Desert Plants

Volume 29, Number 2

Published by The University of Arizona for the Boyce Thompson Arboretum

A Guide to North American Grasslands

David E. Brown and Elizabeth Makings

Relict Great Basin Shrub-Grassland near Wupatki National Monument northeast of Flagstaff, Coconino County, Arizona, 1,650 m (5,413 ft).

Desert Plants

A journal devoted to broadening knowledge of plants indigenous or adapted to arid and sub-arid regions and to encouraging the appreciation of these plants.

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Volume 29, Number 2
Published by The University of Arizona for the Boyce Thompson Arboretum
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From the editor

As Desert Plants begins its 35th year with a new staff, it seems somewhat appropriate that as we begin a new chapter in the history of Desert Plants, we start with *A Guide to North American Grasslands* by David E. Brown and Elizabeth Makings. Probably one of the most quoted, used and reprinted issues of Desert Plants to this day is Volume 4, No. 1-4: *Biotic Communities of the American Southwest - United States and Mexico*, by David E. Brown (editor). Not only are we reaching back to our early years for authorship, I believe we are maintaining the high standards set back then as well. So, we certainly hope that we are off to a great start, even if it is a bit late.

We are very excited about several upcoming issues. We hope to have one issue dedicated to the 25-year field evaluation of various exotic tree species at the Mesa Agricultural Center in Yuma, Arizona and another issue dedicated to a Vascular and Vegetative Flora of the Ironwood Forest National Monument in Pima and Pinal Counties, Arizona. Other issues will include articles on the 5-year Arizona Hedgehog (*Echinocereus triglochidiatus* var. *arizonicus*) salvage project, the role of floral scent in host detection for a solitary specialist bee and an upcoming genus treatment from *Legumes of Arizona* to name a few.

With so many great issues on the horizon and the change in editorship comes the opportunity to rethink what Desert Plants is and could be. Desert Plants is devoted to broadening knowledge of plants indigenous or adapted to arid and sub-arid regions and to encouraging the appreciation of these plants. With such a broad mandate, it is open to various interpretations. We would certainly welcome comments from our readers as to what articles they value most or what they would like to see more of. Another issue confronting us is whether we should move to become a peer reviewed journal. A peer reviewed journal would open us to additional authors but may eliminate others. So, the fundamental question is what type of articles you would prefer.

We have tried in the past to have some variety in most issues, except for the ones dedicated to a flora or given subject. Typically, we tried to maintain a balance between Arizona and international articles, technical and non-technical articles. As Boyce Thompson Arboretum has grown over the years, we believe we can expand in all areas, but first we would like to hear from you.

Please send your comments to Desert Plants, 37615 E US Highway 60, Superior, Arizona 85173 or DesertPlants@cals.arizona.edu.

Again, we hope you enjoy this issue and sorry for the late start.

Desert Plants Journal is included with Boojum Club, Picket Post Society, and Director's Circle level memberships at Boyce Thompson Arboretum. One-year subscriptions are also available: individual $20, individual(foreign) $30, institution $50. Back issues are $5 each, plus $3 shipping and handling. Additional copies of Vol. 29(2) are $20, plus $5 shipping and handling. Mailing address: Boyce Thompson Arboretum 37615 E US Highway 60, Superior, AZ 85173 Website: arboretum.ag.arizona.edu E-mail: DesertPlants@cals.arizona.edu Telephone: 520.689.2723

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Above: *Trachypogon spicatus* Back cover: Semidesert Grassland in the San Simon Valley, just east of the Price Canyon area. August 2010. Photos: Elizabeth Makings

Acknowledgements

The authors would like to gratefully acknowledge Andy Casillas and Stella Ruth, former office mates of co-author Elizabeth Makings at the Tonto National Forest Supervisor's Office. Without their expertise and patience teaching the basics of ArcMap, the grasslands map would not have been possible. The authors are also indebted to the many contributing photographers who were so generous with not only their photos, but also with species-level descriptions that many noted in the captions. The photograpers are: John Taft, John Alcock, Aimee Kessler, Barbara Neuffer, David and Nancy Pearson, Fernando Zuloaga, David Cook, Lee Frataer, Richard E. Brown, Alejandro Velázquez, Raul Valdez, Bonnie Swarbrick, Joey Carboneaux, D. F. Costello, R. R. Humphrey, Ray Turner, Kevin Clark, Ron Cole, David Clendenen, Randall Babb, Louella Brown, Steve Gallizioli, Casa Grande Valley Historical Society, Charles H. Lowe, Jr, and Anibella Flores.

Authors' Preface

This monograph is an expanded treatment of the grasslands originally presented in "Biotic Communities of Southwest U.S. and Northwest Mexico" published in *Desert Plants* 1982 (1-4). This expansion was prompted by comments received from a number of biologists working in North America's "grassland biome" who suggested that we include and compare the Southwest's grasslands with their area of expertise. Ecologists expressing particular interest in such an expansion included Ray Turner, Alberto Burquez, Orie Laucks, Miklos Udvardy, and the late Jim Yoakum.

Co-author David Brown has been to each of the grassland communities presented herein from the arctic-subarctic to the tropic-neotropic. Biotic communities visited included those in the prairie provinces of Canada; the Eastern, Plains, Rocky Mountain, Great Basin, Oregonian, and California regions of the U.S., and in every Mexican state. Tropic-subtropic grasslands and their inhabitants included those observed in Guatemala, Belize, Nicaragua, Honduras and Costa Rica as well as on several Caribbean islands including Cuba.

Not all ecologists will agree with the climatic and biotic delineations separating the grasslands, correctly pointing out the continuum concept of R. H. Whittaker and others showing that few if any species share identical altitudinal and climatic limitations. Nonetheless, we consider the plant and animal assemblages within the various grasslands depicted to not only be varied and large, but to contribute to a better understanding of each grassland's history and evolution. This presentation therefore incorporates the biotic community concepts originally proposed by H. S. Swarth, Forrest Shreve, and V. E. Shelford; applied by D. I. Rasmussen, and formulated by C. H. Lowe, Jr.

Both plants and animals are therefore of prime consideration in the identification and delineation of the grasslands featured herein. The authors may take credit for assembling what is hoped to be a useful and enduring guide to the grasslands of North America, but the real credit goes to the scientists this work has referenced – leaders in grassland ecology including giants such as Daniel Axelrod, Michael Barbour, William Billings, Frederic Clements, Rexford Daubenmire, Aldo Leopold, Jerzy Rzedowski, Forrest Shreve, and John Weaver. Their influential theories and pioneering works laid the foundation for our current biogeographical view of landscapes.

Those biologists contributing significantly to the inclusion of animal inhabitants within the biotic communities presented include Russell Davis (mammals), Janet Ruth (grassland sparrows), R. Roy Johnson (birds), Rich Glinski (raptors) and Randal Babb (herpetofauna).

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January 2014

Introduction

"*Pride of place must certainly go to the Gramineae…the great family.*"

Ronald Good, 1953

Grassland communities can be found on every continent and on most oceanic islands. They occupy extensive areas and their regional names may imprint a specific designation to an entire biotic province. The Eurasian "steppe," the Hungarian "puszta", the "pampas" of Argentina, the "campos" of Uruguay, the Mexican "pastizales" and the South African "veldt" all refer to vegetation types in which grasses or other herbaceous plants are dominant (Appendix 1). The North American "prairie," while the largest grassland in the Nearctic, is only one of the continent's grassland biotic communities--each having a distinctive climatic pattern, evolutionary history, and plant and animal constituency (Map 1). Given these differences, it is essential that biogeographers, botanists, wildlife managers, land planners, and others interested in biodiversity are able to identify the various grasslands and understand their limiting factors, areal extent, regional variations, and management needs.

Grasslands are the biomes that have been the most impacted by human activities. As a result, more of North America's grasslands have been lost through conversion to agriculture, urbanization, and desertification than any other biotic community (see e.g., Brown and Davis 1994, Hoekstra et al. 2005). Hence, these communities are in the most need of protection, a status bestowed upon only a small percentage of those remaining (Briggs et al. 2005). Only Canada (Saskatchewan) has a Grasslands National Park and, despite the United States having some modest-sized grassland preserves, most of that country's remaining grasslands are maintained for reasons other than grassland preservation. None of the smaller countries in North America have any areas specifically dedicated to grassland preservation, and the need to retain and enhance protective measures for some of the smaller grassland biotic communities such as **California Valley Grassland, Gulf Coastal Grassland, Madrean Montane Grassland,** and the continent's tropic-subtropic savanna grasslands is acute.

Wherever they occur, these herb/grass dominated communities share certain physical and climatic attributes that include high solar radiation, frequent and persistent winds, both seasonal and episodic droughts, and most importantly, periodic fires. The properties are not unrelated to the whole, and the cessation of any of these influences can result in the invasion of woody plants and subsequent conversion to scrubland or forest. Other activities, particularly those associated with water developments and livestock grazing have resulted in large scale type conversions to disclimax grasslands, if not desertscrub (McAuliffe 1995, Briggs et al. 2005).

The Climatic Zone Approach: We first categorize grasslands, i.e., terrestrial plant communities dominated

actually or potentially by grasses and/or other herbaceous plants that cover more than 50% of the ground, into four climatic zones developed by Brown et al. (1979, 1998). Minimum temperatures, minimum moisture requirements, and other limiting natural criteria are recognized as major evolutionary controls.

Arctic-Boreal—landscapes having lengthy periods of freezing temperatures with a growing season generally lasting less than 100-150 days, occasionally interrupted by nights of below freezing temperatures. Less than 200 annual days will have a mean temperature minimum >0º C.

Cold Temperate—Freezing temperatures usually of more moderate duration, although of frequent occurrence during winter months. Some periods of extreme cold to be expected but the potential growing season is generally from 100 to 200 days with >200 days per annum having mean minimum temperatures >0°C.

Warm Temperate—Freezing temperatures of short duration but generally occurring every year, with a potential growing season >200 days with less than 150 days per year subject to temperatures below 0ºC, chilling winds, or cold fogs.

Tropical-Subtropical—Infrequent or no 24-hour periods of freezing temperatures, chilling winds, or cold fogs.

The Biogeographic Province Approach: Each grassland is then described as a biotic community, the name of which is derived from the biotic province in which it is found (see e.g., Brown et al. 1998, 2007). Also termed biotic regions (see e.g., Udvardy 1975a, 1975b), biotic provinces are areas characterized by a particular precipitation pattern or other climatic regime, providing the plant and animal species found therein a more or less similar environment. Biotic communities are then regional formations *within* a particular biotic province, each having a distinctive evolutionary history that provides a characteristic biota at the species level.

Nomenclature: For Poaceae, names are synonymized from the *Flora of North America* (FNA 2003, 2007). For all other vascular plants found within North America, we use the United States Department of Agriculture "PLANTS Database" (USDA, NRCS 2012). Species are ordered alphabetically (vs. importance value). Bird nomenclature follows the American Ornithologist's Union checklist of North and Middle American Birds (AOU 2013). Mammalian nomenclature follows Wilson & Reeder (2005). Reptiles and Amphibians are from various sources. For taxa not in the above mentioned, nomenclature is from the original literature.

Evolutionary History of North America's Grasslands: The fossil record determining both the extent and composition of North America's grasslands is imperfectly known. Nonetheless, the origins of most grass genera, [e.g., *Agropyron* (*sensu lato*), *Koeleria,* and *Stipa* (*sensu lato*)] are recognized as probably arriving from Eurasia, while others (e.g. *Bouteloua* and *Muhlenbergia*) apparently originated in the New World. Prior to the latter half of the Tertiary Period, about 20 million years before present, most of the continent was covered by a more or less continuous forest, which was only occasionally broken up into savannas and parklands (Axelrod 1956, 1958, 1966, 1979a, 1979b, 1985). The geologic physiognomy of the Nearctic Realm looked roughly as it does today: the Great Plains and Great Basin were already in place, and the Rocky Mountains were resuming a general uplifting that had begun during Oligocene times 25 to 37 mybp (Kurtén 1972). This rising, accompanied by other uplifts to the west, resulted in a developing series of rain shadows that intercepted Pacific storms and caused a drying of the continent's interior. It was then that most accounts have North America's grasslands originating in what is now the Intermountain West (e.g., Dix 1964, Axelrod 1985, Sims 1988).

By the middle Miocene, around 14-15 mybp, newer, dryer savannas were evolving as habitats became increasingly arid. By 4-5 mybp, several genera of antilocaprids were sharing open landscapes with horses, camels, and other now extinct ungulates (Martin and Wright 1967, Owen-Smith 1987). As the Tertiary's forests continued to retreat, additional savannas and meadow-like parklands emerged and enlarged throughout the Intermountain West where the climate became not only drier, but also possibly warmer, giving rise to drying winds and a potential for fire—ingredients making these landscapes conducive to grassland formation and maintenance (Dix 1964). Whatever their causes, savanna-grasslands of sizable extent were present in the Great Basin by about 4 mybp. Vast, open prairies were yet to come, however (Axelrod 1985).

The advent of the Pliocene after 5 mybp saw a continued rising of the Sierra Nevada, and a cooler Pacific ocean (Axelrod 1985). The drying trend in the Intermountain West accelerated even though winter precipitation averages were considerably greater and less variable than today. Winter temperatures in the interior rose, while summers remained cooler than at present with Arcto-Tertiary grasses expanding in the north and summer-growing C-4 grasses becoming increasingly prevalent in the south. Savannas and shrub-steppe now captured the valley floors and low plains as the forests retreated from all but the mountains and stream bottoms. By the end of the Pliocene (1.8 mybp), conditions in both the Great Basin and Great Plains were drier than had heretofore been experienced (Axelrod 1985). South.

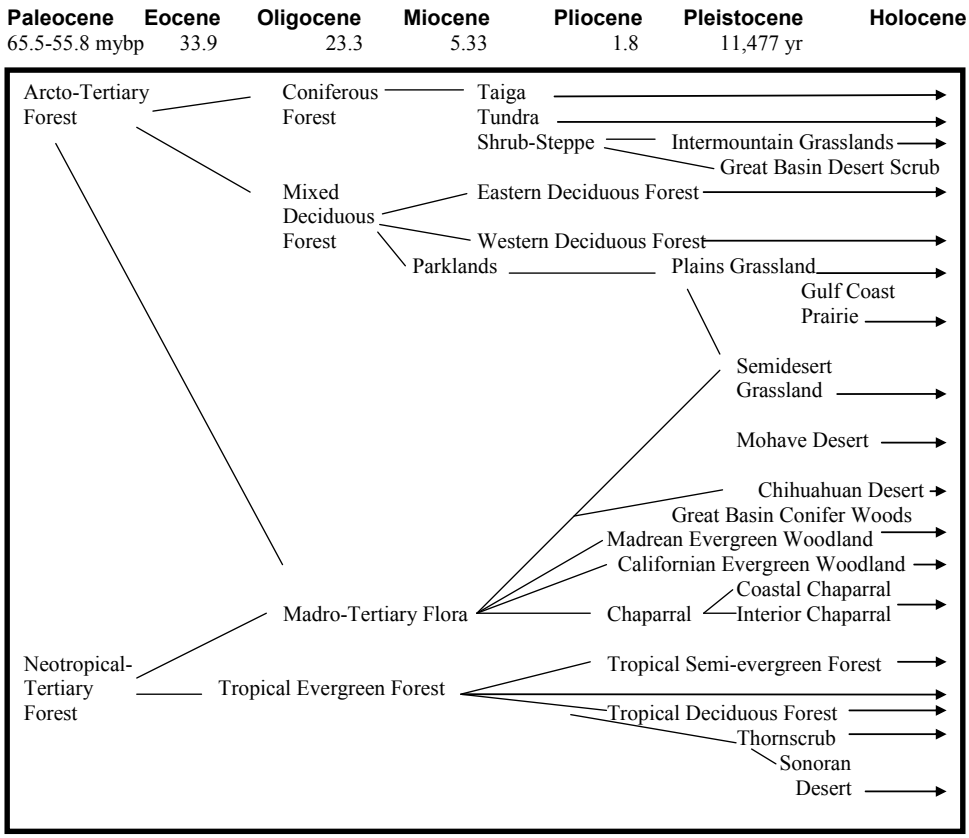


Fig. 11. Cenozoic-Era evolutionary sequences of the origins of certain biotic communities in North America as interpreted from the literature on fossil pollens. Geologic time scale based on Federal Geographical Subcommittee (FGDC 2006).

ward, chaparral, thornscrub, and the components of a new "semidesert" grassland began invading valleys and plains in what are now northern Mexico and the American Southwest (Axelrod 1979a,b; Van Devender 1995; McAuliffe and Van Devender 1998).

The final years of the Pliocene epoch (3.5 to 1.8 mybp) were a time of evolving mammalian divergence with an assemblage of large mammals inhabiting western North America. No fewer than four genera of prongbucks were present ranging in size from the dik-dik sized *Capromeryx* to the nearly pronghorn size *Tetrameryx* (Skinner 1942). North America's diverse fauna, formerly composed mostly of browsing ungulates, was now increasingly joined by ruminants with high, hypsodont molars. Adding to this assemblage was the emergence of the land bridge to South America about 3 mybp, permitting animals to enter North America from the south and join other mammal species arriving from Asia.

Most fossil floras in western North America after 3 mybp suggest cooler temperatures than now with glaciers occupying the coldest areas (Metcalf 2006). Although rainfall may have been 500 mm (20 in) greater than at present on the Pacific coast, the rising Peninsular, Sierra-Nevadan and Rocky Mountain ranges were further interfering with winter precipitation in the interior. By 1-2 mybp, the climate appears to have become increasingly unstable due to rain shadows, cyclonic depressions and changing storm tracks. Winter temperatures became decidedly colder and more severe. Summers, however, may have been warmer than now, with warm-season rainfall occurring particularly in the south. But more than any other factor, it was an increasing variation in temperature extremes that heralded the coming of the Pleistocene epoch in what was still a generally benign climate for large, open-country mammals with a range of sizes, the largest of which were elephants (Kurtén and Anderson 1980).

Much of the continent remained covered by forest or woodland where newly arrived cervids (mammals in the deer family) were evolving in place. Other genera of native North American mammals, including such antilocaprids as *Tetrameryx*, now began to disappear, their place taken by more open country pronghorns including the ancestors of *Antilocapra americana* (Lindsay and Tessman 1974, Kurtén and Anderson 1980, Byers 1997). By 1.75 to 2.5 mybp, a newer grassland fauna was evolving, concomitant with a drier climate, interspecies competition, and accelerating extinctions. Grassland species such as prairie dogs (*Cynomys*) and prairie grouse (*Pedioecétes*, *Tympanúchus*) appeared (Kurtén and Anderson 1980), and it was probably about this time that the

various species of grassland sparrows began to evolve, the genus *Ammodramus* (*Xenospiza*) differentiating into northern prairie forms with species of *Aimophila* (*Peucaea*) evolving in the southern savannas.

Between 2 mybp and 75,000 ybp a series of glacial periods occurred, each followed by an interglacial interval of shorter length (Kurtén and Anderson 1980, Grayson 1993, VanDevender 1995). During the glacials, ice sheets covered the northern portions of the continent, while in the south and west a cooler climate prevailed. Winds increased in frequency and velocity with fluctuating temperatures, the intervening interglacials being warmer than at present. Both the Rocky Mountain and Sierra Nevada uplifts continued, while the interior basins were subjected to significant loess deposition and drainage alteration. The savannas and "shrub-steppes," populated mostly by Arcto-Tertiary species, alternatively expanded and receded, generally expanding during the warmer, drier interglacials with increased incidences of drought and fire.

