plant biodiversity in forests have not been well described, in part because of the difficulty of assessing such changes in ecosystems with longer-lived organisms, and in part, because in many of these ecosystems the herbaceous plants have already been altered by historical N deposition, other pollutants, or habitat alteration.
- Effects of N deposition on forest growth and sustainability. Insufficient data are available to determine critical loads for the effects of increasing N fertility on pest outbreaks, drought, cold tolerance, tree vigor, and multiple stress complexes in general.
- Identification of mechanisms that control plant and ecosystem responses to N deposition. This is a necessary step in refining critical loads estimates, improving their reliability, and laying the groundwork for more complex dynamic models, which are necessary for broad scale assessments, including detailed national maps of empirical critical loads for N.

The objective of future critical-loads-driven research should be to fill in gaps in data and improve the

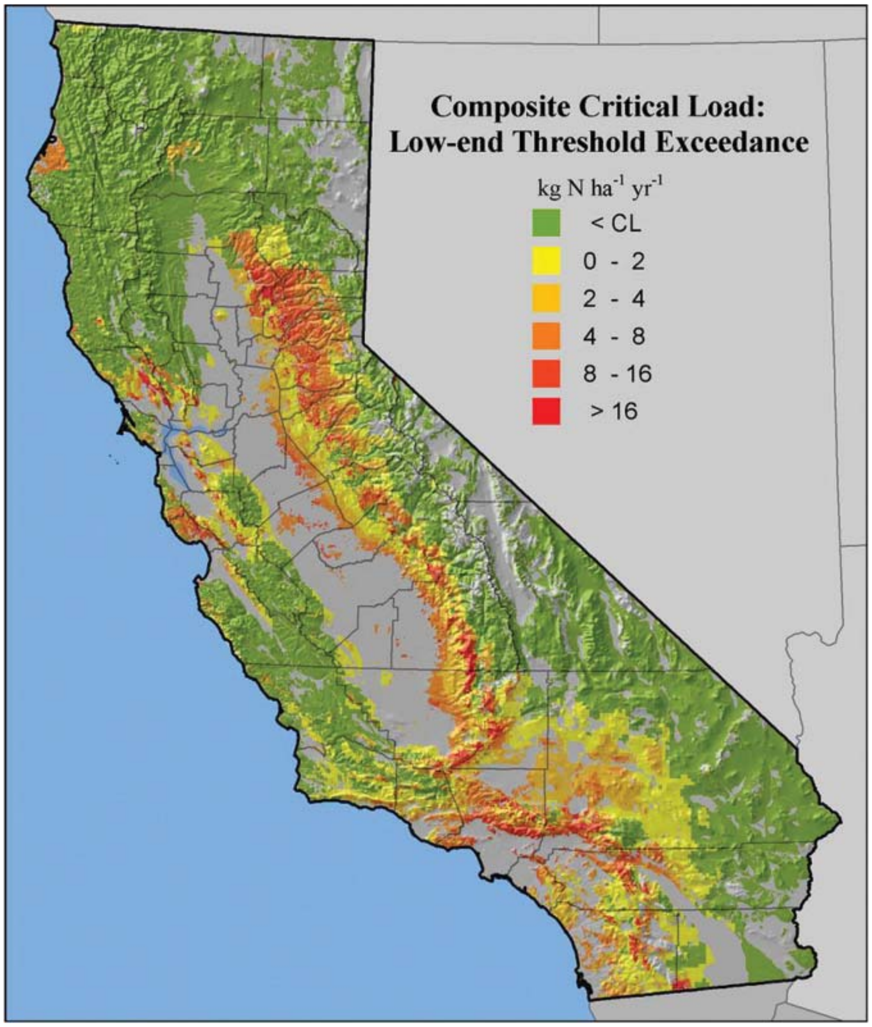

Figure 19.11—Composite showing critical load exceedance for seven vegetation types in California (Fenn et al. 2010).

reliability of estimates. When more data are available, especially data of higher reliability, it will be possible to make a map of empirical critical loads of N such as that developed for California (Figure 19.11; Fenn et al. 2010). This map also utilized N deposition modeled at a much finer grid (4 km x 4 km). One approach for assembling the data necessary to estimate critical loads is using systematically sampled large scale studies (for example the U.S. Forest Service FIA grid sampling) to ensure that a broad gradient in N deposition, climate, and other variables are included in the dataset generated (e.g., Geiser and Neitlich 2007, Jovan 2008). This approach would allow extrapolation of the N critical loads to a broad area with confidence. Better understanding of when the "baseline" response has been altered by prior N deposition is necessary to identify empirical critical loads using N deposition gradient or N addition studies. Long-term monitoring is also necessary to evaluate the scope of particular responses and to assess future responses to reductions in N deposition. The accuracy of empirical N critical loads is limited by the accuracy of the N deposition values used. Thus, improving estimates of total N deposition is essential for improving empirical critical loads and exceedance estimates.

Thus, the highest research priorities should be:

(1) Lichens: systematic sampling of lichens in areas where there are few data in combination with analyzing existing FIA data could yield very useful results for this sensitive indicator.
(2) Diatoms in lake sediments and phytoplankton in lakes: diatoms preserved in lake sediments can be used to identify when and at what atmospheric N deposition amounts critical

thresholds were crossed in the past. The approach has applications far beyond the few locations where it has been applied. Phytoplankton in lakes respond rapidly to changes in limiting nutrients, and far more studies are needed to show how (and how much) N deposition is needed to affect the N:P stoichiometric ratio and subsequent shifts in food webs and ecological processes in oligotrophic lakes. Equally important are studies of whether the removal of N deposition allows the return of N-limited conditions and oligotrophic phytoplankton. A final and key research priority for lakes are experiments to determine the effects of atmospheric N deposition on algal biodiversity.

(3) Herbaceous species: research is needed to identify the most responsive species across a variety of ecosystem types.

(4) Identifying indicator species in general: species which allow evaluation of the ecosystem condition are especially useful for empirical N critical loads estimates.

(5) Long-term low N addition experiments: more long-term low N fertilization studies will help make more accurate determinations of critical loads.

LITERATURE CITED

Aber, J.; McDowell, W.; Nadelhoffer, K.; Magill, A.; Berntson, G.; Kamakea, M.; McNulty, S.; Currie, W.; Rustad, L.; Fernandez, I. 1998. **Nitrogen saturation in temperate forest ecosystems.** BioScience. 48: 921-934.

Aber, J.D.; Goodale, C.L.; Ollinger, S.V.; Smith, M.-L.; Magill, A.H.; Martin, M.E.; Hallet, R.A.; Stoddard, J.L. 2003. **Is nitrogen deposition altering the nitrogen status of Northeastern forests?** BioScience. 53(4): 375-389.

Aber, J.D.; Nadelhoffer, K.J.; Steudler, P.; Melillo, J.M. 1989. **Nitrogen saturation in northern forest ecosystems.** BioScience. 39: 378-386.

Adams, M.B.; DeWalle, D.R.; Peterjohn, W.T.; Gilliam, F.S.; Sharpe, W.E.; Williard, K.W.J. 2006. **Soil chemical responses to experimental acidification treatments.** In: Adams, M.B.; DeWalle, D.R.; Hom, J.L., eds. The Fernow watershed acidification study. Dordrecht, The Netherlands: Springer: 41-69.

Aldous, A.R. 2002. **Nitrogen retention by *Sphagnum* mosses: responses to atmospheric nitrogen deposition and drought.** Canadian Journal of Botany. 80: 721-731.

Allen, E.B.; Rao, L.E.; Steers, R.J.; Bytnerowicz, A.; Fenn, M.E. 2009. **Impacts of atmospheric nitrogen deposition on vegetation and soils in Joshua Tree National Park.** In: Webb, R.H.; Fenstermaker, L.F.; Heaton, J.S.; Hughson, D.L.; McDonald, E.V.; Miller, D.M., eds. The Mojave Desert: Ecosystem processes and sustainability. Las Vegas: University of Nevada Press: 78-100

Allen, E.B.; Temple, P.J.; Bytnerowicz, A.; Arbaugh, M.J.; Sirulnik, A.G.; Rao, L.E. 2007. **Patterns of understory diversity in mixed coniferous forests of southern California impacted by air pollution.** The Scientific World Journal. 7(S1): 247-263.

Amaranthus, M.P. 1998. **The importance and conservation of ectomycorrhizal fungal diversity in forest ecosystems: Lessons from Europe and the Pacific Northwest.** Gen. Tech. Rep. PNW-431. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 15 p.

Arens, S.J.T.; Sullivan, P.F.; Welker, J.M. 2008. **Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a high arctic ecosystem.** Journal of Geophysical Research-Biogeosciences 113: G03509.

Baker, J.P.; Van Sickle, J.; Gagen, C.J.; Baldigo, B.P.; Bath, D.W.; Carline, R.F.; DeWalle, D.R.; Kretser, W.A.; Murdoch, P.S.; Sharpe, W.E.; Simonin, H.A.; Wigington, P.J. 1996. **Episodic acidification of small streams in the northeastern United States: Effects on fish populations.** Ecological Applications. 6: 422-437.

Baron, J.S. 2006. **Hindcasting nitrogen deposition to determine ecological critical load.** Ecological Applications. 16(2): 433-439.