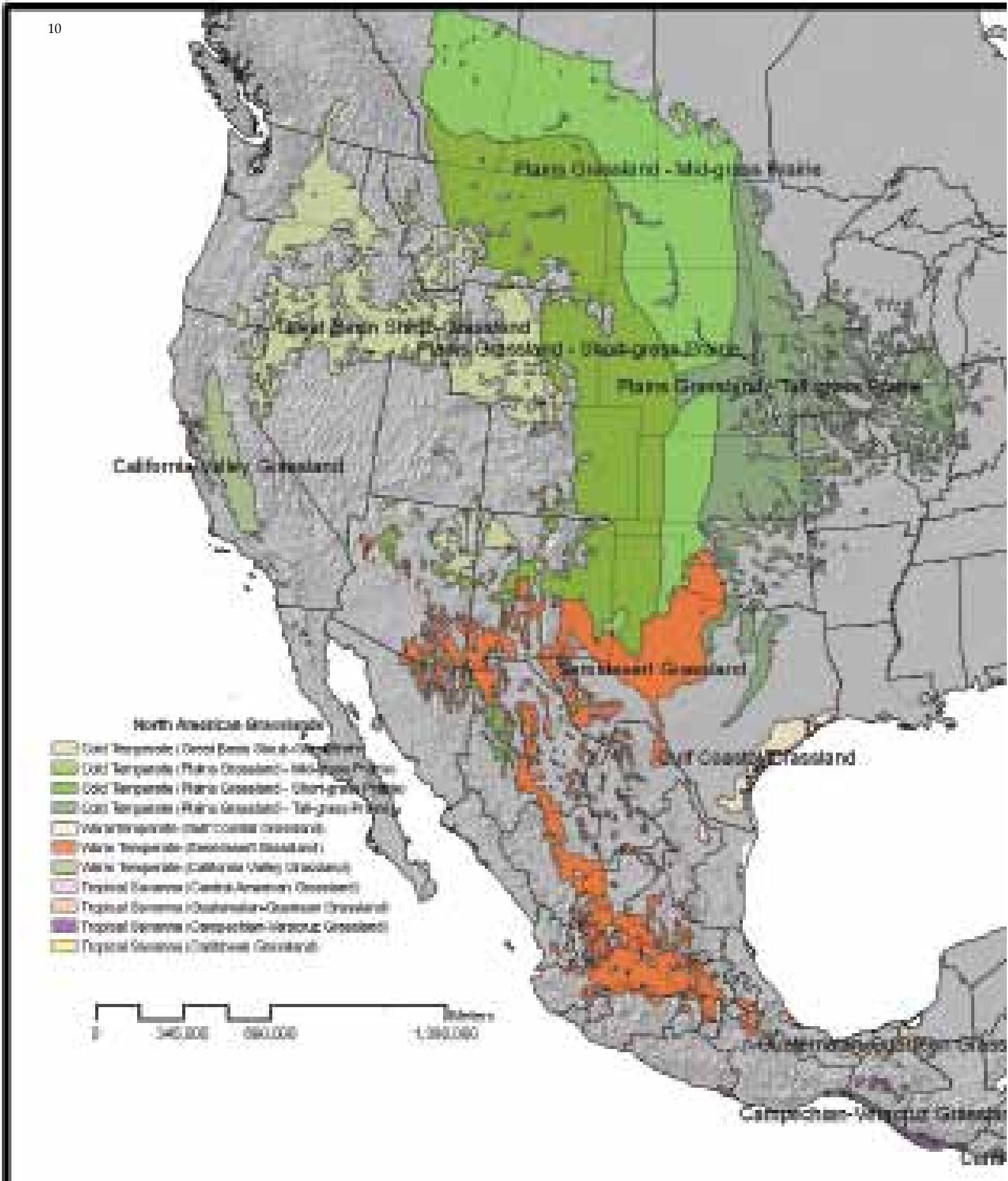
Much of the Great Basin was covered during the early Pleistocene by subalpine forests and tundra, with spruce (*Picea*) and fir (*Abies*) occurring as low as 1,070 m (3,500 ft) (Thompson 1990). Temperate montane species such as Utah juniper (*Juniperus osteosperma*) and Ponderosa pine (*Pinus ponderosa*) had yet to arrive, and the lower valleys appear to have been primarily clothed in spruce parklands, marshy meadows, or sagebrush steppe (*Artemisia* spp.) with subalpine conifers and shrubs dominating the coarser sites (Nowak et al. 1994). During the interglacials, sagebrush and other steppe dominants radiated eastward, westward, and southward, while in the American Southwest, sclerophyllous vegetation expanded northward, westward, and eastward from Mexico (Thompson & Anderson 2000).

What is now western America was inhabited by an array of savanna-inhabiting mammals including several genera of pronghorn, horses, and camels, and the large bison (*Bison priscus*), which first appeared between 1.75 and 0.8 mybp. During the Sangmonian interglacial about 45 thousand years before the present, many of these ruminants were joined by others from Asia, accelerating large mammal diversity and competition. Some, such as the forest and meadow-dwelling bison (*Bison*), elk (*Cervus*), and mammoth (*Mammuthus*) arrived during ice-free periods when such purely grassland species as Saiga antelope (*Saiga tatarica*) were unable to penetrate beyond the Beringian spruce forests. Ruminants consisted of both browsers and grazers with some of the most successful being the native pronghorns, *Antilocapra*, *Capromeryx, Stockocerus,* and *Tetrameryx* (Kurtén and Anderson 1980).

The influx of new arrivals notwithstanding, large mammal diversity now began to decrease due to further climatic shifts and increased competition, the American-derived species being more prone to extinction than their Eurasian counterparts—91% vs. 46%, respectively (Kurtén and Anderson 1980). Although grazers went into decline, open-country species generally continued to fare well with the antilocaprids being represented by several genera, most of which appear to have been specialized to live in savannas (Heffelfinger et al. 2002). The declines in temperatures in the Great Basin and Rocky Mountains during the glacials forced large herbivores to adopt migratory strategies to cope with attenuated growing seasons, while large mammals in the plains may have evolved a more nomadic feeding strategy (Burkhardt 1996). Some of the smaller prairie mammals, such as prairie dogs and thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*) became common and widespread by adapting a hibernation strategy (Kurtén 1972).

During the most recent or Wisconsin glaciation that lasted from about 45 to 11.3 kybp, North America saw significant decreases in growing season temperatures, and although pluvial lake levels may have remained relatively constant, sea levels lowered by *ca.* 100 m (328 ft) due to pack ice formation (Van Devender 1995). Then, with the withdrawal of this last great ice sheet beginning ca. 18,000 ybp, sea and lake levels began to rise, mainly due to the spring thawing of snow packs and glaciers. But even though winter temperatures began to warm, summers remained relatively cool. Summer rainfall shifted eastward and southward in the Great Basin and Northern Plains, with rainfall becoming increasingly erratic after about 14,500 ybp (Axelrod 1985). In the northern Great Basin, open conifer woodlands began replacing steppe, savanna, and tundra (Thompson & Anderson 2000). Then, beginning about 14,000 ybp, pluvial lake and ground water levels dropped dramatically indicating a series of massive droughts (Haynes 1991, Betancourt 2004).

All in all, the Pleistocene had been a time of great extinctions, but one due to plant and animal movement rather than dislocations by new species (Grayson 1991). And, although much of the northern prairie region had been under ice during the full glacial, meadow-like grasslands and savannas generally expanded during the interglacials. In Alaska and northern Canada, forest and muskeg reigned, but further south, a newer "plains grassland" was increasing in size. Here, cool-season (C-3) and warm-season (C-4) grasses alternated in dominance, the former expanding during cold periods when summer rainfall was deficient, the latter shifting northward and westward during warm summer-wet periods (Sims 1988). In the largely glacier-free valleys of the Intermountain West, vegetation changes around 12-13 kybp were more modest with some plant species remaining essen-


Plains Grassland - Mixed-grass Prairie
Tallgrass Prairie
Plains Grassland - Short-grass Prairie
Plains Grassland - Tallgrass Prairie
California Valley Grassland
Desert Grassland
North American Grasslands
Gulf Coastal Grassland
Tropical Savanna (Central American Grassland)
Tropical Savanna (Campechian-Veracruz Grassland)
Miles
0
340,000
680,000
1,360,000

Map 1. North American Grasslands

*See below for list of grasslands that are too small to map at this scale (approximately 1:25,000,000).

Rocky Mountain Alpine And Subalpine
Sierran-Cascade Subalpine
Transvolcanic Alpine And Subalpine
Rocky Mountain Montane
Cascade-Sierran Montane
Madrean Montane
Oregonian Coastal
Tamaulipan Savanna
Sonoran Savanna

tially in place while others "migrated" latitudinally (Nowak et al. 1994). Several species of small mammals did the same while some larger ones went extinct (Grayson 1993). Still others such as bison abandoned California's C-3 grasslands where the forb and shrub-dependent pronghorn persisted (Stock 1992).

Although North America averaged 75 to 100 mm (3 to 4 in) more precipitation between 9 and 11 kybp than at present, and mean temperatures were only 3-4 ºC cooler; some of the winters appear to have been much colder than now with the summers becoming hotter and drier. The result was a mosaic of extreme climatic conditions and local weather disasters as precipitation amounts and temperature fluctuations became increasingly erratic. Although winter precipitation continued to dominate the northern and western portions of the continent, periodic droughts increased in frequency and severity. With the higher mountains clothed in conifers, sagebrush steppe and juniper savanna once again dominated large areas of the Great Basin and Great Plains. Pluvial shorelines lowered, some lakes drying up entirely (Axelrod 1985, Spaulding 1990, Nowak et al.1994, Thompson and Anderson 2000).

Vegetation trends south of the Great Basin at the close of the Wisconsin glaciation are less clear, but the predominant plant cover between 300 and 1,700 m (980 and 5,570 ft) in much of what is now Arizona, California, and northern Mexico appears to have been a mixture of woodland and chaparral populated by pines (*Pinus* spp.), oaks (*Quercus* spp.) and junipers (*Juniperus* spp.) (Van Devender 1990, 1995). The climate was milder and wetter than now, with twice the winter rainfall. Summers were cooler, and summer precipitation, while declining in the north and west, and becoming more erratic elsewhere, remained influential in the south (Betancourt 1990, Connin et al. 1998). In Mexico, mixed and subalpine forest communities occupied areas above 2,000 m (6,600 ft) (Betancourt 1990), while conifer forests, encinal woodlands and chaparral covered extensive tracts of what is now semidesert grassland or desertscrub (Metcalfe et al. 2000). Temperate warm-season grasslands, always localized and restricted to generally level terrain, constituted a major vegetation type in the Central Valley of California and on Mexico's Central Plateau.

Some of the large herbivores prominent in fossil deposits after 45,000 ybp including the camel (*Camelops hesterus*), horse (*Equus conversedens)*, and mammoth (*Mammuthus primigenius*), now began to disappear (Owen-Smith 1987). Only a few of these species were replaced by arrivals crossing over from Eurasia during the interglacials via Beringia. The more recent of these immigrants, including the bison (*Bison occidentalis*), grizzly (*Ursus arctos*), and humans (*Homo sapiens*), were savanna-dwellers, which, coupled with earlier arrivals such as the bighorn (*Ovis canadensis*) and elk (*Cervus elaphus*), now began to displace the older, "native" grazers (Martin and Wright 1967). More than two-thirds of North America's ungulates disappeared between 45,000 and 10,000 ybp, including all but one genus of prongbuck. The formerly widespread *Tetrameryx shuleri* was gone by about 37,000 ybp, *Capromeryx minor* by 11,170 ybp, and *Stockoceros onusrosagris* by 11,500 ybp (Kurtén and Anderson 1980). Despite all five of the cervids present during Wisconsin times surviving, and five of the 9 bovids, none of the species of camels, elephants, and horses persisted in North America much past 10,000 ybp (Grayson 1991). Of the large (>35 kg) native herbivores adapted to open country, only *Antilocapra americana* survived. All in all, 35 genera of large mammals disappeared within the last 45,000 years (Kurtén and Anderson 1980).

The large mammal extinctions occurred due to climate change as argued by, among others, Grayson 1991, Grayson and Meltzer 2002, Tankersly and Redmond 2000. And the best climatic explanation appears to be the winter droughts that began in the Intermountain West about 14,000 ybp and continued on to the megadrought described by Haynes (1991) for southeastern Arizona around 11,000 ybp. Such droughts, punctuated by episodes of extremely low temperatures, not only triggered plant die-offs, expansive fires, and widespread insect outbreaks, they resulted in years in which nutritious vegetation was totally lacking and the reproductive success of large herbivores much decreased. Given the intense competition and predation, it is no wonder that so many open-country herbivores disappeared by ca. 11,000 ybp (Grayson and Meltzer 2002). Competition may well have been a winnowing factor, and it is interesting to note that the only large herbivores to survive were elk in the mountains and bison in the plains--both of these animals being more gramivores than forb eaters.

Man arrived in western North America some time prior to 11,500 ybp, and only a few large grassland mammals remained to be hunted (Martin and Wright 1967, Frison 2004). Of the "megafauna" only bison, elk, mammoths, and mastadons persisted, and these only where summer growing grasses still thrived. Connin et al. (1998) found that late Pleistocene mammal teeth from such species as *Bison* and *Mammuthus* indicated a strong preference for consuming summer growing C-4 grasses, and that both these grasses and their consumers had become increasingly restricted to east of longitude 114º W and south of latitude 35º N prior to perishing in the "Clovis megadrought" that took place ca. 11,000 ybp (Haynes 1991).

By ca. 9,000 ybp, modern rainfall and seasonal drought patterns were largely established (Thompson et al. 1993).

There were three major air masses shaping western North America's climate - a cold and wet air mass centered in the northwest; a warm, moist air mass in the Gulf of Mexico, and an intense but oscillating Pacific air mass. In the West especially, the latter was the most influential, the stronger the "westerlies," the more extensive the droughts. Given these emerging fore-summer weather patterns, North America's deserts and grasslands began to assume their defining characters based on temperature minima and regional drought patterns (Betancourt et al. 1990, Betancourt 2004). Only in the cold Intermountain West and northern Great Plains was winter precipitation reliable enough to maintain a semblance of the conifer-savanna and sagebrush shrub-steppe habitats that had formerly defined so much of western North America.

Eastward, in the continent's midsection, a bi-seasonal rainfall pattern and an influx of C-4 grasses from the south characterized a shifting region of prairie grassland, while to the south and southeast, an even richer summer precipitation pattern favored tall grass and coastal prairie composed of both the older Arcto-Tertiary and newer Madro-Tertiary grasses. In the American Southwest and northern Mexico, a scantier bi-seasonal rainfall pattern, coupled with increasingly warmer winters, resulted in the replacement of most of the C-3 grass dominated grasslands by a semidesert grassland savanna. Here, the higher elevations were occupied by fire-maintained savannas of C-4 bunch-grasses punctuated by *Juniperus* spp. and such southerly derived trees as *Pinus ponderosa* and pinyon pines. Meanwhile, temperate grasslands, populated almost entirely by winter rainfall-responding grasses and forbs—many of them annuals--assumed control of California's valleys (Sims 1988).

Summer temperatures continued to rise after 8,000 ybp and were probably warmer than today's. Rainfall amounts continued to decline in the continent's western interior where summer precipitation became increasingly erratic, opening up much of the remaining woodland to invasion by open savannas and shrub-steppe (Van Devender 1990, Metcalfe et al. 2000). Even greater climatic oscillations occurred during the Altithermal, a hot, dry period between 4,500 and 7,000 ybp, characterized by nearly total winter precipitation failure (Antevs 1955).

By 4,000 ybp such arid-adapted plants as Utah juniper (*Juniperus osteosperma*) and Mormon tea (*Ephedra viridis*) were declining below 1,300 m (4,260 ft) in the Great Basin (Nowak et al. 1994). A few large herbivores also had to vacate much of their former range and occupy new habitats elsewhere. Bison, for example, continued their retreat from California, the Great Basin, and the Southwest while some elk (*Cervus elaphus*) populations moved southward into the highlands of what is now Arizona and New Mexico (Carrera and Ballard 2003). Pronghorn, being C-3 forb-feeders, were more adjusted to these climatic catastrophes, not only in California, but elsewhere in the West. Humans appear to have abandoned much of the Western Plains and Great Basin during this time of advancing aridity and retreating tree-lines (Dix 1964, Axelrod 1985).

Although summer precipitation in the Southwest may have increased after 4,500 ybp, winter rainfall amounts continued to be erratic and the lowest elevations were invaded by an array of cacti and microphyllous tree/shrubs such as whitethorn acacia (*Acacia constricta*) and mesquite (*Prosopis* spp.). Pacific coastal grasslands were invaded by coastalscrub, while in the interior Southwest, the level, more favorable sites, were occupied by a "semidesert grassland" consisting of a mixture of continental grasses and xeric-adapted shrubs and succulents. With even greater aridity, semidesert grasslands in northern Mexico gave way to Chihuahuan desertscrub, while in present-day Sonora, Baja California, and southwest Arizona, cacti and small trees such as foothill palo verde (*Parkinsonia microphylla*) prospered in what would come to be known as the Sonoran Desert (Van Devender et al. 1990). A general warming trend, periodically interrupted by episodes of cooling, prevailed throughout the Holocene; each cooler (and wetter) episode being followed by another warming trend, the most recent occurring after 1890 (Dix 1964) and again during the 1990s. Great fluctuations in temperatures attended these episodes, and the accompanying winds and fires allowed grasslands to spread northward and eastward.

North America's grasslands probably reached their greatest extent sometime between 1600 and 1850 AD when approximately 40% of the continent exclusive of Alaska was an open "prairie" of one type or another (Dix 1964). Adaptations such as intercalary meristems, wind pollination, and the ability to reproduce vegetatively, allowed grasses to withstand grazing and fire, and thrive under disturbance regimes. Additionally, the grasses' sod-forming growth habits, ability to take up silica for protection from herbivorous insects, and C4 photosynthetic capacity contributed to their ecological success. Since that time, with the introduction of exotic ungulates and more erratic rainfall patterns, grasslands have been increasingly replaced by shrub steppe and desertscrub. That North America's grasslands reached their fullest development and extent after the continent's grassland megafauna had been depleted was an accident of evolutionary history, one brought about by the climatic vagaries of the Pleistocene-Holocene transition rather than the increasing aridity attendant with the Holocene.

Arctic - Boreal Grasslands

"Arctic" and "alpine" are climatic modifiers used to describe habitats so far north, or at so high an altitude, as to preclude the presence of trees. These landscapes, sometimes called "barren-ground" have traditionally been lumped together to form a *tundra formation*, which encompasses any landscape, either upland or wetland (wet tundra), beyond the limits of tree growth (Billings 1973). As such, scrublands, grasslands, or desertlands existing under an arctic climatic regime are traditionally included within a tundra formation-class (Bliss 1988, Figure 12). Although unsatisfactory from both a structural and biotic perspective, we retain this usage, and those grass and/or herb dominated landscapes found within the Polar, Greenlandian, and Alaskan biotic provinces are included within tundra formations rather than grasslands (see Brown et al. 1998; Figure 13). In a similar vein, those high altitude communities found in Central America, and populated by such grasses as *Agrostis* spp., *Trisetum* spp., *Festuca amplissima, F. setifolia, Muhlenbergia lehmanniana*, and *Trachypogon plumosus* (Davidse 1985), are considered here as being within a Neotropical *páramo* formation rather than a grassland.

Arctic - boreal grasslands in North America are found in the Cascade-Sierran, Rocky Mountain, and Transvolcanic biotic provinces on those mountains having sufficient height to attain an alpine or subalpine climatic zone. Such grasslands are typically characterized by tall bunch-grasses in company with flowering forbs in a community that is sometimes referred to as "tussock grassland" (see e.g., Walter 1973). More often, these generally high-elevation grasslands in North America are referred to as *subalpine grasslands* or *high mountain meadow grasslands* to distinguish them from the montane meadow grasslands downslope (e.g. Moir 1967, Turner and Paulson 1976, Brown et al. 1994). Alpine and subalpine grasslands may occupy valleys, slopes, and ridges, but reach their best development on undulating or level terrain adjacent to and within subalpine conifer forest. Here their size may vary from small, park-like openings within the forest to landscapes measured in square kilometers. Because of their scale, Arctic-Boreal grasslands are not mapped in Figure 1.

Subalpine grassland soils, while variable, are usually fine-grained, well drained, and possess properties unsuitable for tree growth. Temperatures are often significantly lower, and evaporation rates significantly higher, in the grasslands than in the adjacent forest but it is uncertain whether these microclimatic differences represent cause or effect. Particularly at the highest elevations, a near timberline situation of stunted trees often occurs where 2-m trees at the forest edge may be the same age as 10-m trees only five to six meters back.

Figure 12. Although often lumped in with tundra formations, arctic grasslands such as this Alaskan Grassland near Eielson Visitor Center, Denali National Park and Preserve in Alaska should probably be included within the grassland formation-class. Important grasses in this part of Alaska include *Bromus* spp., bluejoint (*Calamagrostis canadensis*), purple reed grass (*C. purpurascens*), dry fescue (*Festuca altaica*), and downy ryegrass (*Leymus innovatus*). Yarrow (*Achillea millifolium*), monkshood (*Aconitum delphiniifolium*), sage (*Artemisia frigida*), fireweed (*Epilobium angustifolium*), bluebells (*Mertensia paniculata*), and goldenrod (*Solidago multiradiata*), are important forb species (Viereck et al. 1992). August 1996, D.E.B.

Figure 13. Tundra formation above timberline 3,900 m (12,800 ft) near Summit Lake on Mt. Evans, Arapaho National Forest, Colorado. Compact, low growing species of high arctic circumpolar distribution are found in these areas. Families such as *Asteraceae*, *Caryophyllaceae*, *Cyperaceae*, *Poaceae*, and *Saxifragaceae* are consistently well-represented. September 2003, E. M.

Rocky Mountain Alpine and Subalpine Grasslands

Boreal landscapes dominated by tussock-forming grasses up to 1-m tall occur in the Rocky Mountains and mountains of the Great Basin as far north as Alberta and British Columbia to as far south as the Pinaleño Mountains in southeast Arizona. Another boreal grassland community also occurs on the eastern front of the northern Rockies where aspen (*Populus tremuloides*) parklands extend eastward on the Canadian prairie from Alberta to northwestern Manitoba (Scott 1995). Here, as the prairie's northern limits are approached, one finds islands or *mottes* of quaking aspen, balsam poplar (*Populus balsamifera*), and other boreal trees and shrubs within the grassland, and in parkland islands of prairie adjacent to tall aspen and conifer forests (Figures 14, 15). In the mountains, these bunch-grass dominated grasslands may occur as park-like openings within the forests of a particular mountain range, occupy relatively large valleys between mountains (e.g., Jackson Hole in Wyoming), or exist as extensive "prairies" on open slopes, ridges, summits, and valleys. Ranging upward from the lower edge of **Rocky Mountain Subalpine Forest** to **Rocky Mountain Alpine Tundra**, these grasslands are all at sufficient elevation to experience arctic-boreal climatic conditions.

Rocky Mountain Alpine and Subalpine Grassland occupies extensive areas in Alberta, Montana, Idaho, Wyoming, Utah, and Colorado. It reaches its southern terminus in the American Southwest where it occurs between 2,500 – 3,500 m (8,200 – 11,500 ft) in the San Juan Mountains of Colorado, the Sangre de Cristo, Jemez, San Mateo, Sierra Blanca, Magdalena, Mogollon, Chuska, and other mountains in New Mexico; in the Buckskin, San Francisco, Lukachukai, White, Escudilla, and Pinaleño mountains in Arizona; and on more limited areas of Pine Valley and other high elevation mountains in southern Utah. This biotic community does not occur in Mexico.