Baron, J.S.; Ojima, D.S.; Holland, E.A.; Parton, W.J. 1994. **Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: Implications for aquatic systems.** Biogeochemistry. 27: 61-82.

Baron, J.S.; Rueth, H.M.; Wolfe, A.M.; Nydick, K.R.; Allstott, E.J.; Minear, J.T.; Moraska, B. 2000. **Ecosystem responses to nitrogen deposition in the Colorado Front Range.** Ecosystems. 3: 352-368.

Barret, J.E.; Burke, I.C. 2002. **Nitrogen retention in semiarid ecosystems across a soil organic-matter gradient.** Ecological Applications. 12: 878-890.

Belyazid S.; Westling, O.; Sverdrup, H. 2006. **Modelling changes in forest soil chemistry at 16 Swedish coniferous forest sites following deposition reduction.** Environmental Pollution. 144: 596-609.

Berryman, S.; Straker, J. 2008. **Nitrogen loading and terrestrial vegetation—assessment of existing regional monitoring and recommendations.** Sidney, BC: Submitted by CE Jones and Associates.

Berryman, S.; Geiser, L.; Brenner, G. 2004. **Depositional gradients of atmospheric pollutants in the Athabasca Oil Sands region, Alberta, Canada: an analysis of lichen tissue and lichen communities.** Lichen Indicator Pilot Program 2002-2003. Final report submitted to the Terrestrial Environmental Effects Monitoring (TEEM) Science sub-committee of the Wood Buffalo Environmental Association (WBEA). Fort McMurray, AB, Canada: Wood Buffalo Environmental Association.

Blett, T.; Geiser, L.; Porter, E. 2003. **Air pollution-related lichen monitoring in national parks, forests, and refuges: guidelines for studies intended for regulatory and management purposes.** Tech. Rep. NPS-D2292. Denver, CO: U.S. Department of the Interior, National Park Service, Air Resources Division and U.S. Fish and Wildlife Service, Air Quality Branch; Corvallis, Oregon: U.S. Department of Agriculture, Forest Service. 26 p.

Bobbink, R.; Ashmore, M.; Braun, S.; Flückinger, W.; van den Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R., eds. Empirical critical loads for nitrogen. Environmental Documentation No. 164. Berne, Switzerland: Swiss Agency for the Environment, Forests, and Landscape: 43-170.

Bobbink R.; Boxman D.; Fremstad E.; Heil G.; Houdijk A.; Roelofs J. 1992. **Critical loads for nitrogen eutrophication of terrestrial and wetland ecosystems based upon changes in vegetation and fauna.** In: Grennfelt, P.; Thörnelöf, E., eds. Critical loads for nitrogen. Copenhagen: Nordic Council of Ministers: 111-159.

Bobbink, R.; Hicks, K.; Galloway, J.N.; Spranger, T.; Alkemade, R.; Ashmore, M.; Bustamante, M.M.C.; Cinderby, S.; Davidson, E.A.; Dentener, F.; Emmett, B.; Erisman, J.-W.; Fenn, M.; Gilliam, F.; Nordin, A.; Pardo, L.; de Vries, W. 2010. **Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis.** Ecological Applications. 20(1): 30-59.

Bobbink, R.; Hornung, M.; Roelofs, J.G.M. 1998. **The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation.** Journal of Ecology. 86: 738.

Boggs, J.L.; McNulty, S.G.; Gavazzi, M.J.; Moore, J. 2005. **Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forests.** Canadian Journal of Forest Research. 35: 1901-1913.

Boonpragob, K.; Nash, T.H. III; Fox, C.A. 1989. **Seasonal deposition patterns of acidic ions and ammonium to the lichen *Ramalina menziesii* Tayl. in southern California.** Environmental and Experimental Botany. 29: 187-197.

Bowman, W.D.; Larson, J.R.; Holland, K.; Wiedermann, M.; Nieves, J. 2006. **Nitrogen critical loads for alpine vegetations and ecosystem response- are we there yet?** Ecological Applications. 16(3): 1183-1193.

Breiner, J.; Gimeno, B.S.; Fenn, M. 2007. **Calculation of theoretical and empirical nutrient N critical loads in the mixed-conifer ecosystems of southern California.** The Scientific World Journal. 7(S1): 198-205.

Burns, D.A.; Blett, T.; Haeuber, R.; Pardo, L.H. 2008. **Critical loads as a policy tool for protecting ecosystems from the effects of air pollutants.** Frontiers in Ecology and the Environment. 6: 156-159.

Byun, D.W.; Ching, J.K.S., eds. 1999. **Science algorithms of the EPA models-3 Community Multiscale Air Quality model (CMAQ) modeling system. EPA/600/R-99/030.** Washington, DC: U.S. Environmental Protection Agency, Office of Research and Development. Available at http://www.epa.gov/asmdnerl/CMAQ/CMAQscienceDoc.html (Accessed May 12, 2010).

Byun, D.; Schere, K.L. 2006. **Review of the governing equations, computational algorithms, and other components of the Models-3 Community Multiscale Air Quality (CMAQ) modeling system.** Applied Mechanics Reviews. 59: 51-77.

Caffrey, J.M.; Murrell, M.C.; Wigand, C.; McKinney, R. 2007. **Effect of nutrient loading on biogeochemical and microbial processes in a New England salt marsh.** Biogeochemistry. 82: 251-264.

Cape, J.N.; van der Eerden, L.J.; Sheppard, L.J.; Leith, I.D; Sutton, M.A. 2009. **Reassessment of critical levels for atmospheric ammonia.** In: Sutton M.; Reis, S.; Baker; S.M.H., eds. Atmospheric ammonia. Dordrecht, The Netherlands: Springer Science: 15-40.

Clark, C.M.; Hobbie, S.; Venterea, R.; Tilman, D. 2009. **Long-lasting effects on N cycling 12 years after treatments cease despite minimal N retention.** Global Change Biology. 15: 1755-1766.

Clark, C.M.; Tilman, D. 2008. **Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands.** Nature. 451: 712-715.

Clark, J.E.; Hellgren, E.C.; Jorgensen, E.E.; Leslie, D.M. 2005. **Population dynamics of harvest mice (*Reithrodontomys fulvescens* and *R. montanus*) across a nitrogen-amended old field.** American Midland Naturalist. 154: 240-252.

Clark, J.E.; Hellgren, E.C.; Jorgensen, E.E.; Tunnell, S.J.; Engle, D.M.; Leslie, D.M. 2003. **Population dynamics of hispid cotton rats (*Sigmodon hispidus*) across a nitrogen-amended landscape.** Canadian Journal of Zoology-Revue Canadienne De Zoologie. 81: 994-1003.

CEC (Commission for Environmental Cooperation). 1997. **Ecological regions of North America. Toward a common perspective.** Montreal, QC, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

Cornelissen, J.H.C.; Lang, S.I.; Soudzilovskaia, N.A.; During, H.J. 2007. **Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry.** Annals of Botany. 99: 987-1001.

de Vries, W.; Kros, J.; Reinds, G.J.; Wamelink, W.; van Dobben, H.; Bobbink, R.; Emmett, B.; Smart, S.; Evans, C.; Schlutow, A.; Kraft, P.; Belyazid, S.; Sverdrup, H.; Hinsberg, A. van; Posch, M.; Hettelingh, J.P. 2007. **Developments in deriving critical limits and modeling critical loads of**

nitrogen for terrestrial ecosystems in Europe. Alterra Report 1382 [Alterra-rapport 1382]. Wageningen, The Netherlands: Wageningen University, Alterra. 206 p.

de Vries, W.; Wamelink, W.; van Dobben, H.; Kros, H.; Reinds, G.J.; Mol-Dijkstra, J.; Smart, S.; Evans, C.; Rowe, E.; Belyazid, S.; Sverdrup, H.; van Hinsberg, A.; Posch, M.; Hettelingh, J.-P.; Spranger, T.; Bobbink, R. 2010. **Use of dynamic soil-vegetation models to assess impacts of nitrogen deposition on plant species composition: an overview.** Ecological Applications. 20 (1): 60-79.

Dighton, J.; Tuininga, A.R.; Gray, D.M.; Huskins, R.E.; Belton, T. 2004. **Impacts of atmospheric deposition on New Jersey pine barrens forest soils and communities of ectomycorrhizae.** Forest Ecology and Management. 201: 131-144.

Driscoll, C.T; Whitall, D.; Aber, J.; Boyer, E.; Castro, M.; Cronan, C.; Goodale, C.L.; Groffman, P.; Hopkinson, C.; Lambert, K.; Lawrence, G.; Ollinger, S. 2003. **Nitrogen pollution in the northeastern United States: sources, effects, and management options.** BioScience. 53: 357-374.

Duan, L. 2009. **Empirical critical loads of nitrogen in China.** In: Proceedings from a workshop on nitrogen deposition, critical loads, and biodiversity; 2009 November 16-18; Edinburgh, Scotland. Available at http://www.rivm.nl/thema/images/Poster_lei_duan_icpmm_2010_tcm61-48704.pdf [Poster] (Accessed April 21, 2011).

Dupont, J.; Clair, T.A.; Gagnon, C.; Jeffries, D.S.; Kahl, J.S.; Nelson, S.; Peckenham, J. 2005. **Estimation of critical loads of acidity for lakes in northeastern United States and eastern Canada.** Environmental Monitoring Assessment. 109: 275-292.