Annual precipitation means range from 360 mm (14 in) to as high as 1,500 mm (59 in) (Table 1). Other climatic controls such as growing season length and edaphic conditions are more important than precipitation amounts *per se*, most of which falls as snow (Scott 1995). The resulting snow pack commonly covers the ground from October to May and may be of considerable depth. Although subzero air temperatures can be expected during every winter month, soil temperatures below the snow-pack usually remain at or slightly below freezing. Hence, some plants remain green throughout the winter, while others begin growth before the completion of snow melt (Turner and Paulsen 1976). The actual growing season is brief, often less than 100 days and even then, occasionally interrupted by nighttime frosts. As in grasslands everywhere, periodic fires are needed for prairie maintenance, and aspen suckers may extend "up from

Figure 14. Rocky Mountain Subalpine Grassland/aspen parkland west of the Red Deer River on Dry Island Buffalo Jump Provincial Park, northeast of Calgary, Alberta, ca. 670 m (2,200 ft) elevation. The grasses are mostly fescues in this now ungrazed site. The aspen (*Populus tremuloides*), members of a single clone, appear to be advancing outward. May 2010, D.E.B.

Figure 15. Rocky Mountain Subalpine Grassland above and below timberline on the San Juan National Forest, southern Colorado, 3,566 m (10,026 ft). The ground cover is mostly forbs and the bases of grass clumps, the taller portions of the plants having been cropped by livestock the previous summer. Undated photo, David Cook, United States Forest Service (USFS).

underneath the prairie," capturing many prairie sites since 1880 (Scott 1995).

Well-drained sites are commonly dominated, actually or potentially, by perennial bunchgrasses of the genera *Festuca*, *Koeleria, Poa*, needlegrasses such as *Achnatherum*, *Hesperostipa*, and wheat grasses including *Agropyron*, *Elymus*, *Pascopyrum*, and *Thinopyrum*. Of these, the fescues are particularly indicative, with such species as plains rough fescue (*Festuca hallii*) dominating in central Manitoba and west central Alberta, rough fescue (*F. campestris*), and Idaho fescue (*F. idahoensis*) in the northern Rocky Mountains, spike fescue (*Leucopoa kingii*) in the Colorado front range, and Arizona fescue (*F. arizonica*), sheep fescue (*F. ovina*), and Thurber's fescue (*F. thurberi*) in the southern Rockies and Southwest (Allen 1984, Brown 1994, Dick-Peddie 1993, Peet 2000, Scott 1995) (Figure 16). These grasses occur with a greater or lesser accompaniment of others such as pine dropseed (*Blepharoneuron tricholepis*), muttongrass (*Poa fendleriana*), and introduced Kentucky blue grass (*Poa pratensis*). Forbs include regional species of yarrow (*Achillea*), mountain dandelions (*Agoseris*, *Taraxacum*), sage (*Artemisia*), paintbrush (*Castilleja*), larkspur (*Delphinium*), fleabane (*Erigeron*), skyrocket (*Ipomopsis*), lupine (*Lupinus*), cinquefoil (*Potentilla*), goldenrod (*Solidago*), clover (*Trifolium*), and vetch (*Vicia*) (Dick-Peddie 1993, Moir 1967, Scott 1995, Turner and Paulsen 1976). Wetter sites are often occupied by regional sedges of the genera *Carex* and *Cyperus*, as well as spike-rush (*Eleocharis*), *Iris* and rush (*Juncus*).

Aspen parklands are sometimes called "fescue-prairie" (Scott 1995) because of the importance of the genus, especially rough fescues, which occur with shrubby copses of clonal poplars and other shrubs in the drier sites. Heavily-grazed areas are inhabited by species of *Carex*, *Danthonia*, Junegrass (*Koeleria macrantha*), Kentucky bluegrass, needlegrasses, and wheatgrasses.

Lower down, in the moister bottom sites, these high elevation bunch-grass prairies are replaced by wet meadows populated by an even greater abundance of regional sedges and spike-rushes (*Carex, Eleocharis*) occurring in combination with a variety of moisture-dependant grasses and forbs that include bentgrasses (*Agrostis* spp.), bluejoint (*Calamagrostis canadensis*), marsh marigold (*Caltha leptosepala*), tufted hairgrass (*Deschampsia caespitosa*), fleabanes (*Erigeron* spp.), bluegrasses (*Poa fendleriana, P. nemoralis, P. reflexa* et al.), alpine timothy (*Phleum alpinum*), and American bistort (*Polygonum bistortoides*) (Windell et al. 1986). Especially in the northern climes, a heath component of bog laurel (*Kalmia polifolia*), wintergreen (*Gaultheria humifusa*), dwarf bilberry (*Vaccinium caespitosum*), and whortleberry (*V. myrtillus*) may be present along with bogs of *Sphagnum* in the wettest sites. Although both the uplands and lowlands possess a number of distinctive species, there is often much intermingling with grasses and forbs equally representative of **Rocky Mountain Alpine Tundra** above and **Rocky Mountain Montane Grassland** below.

Table 1. Mean precipitation totals and mean days with lows > 0°C for stations within or adjacent to Rocky Mountain Subalpine Grassland and Parkland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)													
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Lows >0°C
Calgary, Alberta, CANADA 51.0° N, 114.0° W	1084 (3556')	11.6	8.8	17.4	23.9	60.3	79.8	67.9	58.8	45.7	13.9	12.3	12.2	412.6 (16.2")	169.3
Edmonton, Alberta, CANADA 53.6° N, 113.5° W	723 (2372')	22.7	13	16	26.3	49.9	87.4	95.2	70.3	47.1	19.8	17.7	17.3	482.7 (19.0")	161.5
Saskatoon, Seskatchewan, CANADA 52.1° N, 106.6° W	501 (1644')	15.2	10.3	14.7	23.9	49.4	61.1	60.1	38.8	30.7	16.7	13.3	15.5	349.7 (13.8")	166.4
Winnipeg, Manitoba, CANADA 49.9° N, 97.1° W	238.7 (781')	19.7	14.9	21.5	31.9	58.8	89.5	70.6	75.1	52.3	36	25	18.5	513.8 (20.2")	170.2
Canmore, Alberta, CANADA 51.1° N, 115.4° W	1350 (4429')	27.5	21.9	23.4	32.4	59.6	61.7	54.2	60.1	42.1	29.4	26.8	33.2	472.3 (18.6")	158.9
Jackson Hole, Wyoming, USA 43.5° N, 110.8° W	1871 (6141')	37.6	25.4	29.5	28.4	47.8	41.9	26.7	29.2	32.8	29	36.6	39.1	404 (15.9")	
Estes Park, Colorado, USA 40.4° N, 105.5° W	2293 (7522')	9.4	11.4	22.1	32.8	51.6	45	56.6	48.3	30	20.8	15.5	12.2	355.7 (14.0")	170.6
Eagle Nest, New Mexico, USA 36.5° N, 105.3° W	2511 (8238')	17	16.3	25.9	27.4	32.2	30	65.8	70.6	33	25.1	18.8	18.3	380.4 (15.0")	

Figure 16. Rocky Mountain Subalpine Grassland at ca. 2,800 m (9,200 ft) in the White Mountains of the Apache-Sitgreaves National Forest, eastern Arizona. The conspicuous grass is Arizona fescue (*Festuca arizonica*). Conifers in background are mostly subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). September 1978, D.E.B.

In some localities, especially within aspen parklands, the grassland may be interspersed with a **Rocky Mountain Subalpine Scrubland** in which silverberry (*Elaeagnus commutata*), chokecherry (*Prunus virginiana*), wild rose (*Rosa* spp.), or buffaloberry (*Shepherdia argentea*) may participate. Other sites will also be populated by aspen clones, either as a consociation or punctuated with successional individuals of blue spruce (*Picea glauca*), common juniper (*Juniperus communis*) or other conifers. These woodlands may be advancing or declining depending on regional/global trends such as fire regime, ungulate densities, and climate change (Scott 1995).

Precipitation and a shorter growing season favor the integrity of **Rocky Mountain Subalpine Grassland** compared to some other grasslands due to the former's lower transpiration rates. Many alpine and subalpine grasslands in the Rocky Mountains have retained their original "wet meadow" characteristics while many of the lower elevation montane meadows have not. Subalpine meadows are often less available to heavy livestock and game use because of lingering snow packs, and hence less prone to being "dried out" by heavy grazing. Their fine alluvial soils, excess soil moisture, frequent cold air inversions, and other temperature differences contribute to making these grasslands more resilient (Daubenmire 1968, Root & Habeck 1972). Indeed, some subalpine meadows and parks have harbored stable grasslands for possibly thousands of years (Peet 2000). Another, and perhaps even more valid explanation for this continued integrity may be the difficulty for the roots of seedling trees to penetrate the dense turf of the bunch-grass sod matrix that is characteristic of these grasslands in good condition (Peet 2000).

Tree encroachment is taking place nonetheless in a number of these grasslands, a phenomenon variously ascribed to fire suppression, drought, and overgrazing (Coop & Givnish 2007, Figure 17). It is also true that few alpine and subalpine grasslands are in a climax condition because of grazing, or less commonly today, because of fire. Past and present misuse of these grasslands allowing overgrazing by sheep and cattle, while common, is not always readily apparent because of the abundant herbaceous cover that may be present and the natural variations in plant composition potential between sites (Figure 18). Generally, introduced Kentucky blue grass (*Poa pratensis*) and common dandelion (*Taraxacum officinale*) have replaced native grasses and forbs where sheep are pastured (Turner & Paulsen 1976). At lower elevations, and especially on the drier and poorer ranges, shrubs such as buffaloberry (*Shepherdia*) and certain sages may occur abundantly.

Those grass-forb and shrubby areas that are sites of recent forest disturbance and which are obviously in a successional

Figure 17. Trees, mostly Engelmann spruce, gradually invading a Rocky Mountain Subalpine Grassland in Arizona's Escudilla Mountains, ca. 2,835 m. (9,300 ft). The advancement is occurring on a sunny, south exposure and ridgeline. *Iris missouriensis* is the conspicuous forb in the foreground; Arizona fescue (*Festuca arizonica*) the dominant bunchgrass. June 2007, E.M.

stage toward subalpine conifer forest are not considered grasslands. Nonetheless, it should be noted that the grassland's edge is often in the process of being invaded by thickets of quaking aspen and small conifers so that the extent of **Rocky Mountain Subalpine Grassland** and aspen parkland is decreasing in many areas.

Of the many vertebrates inhabiting **Rocky Mountain Subalpine Grassland**, burrowing mammals are probably the most representative, including several smaller species that have adapted to the rigorous winters by hibernating, by feeding underground and/or snow, or having evolved other strategies such as porcupines (*Erethizon dorsatum*) that feed on the inner bark of selected trees during the winter months. Representative species include the marmot (*Marmota flaviventris*), gray-collared chipmunk (*Tamias cinereicollis*), least chipmunk (*N. minimus*), several meadow voles (*Microtus montanus*, *M. longicaudus*, *M. mexicanus*, *M. pennsylvanicus*), deer mouse (*Peromyscus maniculatus*), heather vole (*Phenacomys intermedius*), golden-mantled ground squirrel (*Spermophilus lateralis*), Richardson ground squirrel (*S. richardsonii*), pocket gophers (*Thomomys bottae*, *T. talpoides*), jumping mouse (*Zapus princeps*), the shrews (*Sorex cinereus*, *S. nanus, S. obscurus*, *S. vagrans*), and their predators—e.g., the long-tailed weasel (*Mustela frenata*), ermine (*M. erminea),* badger (*Taxidea taxus*), and red fox (*Vulpes vulpes*). The proclivity of the grizzly bear (*Ursus arctos*) for open areas such as subalpine grassland contributed to its near extirpation in the Rocky Mountains while other large mammals seasonally associated with these meadows such as the gray wolf (*Canis lupus*), coyote (*C. latrans*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and bighorn sheep (*Ovis canadensis*) are more or less migratory by necessity. The same is also true for pronghorn (*Antilocapra americana*), which, unlike bison (*Bison bison*), can only use these grasslands if a migratory route to a suitable wintering range is available. The insectivorous bats, e.g. *Lasionycteris noctivagans*, *Lasiurus cinereus,* and *Myotis volans* are also of necessity, summer residents only. On the other hand, snowshoe hares (*Lepus americanus*) and white-tailed jack-rabbits (*Lepus townsendii*) are characteristic residents of **Rocky Mountain Alpine and Subalpine Grassland** within their respective ranges.

No bird is restricted to, or is particularly indicative of

Figure 18. Rocky Mountain Subalpine Grassland subject to grazing on Fish Lake National Forest, Utah. The original bunch grasses have been largely replaced by wheatgrasses, low shrubs and coarse forbs. Engelmann spruce (*Picea engelmannii*) in background; elevation ca. 2,900 m (9,520 ft). Summer 1964, Lee Frataer, USFS.

Rocky Mountain Subalpine Grassland. Avian inhabitants are those species found throughout the higher open landscapes of the West for example, the red-tailed hawk (*Buteo jamaicensis*), common nighthawk (*Chordeiles minor*), raven (*Corvus corax*), horned lark (*Eremophila alpestris*), American kestrel (*Falco sparverius*), savanna sparrow (*Passerculus sandwichensis*), and mountain bluebird (*Sialia currucoides*). Other species seasonally using these high open meadows, such as the blue grouse (*Dendragapus obscurus*), yellow-rumped warbler (*Setophaga coronata*), and robin (*Turdus migratorius*) are more or less confined to the meadow's edge. Important nesting birds in aspen parklands include a host of open country raptors such as the rough-legged hawk (*Buteo lagopus*), ferruginous hawk (*B. regalis*), and Swainson's hawk (*B. swainsoni*), as well as such terrestrial shorebirds as the upland plover (*Bartramia longicauda*), white-rumped sandpiper (*Calidris fuscicollis*), marbled godwit (*Limosa fedoa*), and long-billed curlew (*Numenius americanus*).

As is to be expected in a boreal biotic community, relatively few reptiles or amphibians are present. These include the Western toad (*Bufo boreas*), short-horned lizard (*Phrynosoma douglasii*), gophersnake (*Pituophis melanoleucus*), and Western terrestrial garter snake (*Thamnophis elegans*); while tiger salamanders (*Ambystoma tigrinum*), chorus frogs (*Pseudacris triseriata*), and leopard frogs (*Rana pipiens*) can be found in adjacent subalpine wetlands.

Because of their short growing season, often steep terrain, and other generally untillable characteristics, large areas of **Rocky Mountain Subalpine Grassland** enjoy protective status. Major sites are protected in Banff and Jasper National Parks in Canada; and Glacier, Grand Teton, Rocky Mountain, and Yellowstone National Parks in the United States.

Figure 19. An example of an enclosed Rocky Mountain Subalpine Grassland at 2,775 m (9,100 ft) in the Valle Grande, Valles Caldera National Preserve, Jemez Mountains, New Mexico. Although grazed for more than two centuries this fescue grassland remains remarkably intact. Conspicuous forbs are prairie sagewort (*Artemisia frigida*), bellflower (*Campanula rotundifolia*), and woolly cinquefoil (*Potentilla hippiana*). Bunchgrasses in low, wetter areas of the grand valley are Idaho fescue (*Festuca idahoensis*) and tufted hairgrass (*Deschampsia caespitosa*). Spike muhly (*Muhlenbergia wrightii*) is the abundant bunchgrass in the foreground. Elk herd in the distance. August 2006, E.M.

Important smaller areas are also preserved in the 44,807 sq. km (17,399 sq. mi) Wood Buffalo National Park in the Northwest Territories, and in the 2,978 sq. km (1,150 sq. mi) Riding Mountain National Park in Manitoba (Scott 1995). Some excellent representative examples of this biotic community can also be found in dozens of provincial/state parks and preserves (e.g. Figure 19). In contrast, much aspen-parkland is under the plow, but many remaining parcels of this biotic community are included as managed grasslands under the jurisdiction of the various National Forests found in the Rocky Mountain states. Many of these grasslands are also protected from grazing in "natural areas," and other areas owned and/or managed by private conservation groups such as The Nature Conservancy's Pine Butte Swamp in Montana.

Cascade-Sierran Subalpine Grassland

Grassland and other herbaceous communities analogous to **Rocky Mountain Alpine** and **Subalpine Grassland** also occur within and adjacent to **Cascade-Sierran Subalpine Conifer Forest** from the eastern slopes of the Northern Cascades and the mountains surrounding the Columbia Basin in British Columbia southward through the Cascade and Sierra Nevada ranges to the Transverse Ranges in southern California. Included are elevated portions of such mountainous areas as the Okanogan Highlands of Washington and British Columbia, the east slopes of the Cascades in Washington and Oregon, the Blue Mountains in Oregon, and the Sierra Nevada, Warner, Klamath, Trinity and White mountains in California. Elsewhere in California, this biotic community is represented by small areas on Mounts Lassen and Shasta before reaching its southern terminus in the small parks and meadows found at the highest elevations of the San Bernardino, San Gabriel, and San Jacinto mountains in southern California where they occur as "snow-melt gullies" (Thorne 1977). Further investigation may show that certain high elevation meadow communities (to 2,750 m, 9,000 ft) found at Vallecitos and other valley sites in Baja California's Sierra San Pedro Martir may also qualify as subalpine grasslands in that they occur in the company of lodgepole pine (*Pinus contorta*) and aspen. Most of these "Vallecitos" grasslands, however, are contained within Jeffrey pine forest (*Pinus jeffreyi*) and are probably best considered as cold temperate **Sierran Montane Grassland** until climatic data indicate otherwise.

Examples of the **Cascade-Sierran grassland** biotic community range in size from being measured in km^2 in the mountains surrounding the Columbia Basin to a few square meters scattered within and above **Cascade- Sierran Subalpine Conifer Forest** in the Transverse Range. Too small to show on the color map and only briefly visited by the authors, the information presented here are mostly taken from the succinct summaries provided by Scott 1995, Franklin and Dyrness (1973) and Rundell et al. (1977), who have incorporated the numerous investigative works contributed by Rexford Daubenmire and his students and colleagues (e.g., Daubenmire and Daubenmire 1968).

Elevations vary considerably by latitude and longitude. **Cascade- Sierran Subalpine Grassland** occurs farther upslope on mountains in the drier south and east than in the wetter north and west. In general, the lower altitudinal limits range from 900 m (3,000 ft) in the northern Cascades, to 1,675 m (5,500 ft) in the northern and central Sierra Nevada, to 2,450 m (8,000 ft) in the southern Sierra Nevada (Storer and Usinger 1963, Franklin and Dyrness 1973, Rundell et al. 1977). The amount of precipitation is similar to that received by the **Cascade-Sierra Subalpine Conifer Forest**

Figure 20. Cascade-Sierran Subalpine Grassland meadow at an altitude of 2,150 m (7,050 ft) near Serene Lake in the Sierra Nevada, Nevada County, California. It is July, yet the snow-pack has only recently melted, allowing the forbs and grasses to commence their annual growth. Common yarrow (*Achillea millefolium*), swamp onion (*Allium validum*), cow parsnip (*Heracleum maximum*), Bigelow's sneezeweed (*Helenium bigelovii*), alum-root (*Heuchera micrantha*), yellow cinquefoil (*Potentilla glandulosa*), bird's-foot trefoil (*Lotus oblongifolius*), Sierra checkerbloom (*Sidalcea reptans*), goldenrod (*Solidago* spp.), and lady's tresses (*Spiranthes romanzoffiana*), are just a few of the flowery species likely to be present. July 2001, Richard E. Brown.

and is equally variable, ranging from as low as 200 mm (8 in) in the rain shadowed ranges of eastern Oregon and Washington to above 1,600 mm (63 in) in western Washington and British Columbia (Table 2). Temperatures are uniformly cold, however, and much of this precipitation falls as snow so that these grasslands usually experience less than 70 frost free days during the year. Like their Rocky Mountain counterpart, the physical parameters are determined as much or more by minimum temperatures, edaphic conditions, slope, exposure, and fire history, than by moisture amount.

Also, as in the Rocky Mountains, the flora is often characterized by bunch grass species of *Festuca*. On the eastern Cascade Range in Washington, and in the Wallowa and Blue Mountains of Oregon, the dominant species is greenleaf fescue (*Festuca viridula*), which when heavily grazed is replaced by grass and weed dominated communities of Letterman's needlegrass (*Achnatherum lettermannii*), Western needlegrass (*A. occidentale*), bearded wheatgrass (*Elymus caninus*), oniongrass (*Melica bulbosa*), Kentucky bluegrass (*Poa pratensis*), and half-shrubs like buckwheats (*Eriogonum* spp.). Forbs such as velvet lupine (*Lupinus leucophyllus*), Nuttall gilia (*Gilia nuttallii*), Rydberg's penstemon (*Penstemon rydbergii*), and slender mountain sandwort (*Arenaria capillaris* ssp. *americana*) may also be present (Figure 20). Because of soil loss and increased evapotranspiration rates, many of these changes from bunchgrasses to weed fields are deemed irreversible (Franklin and Dyrness 1973).

Other dominant or principal graminoids within **Cascade-Sierran Subalpine Grassland** include Ross' bentgrass (*Agrostis rossiae*), California brome (*Bromus carinatus*), tufted hairgrass (*Deschampsia caespitosa*), squirreltail (*Elymus elymoides*), Idaho fescue (*Festuca idahoensis*), alpine timothy (*Phleum alpinum*), various bluegrasses (*Poa* spp.), beardless wheatgrass (*Pseudoroegneria spicata*), and spike trisetum (*Trisetum spicatum*), as well as regional species of *Juncus* and *Carex*.