Egerton-Warburton, L.M.; Allen, E.B. 2000. **Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient.** Ecological Applications. 10: 484-496.

Egerton-Warburton, L.M.; Graham, R.C.; Allen, E.B.; Allen, M.F. 2001. **Reconstruction of the historical changes in mycorrhizal fungal communities under anthropogenic nitrogen deposition.** Proceedings of the Royal Society of London. B268: 2479-2484.

Elser, J.J.; Anderson, T.; Baron, J.S.; Bergström, A-K; Kyle, M.; Nydick, K.R.; Steger, L.; Hessen, D.O. 2009. **Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition.** Science. 326: 835-837.

Emmett, B.A.; Reynolds, B. 2003. **The role of models in addressing critical N loading to ecosystems.** In: Canham, C.D.; Cole, J.J.; Lauenroth, W.K., eds. Models in ecosystem science. Princeton, NJ: Princeton University Press: 308-326

Environment Canada. 2008. **Canada-United States air quality agreement progress report 2008.** Ottawa, ON, Canada, and Washington, DC: International Joint Commission. Available at http://www.ec.gc.ca/cleanair-airpur/caol/canus/report/2008CanUs /eng/tdm-toc_eng.cfm (Accessed June 6, 2009).

Epstein, H.E.; Burke, I.C.; Mosier, A.R. 2001. **Plant effects on nitrogen retention in shortgrass steppe 2 years after ^{15}N addition.** Oecologia. 128: 422-430.

Falkengren-Grerup, U. 1995. **Interspecies differences in the preference of ammonium and nitrate in vascular plants.** Oecologia. 102: 305-311.

Fenn, M.E.; Allen, E.B.; Weiss, S.B.; Jovan, S.; Geiser, L.; Tonnesen, G.S.; Johnson, R.F.; Rao, L.E.; Gimeno, B.S.; Yuan, F.; Meixner, T.; Bytnerowicz, A. 2010. **Nitrogen critical loads and management alternatives for N-impacted ecosystems in California.** Journal of Environmental Management. 91(12): 2404-2423.

Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W.; Neitlich, P. 2003a. **Ecological effects of nitrogen deposition in the western United States.** BioScience. 53(4): 404-420.

Fenn, M.E.; de Bauer, L.I.; Quevedo-Nolasco, A.; Rodriguez-Frausto, C. 1999. **Nitrogen and sulfur deposition and forest nutrient status in the Valley of Mexico.** Water, Air, and Soil Pollution. 113: 155-174.

Fenn, M.E.; de Bauer, L.I.; Zeller, K.; Quevedo, A.; Rodríguez, C. and Hernández-Tejeda, T. 2002. **Nitrogen and sulfur deposition in the Mexico City air basin: Impacts on forest nutrient status and nitrate levels in drainage waters.** In: Fenn, M.E.; de Bauer, L.I.; Hernández-Tejeda, T., eds. Urban air pollution and forests: Resources at Risk in the Mexico City air basin. Ecological Studies Series, Volume 156. New York, NY: Springer-Verlag: 298-319.

Fenn, M.E.; Haueber, R.; Tonnensen, G.S.; Baron, J.S.; Grossman-Clarke, S.; Hope, D.; Jaffe, D.A.; Copeland, S.; Geiser, L.; Rueth, H.M.; Sickman, J.O. 2003b. **Nitrogen emission, deposition, and monitoring in the Western United States. Bioscience.** 53(4): 391-403.

Fenn, M.E.; Jovan, S.; Yuan, F.; Geiser, L.; Meixner, T.; Gimeno, B.S. 2008. **Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests.** Environmental Pollution. 155: 492-511.

Fenn, M.E.; Poth, M.A. 1999. **Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California.** Journal of Environmental Quality. 28: 822-836.

Fenn, M.E.; Poth, M.A.; Bytnerowicz, A.; Sickman, J.O.; Takemoto, B.K. 2003c**. Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada.** In: Bytnerowicz, A.; Arbaugh, M.J.; Alonso, R., eds. Developments in environmental science, volume 2: Ozone air pollution in the Sierra Nevada: Distribution and effects on forests. Amsterdam: Elsevier: 111-155.

FWS (U.S. Fish and Wildlife Service). 2005. **Status and trends of wetlands in the conterminous United States 1998 to 2004.** Washington, DC: U.S. Department of Interior, Fish and Wildlife Service. 112 p.

Galloway, J.N. 1998. **The global nitrogen cycle: changes and consequences.** Environmental Pollution. 102: 15-24.

Galloway, J.N.; Aber, J.D.; Erisman, J.W.; Seitzinger, S.P.; Howarth, R.W.; Cowling, E.B.; Cosby, B.J. 2003. **The nitrogen cascade.** BioScience. 53: 341-356.

Geiser, L.H.; Ingersoll, A.R.; Bytnerowicz, A.; Copeland, S.A. 2008. **Evidence of enhanced atmospheric ammoniacal nitrogen in Hells Canyon NRA: Implications for natural and cultural resources.** Journal of the Air & Waste Management Association. 58: 1223-1234.

Geiser, L.H.; Jovan, S.E.; Glavich, D.A.; Porter, M. 2010. **Lichen-/based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA.** Environmental Pollution. 158: 2412-2421.

Geiser, L.H.; Neitlich, P.N. 2007. **Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens.** Environmental Pollution. 145: 203-218.

Gilliam, F.S. 2006. **Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition.** Journal of Ecology. 94: 1176-1191.

Gilliam, F.S. 2007. **The ecological significance of the herbaceous layer in forest ecosystems.** BioScience. 57: 845-858.

Gilliam, F.S.; Adams, M.B.; Yurish, B.M. 1996. **Ecosystem nutrient responses to chronic nitrogen inputs at Fernow Experimental Forest, West Virginia.** Canadian Journal of Forest Research. 26: 196-205.

Gilliam, F.S.; Hockenberry, A.W.; Adams, M.B. 2006. **Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest.** Journal of the Torrey Botanical Society. 133: 240-254.

Glavich, D.A.; Geiser, L.H. 2008. **Potential approaches to developing lichen-based critical loads and levels for nitrogen, sulfur and metal-containing atmospheric pollutants in North America.** The Bryologist. 111: 638-649.

Gotelli, N.J.; Ellison, A.M. 2002. **Nitrogen deposition and extinction risk in the northern pitcher plant, *Sarracenia purpurea*.** Ecology. 83: 2758-2765.

Gotelli, N.J.; Ellison, A.M. 2006. **Forecasting extinction risk with nonstationary matrix models.** Ecological Applications. 16: 51-61.

Grulke, N.E.; Andersen, C.P.; Fenn, M.E.; and Miller, P.R. 1998. **Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California.** Environmental Pollution. 103: 63-73.

Grulke, N.E.; Balduman, L. 1999. **Deciduous conifers: High N deposition and O_3 exposure effects on growth and biomass allocation in ponderosa pine.** Water, Air and Soil Pollution. 116: 235-248.

Grulke, N.E.; Minnich, R.A.; Paine, T.D.; Seybold, S.J.; Chavez, D.J.; Fenn, M.E.; Riggan, P.J.; Dunn, A. 2009. **Air pollution increases forest susceptibility to wildfires: A case study in the San Bernardino Mountains in southern California.** In: Bytnerowicz, A.; Arbaugh, M.J.; Riebau, A.R.; Andersen, C., eds. Wildland fires and air pollution. Developments in environmental science, Volume 8. Amsterdam: Elsevier: 365-403.

Hettelingh, J.-P.; Posch, M.; Slootweg, J., eds. 2008. **Critical load, dynamic modelling and impact assessment in Europe. CCE Status Report 2008.** Bilthoven, The Netherlands: Netherlands Environmental Agency, Coordination Centre for Effects. Netherlands Environmental Assessment Agency. 231 p. Available at www.rivm.nl/cce (Accessed March 30, 2011).

Hurd, T.M.; Brach, A.R.; Raynal, D.J. 1998. **Response of understory vegetation of Adirondack forests to nitrogen additions.** Canadian Journal of Forest Research. 28: 799-807.

Hyvärinen, M.; Walter, B.; Koopmann, R. 2003. **Impact of fertilisation on phenol content and growth rate of *Cladina stellaris*: a test of the carbon-nutrient balance hypothesis.** Oecologia. 134: 176-181.

Inouye, R.S. 2006. **Effects of shrub removal and nitrogen addition on soil moisture in sagebrush steppe.** Journal of Arid Environments. 65: 604-618.

Jones, M.E.; Paine, T.D.; Fenn, M.E.; Poth, M.A. 2004. **Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions.** Forest Ecology and Management. 200: 67-76.

Jorgensen, E.E.; Holub, S.M.; Mayer, P.M.; Gonsoulin, M.E.; Silva, R.G.; West, A.E.; Tunnell, S.J.; Clark, J.E.; Parsons, J.L.; Engle, D.M.; Hellgren, E.C.; Spears, J.D.H.; Bulter, C.E.; Leslie, D.M. Jr. 2005. **Ecosystem stress from chronic exposure to low levels of nitrate.** EPA/600/R-05/087. Cincinnati, OH: U.S. Environmental Protection Agency, National Risk Management Research Laboratory. 35 p.

Jovan, S. 2008. **Lichen bioindication of biodiversity, air quality, and climate: baseline results from monitoring in Washington, Oregon, and California.** Gen. Tech. Rep. PNW-GTR-737. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 56 p.

Jovan, S.; McCune, B. 2005. **Air quality bioindication in the greater Central Valley of California with epiphytic macrolichen communities.** Ecological Applications. 15(5): 1712-1726.

Kelly, V.R.; Lovett, G.M., Weathers, K.C.; G.E. Likens. 2005. **Trends in atmospheric ammonium concentrations in relation to atmospheric sulfate and local agriculture.** Environmental Pollution. 135: 363-369.

Kleijn, D.; Bekker, R.M.; Bobbink, R.; de Graaf, M.C.C.; Roelofs, J.G.M. 2008. **In search for key biogeochemical factors affecting plant species persistence in heathlands and acidic grasslands: a comparison of common and rare species.** Journal of Applied Ecology. 45: 680-687.

Knops, J.M.H; Nash, T.H. III; Boucher, V.L.; Schlesinger, W.L. 1991. **Mineral cycling and epiphytic lichens: implications at the ecosystem level.** Lichenologist. 23: 309-321.

Krupa, S.V. 2003. **Effects of atmospheric ammonia (NH3) on terrestrial vegetation: a review.** Environmental Pollution. 124: 179-221.

Kytöviita, M.-M.; Crittenden, P.D. 2007. **Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*.** Annals of Botany. 100: 1537-1545.

Lafrancois, B.M.; Nydick, K.R.; Johnson, B.M.; Baron, J.S. 2004. **Cumulative effects of nutrients and pH on the plankton of two mountain lakes.** Canadian Journal of Fisheries and Aquatic Science. 61: 1153-1165.

Latimer J.S.; Rego, S.A. 2010. **Empirical relationship between eelgrass extent and predicted watershed-derived nitrogen loading for shallow New England estuaries.** Estuarine, Coastal and Shelf Science. 90: 231-240.

LeBauer, D.S.; Treseder, K.K. 2008. **Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed.** Ecology. 89(2): 371-379.

Lehmann, C.M.B.; Bowersox, V.C.; Larson, S.M. 2005. **Spatial and temporal trends of precipitation chemistry in the United States, 1985-2002.** Environmental Pollution. 135: 347-361.

Lilleskov, E.A. 1999. **Decline of above- and belowground ectomycorrhizal fungal diversity over an atmospheric nitrogen deposition gradient near Kenai, Alaska.** Ithaca, NY: Cornell University. 198 p. Ph.D. dissertation.

Lilleskov, E.A. 2005. **How do composition, structure, and function of mycorrhizal fungal communities respond to nitrogen deposition and ozone exposure?** In: Dighton, J.; White, J.F.; Oudemans, P., eds. The fungal community: its organization and role in the ecosystem. Boca Raton, FL: Taylor and Francis: 769-801.

Lilleskov, E.A.; Fahey, T.J.; Horton, T.R.; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** Ecology. 83: 104-115.

Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient.** Ecological Applications. 11: 397-410.

Lilleskov, E.A.; Wargo, P.M.; Vogt, K.A.; Vogt, D.J. 2008. **Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern US.** Canadian Journal of Forest Research. 38: 1260-1266.

Liu, L.; Greaver, T.L. 2009. **A review of nitrogen enrichment effects on three biogenic GHGs: The CO_2 sink may be largely offset by stimulated N_2O and CH_4 emission.** Ecology Letters. 12: 1103-1117.

Lovett, G.M.; Tear, T.H. 2008. **Threats from above: Air pollution impacts on ecosystems and biological diversity in the eastern United States.** The Nature Conservancy and the Cary Institute of Ecosystem Studies. www.nature.org/wherewework/northamerica/states/maryland (Accessed May 12, 2010).

Lovett, G.M.; Tear, T.; Evers, D.; Findlay, S.E.G.; Cosby, B.J.; Dunscomb, J.; Driscoll, C.; K.C. Weathers. 2009. **Effects of air pollution on ecosystems and biological diversity in the eastern United States.** Annals of the New York Academy of Sciences. 1162: 99-135.

Makkonen, S.; Hurri, R.S.K.; Hyvarinen, M. 2007. **Differential responses of lichen symbionts to enhanced nitrogen and phosphorus availability: An experiment with *Cladina stellaris*.** Annals of Botany. 99: 877-884.

Maser, Z.; Maser, C.; Trappe, J.M. 1985. **Food habits of the northern flying squirrel (*Glacomys sabrinus*) in Oregon.** Canadian Journal of Zoology. 63: 1084-1088.

McCune, B.; Grenon, J.; Mutch, L.S.; Martin, E.P. 2007. **Lichens in relation to management issues in the Sierra Nevada national parks.** Pacific Northwest Fungi. 2: 1-39.

McCune, B.M.; Geiser, L.H. 2009. **Macrolichens of the Pacific Northwest. 2nd Edition.** Corvallis, OR: Oregon State University Press. 400 p.

McKane, R.B; Johnson, L.C.; Shaver, G.R.; Nadelhoffer, K.J.; Rastetter, E.B.; Fry, B.; Giblin, A.E.; Kiellandk, K.; Kwiatkowski, B.L.; Laundre, J.A.; Murray, G. 2002. **Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra.** Nature. 415(6867): 68-71.

McNulty, S.G.; Boggs, J.L. 2010. **A conceptual framework: redefining forest soil's critical acid loads under a changing climate.** Environmental Pollution. 158: 2053-2058.

McNulty, S.G.; Boggs, J.; Aber, J.D.; Rustad, L.; Magill, A. 2005. **Red spruce ecosystem level changes following 14 years of chronic N fertilization.** Forest Ecology and Management. 219: 279-291.

McNulty, S.G.; Cohen, E.C.; Myers, J.A.M.; Sullivan, T.J.; Li, H. 2007. **Estimates of critical acid loads and exceedances for forest soils across the conterminous United States.** Environmental Pollution 149: 281-292.

Meixner, T.; Fenn, M. 2004. **Biogeochemical budgets in a Mediterranean catchment with high rates of atmospheric N deposition—importance of scale and temporal asynchrony.** Biogeochemistry. 70: 331-356.

Michel, T.J.; Saros, J.E.; Interlandi, S.J.; Wolfe, A.P. 2006. **Resource requirements of four freshwater diatom taxa determined by in situ growth bioassays using natural populations from alpine lakes.** Hydrobiologia. 568: 235-243.

Miller, A.E.; Bowman, W.D. 2002. **Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition nitrogen form?** Oecologia. 130: 609-616

Mitchell, R.J.; Truscot, A.M.; Leith, I.D.; Cape, J.N.; van Dijk, N.; Tang, Y.S.; Fowler, D.; Sutton, M.A. 2005. **A study of epiphytic communities of Atlantic oak woods along an atmospheric nitrogen deposition gradient.** Journal of Ecology. 93: 482-492.

Moore, T.; Blodau, C.; Turunen, J.; Roulet, N.; Richard, P.J.H. 2004. **Patterns of nitrogen and sulfur accumulation and retention in ombrotrophic bogs, eastern Canada.** Global Change Biology. 11 (2): 256-367.

NADP (National Atmospheric Deposition Program). 2009. **Atmospheric integrated research monitoring network.** Available at http://nadp.sws.uiuc.edu/airmon/ (Accessed May 17, 2010).

NEG/ECP (New England Governors and Eastern Canadian Premiers) Forest Mapping Group. 2003. **Assessment of forest sensitivity to nitrogen and sulfur deposition in New England and Eastern**

Canada - pilot phase report. Boston: Conference of the New England Governors and Eastern Canadian Premiers.16 p. Available at http://www.ecosystems-research.com/fmi/reports.htm (Accessed May 24, 2010).

NRC (National Research Council). 2004. **Air quality management in the United States.** Washington, D.C.: National Academy of Sciences Press. 462 p. Available at http://www.nap.edu/openbook.php?isbn=0309089328 (Accessed May 12, 2010).

NRCS (National Resources Conservation Service). 2009. **PLANTS database.** Baton Rouge, LA: U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Center. Available at http://plants.usda.gov (Accessed May 12, 2010).

Nilles, M.A.; Conley, B.E. 2001. **Changes in the chemistry of precipitation in the United States, 1981-1998.** Water, Air and Soil Pollution. 130: 409-414.

Nordin, A.; Strengbom, J.; Ericson, L. 2006. **Responses to ammonium and nitrate additions by boreal plants and their natural enemies.** Environmental Pollution. 141: 167-174.

Nordin, A.; Strengbom, J.; Witzell, J.; Näsholm, T.; Ericson, L. 2005. **Nitrogen deposition and the biodiversity of boreal forests: Implications for the nitrogen critical load.** Ambio. 34: 20-24.

Nydick, K.R.; Lafrancois, B.M.; Baron, J.S.; Johnson, B.M. 2004. **Nitrogen regulation of algal biomass, productivity, and composition in shallow mountain lakes, Snowy Range, Wyoming, USA.** Canadian Journal of Fisheries and Aquatic Science. 61: 1256-1268.

Ollinger, S.V.; Aber, J.D.; Lovett, G.M.; Milham, S.E.; Lathrop, R.G. 1993. **A spatial model of atmospheric deposition for the northeastern US. Ecological Applications.** 3: 459-472.