Forbs and other herbaceous plants vary according to location, grazing pressure and ecological condition. A list of the most commonly encountered forbs would include yarrow (*Achillea millefolium*), pale agoseris (*Agoseris glauca*), sandworts (*Arenaria* spp.), paintbrushes (*Castilleja parviflora,* et al.), lanceleaf springbeauty (*Claytonia lanceolata*), larkspurs (*Delphinium* spp.), buckwheats (*Eriogonum flavum, E. heracleoides*, *E. nudum*), hawkweeds (*Hieracium* spp.), scarlet gilia (*Ipomopsis aggregata*), Gray's licorice-root (*Ligusticum grayi*), lupines (*Lupinus breweri*, *L. latifolius*), Jacob's-ladders (*Polemonium* spp.), *Penstemon* spp., Cascade aster (*Eucephalus ledophyllus*), fleabanes (*Erigeron*

breweri, E. peregrinus, *E. speciosus*), woolly sunflower (*Eriophyllum lanatum*), Sierra Nevada pea (*Lathyrus nevadensis*), Cascade parsley (*Lomatium martindalei*), knotweeds (*Polygonum* spp.), cinquefoils (*Potentilla* spp), *Phlox* spp., Western pasqueflower (*Pulsatilla occidentalis*), buttercups (*Ranunculus* spp.), and clovers (*Trifolium* spp.) (Whittaker 1960, Scott 1995, Franklin and Dyrness 1973).

Shrubs include little sagebrush (*Artemisia arbuscula*), big sagebrush (*A. tridentata*), mountainheaths (*Phyllodoce* spp.), currants *(Ribes* spp.), and various species of *Vaccinium*. Particularly in the wetter northwest, some meadow communities can present an exceptionally lush appearance, containing blackandwhite sedge (*Carex albonigra*), fireweed (*Chamerion angustifolium*), fawnlilys (*Erythronium* spp.), cow parsnip (*Heracleum maximum*), purple monkeyflower (*Mimulus lewisii*), Brewer's miterwort (*Mitella breweri*), Western pasque-flower (*Pulsatilla occidentalis*), American saw-wort (*Saussurea americana*), Sitka valerian (*Valeriana sitchensis*), and false hellebore (*Veratrum viride*).

Franklin and Dyrness (1973) also describe a luxuriant Idaho fescue-snowberry (*Symphoricarpos albus*) association along the eastern margins of the Columbia Basin in which the following grasses are dominant—*Festuca idahoensis*, *Koeleria macrantha*, *Poa secunda*, and *Pseudoroegneria spicata*, to name only a few. Also present are a great variety of perennial forbs including common yarrow (*Achillea millefolium*), Palouse milkvetch (*Astragalus arrectus*), arrowleaf balsamroot (*Balsamorhiza sagittata*), yellow paintbrush (*Castilleja lutescens*), sticky geranium (*Geranium viscosissimum*), old man's whiskers (*Geum triflorum*), false sunflower (*Helianthella uniflora*), hawkweeds (*Hieracium* spp.), silky lupine (*Lupinus sericeus*), slender cinquefoil (*Potentilla gracilis*), and many more. In addition to snowberry, shrubs such as big sagebrush, threetip sagebrush (*Artemisia tripartita*), parsnipflower buckwheat (*Eriogonum heracleoides*), bitterbrush (*Purshia tridentata*), and skeletonweed (*Pleiacanthus spinosus*) were recorded.

Other lush communities, particularly those on rocky sites and cool north slopes, may be dominated by heathers such as Western moss heather (*Cassiope mertensiana*), pink mountainheath (*Phyllodoce empetriformis*), and *Vaccinium* spp. (Franklin and Dyrness 1973). These communities might be more properly considered tundra rather than alpine or subalpine grassland, however.

Farther south in the Sierra Nevada, Bennett (1965) divided subalpine meadows into three basic types, one of which (his wet meadow) is probably best considered a wetland. The other two types, woodland meadows and short-hair sedge meadows are southern extensions of the communities described by Franklin and Dyrness (1973) and are in turn dominated by grasses/forbs/rushes and sedges. The drier woodland meadows above 1,800 m (5,900 ft) elevation are typified by scattered bunch-grasses and forbs interspersed with wooded areas of lodgepole pine (*Pinus contorta*), black cottonwood (*Populus balsamifera*), aspen (*P. tremuloides*), and willows (*Salix* spp.). Principal species among the grasses are Western needlegrass (*Achnatherum occidentale*), *Agropyron* spp., California brome (*Bromus carinatus*), reedgrass (*Calamagrostis breweri*), greenleaf fescue (*Festuca viridula*), blue wildrye (*Elymus glaucus*), Sierra false needlegrass (*Ptilagrostis kingii*), and spike trisetum (*Trisetum spicatum*). Forb participants include pussypaws (*Cistanthe umbellata*), talus fleabane (*Erigeron algidus*), naked buckwheat (*Eriogonum nudum*), alpine laurel (*Kalmia microphylla*), *Lupinus* spp., tundra aster (*Oreostemma alpigenum*), Sierra beardtongue (*Penstemon heterodoxus*), and dwarf bilberry (*Vaccinium cespitosum*). A variety of carices (*Carex microptera*, *C. filifolia*, *C. scopulorum*, *C. utriculata*), fewflower spikerush (*Eleocharis quinqueflora*), and *Juncus* spp. complete the graminoid component (Strand 1972, Rundel et al. 1977, Sawyer and Keeler-Wolf 1995). Indeed, dwarf and hair sedge communities of *Carex* spp. are characteris-

Table 2. Mean precipitation totals for stations located within or adjacent to Cascade-Sierran Subalpine Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Oct.-Mar.	%
Rainier Paradise R.S., Washington, USA 46.8° N, 121.7° W	1654 (5427')	465	348	304	155	105	81	50	71	126	227	437	460	2829 (111.4")	2241	79
Crater Lake, National Park, Oregon, USA 42.9° N, 122.1° W	1974 (6475')	245	198	201	83	76	50	17	33	60	121	268	275	1627 (64.1")	1308	80
Twin Lakes, California, USA 38.7° N, 120.0° W	2438 (8000')	210	123	169	104	52	29	15	24	35	72	183	191	1257 (49.5")	998	79
Gem Lake, California, USA 37.8° N, 119.1° W	2734 (8970')	86	70	71	41	19	15	16	19	23	24	70	77	532 (21.0")	398	75
Lake Sabrina, California, USA 37.2°N, 118.6°W	2763 (9065')	75	59	51	33	16	10	11	12	20	18	50	58	413 (16.3")	311	75

tic throughout the range of **Cascade-Sierran Alpine and Subalpine Grassland**, where these communities are an important forage resource for domestic sheep.

Associated trees may be such Krumholtz forming species as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce, with stands of Pacific silver fir (*Abies amabilis*), Western juniper (*Juniperus occidentalis*), lodgepole pine (*Pinus contorta*), and mountain hemlock (*Tsuga mertensiana*) in western Canada and Washington. In the eastern slopes of the Cascades and in the Okanogan Mountains the deciduous and flame-foilaged subalpine larch (*Larix lyalli*) presents a most spectacular autumn appearance. On the more xeric sites, the white-bark pine (*Pinus albicaulis*) is the most common conifer—a phenomenon no doubt assisted by the Clark nutcracker (*Nucifraga columbiana*), which disperses its seeds not only throughout the subalpine forest but the grassland as well (Franklin and Dyrness 1973). These trees, although often occurring in groups, ordinarily do not include aspen as a participant as is so often the case in the aspen parklands and Rocky Mountains. Nonetheless, the forest establishment procedure appears to be the same, the trees radiating outward from a single clump of pioneers. And although some subalpine meadows have remained stable for many years, others have experienced massive tree invasions during the 20th Century (Franklin and Dyrness 1973). Whether this phenomenon is due to the upward movement of timberline from a warmer, drier climate since 1925 or to fire suppression is much debated.

As within **Rocky Mountain Subalpine Grassland**, one may also encounter 0.5 to 3 m (1-10 ft) tall patches of a **Cascade-Sierran Subalpine Scrubland** of black hawthorn (*Crataegus douglasii*), chokecherry (*Prunus virginiana*), bitterbrush (*Purshia tridentata*) and/or Nutka rose (*Rosa nutkana*), in addition to snowberry and other boreal shrubs with nettleleaf giant hyssop (*Agastache urticifolia*) commonly being the only herbaceous plant present. Other sites, although populated by herbaceous plants such as the sedge and moss bogs found below seepage areas, are more properly considered wetlands. In a similar vein, the sparsely vegetated "pumice deserts" such as those found south of Mount Jefferson in the Cascade Range and in Crater Lake National Park's "Cinder Desert" are probably best regarded as successional subalpine and cold temperate desertscrub communities in that they are edaphically prevented from attaining grassland status. Indeed, the species of plant participants listed for these areas are somewhat unique in their adaptations to these barren situations e.g., Crater Lake sandwort (*Arenaria pumicola*), Brewer's sedge (*Carex breweri*), cobwebby Indian paintbrush (*Castilleja arachnoidea*), Mt. Hood pussypaws (*Cistanthe umbellata*), marumleaf buckwheat (*Eriogonum marifolium*), Shasta buckwheat (*E. pyrolifolium*), Cascade parsley (*Lomatium martindalei*), desert lupine (*Lupinus aridus*), littleflower penstemon (*Penstemon procerus*), Davis' knotweed (*Polygonum davisiae*), and silky raillardella (*Raillardella argentea*) (Horn 1968).

According to Storer and Usinger (1963), many of the animals are open-space adapted species shared with **Rocky Mountain Alpine and Subalpine Grassland**. Included among the mammals are the Sierra subspecies of bighorn sheep (*Ovis canadensis californiana*), pocket gophers, and meadow mice. Ground squirrels are more poorly represented than in the Rocky Mountains, however, and only a few species such as the Cascade golden-mantled ground squirrel (*Spermophilus saturatus*) are endemic to this biotic community. The Columbian ground squirrel (*S. columbianus*) is confined to the northern fasciations, and both the hoary marmot (*Marmota caligata*) of the north and yellow-bellied marmot (*M. flaviventris*) of the south are shared with **Rocky Mountain Alpine and Subalpine Grassland** (Hall and Kelson 1959).

Many bird species are also shared between the two biotic communites but with differentiation at the subspecies level. One such example is the blue or dusky grouse (*Dendragapus obscurus*), which occurs in the Rocky Mountains as *D. o. obscurus* and in the Sierra Nevada as *D. o. sierra*.

Although heavily used for recreation and livestock grazing, many areas **of Cascade-Sierran Alpine and Subalpine Grassland** are protected and/or managed within an extensive system of National Parks, Provincial Parks, National Forests, and State areas with a number of wilderness and natural areas. Some of the larger national parks are the North Cascades, Olympic, and Mount Rainer in Washington state; and Yosemite, Kings Canyon and Sequoia in California.

Transvolcanic Alpine and Subalpine Grassland

Tall bunch-grass communities up to a meter in height and variously termed alpine meadows, *páramo de altura*, and *zacatonales* occur on the Eje Volcanico from elevations of 3,500 m (11,500 ft) to above timberline at 4,300 m (14,100) ft) (Miranda 1952, Rzedowski 1988, Almeida et al. 1994, Velázquez et al. 2000). Because these grasslands are neither closely related to North America's alpine and subalpine grasslands, nor to the *páramos* of Central and South America, the local term *zacatonal* has been used to describe this biotic community, confined to El Popocatepétl, El Ixtaccíhuatl, La Malinche, El Nevada de Toluca, El Cofre de Perote, El Tancitaro and Pico de Orizaba in central Mexico (Cruz 1969, Almeida et al. 1994, Velázquez et al. 2000). The climate of these *zacatonales* is imperfectly known but the mean annual temperature at 3,900 m (12,800 ft) on Iztaccihuatl (the White Lady) was reported to be from 3 to 5º C (37 – 41 F) with lower limits around -10 ºC (14 F) and an annual precipitation varying from 600- 1,300 mm (24 -51 in), the majority of which falls as snow (Beaman 1962, Rzedowski 1988). Although Iztaccihuatl has (had) the only alpine glacier in Mexico, there is no permafrost in the Eje Volcanico.

Velázquez et al. (2000) describe a subalpine *zacatonal* dominated by a densely layered community of 50-cm (19 in) tall Toluca fescue (*Festuca tolucensis*) and Toluca reedgrass (*Calamagrostis tolucensis*) on deep soils with abundant plant litter occurring in the valley flats of volcanic craters ca. 3,500 m (11,480 ft) (Figure 21). These plants are adjacent to or above an open forest of Hartweg and/or Montezuma pines (*Pinus hartwegii, P. montezumae*) where they form an open ground layer joined by *Juniperus monticola* and such grasses and forbs as *Arenaria bryoides, Descurainia impatiens*, *Draba jorullensis, Lupinus montanus*, *Muhlenbergia pusilla*, *M. quadridentata*, *Oxalis* sp., *Pedicularis orizabae*, *Penstemon gentianoides*, *Poa annua*, *Potentilla staminea*, *Sicyos parviflorus*, and *Trisetum spicatum* (Rzedowski 1988, Velázquez et al 2000). At slightly higher elevations, ca. 3,800 m (12,500 ft), the *zacatonal* is often dominated by *Muhlenbergia quadridentata* before being replaced by a community dominated by *Calamagrostis tolucensis* at 3,800 to 4,200 m (12,5000 -13,800 ft). At still higher elevations, ca. 4,300 m (14,100 ft), *Festuca livida* becomes dominant along with *Arenaria bryoides*. Other plants at this alpine location include *Festuca tolucensis* and species of *Carex*, *Cerastium*, *Cirsium*, *Draba*, *Eryngium*, *Gnaphalium*, *Lupinus*, *Luzula*, *Oxylobus*, *Phacelia*, *Plantago*, *Potentilla*, *Ranunculus* and *Senecio*, as well as a number of ferns, mosses, and lichens (Rzedowski 1988).

The climatic status of two other herbaceous communities found in the Valley of Mexico and on its volcanoes is less certain. Here, between 3,000 and 3,300 m (9,800 -10,800 ft), on poorly drained soils, Cruz (1969) reported the flatlands surrounding certain volcanic cones to contain heavily

Figure 21. Transvolcanic Alpine and Subalpine Grassland southeast of Mexico City, Mexico, D.F. Important grass species in this "zacatonal" are high elevation species of *Festuca*, *Muhlenbergia* and *Stipa*. The snow-capped peak in the background is Volcán Popocatápetl, 5,452 m (17,888 ft). Undated, Alejandro Velázquez.

disturbed meadows or *praderas* populated by a single ground layer of forbs and grasses. Cruz (1969) reported these *praderas* to be dominated by such plants as *Potentilla candicans* and *Stipa ichu*, with *Alchemilla procumbens*, *Astragalus micranthus*, *Bidens triplinervia*, *Commelina alpestris*, *Gnaphalium seemannii*, *Hedeoma piperita*, *Reseda luteola*, *Salvia* spp., and *Vulpia myuros* being important constituents.

Another possible subalpine grassland occurs between 3,090 and 3,340 m (10,100 – 11,000 ft) on the dissected rocky slopes of volcanoes such as Pelado and Tláloc, where Velázquez et al. (2000) reported an herbaceous community dominated by *Furcraea parmentieri*, an agave with stalks from 0.5 to 5.3 m (1.6-17 ft) tall. The accompanying plants on these mostly shallow soils, while floristically rich, formed a relatively open herb layer, which was reported to include *Alchemilla procumbens*, *Festuca amplissima, Geranium potentillaefolium*, *Gnaphalium oxyphyllum*, *Laennecia schiedeana*, *Muhlenbergia macroura*, *M. quadridentata*, *Senecio angulifolius*, *Sibthorpia repens*, *Stipa ichu*, and *Symphoricarpos microphylla*.

The *zacatonales* are the home of the now nearly extinct Sierra Madre sparrow (*Xenospiza baileyi*), at least one shrew (*Cryptotis goldmani alticola*), the volcano mouse (*Neotomodon alstoni*), the volcano harvest mouse (*Reithrodontomys chrysopsis*), and the volcano rabbit (*Romerolagus diazi*), as well as hosts of amphibians, reptiles and insects, which like the flora, is distinctive with a great amount of endemism (Rzedowski 1988). Unfortunately, a long history of dense human population pressures including grazing abuses and unregulated burning have resulted in many of these communities being either depauperate, seral, or in a disclimax state regardless of a protective status initiated in 1935 that included nearly 4,000 km² (1,544 mi²) of lands with the potential to support this biotic community (World Conservation Monitoring Centre 1992). Altogether, the **Transvolcanic Alpine and Subalpine Grassland** covers only 0.02% of Mexico (Velázquez et al. 2000).

Another herbaceous biotic community found in the boreal climatic zone —**Guatemalan Subalpine Grassland**— occurs in small patches from 0.5 to 2 m (1.6 – 6.6 ft) tall above 3,050 m (10,000 ft) on the high volcanoes bordering Mexico and Guatemala (Miranda 1952, Wagner 1964). One of the best developed of these resides above a 4,000 m

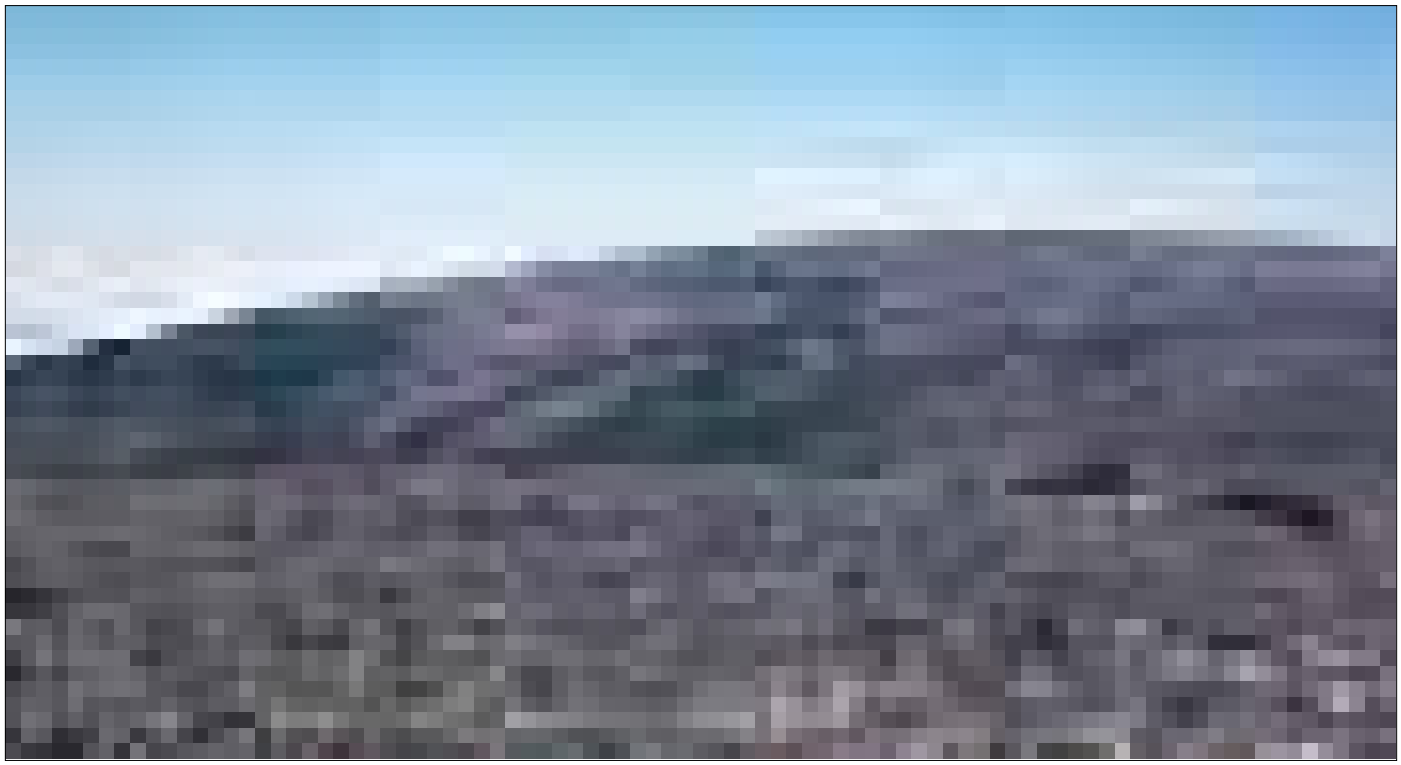


Figure 22. “Meadow” community atop Cerro Potosí, Nuevo León, Mexico, at ca. 3,700 m (12,410 ft) populated by short-statured forbs such as *Arenaria* spp., *Bidens muelleri*, *Castilleja bella*, *Lupinus cacuminis*, *Potentilla leonina*, and *Senecio scalaris* (Beaman and Andersen 1966). The almost total lack of grasses in this “alpine meadow” may be at least partially due to grazing pressure. Nonetheless, the abundance of bare rock and the prostate nature of the vegetation argue that this is a singular example of Madrean Alpine Tundra rather than Subalpine Grassland. June 2003, D.E.B.

Figure 23. Pumice and other substrates that prevent biotic communities from attaining climax status present a conundrum when classifying the type of vegetation present whether in subalpine or temperate environments. Here in Lava Beds National Monument, Idaho, one encounters a “desertscrub” formation within what would normally be Rocky Mountain Montane Conifer Forest. September 1993, D.E.B.