Ouimet, R.; Arp, P.A.; Watmough, S.A.; Aherne, J.; Demerchant, I. 2006. **Determination and mapping critical loads of acidity and exceedances for upland forest soils in eastern Canada.** Water, Air and Soil Pollution. 172: 57-66.

Pardo, L.H. 2010. **Approaches for estimating critical loads of N and S deposition for forest ecosystems on U.S. Federal lands.** Gen. Tech. Rep. NRS-71. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 25 p.

Poikolainen, J.; Lippo, H.; Hongisto, M.; Kubin, E.; Mikkola, K.; Lindgren, M. 1998. **On the abundance of epiphytic green algae in relation to the nitrogen concentrations of biomonitors and nitrogen deposition in Finland.** Environmental Pollution. 102: 85-92.

Porter, E.; Blett, T.; Potter, D.; Huber, C. 2005. **Protecting resources on federal lands: Implications of critical loads for atmospheric deposition of nitrogen and sulfur.** BioScience. 55: 603-612.

Porter, M.K. 2007. **Regional modeling of nitrogen, sulfur and mercury atmospheric deposition in the Pacific Northwest.** Pullman, WA: Washington State University. 127 p. M.S. thesis.

Posch, M.; de Smet, P.A.M.; Hettelingh, J.-P.; Downing, R.J., eds. 1995. **Calculation and mapping of critical thresholds in Europe.** Status Report 1995. RIVM Rep. No. 259101004. Bilthoven, Netherlands: National Institute for Public Health and the Environment, Coordination Center for Effects. Available at http://www.mnp.nl/cce/publ/ (Accessed May 12, 2010).

Posch, M.; de Smet, P.A.M.; Hettelingh, J.-P.; Downing, R.J., eds. 2001. **Modelling and mapping of critical thresholds in Europe.** Status report 2001. RIVM Rep. No. 2591010xx. Bilthoven, The Netherlands: National Institute for Public Health and the Environment, Coordination Center for

Effects. Available at http://www.mnp.nl/cce/publ/ (Accessed May 12, 2010).

Posch, M.; Hettelingh, J.-P.; Sverdrup H.U.; Bull, K. 1993. **Guidelines for the computation and mapping of critical loads and exceedances of sulphur and nitrogen in Europe.** In: Downing, R.J.; Hettelingh, J.-P; de Smet, P.A.M., eds. Calculation and mapping of critical loads in Europe. CCE Status report 1993. RIVM Rep. No. 259101003. Bilthoven, The Netherlands: National Institute for Public Health and the Environment, Coordination Center for Effects. Available at http://www.mnp.nl/cce/publ/ (Accessed May 12, 2010).

Pypker, T.G. 2004. **Influence of canopy structure and epiphytes on the hydrology of Douglas-fir forests.** Corvallis, OR: Oregon State University. 180 p. Ph.D. Thesis.

Rabalais, N.N. 2002. **Nitrogen in aquatic systems.** Ambio. 31: 102-112.

Rao, L.E.; Allen, E.B. 2010. **Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts.** Oecologia. 62: 1035-1046.

Rao, L.E.; Allen, E.B.; Meixner, T. 2010. **Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts.** Ecological Applications. 20: 1320-1335.

Rao, L.E.; Parker, D.R.; Bytnerowicz, A.: Allen, E.B. 2009. **Nitrogen mineralization across an atmospheric nitrogen deposition gradient in southern California deserts.** Journal of Arid Environments. 73: 920-930.

Rochefort, L; Vitt, D.H.; Bayley, S.E. 1990. **Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions.** Ecology. 71(5): 1986-2000.

Rockström, J.; Steffen, W.; Noone, K.; Persson, Å; Chapin, F.S. III; Lambin, E.F.; Lenton, T.M.; Scheffer, M.; Folke, C.; Schellnhuber, H.J.; Nykvist, B.; de Wit, C.A.; Hughes, T.; van der Leeuw, S.; Rodhe, H.; Sörlin, S.; Snyder, P.K.; Costanza, R.; Svedin, U.; Falkenmark, M.; Karlberg, L.; Corell, R.W.; Fabry, V.J.; Hansen, J.; Walker, B.; Liverman, D.; Richardson, K.; Crutzen, P.; Foley, J.A. 2009. **A safe operating space for humanity.** Nature. 461: 472-475.

Rueth, H.M.; Baron, J.S. 2002. **Differences in Englemann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA.** Ecosystems. 5: 45-57.

Rueth, H.M.; Baron, J.S.; Allstott, E.J. 2003. **Responses of Engelmann spruce forests to nitrogen fertilization in the Colorado Rocky Mountains.** Ecological Applications. 13: 664-673.

Saros, J.E.; Michel, T.J.; Interlandi, S.J; Wolfe, A.P. 2005. **Resource requirements of *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations.** Canadian Journal of Fisheries and Aquatic Science. 62: 1681-1689.

Schaberg, P.G.; DeHayes, D.H.; Hawley, G.J.; Murakami, P.F.; Strimbeck, G.R.; McNulty, S.G. 2002. **Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon storage in montane red spruce.** Canadian Journal of Forest Research. 32: 1351-1359.

Sickman, J.O.; Melack, J.M.; Stoddard, J.L. 2002. **Regional analysis of inorganic nitrogen yield and retention in high-elevation ecosystems of the Sierra Nevada and Rocky Mountains.** Biogeochemistry. 57: 341-374.

Slootweg, J.; Posch, M.; Hettelingh, J.-P., eds. 2007. **Critical loads of nitrogen and dynamic modelling: CCE Progress Report 2007.** MNP Report 500090001. Bilthoven, The Netherlands: Netherlands Environmental Assessment Agency, Coordination Centre for Effects. 201 p. Available at http://www.rivm.nl/en/themasites/cce/publications/cce-progress-report-2007/index.html (Accessed March 30, 2011).

Stevens, C.J.; Dise, N.B.; Mountford, J.O.; Gowing, D.J. 2004. **Impact of nitrogen deposition on the species richness of grasslands.** Science. 303: 1876-1879.

Strengbom, J.; Walheim, M.; Näsholm, T.; Ericson, L. 2003. **Regional differences in the occurrence of understory species reflect nitrogen deposition in Swedish forests.** Ambio. 32: 91-97.

Sullivan, T.J.; Cosby, B.J.; Tonnessen, K.A.; Clow, D.W. 2005. **Surface water acidification responses and critical loads of sulfur and nitrogen deposition in Loch Vale watershed, Colorado.** Water Resources Research. 41: W01021.

Suding, K.N.; Gross, K.L.; Houseman, G.R. 2004. **Alternative states and positive feedbacks in restoration ecology.** Trends in Ecology & Evolution. 19: 46-53.

Sutton M.; Reis, S.; Baker; S.M.H., eds. 2009. **Atmospheric Ammonia.** Springer Science. 464 p.

Theodose, T.A.; Bowman, W.D. 1997. **Nutrient availability, plant abundance, and species diversity in two alpine tundra communities.** Ecology. 78: 1861-1872.

Thomas, R.Q.; Canham, C.D.; Weathers, K.C.; Goodale, C.L. 2010. **Increased tree carbon storage in response to nitrogen deposition in the US.** Nature Geoscience. 3: 13-17.

Tilman, D. 1987. **Secondary succession and the pattern of plant dominance along experimental nitrogen gradients.** Ecological Monographs. 57: 189-214.

Tilman, D. 1993. **Species richness of experimental productivity gradients: How important is colonization limitation.** Ecology. 74: 2179-2191.

Tonnesen, G.; Wang, Z.; Omary, M.; Chien, C.J. 2007. **Assessment of nitrogen deposition: modeling and habitat assessment.** CEC-500-2005-032. Sacramento, CA: California Energy Commission, PIER Energy-Related Environmental Research. 105 p. Available at http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF (Accessed may 12, 2010).

UBA (UmweltBundesAmt). 2004. **Manual on methodologies and criteria for mapping critical levels/loads and geographical areas where they are exceeded.** Berlin: Federal Environmental Agency (UmweltBundesAmt). Available at http://www.icpmapping.org (Accessed May 12, 2010).

US EPA (U.S. Environmental Protection Agency). 1993. **Air quality criteria for oxides of nitrogen.** Rep. No. EPA/600/8-91/049aF-cF.Research Triangle Park, NC: Office of Health and Environmental Assessment, Environmental Criteria and Assessment Office. 3v.

US EPA (U.S. Environmental Protection Agency). 2007. **Acid rain and related programs: 2007 progress report.** Washington, DC: U.S. Environmental Protection Agency. Available at http://www.epa.gov/airmarkets/progress/docs/2007ARPReport.pdf (Accessed May 12, 2010).

US EPA (U.S. Environmental Protection Agency). 2008. **Integrated science assessment (ISA) for oxides of nitrogen and sulfur–ecological criteria (final report).** EPA/600/R- 08/082F. Research Triangle Park, NC: U.S. Environmental Protection Agency, National Center for Environmental Assessment–RTP Division, Office of Research and Development. Available at http://cfpub.epa.gov/ncea/cfm/recordisplay.cfm?deid=201485.

USFS (U.S. Forest Service). 2001. **U.S. forest facts and historical trends.** FS-696. Washington, DC: U.S. Department of Agriculture, Forest Service. 20 p.

van den Berg, L.J.L; Dorland, E.; Vergeer, Philippine; Hart, M.A.C.; Bobbink, R.; Roelofs, J.G.M. 2005.

Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity in combination with low pH. New Phytologist. 166: 551-564.

van Diepen, L.T.A. 2008. **The role and diversity of arbuscular mycorrhizal fungi in *Acer saccharum* dominated forest ecosystems under natural and N-amended conditions.** Houghton, MI: Michigan Technological University. 99 p. Ph.D. dissertation.

van Diepen, L.T.A.; Lilleskov, E.A.; Pregitzer, K.S.; Miller, R.M. 2007. **Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions.** New Phytologist. 176: 175-183.

van Herk, C.M.; Mathijssen-Spiekman, E.A.M.; de Zwart, D. 2003. **Long distance nitrogen air pollution effects on lichens in Europe.** The Lichenologist 35: 347-359.

Vitt, D.H.; Wieder, K.; Halsey, L.A.; Turetsky, M. 2003. **Response of *Sphagnum fuscum* to nitrogen deposition: A case study of ombrogenous peatlands in Alberta, Canada.** The Bryologist. 1062: 235-245.

Wallander, H. 1995. **A new hypothesis to explain allocation of dry matter between mycorrhizal fungi and pine seedlings in relation to nutrient supply.** Plant and Soil. 169:243-248.

Weathers, K.C.; Simkin, S.M.; Lovett, G.M.; Lindberg, S.E. 2006. **Empirical modeling of atmospheric deposition in mountainous landscapes.** Ecological Applications. 16(4): 1590-1607.

Wedin, D.A.; Tilman, D. 1996. **Influence of nitrogen loading and species composition on the carbon balance of grasslands.** Science. 274: 1720-1723.

Weiss, S.B. 1999. **Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species.** Conservation Biology. 13: 1476-1486.

Whytemare, A.B.; Edmonds, R.L.; Aber, J.D.; Lajtha, K. 1997. **Influence of excess nitrogen deposition on a white spruce (*Picea glauca*) stand in southern Alaska.** Biogeochemistry. 38: 173-187.

Wigand, C.; McKinney, R.A.; Charpentier, M.A.; Chintala, M.M.; Thursby, G.B. 2003. **Relationships of nitrogen loadings, residential development, and physical characteristics with plant structure in New England salt marshes.** Estuaries. 26: 1494-1504.

Williams, M.W.; Tonnessen, K.A. 2000. **Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA.** Ecological Applications. 10(6): 1648-1665.

Wolfe, A.P.; Baron, J.S.; Cornett, R.J. 2001. **Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA).** Journal of Paleolimnology. 25: 1-7.

Wolfe, A.P.; Van Gorp, A.C.; Baron, J.S. 2003. **Recent ecological and biogeochemical changes in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to anthropogenic nitrogen deposition.** Geobiology. 1(2): 153-168.

Wu, W.; Driscoll, C.T. 2010. **Impact of climate change on three-dimensional dynamic critical load functions.** Environmental Science and Technology. 44: 720-726.

Yoshida, L.C.; Allen, E.B. 2004. **^{15}N uptake by mycorrhizal *Artemisia californica* and the invasive *Bromus madritensis* of a N-eutrophied shrubland.** Biology and Fertility of Soil. 39: 243-248.

APPENDIX 1.—PLANT SPECIES COMMON AND SCIENTIFIC NAMES

Life form	Common name	Latin name	Alternate name
Tree/shrub	Acacia	*Acacia* Mill.	
Shrub/subshrub//Forb/ herb	Agave	*Agave* L.	
Tree/shrub	Alder	*Alnus* Mill.	
Forb/herb	Alpine chickweed	*Cerastium alpinum* L.	
Graminoid	Alpine fescue	*Festuca brachyphylla* Schult. ex Schult. & Schult. f.	
Tree	American chestnut	*Castanea dentata* (Marsh.) Borkh.	
Shrub	American tarwort	*Flourensia cernua* DC.	Tarbrush
Forb/herb	Annual ragweed	*Ambrosia artemisiifolia* L.	
Shrub	Antelope bitterbrush	*Purshia tridentata* (Pursh) DC.	Antelope brush; buckbrush
Graminoid	Arctic bluegrass	*Poa arctica* R. Br.	
Lichen	Arctic kidney	*Nephroma arcticum* (L.) Torss.	
Subshrub/shrub	Arctic willow	*Salix arctica* Pall.	
Graminoid	Arrow grass	*Triglochin* L.	
Lichen	Asahina's cartilage lichen[d]	*Ramalina asahinae* (L.) Ach.	
Tree	Ash	*Fraxinus* L.	
Tree	Balsam fir	*Abies balsamea* (L.) Mill.	
Tree	Balsam poplar	*Populus balsamifera* L.	
Tree	Basswood	*Tilia* L.	
Shrub	Bearberry	*Arctostaphylos alpina* (L.) Spreng.	alpine bearberry
Lichen	Beard lichen[a]	*Usnea* Dill. ex Adans.	
Tree	Beech	*Fagus* L.	
Graminoid	Big bluestem	*Andropogon gerardii* Vitman	
Tree	Big leaf maple	*Acer macrophyllum* Pursh	
Tree/Shrub	Big sagebrush	*Artemisia tridentata* Nutt.	
Tree	Bigtooth aspen	*Populus grandidentata* Michx.	
Tree/shrub	Black cherry	*Prunus serotina,* Ehrh.	
Tree/shrub	Black mangrove	*Avicennia germinans* L.	
Tree	Black oak	*Quercus velutina,* Lam.	
Tree	Black spruce	*Picea mariana* (Mill.) Britton, Sterns & Poggenb.	
Graminoid	Blue grama	*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths	
Tree	Blue oak	*Quercus douglasii* Hook. & Arn.	
Graminoid	Bluestem	*Andropogon* L.	
Tree	Box elder	*Acer negundo* L.	
Forb/herb	Bracken fern	*Pteridium aquilinum* var. *pubescens*	
Tree	Bristlecone pine	*Pinus aristata* Engelm.	
Subshrub/Shrub	Brittlebush	*Encelia* Adans.	
Shrub	Buckbrush	*Ceanothus cuneatus* (Hook.) Nutt.	
Graminoid	Buffalo grass	*Bouteloua dactyloides* (Nutt.) J.T. Columbus	*Buchloe dactyloides*
Tree/shrub	Buttonwood	*Conocarpus erectus* L.	
Tree/shrub	California ash	*Fraxinus dipetala* Hook. & Arn.	
Tree/shrub	California black oak	*Quercus kelloggii* Newberry	
Tree/shrub	California buckeye	*Aesculus californica* (Spach) Nutt.	
Tree	California foothill pine	*Pinus sabiniana* Douglas ex Douglas	Digger pine

continued

Appendix 1.—continued

Life form	Common name	Latin name	Alternate name
Tree	California redwood	*Sequoia sempervirens* (Lamb. ex D. Don) Endl.	
Forb/herb	Canada goldenrod	*Solidago Canadensis* L.	
Forb/herb	Canadian sandspurry	*Spergularia canadensis* (Pers.) G. Don	
Shrub	Ceanothus (California lilac)	*Ceanothus spp.*	
Lichen	Cetraria lichen[a]	*Cetraria ericetorum* Opiz	
Lichen	Cetraria lichen[b]	*Cetrariella delisei* (Bory ex Schaerer) Karnefelt & A. Thell	
Lichen	Cetraria lichen[b]	*Flavocetraria cucullata* (L.) Karnefelt & A. Thell	
Lichen	Cetraria lichen[b]	*Flavocetraria nivalis* (Bellardi) Karnefelt & A. Thell	
Shrub	Chamise	*Adenostoma fasciculatum* Hook. and Arn.	
Graminoid	Cheatgrass	*Bromus tectorum* L.	
Tree	Chestnut oak	*Quercus prinus* L.	
Shrub (cactus)	Cholla	*Cylindropuntia* spp.	
Forb/herb	Clover	*Trifolium* spp.	
Tree	Coast Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*	
Tree/shrub	Coast live oak	*Quercus agrifolia* Née var. *oxyadenia* (Torr.) J.T. Howell	
Shrub	Coastal sagebrush	*Artemisia californica* Less.	California sagebrush
Tree/subshrub/shrub	Coco plum	*Chrysobalanus icaco* L.	
Graminoid	Common Mediterranean grass	*Schismus barbatus* (Loefl. ex L.) Thell.	Mediterranean splitgrass
Graminoid	Cordgrass	*Spartina* spp.	
Graminoid	Cotton grass[a]	*Eriophorum* L.	
Shrub	Creosote bush	*Larrea tridentata* (DC.) Coville	
Lichen	Cumberland xanthoparmelia lichen	*Xanthoparmelia cumberlandia* (Gyelnik) Hale	
Lichen	Cup lichen	*Cladonia* P. Browne	Reindeer lichen[c]
Graminoid	Curly sedge	*Carex rupestris* All.	
Bryophyte	Dicranum moss[a]	*Dicranum polysetum* Sw.	
Bryophyte	Dicranum moss[a]	*Dicranum scoparium* Hedw.	
Tree/shrub	Dogwood	*Cornus* L.	
Tree	Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco	
Shrub/subshrub	Dwarf birch	*Betula nana* L.	
Tree	Eastern hemlock	*Tsuga canadensis* (L.) Carrière	
Subshrub/shrub	Eastern Mojave buckwheat	*Eriogonum fasciculatum* Benth.	California buckwheat
Tree	Eastern red cedar	*Juniperus virginiana* L.	
Tree	Eastern white pine	*Pinus strobus* L.	white pine
Forb/herb	Eelgrass	*Zostera* spp.	
Tree	Elm	*Ulmus L.*	
Tree	Engelmann oak	*Quercus engelmannii* Greene	
Tree	Engelmann spruce	*Picea engelmannii* Parry ex Engelm.	
Subshrub/shrub/forb/herb	Entireleaf mountain avens	*Dryas integrifolia* Vahl	
Tree	Eucalyptus	*Eucalyptus camaldulensis* Dehnh.	

continued

Appendix 1.—continued

Life form	Common name	Latin name	Alternate name
Lichen	Felt lichen[a]	*Peltigera aphthosa* (L.) Willd.	
Lichen	Felt lichen[a]	*Peltigera polydactylon* (Necker) Hoffm.	
Tree	Florida slash pine	*Pinus elliottii* Engelm.	
Tree/shrub	Flowering dogwood	*Cornus florida* L.	
Tree	Fremont cottonwood	*Populus fremontii* S. Watson	
Graminoid	Galleta grass	*Hilaria jamesii* (Torr.) Benth.	*Pleuraphis jamesii* Torr.; James galleta
Tree	Giant sequoia	*Sequoiadendron giganteum* (Lindl.) J. Buchholz	
Graminoid	Grama grass	*Bouteloua* spp.	
Tree	Grand fir	*Abies grandis* (Douglas ex D. Don) Lindl.	
Shrub	Greasewood	*Sarcobatus* Nees	*Sarcobatus vermiculatus* (Hook.) Torr.
Subshrub/Forb/herb	Great ragweed	*Ambrosia trifida* L.	
Subshrub/Forb/herb	Green pitcher plant	*Sarracenia oreophila* (Kearney) Wherry	
Lichen	Greygreen reindeer lichen	*Cladonia rangiferina* (L.) F. H. Wigg.	
Tree/shrub	Gumbo limbo	*Bursera simaruba* (L.) Sarg.	
Tree/shrub	Hackberry	*Celtis occidentalis* L.	
Tree/shrub	Hawaiian holly	*Ilex anomala* Hook. & Arnott	
Shrub	Heather	*Calluna vulgaris* (L.) Hull	
Tree	Hickory	*Carya* Nutt.	
Lichen	Horsehair lichen [a]	*Bryoria capillaris* (Ach.) Brodo & D. Hawksw.	
Lichen	Horsehair lichen[a]	*Bryoria* Brodo & D. Hawksw.	
Lichen	Hydrothyria lichen	*Peltigera hydrothyria* Miadl. & Lutzoni	*Hydrothyria venosa*
Lichen	Inactive tube lichen	*Hypogymnia inactiva* (Krog) Ohlsson	
Tree	Incense cedar	*Calocedrus decurrens* (Torr.) Florin	
Graminoid	Indian ricegrass	*Oryzopsis hymenoides* (Roem. & Schult.) Ricker ex Piper	*Achnatherum hymenoides* (Roem. & Schult.) Barkworth
Graminoid	Indiangrass	*Sorghastrum nutans* (L.) Nash	
Tree	Jack pine	*Pinus banksiana* Lamb.	
Tree	Jeffrey pine	*Pinus jeffreyi* Balf.	
Tree/shrub	Joshua tree	*Yucca brevifolia* Engelm.	
Tree/shrub	Juniper	*Juniperus* L.	
Bryophyte	Juniper polytrichum moss	*Polytrichum juniperinum* Hedw.	
Graminoid	Kentucky bluegrass	*Poa pratensis* L.	
Tree	Koa	*Acacia koa* A. Gray	
Shrub	Labrador tea	*Ledum* L.	
Shrub/subshrub	Lingonberry	*vaccinium vitis-idaea* L.	
Graminoid	Little bluestem	*Schizachyrium scoparium* (Michx.) Nash	
Tree	Live oak	*Quercus virginiana* Mill.	Virginia live oak
Tree	Lodgepole pine	*Pinus contorta* Douglas ex Louden	
Bryophyte	Magellan's sphagnum	*Sphagnum magellanicum* Brid.	
Tree	Mahogany	*Swietenia mahogani* (L.) Jacq.	
Shrub	Manzanita	*Arctostaphylos* Adans.	
Tree	Maple	*Acer* L.	

continued

Appendix 1.—continued

Life form	Common name	Latin name	Alternate name
Subshrub/forb/herb	Marsh rosemary	*Limonium californicum* (Boiss.) A. Heller	
Lichen	Menzies' cartilage lichen	*Ramalina menziesii* Taylor	
Tree/shrub	Mesquite	*Prosopis* L.	
Tree	Mexican mountain pine	*Pinus hartwegii* Lindl.	
Subshrub/shrub	Mountain heather	*Cassiope* D. Don	
Tree	Mountain hemlock	*Tsuga mertensiana* (Bong.) Carrière	
Shrub	Mountain-avens	*Dryas* L.	
Graminoid	Muhly grass	*Muhlenbergia* Schreb.	
Tree	Nemoca cimarrona	*Ocotea spathulata* Mez	
Tree/shrub	Netleaf hackberry	*Celtis laevigata* Willd. var. *reticulata* (Torr.) L.D. Benson	
Tree	Nootka cypress	*Callitropsis nootkatensis* (D. Spach)	Alaska yellow-cedar; *Cupressus nootkatensis* D. Don
Tree	Northern red oak	*Quercus rubra* L.	Red oak
Tree	Northern white-cedar	*Thuja occidentalis* L.	
Tree	Norway spruce	*Picea abies* (L.) Karst.	
Tree	Oak	*Quercus* L.	
Tree/shrub	Ohi'a lehua	*Metrosideros polymorpha* Gaud	
Tree	Olapa	*Cheirodendron*	
Lichen	Orange wall lichen[a]	*Xanthoria* (Fr.) Th. Fr.	
Lichen	Orange wall lichen[e]	*Xanthomendoza* S. Kondr. & Kärnefelt	
Lichen	Orange wall lichen[e]	*Xanthomendoza fallax* (Hepp ex Arnold) Søchting, Kärnefelt & S. Kondr.	
Tree	Oregon ash	*Fraxinus latifolia* Benth	
Tree/shrub	Oregon white oak	*Quercus garryana* Douglas ex Hook.	Garry oak
Tree	Pacific madrone	*Arbutus menziesii* Pursh	
Tree	Pacific silver fir	*Abies amabilis* (Douglas ex Louden) Douglas ex Forbes	silver fir
Tree/shrub	Palo Colorado	*Cyrilla racemiflora L.*	Swamp titi
Tree/shrub	Paloverde	*Parkinsonia* L.	
Tree	Paper birch	*Betula papyrifera* Marsh.	White birch
Lichen	parmotrema lichen[a]	*Parmotrema stuppeum* (Taylor) Hale	
Tree	Persimmon	*Diospyros virginiana* L.	common persimmon
Tree	Pignut hickory	*Carya glabra* (Mill.) Sweet	
Tree	Pine	*Pinus* L.	
Bryophyte	Polytrichum moss	*Polytrichum commune* Hedw.	
Tree	Ponderosa pine	*Pinus ponderosa* C. Lawson	
Shrub (cactus)	Prickly pear cactus	*Opuntia* Mill.	
Forb/herb	Purple mountain saxifrage	*Saxifraga oppositifolia* L.	
Subshrub/forb/herb	Purple pitcher plant	*Sarracenia purpurea* L.	
Graminoid	Quackgrass	*Agropyron repens* (L.) P. Beauv.	*Elymus repens* (L.) Gould
Tree	Quaking aspen	*Populus tremuloides* Michx.	Trembling aspen
Graminoid	Quillworts	*Isoetes* L.	
Shrub	Rabbit brush	*Chrysothamnus* spp.	