(13,100 ft) "tree-line" of scrub *Juniperus standleyi* atop Volcán Tacaná (on the border between Chiapas and Guatemala (Wagner 1964, Breedlove 1973). Dominated by 1 m (3 ft) tall communities of *Lupinus montanus* and tussocks of *Calamagrostis vulcanica*, this little studied biotic community reportedly has a ground layer of mosses along with such more or less endemic constituents as *Alchemilla pinnata*, *Arenaria bryoides*, *Draba volcanica*, *Festuca tolucensis*, *Gentiana pumilio*, *Gnaphalium salicifolium*, *Haplopappus stolonifer*, *Lobelia nana*, *Luzula racemosa*, *Pernettya prostrata, Potentilla heterosepala*, *Viola nannei*, *Weldenia candida*, and *Werneria nubigena*, with the moss *Racomitrium crispulum* dominating rocky outcrops (Breedlove 1973, Islebe and Velázquez 1994). Other dominants on these high volcanoes, including Guatemala's Volcán Tajumulco (4,220 m, 13,800 ft), include the grasses *Bromus carinatus, Briza rotunda, Festuca amplissima*, *Muhlenbergia gigantea*, *M. macroura*, *M. robusta*, *Piptochaetium virescens*, *Stipa ichu*, and *Trisetum irazuense* (Breedlove 1973). The only endemic animal heretofore assigned to this little studied community is the narrow-nosed harvest mouse (*Reithrodontomys tenuirostris*) (Hall and Kelson 1959).

Another isolated herbaceous alpine community occurs above Hartweg pine (*Pinus hartwegii*) forest and *Pinus culminicola* scrub atop Cerro Potosí (3,650 m, 12,000 ft) in the Sierra Madre Oriental of Nuevo Leon (Beaman and Andresen 1966, Cruz 1969). Grasses are sparse above 3,500 m (11,500 ft), however, and this flower-strewn herbland may best be regarded as a lone representative of a **Sierra Madrean Alpine Tundra** biotic community (Figures 22, 23).

Cold Temperate Grasslands

Extensive grasslands recently existed throughout the world's temperate zones under semi-arid and wind-swept conditions, and in other areas unfavorable for tree or scrub growth. These grass and/or herb dominated landscapes reached maximum size and development in the Eurasian "steppe" and the North American "prairie," both of which evolved within a continental type climatic regime characterized by cold, harsh winters with a substantial portion of the limited precipitation falling during a more or less arid growing season (see, e.g. Walter 1973). In North America, **Plains Grassland** (tall-grass, mid-grass, short-grass prairie, etc.) is, along with the older **Intermountain Grassland**, the most important biotic community in the evolutionary history and development of our continent's grassland biota. **Plains Grassland** is a mid-summer flowering grassland extending from approximately 55° N latitude in the Canadian provinces of Alberta and Saskatchewan southward to below latitude 30° N in Mexico, and once covered much of the American "Midwest" from the eastern deciduous forest westward to the Rocky Mountains. More than 75% (some estimates as high as 90%) of **Plains Grassland** is now under cultivation, has been converted to urban infrastructure, or otherwise transformed by people (see e.g., Garrison et al. 1977, Gibson 2009).

Centered in the Columbia Basin of eastern Washington and northeastern Oregon is a grassland region commonly referred to as the "Palouse Prairie" (see e.g., Shelford 1963:350). This spring-flowering Great Basin or **Intermountain Grassland** is generally restricted to those areas west of the Rockies and east of the Sierra-Cascades possessing suitable precipitation, soils, and grazing history. Much of it is appropriately described as a shrub-steppe in that pure grass landscapes without such shrubs as *Artemisia tridentata* are limited (Franklin and Dyrness 1973). It should also be noted that extensive areas of **Intermountain Grassland** merge with the generally wetter **Plains Grassland** over a large transition area adjacent to the Rocky Mountains in Montana, Wyoming, Colorado, New Mexico and Arizona. Much of this grassland and shrub-steppe has also been converted to cropland through irrigation and nearly all of the remainder has been subject to livestock grazing and fire suppression.

In addition to Plains and Intermountain Grassland, cold temperate grasslands in North America are represented by other, smaller grass and herb dominated areas in the Pacific Northwest (**Oregonian Grassland**), in the Rocky, Sierra Nevada, and Sierra Madre mountains (montane meadow grasslands) and by select areas within the **Northeastern Deciduous Forest** (e.g., **Northeastern Grassland** on Martha's Vineyard, MA).

Rocky Mountain Montane Grassland

Montane meadow grasslands (also too small to show on the color map) within and adjacent to **Rocky Mountain Montane Conifer Forest** are typically encountered as natural openings or "parks" within the forest on flatlands possessing heavy, poorly drained soils (Figures 24 and 25). Such soils are unfavorable for tree growth, and the forest edge can be abrupt, producing a marked "edge effect." **Otherwise, Rocky Mountain Montane Grasslands** share the same general elevations and climatic parameters as those found within **Rocky Mountain Montane Conifer Forest** communities (Table 3).

Herbs, and forbs or "weeds" can outnumber the grasses making these lower elevation "flower meadows" distinct from the higher, colder, and sometimes adjacent subalpine grasslands, which are more often dominated by bunchgrasses. Also not to be confused with montane meadow grasslands are extensions of **Plains and Intermountain Grassland** into the lower reaches of Ponderosa pine forest on plateaus and mesas.

Where not grazed too heavily, a great variety of summer flowering perennial forbs and grasses may be present (Figure 26). Surprisingly, many of the same characteristic meadow species are present in montane grasslands in the Rocky Mountains, the Sierra-Nevada, and the Sierra Madre including such widespread and conspicuous native plants as monkey flower (*Mimulus* spp.*),* mountain muhly (*Muhlenbergia montana*), brackenfern (*Pteridium aquilinum*), Western wheatgrass (*Pascopyrum smithii*), blackeyed Susan (*Rudbeckia hirta*), corn-lily (*Veratrum californicum*), and such established exotics as orchard grass (*Dactylis glomerata*), Kentucky bluegrass (*Poa pratensis*), and mullein (*Verbascum thapsus*). Another shared species is *Iris missouriensis* (see Figure 17) which may completely dominate heavily grazed meadows. Nonetheless, many of the participants are regionally restricted as is to be expected within a distinctive large biotic community.

Rocky Mountain Montane Meadow Grassland typically supports a large number of showy herbs in the genera *Astragalus*, *Campanula*, *Erigeron, Helianthus*, *Ipomopsis, Lathyrus*, *Lotus*, *Lupinus*, *Penstemon*, *Pseudocymopterus*, *Senecio*, *Solidago, Sphaeralcea*, *Vicia*, and *Viola*. Because of this initially abundant herbage, these meadow grasslands have been, and still are, centers for livestock operations that often subject the meadows to heavy grazing pressures. Such overgrazing commonly results in changes in plant composition from grasses and forbs to shrubs (especially species of *Artemisia* and *Chrysothamnus*). In many cases, forest trees, mostly Ponderosa pine (*Pinus ponderosa*) are also invading the meadows, and, should the trampling, drying, and erosion continue, the soils will lose their binding character and the grassland itself will be irretrievably lost (Figure 27).

Figure 24. Rocky Mountain Montane Grassland northwest of Saint Mary on the Blackfoot Indian Reservation, Montana—early spring aspect. This grassland at 1,368 m (4,488 ft), although heavily used by horses and other stock, has maintained its montane integrity despite merging with Plains Grassland to the east. June 1990, D.E.B.

Figure 25. Rocky Mountain Montane Grassland in Valle Santa Rosa, on the Valles Caldera National Preserve, NM. Constraints on conifer growth in the valley bottoms resulting in reversed tree line effect – a function of several biotic and abiotic processes, especially differences in well-drained slopes vs. fine textured, moist, meadow soils; very cold nightly temperatures which puts restraints on seedling recruitment; and competition from grasses (Coop & Givnish 2007). Blue spruce (*Picea glauca*) are the conifers lining valleys in this system. August 2007, E. M.

Table 3. Mean precipitation totals for stations located within and adjacent to Rocky Mountain Montane Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Apr-Sept	%
Smithers, British Columbia, CANADA 54.8° N, 127.2° W	524 (1718')	55	30	24	22	32	40	49	39	48	60	56	57	512 (20.2")	230	45
Prince George, British Columbia, CANADA 53.9° N, 122.7° W	676 (2218')	59	43	32	30	42	58	58	73	56	61	55	54	621 (24.4")	317	51
Jasper, Alberta, CANADA 52.9° N, 118.1° W	1061 (3480')	30	24	15	23	35	50	48	48	35	30	33	33	404 (15.8")	239	59
Kleena Kleene, British Columbia, CANADA 52.0° N, 124.9° W	899 (2950')	44	18	15	20	25	40	29	34	20	32	36	45	358 (14.1")	168	47
Big Creek, British Columbia, CANADA 51.7° N, 123.0° W	1134 (3720')	28	18	22	16	30	52	33	46	27	19	20	29	340 (13.4")	204	60
Kimberley, British Columbia, CANADA 49.7° N, 115.8° W	919 (3016')	42	27	22	18	35	52	21	32	24	28	35	42	378 (14.9")	182	48
Libby Ranger Station, Montana, USA 48.4° N, 115.5° W	639 (2096')	55	37	31	27	41	41	28	26	29	34	61	53	463 (18.2")	192	41
Seeley Lake Ranger Station, Montana, USA 47.2° N, 113.5° W	1250 (4100')	75	61	40	33	50	54	28	33	36	32	52	53	547 (21.5")	234	43
Lincoln Ranger Station, Montana, USA 46.9° N, 112.7° W	1394 (4575')	54	35	29	31	59	51	29	36	34	29	35	50	472 (18.6")	240	51
S. Livingston, Montana, USA 45.5° N, 110.6° W	1484 (4870')	18	12	27	33	75	65	38	38	49	35	23	17	430 (17.0")	298	69
Swan Valley, Idaho, USA 43.5° N, 111.3° W	1634 (5360')	38	27	26	38	59	42	32	33	41	29	38	31	434 (17.1")	245	56
Colorado Springs, Colorado, USA 38.8° N, 104.7° W	1856 (6090')	7	10	26	30	55	57	74	77	34	21	12	14	417 (16.4")	327	78
Chama, New Mexico, USA 36.8° N, 106.6° W	2393 (7850')	45	40	51	32	28	28	57	72	57	50	22	46	528 (20.8")	274	52
Fort Valley, Arizona, USA 35.3° N, 111.7° W	2239 (7347')	55	42	54	41	18	16	75	88	43	36	34	57	559 (22.0")	281	50
Ruidoso, New Mexico, USA 33.3° N, 105.7° W	2060 (6760')	27	27	33	17	22	50	109	76	64	27	17	40	509 (20.0")	338	66
Mt. Lemmon, Arizona, USA 32.5° N, 110.8° W	2371 (7779')	59	39	62	25	7	23	147	##	51	40	38	51	681 (26.8")	392	58

Although not often extensive, these attractive landscapes are nonetheless important to the meadow-affiliated animals of the **Rocky Mountain Montane Conifer Forest**; such species in the appropriate geographic area as elk (*Cervus elaphus*), Pacific-slope flycatcher (*Empidonax difficilis*), wild turkey (*Meleagris gallopavo*), meadow voles (*Microtus californicus, M. mexicanus*, etc.), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and Western bluebird (*Sialia mexicana*), and pocket gophers (*Thomomys bottae*, et al.). The larger meadows may also serve as more or less seasonal habitats for such grassland species as the pronghorn (*Antilocapra americana*), American kestrel (*Falco sparverius*), and meadowlarks (*Sturnella magna* and *S. neglecta*).

Where streams course through the meadows, leopard frogs (*Rana pipiens*) and garter snakes (*Thamnophis elegans*) are normally present and should be abundant. Wet meadows without stream development, but with small ponds at lower ends, often support populations of tiger salamanders or water-dogs (*Ambystoma tigrinum*) and chorus frogs (*Pseudacris triseriata*), as do the subalpine meadows higher up. Thus, the amphibian species in montane meadow grasslands are usually found in the lower wetland portions of the meadows where wetland graminoids (*Carex, Cyperus, Eleocharis, Juncus*, etc.) are to be expected.

Figure 26. Rocky Mountain Montane Grassland on the Apache-Sitgreaves National Forest, Apache County, Arizona. This "flower meadow" of forbs at an altitude of 2,157 m (7,977 ft) shows the effects of grazing—summer aspect with Escudilla Mountain in the background. June 1969, D.E.B.

Figure 27. Bunch-grasses, mainly *Festuca arizonica* and *Muhlenbergia montana* in this photo, dominate in this southwestern extension of Rocky Mountain Montane Grassland in Government Prairie at ca. 2,220 m (7,270 ft) on the South Kaibab National Forest west of Flagstaff, Arizona. The encroaching trees are Ponderosa pine (*Pinus ponderosa*). Undated, D.E.B.

Cascade-Sierran Montane Grassland

Located within or adjacent to **Cascade-Sierran Montane Conifer Forest,** one can encounter grass and herb strewn meadows ranging in size from a few to several hundred hectares. Analogous to, and only partially differentiated from its Rocky Mountain counterpart, C**ascade-Sierran Montane Meadow Grassland** is found in the foothills and valleys of south-central British Columbia west of the Columbia Basin, southward through the Cascade and Sierra Nevada ranges, through the Transverse and Peninsular ranges of southern California, to the vicinity of Vallecitos in the Sierra San Pedro Martir (Franklin and Dyrness 1973, Barbour and Major 1977, Scott 1995). Generally speaking, precipitation amounts are greater in this biotic community than in **Rocky Mountain Montane Meadow Grassland** due to the reduced rain shadow.

The mean annual precipitation is that of the adjacent or surrounding forest, ranging from as high as 1,500 to 2,800 mm (59 - 110 in) in the wetter northwest through a declining summer precipitation regime to as low as 500 mm (20 in) in the arid Californias (Franklin and Dyrness 1973, Brown 1994, Table 4). The elevation range is also great, rising from 600-1,300 m (1,970-4,260 ft) in the Northern Cascades of Washington State, through 900-2,000 m (2,950-6,600 ft) in southern Washington and the Sierra Nevada, up to 2,300-2,750 m (7,600-9,020 ft) in the southern Sierra Nevada and Transverse ranges, again depending upon the effects of rain shadow and slope exposure.

In their natural state, or where protected from grazing, the vegetation may take on the appearance of a bunch-grass-herb parkland nestled within the Douglas-fir and Jeffrey pine zones (*Pinus ponderosa*, *P. jeffreyi*; Figure 28). The size of any given parcel may range from square kilometers as in the Fraser and southern Kootenay valleys in southern British Columbia and in the Okanagan Valley in Washington, through more moderate sized areas such as Yosemite Valley in the Sierra Nevada, to small "postage stamp" snow melt meadows in the San Gabriel and San Bernardino mountains in California (Thorne 1977).

Unlike **Cascade-Sierran Subalpine Grassland**, forbs commonly outnumber the grasses, which may include Indian ricegrass (*Achnatherum hymenoides*), Thurber's needlegrass (*Achnatherum thurberianum*), crested wheatgrass (*Agropyron cristatum*), cheatgrass (*Bromus tectorum*), pinegrass (*Calamagrostis rubescens*), wild rye (*Elymus canadensis*), rough fescue (*Festuca campestris*), Idaho fescue (*F. idahoensis*), needle and thread (*Hesperostipa comata*), junegrass (*Koeleria macrantha*), and *Poa pratensis* (Watson and Murtha 1978, Sawyer and Keeler-Wolf 1995). Not only does this biotic community share many of the same species as **Rocky Mountain Montane Grassland**, it often also merges almost imperceptibly with

Intermountain Grassland on the Sierra's eastern slopes and adjacent lower valleys. Here, the grasslands usually contain such bunch-grasses as squirreltail (*Elymus elymoides*), beardless wheatgrass (*Pseudoroegneria spicata*), and the seemingly invasive big sagebrush (*Artemisia tridentata*), the latter sometimes accompanied or replaced by prairie sagewort (*A. frigida*) and threetip sagebrush (*A. tripartita*). In the lower elevation grasslands to the west one is more likely to encounter species more typical of **Oregon Coastal Grassland** and **California Valley Grassland**.

In the Rocky Mountains, it is an abundance of flowering herbs that primarily distinguishes this biotic community from the higher elevation subalpine meadows upslope. Montane forbs listed by Franklin and Dyrness (1973) for Washington and Oregon include many genera typical of **Sierra Nevada Montane Meadow Grassland**— *Castilleja parviflora*, *Claytonia lanceolata*, *Chamerion angustifolium*, *Erythronium grandiflorum, Eucephalus ledophyllus*, *Lupinus latifolius*, *Phlox diffusa*, *Potentilla flabellifolia*, *Senecio triangularis*, and *Solidago canadensis* to name only a few. Bracken fern (*Pteridium aquilinum*) and thimbleberry (*Rubus parviflorus*) are often abundant enough to be regarded as dominants, with sagebrushes, (*Artemisia arctica, A. ludoviciana*) locally common. Lewis monkeyflower *Mimulus lewisii* may almost exclusively occupy wet areas in company with the appropriate species of *Carex*, *Cyperus* and *Juncus*.

In the Blue Mountains of the southeastern Walla Walla Mountains, and locally elsewhere, one can find limited areas occupied by a 0.5 to 3-m tall (1.6 – 10 ft) **Cascade-Sierran Montane Scrubland** (Franklin and Dyrness 1973). Here the principal species may be *Artemisia arbuscula*, *Ceanothus velutinus*, *Cercocarpus ledifolius*, *Prunus emarginata*, *Purshia tridentata*, *Rosa nutkana*, *Salix scouleriana*, and higher up, kinnikinnick (*Arctostaphylos uva-ursi*). Herbaceous species are often sparse or lacking and the only herbaceous plant in these thickets may be nettleleaf giant-hyssop (*Agastache urticifolia*).

Although the origin of these meadows is sometimes attributed to the filling in of glacial lakes and valleys (Storer and Unsinger 1963), Ratliff (1974) proposed an alternative hypothesis by which such densely structured species as bog laurel (*Kalmia polifolia*) and *Vaccinium* spp., in conjunction with various mosses, formed vegetative mats upon which tussock grasses such as *Calamagrostis breweri* eventually took hold, thereafter precluding the invasion of trees by maintaining a dense matrix of grass and sedge roots and a high water table (Rundel et al. 1977). Moreover, Wood (1975) showed that many meadows between 1,500 and 2,500 m (4,900 –

Table 4. Precipitation totals for stations located within or adjacent to Cascade-Sierran Montane Grasslands

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Oct - Mar	%
Revelstoke, British Columbia, CANADA 51.0° N, 118.2° W	456 (1497')	151	109	72	57	51	74	57	64	76	106	121	158	1096 (43.1")	717	65
Newport, Washington, USA 48.2° N, 117.1° W	651 (2136')	84	64	56	47	56	47	29	34	34	42	93	101	687 (27.1")	440	64
Lake Wenatchee, Washington, USA 47.8° N, 120.8° W	611 (2005')	211	112	72	44	31	24	13	21	32	79	156	194	989 (38.9")	824	83
Packwood, Washington, USA 46.6° N, 121.7° W	323 (1060')	254	167	128	86	61	49	23	35	62	115	214	238	1432 (56.4")	1116	78
Mt. Adams, R.S., Washington, USA 46.0° N, 121.5° W	597 (1960')	204	151	118	52	33	25	9	21	27	75	183	205	1103 (43.4")	936	85
Oakridge Fish Hatchery, Oregon, USA 43.8° N, 122.5° W	389 (1275')	165	123	123	92	66	43	16	28	45	84	155	163	1103 (43.4")	813	74
Mount Shasta, California, USA 41.3° N, 122.3° W	1094 (3590')	160	131	130	67	39	21	9	12	21	61	146	142	939 (37.0")	770	82
Manzanita Lake, California, USA 40.5° N, 126.6° W	1752 (5750')	145	126	138	83	61	38	10	23	38	84	149	138	1033 (40.7")	780	75
Donner Memorial S.P., California, USA 39.3° N, 120.2° W	1810 (5937')	172	149	140	69	32	24	11	17	24	60	146	158	1002 (39.4")	825	82
Huntington Lake, California, USA 37.2° N, 119.2° W	2140 (7020')	165	160	151	84	32	9	5	6	28	48	117	132	937 (36.9")	773	82
Big Bear Lake, California, USA 34.3° N, 116.9° W	2070 (6790')	102	95	90	39	15	3	21	25	16	17	65	88	576 (22.7")	457	79

Figure 28. A flower meadow typical of Cascade-Sierran Montane Meadow grassland at ca. 2,100 m (6,890 ft) in the Sierra Nevada of California. The vegetation on the hill in the background is an interface between Cascade-Sierran Montane Conifer Forest and Cascade-Sierran Montane Scrubland. July 2001, Richard E. Brown.

8,200 ft) in the Sierra Nevada lie in non-glaciated valleys and contain tree stumps.

Heavy grazing increases the presence of more loosely-rooted plants as *Bromus tectorum* and *Poa pratensis,* and dries the meadow out, predisposing the grassland to invasion by trees and such shrubs as *Artemisia tridentata*. Although the presence of the latter is readily controlled by burning, fire does little to restore soil moisture.