continued

Appendix 1.—continued

Life form	Common name	Latin name	Alternate name
Lichen	Ragged lichen[a]	*Platismatia glauca* (L.) W. L. Culb.. & C. F. Culb.	
Tree	Red alder	*Alnus rubra* Bong.	
Graminoid	Red brome	*Bromus rubens* L.	
Tree/shrub	Red mangrove	*Rhizophora mangle* L.	
Tree	Red maple	*Acer rubrum* L.	
Tree	Red pine	*Pinus resinosa* Ait.	
Tree	Red spruce	*Picea rubens* Sarg.	
Lichen	Reindeer lichen[c]	*Cladonia mitis* Sandst.	
Lichen	Ring lichen[a]	*Evernia mesomorpha* Nyl.	
Tree	River birch	*Betula nigra* L.	black birch
Tree	Rocky Mountain Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco	
Forb/herb	Round head lespedeza	*Lespedeza capitata* Michx.	Round-head bush-clover
Forb/herb	Roundleaf sundew	*Drosera rotundifolia* L.	
Forb/herb	Russian Thistle	*Salsola iberica* (Sennen & Pau) Botsch. ex Czerep.	*Salsola tragus* L.
Subshrub/shrub	Sacahuista	*Nolina microcarpa* S. Watson	
Tree	Sacred fir	*Abies religiosa* (H.B.K.) Schl. et Cham.	
Forb/herb	Sage	*Salvia* L.	
Subshrub/shrub	Sagebrush	*Artemisia* L.	
Tree (cactus)	Saguaro	*Cereus gigantea* Engelm.	*Carnegiea gigantea* (Engelm.) Britton & Rose
Shrub	Saltbush	*Atriplex* L.	
Graminoid	Saltgrass	*Distichlis spicata* (L.) Greene	
Graminoid	Saltmeadow cordgrass	*Spartina patens* (Aiton) Muhl.	
Tree/shrub	Saw palmetto	*Serenoa repens* (Bartram) Small	
Tree	Scarlet oak	*Quercus coccinea* Münchh.	
Bryophyte	Schreber's big red stem moss	*Pleurozium schreberi* (Brid.) Mitt.	
Tree	Scots pine	*Pinus sylvestris* L.	Scotch pine
graminoid	Sheep fescue	*Festuca ovina* L.	
Lichen	Shield lichen[a]	*Parmelia sulcata*	
Tree	Sitka spruce	*Picea sitchensis* (Bong.) Carrière	
Lichen	Skin lichen[a]	*Leptogium rivale* Tuck.	
Graminoid	Smooth cordgrass	*Spartina alterniflora* Loisel.	
Lichen	Snow lichen[a]	*Stereocaulon* Hoffm.	
Lichen	Snow lichen[a]	*Stereocaulon paschale* (L.) Hoffm.	
Tree/shrub	Soaptree yucca	*Yucca elata* (Engelm.) Engelm.	
Tree/shrub	Southern California walnut	*Juglans californica* S. Watson	
Tree	Southern oak	*Quercus falcata* Michx.	Southern red oak
Tree	Spanish fir	*Abies pinsapo* Boiss.	
Bryophyte	Sphagnum	*Sphagnum fuscum* (Schimp.) Klinggr.	brown peatmoss
Bryophyte	Sphagnum[a]	*Sphagnum* L.	
Bryophyte	Sphagnum[a]	*Sphagnum fuscum* (Schimp.) Klinggr.	
Bryophyte	Splendid feather moss	*Hylocomium splendens* (Hedw.) Schimp.	

continued

Appendix 1.—continued

Life form	Common name	Latin name	Alternate name
Lichen	Star reindeer lichen	*Cladonia stellaris* (Opiz) Pouzar & Vězda	
Forb/herb	Stickywilly	*Galium aparine* L.	
Forb/herb	Stork's bill	*Erodium cicutarium* (L.) L'Hér. ex Aiton	
Tree/shrub/vine	Strangler fig	*Ficus aurea* Nutt.	
Tree	Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.	
Tree	Sugar maple	*Acer saccharum* Marsh.	
Tree	Sugar pine	*Pinus lambertiana* Douglas	
Tree	Sweet gum	*Liquidambar styraciflua* L.	
Graminoid	Switchgrass	*Panicum virgatum* L.	
Tree	Tabonuco tree	*Dacryodes excels* Vahl	
Graminoid	Tall fescue	*Schedonorus phoenix* (Scop.) Holub	*Festuca arundinacea* Schreb.
Tree	Tamarack	*Larix larcina* (Du Roi) K. Koch	American larch
Tree/shrub	Texas live oak	*Quercus fusiformis* Small	
Graminoid	Threeawn	*Aristida* L.	
Graminoid	Tobosagrass	*Pleuraphis mutica Buckley*	*Hilaria mutica*
Tree/shrub	Toyon	*Heteromeles arbutifolia* (Lindl.) M. Roem.	
Lichen	Tube lichen[a]	*Hypogymnia enteromorpha* (Ach.) Nyl.	
Lichen	Tube lichen[a]	*Hypogymnia physodes* (L.) Nyl.	
Forb/herb	Tule	*Schoenoplectus acutus* (Muhl. ex Bigelow) A. Löve & D. Löve var. *occidentalis* (S. Watson) S.G. Sm.	
Graminoid	Tussock cottongrass	*Eriophorum vaginatum* L.	
Subshrub/forb/herb	Virginia glasswort	*Salicornia depressa* Standl.	*Salicornia virginica* L.
Graminoid	Wavy hairgrass	*Deschampsia flexuosa* (L.) Trin.	
Tree	Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.	
Tree	Western juniper	*Juniperus occidentalis* Hook.	
Tree	Western red cedar	*Thuja plicata* Donn ex D. Don	
Tree	Western white pine	*Pinus monticola* Douglas ex D. Don	
Graminoid	Wheatgrass	*Agropyron* Gaertn.	
Tree	White ash	*Fraxinus americana* L.	
Tree	White fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.	
Tree/shrub	White mangrove	*Laguncularia racemosa* (L.) Gaertn. f.	
Tree	White spruce	*Picea glauca* (Moench)Voss	
Subshrub/shrub	Whortleberry	*Vaccinium myrtillus* L.	
Tree/shrub	Willows	*Salix* L.	
Lichen	Witch's hair lichen[a]	*Alectoria nigricans* (Ach.) Nyl.	
Lichen	Witch's hair lichen[a]	*Alectoria ochroleuca* (Hoffm.) A. Massal.	
Lichen	Witch's hair lichen[a]	*Alectoria sarmentosa* (Ach.) Ach.	
Lichen	Wolf lichen	*Letharia vulpina* (L.) Hue	
Tree	Yellow birch	*Betula alleghaniensis* Britt.	
Tree	Yellow-poplar	*Liriodendron tulipifera* L.	Tulip tree

[a] The same common name is used for all species in the genus.

[b] This common name has not been updated in the NRCS plants database (NRCS 2010) since the genus name changed.

[c] General common name for species that were formerly in the genus *Cladina.*

[d] This common name is not listed in the NRCS plants database (NRCS 2010), but follows NRCS naming conventions.

[e] General common name for species that were formerly in the genus *Xantharia;* this common name has not been updated in the NRCS plants database (NRCS 2010) since the genus name changed.

NRCS (National Resources Conservation Service). 2010. PLANTS database. Baton Rouge, LA: U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Center. Available at: http://plants.usda.gov (Accessed February 9, 2011).

APPENDIX 2.—CHEMICAL APPENDIX

Chemical formula or abbreviation	Chemical name or terminology
Al	Aluminum
ANH_4I	Aitken mode ammonium mass
ANH_4J	Accumulation mode ammonium mass
ANO_3I	Aitken mode aerosol nitrate mass
ANO_3J	Accumulation mode nitrate mass
C	Carbon
$C_{18}H_{16}O_7$	Usnic acid
CH_4	Methane
CO_2	Carbon dioxide
Ca	Calcium
HNO_3	Nitric acid
HONO	Nitrous acid
H_2S	Hydrogen sulfide
H_2SO_4	Sulfuric acid
Hg	Mercury
K	Potassium
KH_2PO_4	Potassium dihydrogen phosphate
MA-PAN	PAN analogue formed from methacrolein (C_4H_6O)
Mg	Magnesium
N	Nitrogen
NH_3	Ammonia
NH_4^-	Ammonium
NH_4Cl	Ammonium chloride
NH_4NO_3	Ammonium nitrate
$(NH_4)_2SO_4$	Ammonium sulfate
NH_x	NH_3 and NH_4^-
NO	Nitric oxide
NO_2	Nitrogen dioxide
NO_3^-	Nitrate
NO_x	Nitric oxides
NO_y	NO, NO_2, nitric acid (HNO_3), organic and inorganic nitrates
N_2	Nitrogen gas
N_2O	Nitrous oxide
N_2O_5	Dinitrogen pentoxide
$NaNO_3$	Sodium nitrate
O_3	Ozone
P	Phosphorus
PAN ($C_2H_3NO_5$)	Peroxyacetyl nitrate
PAN2 (RCO_5N)	Higher peroxyacetyl nitrate (based on peroxypropyl nitrate)
PBZN ($C_7H_5NO_5$)	Peroxybenzoyl nitrate
RNO_3	Organic nitrates
S	Sulfur
SO_2^-	Sulfur dioxide
SO_4^{2-}	Sulfate
SO_x	Sulfur oxides

Pardo, L.H.; Robin-Abbott, M.J.; Driscoll, C.T., eds. 2011. **Assessment of Nitrogen deposition effects and empirical critical loads of Nitrogen for ecoregions of the United States.** Gen. Tech. Rep. NRS-80. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 291 p.

This report synthesizes current research relating atmospheric nitrogen (N) deposition to effects on terrestrial and aquatic ecosystems in the United States and to identify empirical critical loads for atmospheric N deposition. The report evaluates the following receptors: freshwater diatoms, mycorrhizal fungi and other soil microbes, lichens, herbaceous plants, shrubs, and trees. The main responses reported fell into two categories: (1) biogeochemical; and (2) individual species, population, and community responses. The range of critical loads for nutrient N reported for U.S. ecoregions, inland surface waters, and freshwater wetlands is 1 to 39 kg N ha^{-1} y^{-1}. This range spans the range of N deposition observed over most of the country. The empirical critical loads for N tend to increase in the following sequence for different life forms: diatoms, lichens and bryophytes, mycorrhizal fungi, herbaceous plants and shrubs, trees.

KEY WORDS: air pollution, atmospheric N deposition, critical nitrogen loads, biodiversity, nitrate leaching, nitrogen saturation, plant nitrogen concentration, natural resource protection, vegetation type conversion

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