Representative vertebrates are few and include a number of species shared with **Rocky Mountain Montane Grassland** including the porcupine (*Erethizon dorsatum*), which uses these meadows during summer months, the golden-mantled ground squirrel (*Spermophilus lateralis*), several pocket gophers, mountain bluebird, etc. (Storer and Unsinger 1963). Many forms are only differentiated at the subspecies level, e.g. the Western skink (*Eumeces skiltonianus skiltonianus*), and Sierra bighorn sheep (*Ovis canadensis californiana*). Other Rocky Mountain animals such as the wolf (*Canis lupus*) and elk (*Cervus canadensis*) are lacking from the southern reaches of this biotic community. Also, unlike the Rocky Mountains, only a few ground squirrels are represented, one of these being the endemic Cascade golden-mantled ground squirrel (*Spermophilus saturatus*). And although the Belding ground squirrel *(S. beldingi*) is found in both biotic communities, the Columbian ground squirrel (*S. columbianus*) is limited mainly to the Rocky Mountains.

As is the case with **Sierran Cascade Alpine and Subalpine Grassland**, numerous representative areas of this biotic community are protected within National Parks and other Wilderness or Natural areas. Moreover, many meadows are receiving some modicum of protection, at least from development, as they reside within the various lands managed by the United States Forest Service.

Madrean Montane Grassland

Mountain meadows are also found above 2,400-2,500 m (7,900-8,200 ft) elevation in both the Sierra Madre Occidental and Sierra Madre Oriental within and adjacent to **Madrean Montane Conifer Forest**. Although most of these grasslands occupy only a few acres, some are extensive enough to suggest that a distinctive montane grassland flora and fauna evolved on particular soil types within the same climatic regime as the forest (Table 5). Formerly composed of herbaceous forbs and tall bunchgrasses (Figure 29), these montane meadows extend(ed) southward from the Chiricahua and Huachuca mountains of Arizona to the Trans Mexican Volcanic Belt in central-southern Mexico. Knowledge of the community composition is limited, however, as few botanical or ecological studies have been conducted in these meadows, most of which have been grazed for so long that their original constituents can only be speculated upon (Figure 30).

An exception to the above is a study by Mills Tandy who conducted a floristic survey of a portion of ungrazed meadow in the Huachuca Mountains in extreme southern Arizona in 2005. One of Tandy's (pers. com.) transects sampled an area of **Madrean Montane Grassland** at 2,584 m (8,500 ft) that he described as a "*Helianthella*-forb" grassland. Other dominants in the community in addition to the five-nerve sunflower (*Helianthella quinquenervis*) were such grasses as pine dropseed (*Blepharoneuron tricholepis*), fringed brome (*Bromus ciliatus*), and Junegrass (*Koeleria macrantha*). A variety of Madrean forbs and sedges were also present in addition to such dominants as Fendler's flatsedge (*Cyperus fendlerianus*) and Dakota mock vervain (*Glandularia bipinnatifida*). Tandy considered 60% of the meadow's species to be of Madrean origin.

Gentry (1946a) described a pine forest meadow in the Sierra Tacuichamona, a Sierra Madre outlier in the State of Sinaloa, Mexico. He stated that the dominant grasses in this site were mostly *Aristida schiedeana* and *Muhlenbergia rigida*, accompanied by such shrubs as *Erythrina montana* and *Triumfetta chihuahuensis*. Many herbs including *Ipomoea decasperma* were also described as present.

The composition of similar meadows in the Sierra Madre proper would be of much interest from both a floristic and a comparative standpoint. Farther south, near El Guarda, Mexico, D. F., Rzedowski (1988) illustrates a *Festuca amplissima- Muhlenbergia macroura* meadow at 2,800 m (9,200 ft) elevation within **Transvolcanic Montane Conifer Forest**. Other grasses listed by Rzedowski for these mountainous zones belonged to such genera as *Andropogon*, *Bouteloua*, *Bromus*, *Deschampsia*, *Hilaria*, *Stipa*, *Trachypogon* and *Trisetum* – the species of which were presumably different than those

found in **Rocky Mountain** and **Cascade-Sierran Montane Meadow Grasslands**.

Both the vertebrate and invertebrate fauna of these grasslands is poorly known, but might include the Sierra Madre ground squirrel (*Callospermophilus madrensis*), white-sided jack-rabbit (*Lepus callotis*), and Sierra Madre sparrow (*Xenospiza baileyi*).

Figure 29. Above left. A Madrean Montane Meadow as it appeared in 1922. The grass in foreground is probably bullgrass (*Muhlenbergia emersleyi*), a tall bunch-grass that tends to disappear with heavy grazing. Note also the size and appearance of the Ponderosa pines prior to logging and fire protection. Photo taken at ca. 2,360 m (7,185 ft) en route to Colonia Pacheco, Chihuahua, Mexico, by L. A. Carlton; photo courtesy of Raul Valdez, New Mexico State University.

Figure 30. Remains of a Madrean Montane Meadow near Chuichupa, Chihuahua, at an elevation of ca. 2,060 m (6,890 ft). Once planted to corn and heavily grazed for years, this small meadow would probably have disappeared had it not been protected from erosion by the trincheras built by prehistoric peoples. The original grasses have been replaced by a few clumps of blue grama (*Bouteloua gracilis*), annuals and short-term weeds; the trees are Ponderosa pine and alligator juniper (*Juniperus deppeana*). 1988, D.E.B.

Table 5. Mean precipitation totals for stations located within or adjacent to Madrean Montane Meadow Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Jun-Sept.	%
Dolores, Chihuahua, MEXICO 28.9°N, 108.5°W	1926 (6897')	52	32	19	5	20	103	211	178	115	56	28	51	869 (34.2")	607	70
Creel, Chihuahua, MEXICO 27.8° N, 107.6° W	2345 (7694')	54	28	21	12	15	70	174	142	87	47	31	48	729 (28.7")	473	65
Guadalupe y Calvo, Chihuahua, MEXICO 26.1° N, 107.0° W	2400 (7874')	60	57	35	6	24	84	257	221	157	64	29	83	1076 (42.4")	719	67
Guanacevi, Durango, MEXICO 25.9° N, 106.0° W	2200 (7218')	20	10	9	5	11	62	134	135	117	38	13	31	584 (23.0")	448	77

Plains Grassland

Plains Grassland, or as it is often called, "prairie grassland" encompasses some 2,341,000 km^2 (903,860 mi^2) and constitutes one of the largest biotic communities in North America (Brown et al. 2007). Traveling from east to west, they become increasingly arid approaching the 100th Meridian. **Plains Grassland** then expands westward with decreasing precipitation and increasing incidences of drought to ca. 116 degrees W. longitude. The latitudinal expanse is even greater, extending from 54 degrees N. latitude in Alberta to at least 26 degrees N. Latitude in Chihuahua, Mexico–a north south distance of more than 3,000 km (1,864 mi.). Elevations range from less than 200 m (650 ft) in central Texas to more than 2,000 m (6,550 ft) in the highlands of Chihuahua. Soil types, are not only important in determining which species of grass are present, they are also important in delineating the extent of the grassland proper, with certain grassland fasciations occurring on sandy substrates as far east as New England.

Although dominated visually by grasses and grass-like plants, forbs and small shrubs are almost always common and important associates, and often outnumber the perennial grasses (Figure 31). Composites (Asteraceae) are especially prevalent, with legumes (Fabaceae) second in importance. The presence of both growing and residual plants is also an important facet of the grassland's structure in that the vegetation is layered both above and below ground, the grasses typically having a deeper and finer root system than the forbs.

As befits its recent evolutionary development, relatively few of the taxa are Nearctic endemics, and this biotic community has only attained its present character and composition during the last 10,000 years (Sims 1988). Further evidence of the prairie's relatively recent formation is a sparse fauna of large mammals when compared to the grasslands of Asia and Africa.

Little if any **Plains Grassland** vegetation remains unaltered by livestock grazing and/or past conversion to cropland. Nonetheless, a large and diverse assemblage of human-affected grassland remains, and because of their great economic and biologic importance, **Plains Grassland** communities have been studied by some of the foremost ecologists of the 20th Century. Excellent summaries of many of these studies, including the works of Robert Vestal (1914), Frederic Clements (1916, 1920), Per Axel Rydberg (1932), and Victor Shelford (1963) have recently been published by Sims (1988, 2000) for the U. S., and Scott (1995) for Canada.

As the name implies, this grassland is centered in the Great Plains, with outliers historically present as far East as Martha's Vineyard, Massachusetts, and on Long Island,

Figure 31. Loda Cemetery Prairie Nature Preserve, Iroquois County, Illinois. Cemeteries were often spared from the plow and sometimes represent the best examples of remnant Plains Grassland tall-grass prairie. The shrub in the middle is *Amorpha canescens*, surrounded by *Eryngium yuccifolium*, *Parthenium integrifolium, Solidago heterolepis*, among other species. This site had mean species density of 14.6 species/0.25 m2 (Taft, et al. 2009). Tall-grass prairie historically contained a remarkable diversity of plants - as many as 150 species can occur in less than 5 acres (Betz and Lamp 1992). July 2007, John. B. Taft.

New York (Stalter et al. 1991, Scott 1995). It is nonetheless a largely "continental" biotic community, as **Plains Grassland** rarely comes in direct contact with the seacoast. In the east and northeast, the primary contact is with **Northeastern Deciduous Forest**, and to the north, the contact is with boreal forests and grassland. **Plains Grassland,** integrating with "aspen parklands" and **Canadian Taiga,** covers a broad region that extends from just east of Winnipeg, Manitoba, westward to the vicinity of Edmonton, Alberta (Scott 1995). Other contacts include Ponderosa pine forest "islands" (**Rocky Mountain Montane Conifer Forest**) in Nebraska, South Dakota, and

Figure 32. Plains Grassland short grass community, on Thunder Basin National Grassland in northeastern Wyoming having characteristics of both Plains Grassland and Great Basin Shrub-Grassland, ca. 1,340 m (4,400 ft). The principal grasses here are western wheatgrass (*Pascopyrum smithii*) and blue grama (*Bouteloua gracilis*) depending on year and location. These and other grasses along with short-statured sagebrushes (*Artemisia* spp.) are shared by these two biotic communities along a broad transition that extends from Canada southward to northern Arizona and New Mexico (see also Figure 1). September 2003, D.E.B.

Figure 33. A short-grass prairie community of Plains Grassland being invaded by mesquite (*Prosopis glandulosa*) near Menard, Texas, ca. 638 m (2,093 ft). Although the temperature regime and continuity of a blue grama sod grass cover still makes this site Plains Grassland rather than Semidesert Grassland, the transition from the former to the latter is taking place over large areas wherever these two biotic communities meet. This transition has been particularly striking in west Texas where former prairies are now choked with both mesquite and "cedars" (*Juniperus monosperma*, et al.). September 2001, D.E.B.

other sites east of and in the Rocky Mountains. **Plains Grassland** also meets or merges along a broad front with **Great Basin Conifer Woodland** and **Great Basin Shrub-Grassland** from eastern Wyoming southward to Texas, New Mexico and north-central Arizona, the two grasslands being separated by the latter's presence of sagebrush and other short-statured shrubs along with a general dominance of *Pascopyrum* and other C3 grasses (Figure 32). Other western contacts involve isolated forests of ponderosa pine and other montane trees. In the "Southwest," **Plains Grassland** gradually morphs into **Semidesert Grassland**, the arrival of the latter being announced by the increasing occurrence of bare ground and the presence of *Opuntia, Prosopis*, *Yucca*, and other dry-tropic plants (Figure 33). Elsewhere in the Southwest, **Plains Grassland** borders **Madrean Evergreen Woodland**, and locally, as near Prescott, Arizona, **Interior Chaparral.** At its southern and southeastern extremities in Texas, where not grading into **Semidesert Grassland**, **Plains Grassland** may come in contact with **Southeastern Deciduous** and **Evergreen Forest** and **Balcones Mixed Evergreen Woodland**.

The climatic regime of **Plains Grassland** is very much continental and characterized by cold winters, hot summers, and great ranges in daily temperatures. But, as is to be expected in so vast an area, the climate is highly variable between regions. It is also highly variable between years, with evaporation exceeding precipitation in all but the most mesic tall-grass regions (Sims 2000). Mean precipitation ranges from more than 1,000 mm (39 in) in Midwest "tall-grass prairies" to less than 300 mm (12 in) in the west's short-grass plains (Table 6). Although snow is of regular occurrence, most of the precipitation falls as rain during the April through September growing season, and the changes of season are heralded by a time of droughty winds. Prior to livestock grazing by Europeans, these winds periodically drove fires, which were facilitated by a deficiency in rainfall and fueled by cured grasses from past growing seasons. These fires were, and remain, important to the prairie's maintenance, as without them, shrubs and trees will eventually alter their composition (Briggs, et al. 2005). Winds also play an important role during the winter months, greatly heightening chill factors and moving widely fluctuating snow accumulations that assist in maintaining an open landscape.

Ungrazed grasslands appear green only during the spring and summer growing season, the average number of days between freezes ranging from just over 100 in the northern

Table 6. Mean precipitation totals for locations within or adjacent to Plains Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Jun-Sept.	%
Dayton, Ohio, USA[1]																
39.9° N, 84.2° W	303 (995')	54	55	87	88	99	97	90	81	65	63	78	74	931 (36.6")	520	56
Rensseleer, Indiana, USA[1]																
40.9° N, 87.2° W	198 (650')	45	42	78	90	107	97	89	90	86	71	78	73	946 (37.2")	559	59
Urbana, Illinois, USA[1]																
40.1° N, 88.2° W	226 (743')	46	50	84	100	101	103	113	102	85	68	79	77	1008 (39.7")	604	60
Arlington, Wisconsin, USA[2]																
43.3° N, 89.4° W	209 (1080')	28	24	49	72	54	97	87	99	109	60	54	37	770 (30.3")	518	67
Stockton, Illinois, USA[2]																
42.4° N, 90.0° W	293 (960')	31	31	38	86	90	103	89	107	103	71	65	46	860 (33.9")	578	67
Prairie du Chien, Wisconsin, USA[2]																
43.0° N, 91.2° W	201 (658')	24	29	52	77	90	88	89	100	84	59	50	36	778 (28.7")	528	68
Osage, Iowa, USA[2]																
43.6° N, 92.8° W	357 (1170')	22	22	53	83	99	110	109	114	104	64	42	32	854 (33.7")	619	72
Wells, Minnesota, USA[2]																
43.8° N, 93.7° W	365 (1197')	14	14	48	63	84	111	113	96	77	53	32	23	728 (28.7")	544	75
Fort Dodge, Iowa, USA[2]																
42.5° N, 94.2° W	340 (1115')	22	22	55	82	103	124	115	110	100	63	11	28	835 (32.9")	634	76
Holton, Kansas, USA[2]																
39.5° N, 95.7° W	341 (1120')	23	23	61	81	114	88	93	110	121	81	49	34	878 (34.6")	607	69
La Grange, Texas, USA[3]																
29.9° N, 96.9° W	109 (357')	70	73	57	76	110	100	57	65	118	94	80	70	970 (38.2")	526	54
Austin, Texas, USA[3]																
30.3° N, 97.7° W	179 (587')	43	55	47	65	121	94	52	52	84	87	60	48	808 (31.9")	468	58
Wichita Falls, Texas, USA[2]																
34.0° N, 98.5° W	303 (994')	26	37	56	76	103	89	44	63	97	70	39	33	733 (28.9")	472	64
Hays, Kansas, USAº																
38.9° N, 99.3° W	613 (2010')	9	13	45	50	69	85	88	67	56	36	24	13	555 (21.8")	415	75
Brandon, Manitoba, CANADAº																
49.9° N, 100.0° W	366 (1200')	22	18	26	35	54	84	72	66	45	24	22	21	489 (19.2")	356	73
Valentine, Nebraska, USAº																
42.9° N, 100.6° W	789 (2587')	7	11	26	42	80	73	78	58	39	23	15	9	461 (18.2")	370	80
Hooker, Oklahoma, USAº																
36.9° N, 101.2° W	913 (2995')	10	15	29	35	75	75	58	59	52	24	20	10	462 (18.2")	354	77
Dickinson, North Dakota, USAº																
46.9° N, 102.8° W	750 (2460')	9	9	18	48	65	82	54	37	42	24	11	10	409 (16.1")	328	80
Clovis, New Mexico, USA*																
34.4° N, 103.2° W	1307 (4290')	10	13	15	21	47	72	65	81	55	28	19	14	440 (17.3")	341	78
Cheyenne, Wyoming, USA*																
41.2° N, 104.8° W	1867 (6126')	10	10	26	35	61	53	53	43	32	19	13	11	366 (14.4")	277	76
Fort Collins, Colorado, USA*																
40.6° N, 105.1° W	1525 (5004')	11	10	34	45	68	48	46	32	33	25	18	13	383 (15.1")	272	71
Saskatoon, Saskatchewan, CANADA^																
52.2° N, 106.7° W	501 (1645')	18	18	17	21	34	57	53	45	33	19	19	18	352 (13.9")	243	69
Namiquipa, Chihuahua, MEXICOº																
29.3° N, 107.4° W	1828 (5998')	16	7	6	5	8	36	97	108	91	33	11	20	438 (17.3")	345	79
N. Battleford, Saskatchewan, CANADA																
52.8° N, 108.3° W	547 (1796')	20	16	18	21	33	59	65	51	25	21	18	20	367 (14.4")	254	69
Ft. Assinniboine, Montana, USAº																
48.5° N, 109.8° W	796 (2618')	21	18	20	23	29	55	69	50	36	18	16	18	373 (14.7")	262	70
Canelo, Arizona, USA*																
31.5° N, 110.5° W	1527 (5010')	29	23	23	11	5	13	106	96	52	33	21	40	452 (17.8")	283	62
Coronation, Alberta, CANADAº																
52.1° N, 111.5° W	798 (2618')	21	18	20	23	29	55	69	50	36	18	16	18	373 (14.7")	262	70
Seligman, Arizona, USA*																
35.3° N, 112.9° W	1448 (5249')	24	23	31	13	12	9	54	54	27	21	24	27	319 (12.6")	169	53
Red Deer, Alberta, CANADA^																
52.2° N, 113.9° W	904 (2965')	21	19	20	25	45	83	79	63	39	23	16	17	450 (17.7")	334	74

[1]Forest edge [2]Tall-grass prairie [3]Blackland prairie transition to Gulf Coastal Grassland
*Short-grass prairie community ºMixed or mid-grass prairie ^Aspen parkland

Figure 34. Tall-grass prairie representative of the "Bluestem Prairie" that once dominated the 364,500 ha (900,000 acre) "Grand Prairie" of Arkansas as well as other "Blackland" areas in northern Louisiana and east Texas. This 101 ha (250 acre) Railroad Prairie Natural Area is a remnant of a southeastern fasciation of Plains Grassland in Prairie County, Arkansas, and is jointly managed by The Nature Conservancy and the state of Arkansas, ca. 68 m (225 ft). Important grass species include big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), little bluestem (*Schizachyrium scoparium*), and Indiangrass (*Sorghastrum nutans*). Summer 2005, D.E.B.

states and provinces to 200 or more in the "Blackland Prairies" of Texas (Figure 34). The remainder of the year, the "natural" situation is for the prairie to present a pattern of yellows, browns, tans, and even grays as the various grasses "pattern" and cure before becoming dormant (Figure 35). The climate is nonetheless cold temperate everywhere, and even the southeastern locales are subject to periodic cold snaps or *northers* sweeping southeast out of the Great Plains. Accompanied by freezing temperatures that may last for several days, these *northers* are devastating to sub-tropical plants. Another principal unifying feature of **Plains Grassland** is the wind, with most **Plains Grassland** communities registering mean annual wind speeds in excess of 15 kph (10 mph).

The latitudinal composition of **Plains Grassland** varies with changes in minimum temperatures, while the east-west composition varies with changes in minimum precipitation. Due to their lower rates of evapotranspiration, northern prairies require less precipitation for maintenance than do the more southern grasslands. Cool-season or C-3 grasses such as western wheatgrass (*Pascopyrum smithii*) are generally more sensitive to water stress than warm-season (C-4) grasses such as blue grama (*Bouteloua gracilis*). C-3 grasses also tend to flower earlier, be more deep-rooted, and more often occur as "bunch-grasses" than C-4 species, which are more likely to form sod and resist drought. Cool-season grasses function best under winter rainfall regimes and in the colder climates–hence these species tend to predominate in the north, and at higher elevations. Warm-season grasses are more characteristic of summer rainfall regimes and mostly flower during the summer months. Hence, the more mixed grasslands in the northern states and Canada tend to display a bimodal period of productivity, while those in the southern plains usually have a single growing season (Sims 1988).

Numerous fasciations and series have been described for **Plains Grassland** (see e.g., Shantz and Zon 1924, Küchler 1964). For purposes of convenience, this biotic community has been divided into subdivisions, each having a more or less distinctive climate, geographical extent, and list of associated species. The most commonly accepted subdivi-

Figure 35. Fall aspect of a Plains Grassland short-grass prairie/intermountain grassland community in Campbell County, Wyoming, ca. 1,450 m (4,780 ft). Note the subtle variations in color and texture (patterning) due to the different plant species and the time of their maturation. September 2004, D.E.B.

Figure 36. A southern extension of a Plains Grassland mid-grass prairie at an altitude of ca. 1,675 m (5,500 ft) west of El Sueco Junction, Chihuahua, Mexico. The principal species is sideoats grama (*Bouteloua curtipendula*), but *Andropogon gerardii*, *Bouteloua gracilis*, *Schizachyrium scoparium*, and *Sporobolus heterolepis*, are also present at this site along with numerous forbs. February 1999, D.E.B.

sions are: a tall-grass or true prairie community, a mid-grass community, a short-grass community, and an aspen parkland (Clements and Shelford 1939, Shelford 1963, and Sims 1988). Other ecologists have divided the tall-grass prairie into fasciations that include Fayette prairie, Blackland prairie, Eastern prairie, and savanna (Tharp 1939, Shelford 1963). While these classifications are useful for discussion purposes, it should be remembered that, as is the case with subdivisions of biotic communities, the boundaries are of necessity somewhat arbitrary, and series and associations found in a tall-grass community may also occur within other subdivisions depending upon local climate and/or substrate. Also, the boundaries of some subdivisions are elastic, and can change with long term climatic fluctuations, fire history,

Figure 37. Plains Grassland community of mostly big and little bluestem (*Andropogon gerardii*, *Schizachyrium scoparium*), Shinnery oak (*Quercus havardii*) and soapweed yucca (*Yucca glauca*) on a sand substrate in Roosevelt County, New Mexico, ca. 1,400 m (4,600 ft). December 1969, D.E.B.

and grazing intensity.

Tall-grass Prairie: Sometimes termed "Bluestem prairie" or "True prairie," this subdivision contains a variety of series or communities based primarily on plant height (Shelford 1963). Tall-grass prairie is generally considered to reside east of a line drawn from the Red River Basin in southern Manitoba through east-central North and South Dakota and Nebraska to north-central Kansas where it veers off into eastern Oklahoma and Texas (Map 1). Disjunctive but important areas of tall-grass prairie can be found as far west as southeastern New Mexico, with some tall-grass species extending westward to southeastern Arizona and northern Chihuahua, Mexico (Figure 36). Isolated patches of tall-grass prairie also extend eastward to southwest Ontario where 1,200 sq km (463 sq mi) of tall-grass prairie and oak parklands occur on the sandy plains of the "prairie peninsula," which reaches into Ohio before terminating on the Rice Lake Plains north of central Lake Ontario (Scott 1995). Other isolated patches of tall-grass prairie can be found even farther east as in Martha's Vineyard with a tiny 8 ha (20 acre) grassland in Hampstead Plains, NY (Scott 1995, Sims 1988).

Tall-grass prairie has the largest and greatest north-south grass diversity of any **Plains Grassland** subdivision. The dominants tend to be long-lived bunch and sod-forming grasses from 50 to 150 cm (20-60 in) tall, which present a relatively homogeneous physiognomy. Extreme examples can reach 2 m (80 in) as within the Wright Patterson Field near Dayton, OH (Orie Laucks, pers. com). Annual precipitation amounts range from a low of ca. 500 mm (20 in) to more than 1,000 mm (40 in) (Table 6).

As the term "bluestem prairie" suggests, big bluestem (*Andropogon gerardii*), often dominates, with other important constituents being prairie sandreed (*Calamovilfa longifolia*), porcupinegrass (*Hesperostipa spartea*), switchgrass (*Panicum virgatum*), little bluestem (*Schizachyrium scoparium*), rivergrass (*Scolochloa festucacea*), Indiangrass (*Sorghastrum nutans),* and prairie dropseed (*Sporobolus heterolepis*); some of these being locally important or even dominant (Shelford 1963, Sims 1988, Gibson 2009).

Deep rooted perennials are generally more drought resis-

tant than the shallow rooted species, which may include thistles (*Cirsium* spp.), scarlet gaura (*Gaura coccinea*), blazing stars (*Liatris* spp.), four-o-clocks (*Mirabilis* spp.), scarlet globemallow (*Sphaeralcea coccinea*), and scurfpeas (*Psoralidium* spp.). These and certain species of *Amaranthus*, *Chenopodium*, and *Opuntia* are grassland invaders during times of drought, which is an important tall-grass prairie characteristic as it facilitates the fires that prevent tree and shrub encroachment and inhibits competition from such cool-season invaders as *Bromus inermis* and *Poa pratensis* (Sims 2000).

The times of the year are apportioned out by flowering sequence: sedges such as *Carex pensylvanica* blooming in late winter or early spring (prevernal), cool-season grasses and forbs, e.g., *Koeleria macrantha*, typically flower in the spring (vernal), while the warm-season *Andropogon, Bouteloua*, and buffalograss (*Buchloe dactyloides*) bloom in summer (aestival) or early fall (serotinal). Other plants bloom even later (autumnal), and a number of insect life histories follow these sequences accordingly (Shelford 1963).

Sand substrate may favor certain species of graminoids such as sand bluestem (*Andropogon halli*), prairie sandreed (*Calamovilfa longifolia*), C*yperus schweinitzii*, *Dichanthelium villosissimum*, *Eragrostis* spp., *Hesperostipa spartea*, *Hilaria jamesii*, *Koeleria macrantha,* sandhill muhly (*Muhlenbergia pungens*), *Sporobolus airoides*, and *S. cryptandrus*. Sand-loving forbs include *Ambrosia psilostachya*, *Antennaria* spp., *Chamaecrista fasciculata*, *Dalea* spp., *Helianthus petiolaris*, *Ionactis linariifolia, Lithospermum caroliniense*, *Lygodesmia juncea*, *Nuttallanthus canadensis*, *Oenothera rhombipetala*, *Stillingia sylvatica* and *Tephrosia virginiana* (Shelford 1963, Sims 1988). In some areas, shrubs such as sandsage (*Artemisia filifolia*), Chickasaw plum (*Prunus angustifolia*), Shinnery oak (*Quercus havardii*), sumac (*Rhus aromatica*), and buffaloberry (*Shepherdia* sp.), singularly or accompanied by yuccas, and such cacti as *Opuntia humifusa*, may form dense thickets in a **Plains Deciduous Scrubland** (Brown et al. 2007) (Figure 37).

Although grasses normally account for 80 to 90% of the biomass (Sims 1988), the species of forbs commonly outnumber the grasses by three or four to one. Most of the canopy is less than 1 m tall, although the height of some eastern communities may approach or even exceed 2 m. According to Sims (1988), the height of grazed and/or mowed tall-grass prairie at the beginning of the growing season averages ca. 25 cm (10 in), this height increasing to ca. 50 cm (20 in) by late summer. However, under natural conditions, and if not burned off, there would also be a significant amount of residual grass remaining from the previous year.

A few important remnants of tall grass prairie remain, such as the 15,000 ha (39,000 acre) Tall Grass Prairie Preserve in Osage County, Oklahoma-the largest remaining tract of tall grass prairie, and the 3,487 ha (8,600 acre) Konza Prairie Biological Station in the Flint Hills of eastern Kansas, managed by The Nature Conservancy and Kansas State University. Excellent examples are also contained within the 1,200 ha (3,000 acre) Nachusa Grasslands Preserve in central Illinois managed by The Nature Conservancy (Figure 38), and the 28,300 ha (70,000 acre) Sheyenne National Grassland in North Dakota managed by the U. S. Forest Service. Other exquisite relicts are also to be found in the numerous private and state preserves scattered throughout the eastern U. S. ranging from the recently designated 7,756 ha (19,165 acre) Midewin National Tallgrass Prairie southwest of Chicago, Illinois to the 40 ha (100 acre) Huffman Prairie near Dayton, Ohio. According to Scott (1995) less than 5% remains of the tall-grass prairie in Canada, which once stretched from Manitoba to Ontario, including 4 km² (988 acres) of pure tall-grass prairie within the 2,000 ha (5,000 acre) Manitoba Tall-Grass Prairie Preserve near Winnipeg. Though these areas are invaluable relicts, it must be noted that most such areas were marginally arable when compared with lands that are now under cultivation, and as such, do not represent the original prairie at its productive best.

Fayette and Blackland Prairies: These isolated grasslands in the Texas "Crosstimbers" are here considered as southeastern extensions of tall-grass prairie. Although the soils may differ, the dominant grasses and animals are similar to those found in tall-grass prairie communities farther north in Arkansas, Missouri, and elsewhere (see Figure 34).

The "Fayette Prairie" (Tharp 1939) is (was) centered in Fayette County, Texas on Blackland soils and rolling terrain. Dominant grasses growing among the taller bluestems were needlegrasses (*Achnatherum, Hesperostipa, Nassella*), *Buchloe dactyloides*, and *Sporobolus* spp., with curley mesquite (*Hilaria belangeri*) as a sod-forming short-grass (Dyksterhuis 1948, 1949; Shelford 1963; Sims 1988). Wildflowers could be numerous and included such species as camas (*Camassia scilloides*), day flower (*Commelina* spp.), *Juncus*, *Mirabilis*, crow poison (*Nothoscordum bivalve*), spider-wort (*Tradescantia occidentalis*), and many others (Tharp 1939). Like other East Texas grasslands subject to *northers*, the surrounding vegetation mostly consisted of oak-hickory forest communities. The eastern border (Eastern Cross-Timbers) was mostly oak-hickory forest, and to the west, the grassland bordered the oak-cedar forest of the Edward's Plateau or "Western Cross-Timbers" or **Balcones Mixed Evergreen Woodland** subdivsion of the **Southeastern Mixed Deciduous and Evergreen Forest** (Brown et al. 2007). To the south, the "prairie" gives way to either **Semidesert Grassland** or "Texas brush" in which *granejo* (*Celtis pallida*), condalia (*Condalia* spp.), prickly-pear (*Opuntia* spp.), and mesquite (*Prosopis*)

Figure 38. Plains Grassland Tall-grass prairie (late summer aspect) on The Nature Conservancy's Nachusa Grasslands, a 1012 ha (2,500 acre) preserve near Franklin Grove, Illinois. The tall, dominant grass is big bluestem (*Andropogon gerardii*). The yellow composite is prairie coneflower (*Ratibida pinnata*). Summer 2008, Bonnie Swarbrick.

are important participants. Also, unlike more northern prairie communities which have lower evapotranspiration rates, those small areas of Fayette Prairie remaining require a greater amount of precipitation and lower evapotranspiration rates to maintain their tall-grass character. (Table 6).

Less than one percent of the original vegetation of Blackland prairies remains today, 80% being lost to cultivation in the early part of the 20th Century and much of the remainder lost due to urbanization (Bland and Jones, 1993). Of the few remnants remaining, many are utilized as intensive pastures. Studies of relict areas have nonetheless shown the persistence of native grasses such as sideoats grama (*Bouteloua curtipendula*), hairy grama (*B. hirsuta*), *Schizachyrium scoparium, Sorghastrum nutans*, and dropseeds (*Sporobolus* spp.) (Tharp 1939, Dyksterhuis 1946, 1948; Shelford 1963). As in tall-grass communities farther north, grazing tends to favor the shorter growing grasses such as threeawns (*Aristida* spp.), *Buchloe dactyloides,* Bermuda grass (*Cynodon dactylon*), Texas wintergrass (*Nassella leucotricha) and* thin paspalum (*Paspalum setaceum*). Much of this prairie was formerly a "savanna", the overstory trees mostly being blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*). Prior to settlement, it is thought that Blackland prairies probably burned about once every 10 years, and the prairie's tree and shrub components are now much more extensive than formerly (Sims 1988)

Mixed-grass Prairie: Also called "mid-grass prairie," this **Plains Grassland** subdivision resides between the tall-grass prairie in the east and short-grass prairie in the west (Clements 1920, Shelford 1963). As its name implies, the plant communities contained within are mixtures of both tall and short grass species, and the boundaries of this subdivision are loosely defined and fluctuating. Mixed-grass prairie irregularly occurs west of Manitoba's tall-grass communities, in Canada's southern prairie provinces, and in the northern tier of states in western North Dakota, western South Dakota, eastern Montana, and northeastern Wyoming (Figures 39a and b). Southward, it extends through to central and western Kansas, Oklahoma, and Texas (Map 1).

Precipitation ranges between 500 and 750 mm (20 and 30 in) and is exceeded by evaporation (Table 6). Although several community types are recognized (Scott 1995), this 30 to 60 cm tall (12 to 24 in) grassland is essentially an ecotone

Figure 39a. Mid-grass prairie community of Plains Grassland on Chimney Rock National Historic Site, Morrill County, Nebraska, elevation 1,476 m (4,243 ft). Were it not for this area being protected from grazing, the species and composition of the grasses and forbs would take on the appearance of a short-grass prairie community. April 2002, D.E.B.

Figure 39b. Mid-grass prairie *Elymus lanceolatus-Hesperostipa curtiseta* association along North Dakota/ Saskatchewan border. June 2011, Joey Carboneaux.

between the tall-grass and short-grass communities (Shelford 1963). Characterized by both a mixture of cool-season grasses of intermediate height and a number of short-statured warm-season grasses, the large number of forbs present makes this subdivsion the richest if not most diverse of North America's grasslands. Dominants, depending upon location, may include *Aristida* spp., *Bouteloua curtipendula, Calamovilfa longifolia*, *Elymus* spp., *Muhlenbergia* spp., needlegrasses, *Schizachyrium scoparium*, *Sporobolus* spp., in combination with several tall-grass species in the more mesic situations or succeeding a series of wet years. Some of the most common participants in these wetter sites are sedges such as

Carex atherodes, C. *filifolia*, *C. gravida*, *C. obtusata*, and *C. rostrata*, along with *Bouteloua gracilis, Festuca ovina*, *Hesperostipa comata, H. spartea*, *Koeleria macrantha*, *Nassella viridula*, *Pascopyrum smithii*, *Poa secunda*, and *Schizachyrium scoparium* (Sims 1988). Other grasses important in the local make-up may include nearly all of the tall-grass species as well as individual clumps of such montane grasses as *Danthonia intermedia, D. parryi*, *Elymus trachycaulus*, and *Festuca idahoensis*. Southward, these and other cool-season grasses, including *Elymus canadensis* and *Poa arida*, increasingly give way to warm-season species such as *Bouteloua curtipendula, B. hirsuta, Buchloe dactyloides,* and *Sporobolus compositus* var. *drummondii* with alkali cordgrass (*Spartina gracilis*) occurring in saline depressions. As a general rule, the sod-forming warm-season grasses typically increase after heavy grazing, fire, and/or drought, with the caveat that winter fires, while unusual, tend to favor cool-season species (Sims 1988).

Forbs can be abundant with such species as *Echinacea angustifolia, Helianthus pauciflorus*, *Sphaeralcea coccinea*, and *Symphyotrichum ericoides* being especially prominent. Also heavily represented may be *Ambrosia psilostachya*, *Amorpha canescens*, *Astragalus* spp., *Echinacea pallida*, *Erigeron strigosus*, *Liatris punctata*, *Psoralidium tenuiflorum*, *Salvia azurea*, *Verbena stricta*, *Vernonia baldwini*, and *Vicia* sp., along with such annuals as Russian thistle (*Salsola tragus*) (Shelford 1963, Sims 1988).

Shrubs are generally restricted to "scablands" and rocky ridges where one may encounter snowberry (*Symphoricarpos occidentalis*) and sagebrushes (*Artemisia* spp.). Leaf succulents, principally species of *Yucca*, occupy the driest sites as do certain cacti such as *Coryphantha vivipara* and *Opuntia fragilis*.

After the drought of the 1930s, short-grass species tended to increase and expand their ranges into mixed-grass prairie. In addition to blue grama and buffalograss, these "invaders" included thin paspalum (*Paspalum setaceum*), which increased largely at the expense of sand dropseed (*Sporobolus cryptandrus*) (Sims 1988). These, and other changes are fortunately well monitored due to 1,000,000 ha (2.4 million acres) of "mid-grass prairie" having been maintained in seven National Grasslands. These grasslands, including the more than 200,000 ha (500,000 acre) Thunder Basin National Grassland in Wyoming, are administrated by the U. S. Forest Service. Ungrazed examples are few, however, and even the large areas of prairie in the Wichita National Wildlife Refuge in Oklahoma are subject to grazing by bison, elk and longhorn cattle. A large number of national and state parks in Canada also act as grassland preserves including the 90,640 ha (223,970 acre) Grasslands National Park in Saskatchewan.

Short-grass Prairie: is generally found west of "mixed-grass prairie" and occurs mostly east of the Rocky Mountains (Map 1). As such, its primary distribution is from the extreme southwest limits of Canada's "prairie provinces" southward into eastern New Mexico and west Texas, with disjunct tracts in such places as the Animas Valley in New Mexico's "boot-heel," Arizona's San Rafael and Chino valleys, and certain intermountain valleys of northern Chihuahua (Figure 40). Wherever it occurs, this grassland subdivision is dominated by grasses from 5 to 40 cm (1.2 to 16 in) in height, usually forming a more or less discontinuous sod cover. Annual precipitation averages less than 500 mm (20 in) and evaporation always exceeds precipitation (Table 6). As a general rule, more than half of the precipitation will fall during the late April to early September growing season.

The composition of short-grass prairie changes with time and livestock pressure, but it is not always a "disclimax" mixed-grass prairie as suggested by Weaver and Clements (1938). Nonetheless, in many locations, especially in the eastern portions of its range, short-grass prairie is often replaced by mixed-grass prairie when rested from grazing (Figure 41). Several vegetation series have been recognized as occurring in both the U.S. and Canada, each based on variations in seasonal precipitation and soil moisture. Nor is it unusual for shrub and tree communities to interrupt the grassland on shallow soils and in sheltered depressions (Sims 1988, Scott 1995).

Major grassland dominants include the sod-forming blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and in the eastern areas, buffalograss (*Buchloe dactyloides*). More often than not, however, these dominants are accompanied by greater or lesser numbers of other short and mid-statured grasses which may include three-awns (*Aristida* spp.), side oats grama (*Bouteloua curtipendula*), galleta (*Hilaria jamesii*), needle and thread (*Hesperostipa* spp.), Junegrass (*Koeleria macrantha*), and sand dropseed (*Sporobolus cryptandrus*). Forbs include such early flowering species as pasqueflower (*Pulsatilla* spp.) to be followed later in the year by *Artemisia glauca*, *Liatris punctata*, *Packera streptanthifolia*, *Solidago missouriensis, Sphaeralcea coccinea*, and *Symphyotrichum ericoides* (Shelford 963, Sims 1988). Annuals and Russian thistle (*Salsola tragus*) invade formerly farmed and severely overgrazed areas as do such grasses as red three-awn (*Aristida purpurea*), ring muhly (*Muhlenbergia torreyi*), and burrograss (*Scleropogon brevifolius*). Perennial invaders include fringed and sand sagebrush (*Artemisia filifolia*, *A. frigida*) in eastern sandy areas, and a whole suite of shrub and half-shrub composites, the most successful of which is snakeweed (*Gutierrezia* spp.). Cacti are also common increasers with fire suppression and cattle grazing, particularly prickly-pears (*Opuntia macrorhiza, O. polyacantha*) tree cholla (*Cylindropuntia imbricata*) and yuccas (*Yucca glauca*, et al.), all of which are indicators of past range abuse and/or a transition to **Semidesert Grassland** (Figures 42, 43)

Figure 40. Top. Plains Grassland—a short-grass prairie community on the Gray Ranch in the Animas Valley, Hidalgo County, New Mexico, ca. 1,535 m (5,050 ft). Although grazed by cattle and horses for more than a century, this conservatively managed grassland continues to take on the aspect and species of a mixed grass or mid-grass community. March 2000, D.E.B.

Protected, or at least well managed examples of short-grass prairie can be found on a number of both public and private reserves from the 78,100 ha (193,000 acre) Pawnee and 106,820 ha (263,954 acre) Kiowa and Rita Blanca national grasslands in Colorado and New Mexico to the small 3,238 ha (8,000 acre) Audubon Research Ranch in southeastern Arizona.

Naturally, this biotic community contacts and interfaces with many others. In addition to **Canadian Taiga** in the far north, **Plains Grassland** comes in contact with **Northeastern Deciduous Forest** from south of 30 degrees N to 48 degrees N latitude, a distance of 1,920 km (1,200 mi). Here, red oak (*Quercus rubra*) and basswood (*Tilia americana*) are the common savanna species in the northeast with burr oak (*Quercus macrocarpa*) in the north. To the west, **Plains Grassland** commonly comes in contact with **Rocky Mountain Montane Conifer Forest** trees (e.g., Ponderosa pine in South Dakota and

Figure 41. Bottom. Plains Grassland on Custer State Park, South Dakota, ca. 1,215 m (3,990 ft). This mid-grass prairie has recently burned, releasing the green shoots of both forbs and grasses and taking on the appearance if not the composition of a short-grass community. September 2006, D.E.B.

Figure 42. – Plains Grassland near Walsenburg, Huerfano County, Colorado, 1,850 m (6,070 ft), distinguished by its characteristic short grass species blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*). In this area, compositional changes induced by grazing have resulted in increase cover of unpalatable species such as hedgehog cactus (*Echinocereus viridiflorus*), snakeweed (*Gutierrezia* spp.), plains prickly-pear (*Opuntia polyacantha*), and soapweed yucca (*Yucca glauca*). Shallow, rocky soils are indicated by the stand of pinyon pine (*Pinus edulis*) in the background. September 2008, E.M.

Nebraska, and white pine in Wyoming). **Great Basin Conifer Woodland** of Rocky Mountain pinyon (*Pinus edulis*) and junipers (*Juniperus* spp.) are a common contact in central New Mexico, with **Madrean Evergreen Woodland** a major contact in north-central Chihuahua, southeastern Arizona, and southwest New Mexico. More minor interfaces occur with **Interior Chaparral** near Prescott, Arizona, and **Great Basin Shrub-Grassland** in north-central New Mexico and Arizona. Fire is a requirement for maintenance, and without it, the trees and shrubs of these contact communities have invaded the grasslands as have such successional species as eastern red cedar (*Juniperus virginiana*) in the east and single-seed juniper (*Juniperus monosperma*, et al.) in the west.

Plains Grassland also interacts with riverine or flood-plain forests, making for additional mosaics of habitat-types. In Canada, these "gallery forests" may be 100 to 200 m (300 to 650 ft) wide, and include American white elm (*Ulmus americana*), basswood (*Tilia americana*), box-elder (*Acer negundo*) and green ash (*Fraxinus pennsylvanica*) (Scott 1995). Farther south into the prairie, these trees may be joined or replaced by cottonwoods (*Populus* spp.) and willows (*Salix* spp.) along the flood-plain proper, or in former river channels by more moderate sized trees such as hackberry (*Celtis occidentalis*), dogwood (*Cornus drummondii*), persimmon (*Diospyros virginiana*), wild plum (*Prunus americana*), western soapberry (*Sapindus drummondii*) and elm (*Ulmus* spp.). These and a host of intervening scrubland plants provide refugia for forest-prairie ecotone animals, some of the more notable being bobwhite (*Colinus virginianus*), sharp-tailed grouse (*Pedioecetes phasianellus*), and numerous passerines.

Also important are groves of trees within the prairie proper, called "bluffs" in Canada, and "mottes" in Texas and Oklahoma. These "island" forests stand in marked contrast to "savannas," which are grasslands thinly populated by trees, and "parklands", in which the grassland is surrounded by trees. Mottes in contact areas between **Plains Grassland** and **Northeastern Deciduous Forest** are often composed of any of several hickories (*Carya* spp.), black walnut (*Juglans*

Figure 43. A Plains Grassland short-grass community dominated by blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), et al., accompanied by plains prickly-pear (*Opuntia polyacantha*), west of Boyer, Lincoln County, Colorado, ca. 1,437 m (4,730 ft). 1936, D. F. Costello, USFS.

nigra), bur oak (*Quercus macrocarpa*), red oak (*Q. rubra*), slippery elm (*Ulmus rubra*), and basswood (*Tilia americana*), either as single species consociations or in various combinations. The undergrowth in these groves or mottes contains plants typical of the forest understory, and the tree-line margins ebb and flow as trees die during times of drought or fire, re-invading with fire protection or the return of wetter conditions (Sims 1988). Although bur oak continues westward to the Black Hills and the 100th Meridian, most of the trees in the western regions of **Plains Grassland** are montane forest and riparian species and not characteristic of the grassland proper. The same is true farther south where both the mottes and riparian forests are commonly represented by blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), and in the far southeast, live oak (*Q. virginiana*). It should also be emphasized that hundreds of square miles of **Plains Grassland** east of the Llano Estacado along the Canadian River and around Palo Duro Canyon in west Texas are now so invaded by western honey mesquite (*Prosopis glandulosa*) and cedars (*Juniperus monosperma*, et al.) that it's hard to image these lands as former "buffalo country."

Plains Grassland animals tend to be either fossorial or cursorial in their habits, and many species are also gregarious. The only large gramivore was the bison, the herds of which were largely migratory or nomadic, thus allowing the grasslands to recover from their grazing. Elk, while also grass and forb-eaters, were more often confined to the grassland's edges and river bottoms, and pronghorn depend almost entirely on forbs and shrubs for sustenance. As a result, only bison and elk ranged eastward into the **Northeastern Deciduous Forest**, pronghorn having evolved in open shrub-grasslands and avoiding "tall-grass" communities.

For characteristic representatives of **Plains Grassland** animal species, see appendix 2.

Great Basin Shrub-Grassland

This "Intermountain Grassland" of Sims (1988) also includes the "Palouse Prairie," "Shrub-Steppe," and "Sagebrush Steppe" of Shelford (1963), Küchler (1964), Franklin and Dyrness (1977) and West (1988). It originally resided from southern British Columbia, southward through eastern Washington and Oregon, southern Idaho, southwestern Montana, central Wyoming, and western Colorado, Utah, Nevada, and northeastern California to northern Arizona and New Mexico (Figure 44). In eastern Montana and Wyoming, the merging with **Plains Grassland** to the east is gradual and with many reversions, some **Great Basin Shrub-Grassland** communities extending as far eastward as western Nebraska. More than 80% of the native grass cover was originally composed of perennial bunch-grasses, often accompanied by one or more species of intermountain shrubs. Elevations range from as low as 30 m (100 ft) in the northwest to more than 3,000 m (9,850 ft) in the rain-shadowed mountains of the Great Basin where this biotic community merges into, or replaces, montane meadow grasslands. Although these "shrub-steppes" exhibit certain affinities with **Oregon Coastal Grassland**, **Plains Grassland**, and **California Valley Grassland,** they form a distinctive biotic community between the more arid **Great Basin Desertscrub** to the south and at lower elevations, and such piedmont and montane communities as **Great Basin Conifer Woodland** and **Scrubland**, which typically reside at higher elevations and/or on steeper or more rocky soils (West 1988).

The climate is distinctly cold-temperate with the average January minimums usually below 0°C (Sims 1988). Spring is often late and winters arrive early so that many shrub-steppe plants have a growing season of less than four to five months. More than 60% of the precipitation, much of which falls as snow, is received during the low sun months of October through March (Table 7). Annual means may be as low as 160-190 mm (6-7 in) in some of the more arid shrub-steppe locations to more than 500 mm (20 in) in the "Palouse" grasslands of Washington state. This great variation in average rainfall results in a landscape aspect ranging from sparsely vegetated "scab-lands" in which as little as 50% of the ground has perennial plant cover, through to herb-rich "meadows" in which grasses and forbs cover 80% or more of the ground (Figure 45)

Because of their use as rangelands, these often only moderately diverse grasslands have been much studied (see, e.g., Tisdale 1947, Shelford 1963, Franklin and Dyrness 1973, Sims 1988, West 1988). Many of these investigations were conducted by Rexford Daubenmire (e.g., 1966, 1970) and his students, who identified numerous grass and shrub dominated habitat-types within this biotic community, each

Figure 44. A Great Basin Shrub-Grassland community of wheatgrasses, alkali sacaton (*Sporobolus airoides*), and other Intermountain grasses mixed in with blue grama on the North Plains, Catron County, New Mexico, ca. 1,950 m (6,400 ft). The shrub is southwestern rabbitbrush (*Chrysothamnus pulchellus*). Grasslands having characteristics of both Plains Grassland and Great Basin Shrub-Grassland include New Mexico's San Augustine Plains and the plains forming much of the Little Colorado River watershed in northern Arizona. September 1998, D.E.B.

Figure 45. A "Palouse grassland" community of Great Basin Shrub-Grassland on the National Bison Range near Moise, Montana, ca. 1,907 m (6,259 ft). This 7,493 ha (18,500 acre) refuge harbors a dense cover of C-3 bunch-grasses, numerous forbs and nearly every species of wild ungulate found in the United States. Summer 2001, D.E.B.

depending on a particular soil type, soil moisture regime, and precipitation pattern.

The unifying vegetative pattern of **Great Basin Shrub-Grassland** is, or was, a sparse to luxuriant cover of spring-active or cool-season bunch-grasses from 30 to 40 cm (12 to 16 inches) tall (West 1988). Depending upon location, site characteristics, and grazing and fire history, these include species of wheatgrasses (e.g., *Elymus lanceolatus, Pascopyrum smithii, Pseudoroegneria spicata*), fescues (e.g., *Festuca idahoensis, F. campestris*), wild ryes (e.g., *Elymus elymoides, E. flavescens, E. triticoides,*), and needlegrasses (e.g., *Achnatherum aridum, A. nelsonii, A. occidentale, A. speciosum, A. thurberianum, Hesperostipa comata*) in association with onespike oatgrass (*Danthonia unispicata*), Junegrass (*Koeleria macrantha*), and bluegrasses (*Poa cusickii*, *P. secunda*). In drier locales, and to the south and east, these species may be joined or replaced by Indian ricegrass (*Achnatherum hymenoides*), purple threeawn (*Aristida purpurea*), James' galleta (*Hilaria jamesii*), ring muhly (*Muhlenbergia*

Figure 46. Disclimax Great Basin Shrub-Grassland in Monument Valley on the Hopi Indian Reservation in northeastern Arizona. Blackbrush community (*Coleogyne ramosissima*) with *Ephedra torreyana*, *Gutierrezia sarothrae*, *Yucca angustissima*. Indian ricegrass (*Achnatherum hymenoides*) was probably abundant in this area before livestock grazing. Sept. 2008, E.M.

torreyi), and sand dropseed (*Sporobolus cryptandrus*) as well as several summer-active **Plains Grassland** species such as blue grama (*Bouteloua gracilis*). Saline depressions are typically dominated by saltgrass (*Distichlis spicata*) and Basin wildrye (*Leymus cinereus*), often accompanied by greasewood (*Sarcobatus vermiculatus*) and other halophytic plants (Franklin and Dyrness 1973).

Shrubs, usually less than one meter tall, including big sagebrush (*Artemisia tridentata*) and other sages such as *A. arbuscula, A. bigelovii*, *A. cana, A. filifolia*, *A. rigida,* and *A. tripartita* are commonly in attendance and may constitute up to 80% of the plant cover (West 1988). Other important widespread and prevalent shrub species include fourwing saltbush (*Atriplex canescens*), rabbitbrushes (*Chrysothamnus viscidiflorus, Ericameria nauseosa*), Mormon tea (*Ephedra* spp.), hopsage (*Grayia spinosa*), winterfat (*Krascheninnikovia lanata*), bitterbrush (*Purshia tridentata*), horsebrush (*Tetradymia canescens*), and in the south, blackbrush (*Coleogyne ramosissima*) (Figure 46). Local shrubs might include serviceberry (*Amelanchier* spp.), hawthorn (*Crataegus* spp.), mockorange (*Philadelphus lewisii*), common chokecherry (*Prunus virginiana*), smooth sumac (*Rhus glabra*), Nootka rose (*Rosa nutkana*), buffaloberry (*Shepherdia* spp.), and snowberry (*Symphoricarpos* spp.) (Franklin and Dyrness 1973). **Great Basin Shrub-Grasslands/Great Basin Montane Scrubland** ecotones may include species such as *Cercocarpus ledifolius* and *Juniperus* spp. Smaller "half-shrubs" of buckwheat (*Eriogonum* spp.) and longleaf phlox (*Phlox longifolia*) are also commonly encountered.

Broadleaf herbs, the composition and occurrence of which often depends on grazing history, may be abundant and numerous. Typical genera and species found in this biotic community are common yarrow (*Achillea millefolium*), *Agoseris* spp., sandworts (*Arenaria* spp.), milkvetches (*Astragalus* spp.), balsamroots (*Balsamorhiza sagittata, et al.*), brodiaeas (*Brodiaea* spp.), mariposa lilies (*Calochortus macrocarpus, et al.*), evening primroses (*Camissonia tanacetifolia, et al.*), paintbrushes (*Castilleja* spp.), hawksbeards (*Crepis occidentalis, et al.*), larkspur (*Delphinium* spp.), woolly sunflower (*Eriophyllum lanatum*), *Geum* spp., *Helianthella* spp., woodland-star (*Lithophragma glabrum*), stoneseeds (*Lithospermum ruderale, et al.*), *Lomatium* spp., *Lupinus* spp., beardtongue (*Penstemon breviflorus, et al.*), yellow scurfpea (*Psoralidium lanceolatum*), docks (*Rumex* spp.),

Table 7. Mean precipitation totals for stations located within and adjacent to Great Basin Shrub-Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Dec - May	%
Penticton, British Columbia, CANADA																
49.5° N, 119.6° W	342 (1121')	32	23	17	23	28	36	25	22	18	20	26	31	301 (11.9")	154	51
Kamloops, British Columbia, CANADA																
50.7° N, 120.3° W	379 (1243')	33	10	8	13	23	33	25	28	22	19	20	35	269 (10.6")	122	72
Ellensberg, Washington, USA																
47.0° N, 120.5° W	451 (1480')	32	23	18	14	14	14	6	10	12	14	35	40	232 (9.2")	141	61
Missoula, Montana, USA																
46.9° N, 114.1° W	974 (3187')	31	20	25	24	45	45	23	30	28	19	21	29	340 (13.4")	174	51
Pullman, Washington, USA																
46.8° N, 117.2° W	776 (2545')	69	42	53	40	40	36	19	23	25	36	55	72	510 (20.1")	316	62
Helena, Montana, USA																
46.6° N, 112.0° W	1167 (3828')	16	10	19	25	45	47	28	33	29	15	16	15	298 (11.7")	130	44
Walla Walla, Washington, USA																
46.1° N, 118.3° W	355 (1166')	58	47	53	43	40	26	14	21	24	39	67	64	496 (19.5")	305	61
Boise, Idaho, USA																
43.6° N, 116.2° W	865 (2838')	37	27	33	31	27	21	9	11	20	19	38	35	308 (12.1")	190	62
Shoshoni, Wyoming, USA																
43.2° N, 108.1° W	1472 (4830')	5	7	6	23	37	28	12	14	17	15	6	5	175 (6.9")	83	47
Hart Mountain NWR, Oregon, USA																
42.6° N, 119.7° W	1712 (5616')	22	19	31	34	36	34	11	15	21	25	29	29	306 (12.1")	171	56
Twin Falls, Idaho, USA																
42.6° N, 114.4° W	1207 (3960')	28	23	27	23	27	22	7	12	18	19	31	28	265 (10.4")	159	60
McDermitt, Nevada, USA																
42.0° N, 117.7° W	1380 (4527')	23	18	22	22	28	28	9	14	15	17	26	26	248 (9.7")	139	56
Richmond, Utah, USA																
41.9° N, 111.8° W	1427 (4682')	37	39	50	56	56	38	22	26	38	47	44	41	494 (19.4")	279	56
Fort Bidell, California, USA																
41.9° N, 120.1° W	1372 (4500')	58	51	46	33	28	23	8	15	18	28	51	64	423 (16.7")	280	66
Walden, Colorado, USA																
40.7° N, 106.3° W	2475 (8120')	13	14	19	23	31	26	31	28	30	23	19	16	273 (10.8")	116	42
Reno, Nevada, USA																
39.5° N, 119.8° W	1342 (4404')	27	25	18	10	18	12	7	8	10	10	22	25	192 (7.5")	123	64
Modena, Utah, USA																
37.8° N, 113.9° W	1664 (5460')	17	17	28	23	17	9	35	32	26	24	19	15	262 (10.3")	117	45
Taos, New Mexico, USA																
36.4° N, 105.6° W	2123 (6965')	15	14	21	21	23	27	41	50	38	38	27	20	335 (13.2")	114	34
Chaco Canyon, New Mexico, USA																
36.0° N, 107.9° W	1882 (6174')	11	14	16	11	16	12	31	32	33	27	18	16	237 (9.3")	84	35
Holbrook, Arizona, USA																
34.9° N, 110.2° W	1545 (5070')	15	15	15	9	9	4	28	40	28	24	16	17	220 (8.7")	80	36

and mule ears (*Wyethia* spp.). Biological crusts of mosses, lichens, and/or algae are found in the interspaces of less disturbed soils (West 1988).

Today, much of the better habitats are cultivated for wheat, peas, alfalfa, and other herbaceous crops, or have been replaced by fruit orchards. Native gramivores such as bison were always outnumbered by forb and shrub feeders such as the pronghorn, and neither species was probably as abundant as in **Plains Grassland**. As a result, these grasslands had been lightly grazed, if it all, for nearly 12,000 years. Perhaps for this reason, the native bunch-grasses proved poorly adapted to heavy livestock use, and the stocking of cattle and sheep during spring months, not to mention the yearlong use by feral horses, caused an increase in sagebrush and other shrubbery at the expense of the native grasses, most of which are poor seed producers (West 1988). As a result range managers often re-seed depleted rangelands with a variety of Old-World grasses to replace the herbaceous forage that was lost.

Nothing has changed these grasslands so much as the introduction and proliferation of Old World annuals. Although exotic grasses and forbs were undoubtedly first introduced with the arrival of livestock prior to 1900, it was not until the 1940s and 1950s that disclimax grasslands dominated by cheatgrass (*Bromus tectorum*) became commonplace and generated serious concern. Since then, cheatgrass, along with a host of other exotic bromes, Kentucky bluegrass (*Poa pratensis*), medusa-head (*Taeniatherum caput-medusae*), and other annual grasses have continued to replace the native perennials. Cheatgrass is an especially aggressive invader as it begins growth with the first fall rains, and continues to grow through the winter. On drying in midsummer, cheatgrass

Figure 47. A disclimax shrub community of Great Basin Shrub-Grassland composed of rubber rabbitbrush (*Ericameria nauseosa*) with some big sage (*Artemisia tridentata*) and other shrubs near McDermitt on the Oregon-Nevada border, ca. 1,465 m (4,808 ft). The shrubs increase with grazing but cannot tolerate fire. Burning these communities often results in a total type conversion to cheatgrass (*Bromus tectorum*). 1997, D.E.B.

Figure 48. Shrub and tree species encroaching on a Great Basin Shrub-Grassland. Big sage (*Artemisia tridentata*), snakeweed (*Gutierrezia sarothrae*), and oneseed juniper (*Juniperus monosperma*) in this photo north of Chambers, Arizona, on the Navajo Indian Reservation, ca. 1,795 m (5,890 ft). The grasses have been essentially eliminated at this site due to livestock grazing. Undated, D.E.B.

also provides a highly flammable fuel. An abundant seed producer, cheatgrass not only out competes the native grasses in the race for reestablishment, its tendency to burn allows cheatgrass to replace the more fire sensitive sagebrush and bitterbrush, which do not have the ability to stump-sprout after burning (West 1988; Figure 47).

In addition to promoting cheatgrass and other annual grasses, the increasing incidence of late season fires benefits herbaceous weeds, both foreign and domestic. These include goat-grass (*Aegilops cylindrica*), fiddleneck (*Amsinckia menziesii*), pussytoes (*Antennaria parvifolia*), knapweeds (*Centaurea* spp.), sunflowers (*Helianthus* spp.), Dyer's woad (*Isatis tinctoria*), wild lettuce (*Lactuca* spp.), woodland-star (*Lithophragma glabrum*), Indian wheat (*Plantago patagonica*), and Mediterranean sage (*Salvia aethiopis*); while reducing the presence of such plants as tansy-mustard (*Descurainia pinnata*), tumblemustard (*Sisymbrium altissimum*), and cacti (*Opuntia* spp.) (West 1988).

Grazing, coupled with the increasing establishment of annuals, has converted hundreds of thousands of acres of **Great Basin Shrub-Grassland** into a seasonal rangeland–a change that appears irreversible (Sims 1988). Other more or less permanent changes, depending upon site and location, include the cessation of natural occurring fires, the replacement of native bunch grasses by exotic and summer-active perennials, the proliferation and invasion of sagebrush and other shrubbery in some places and their disappearance in others, and the advancement and increase of junipers and other trees at the grassland's edge (Figures 48). In many cases, even a complete rest from grazing and a total protection from fire has failed to restore the native bunch-grasses. Moreover, the mechanical removal of junipers, pinyons and other woody plants often fails to reestablish the native vegetation, and once established, introduced species such as cheatgrass and medusahead so increase the likelihood of off-

Figure 49. A relict stand of spring-active grasses and forbs within a "Palouse Prairie" community of Great Basin Shrub-Grassland on Steptoe Butte State Park north of Colfax, Whitman County, Washington, ca. 1,066 m (3,500 ft). Most such communities have been virtually eliminated in southeastern Washington and replaced by irrigated fields of wheat and other crops. Spring 2001, D.E.B.

season fires that their dominance is difficult to overcome. Combined with possible climate change, the best remaining examples of native bunch-grass communities are now mostly restricted to the higher, wetter, and/or protected sites.

A number of mammals are characteristic of **Great Basin Shrub-Grassland**, or at least certain habitats within it. Examples include the pygmy rabbit (*Brachylagus idahoensis*), white-tailed prairie dogs (*Cynomys gunnisoni, C. leucurus* and *C. parvidens*), sagebrush vole (*Lemmiscus curtatus*), white-tailed jack rabbit (*Lepus townsendii*), northern grasshopper mouse (*Onychomys leucogaster*), Great Basin pocket mouse (*Perognathus parvus*), Washington ground squirrel (*Spermophilus washingtoni*), least chipmunk (*Tamias minimus*), and Western jumping mouse (*Zapus princeps*). Bison (*Bison bison*) were historically present although not in the numbers found in **Plains Grassland**. The same can be said for the forb and shrub feeding pronghorn (*Antilocapra americana*) despite now being the most numerous big game animal in **Great Basin Shrub-Grassland** (O'Gara and Yoakum 2004).

Birds are also relatively well represented in **Great Basin Shrub-Grassland** and include such "indicator species" as the sage grouse (*Centrocercus urophasianus*) and Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*), even though the introduced rock partridge (*Alectoris graeca*) is now this biotic community's best known game bird. Other characteristic breeding birds include the grasshopper sparrow (*Ammodramus savannarum*), sage sparrow (*Artemisiospiza belli*), lark sparrow (*Chondestes grammacus*), savannah sparrow (*Passerculus sandwichensis*), vesper sparrow (*Pooecetes gramineus*), Brewer's sparrow (*Spizella breweri*), ferruginous hawk (*Buteo regalis*), horned lark (*Eremophila alpestris*), prairie falcon (*Falco mexicanus*), northern shrike (*Lanius excubitor*), sage thrasher (*Oreoscoptes montanus*), and common magpie (*Pica pica*).

Reptiles and amphibians are less well represented, but as their names indicate, those present include a number of characteristic species that include the Western yellow-bellied racer (*Coluber constrictor mormon*), striped whipsnake (*Masticophis taeniatus*), short-horned lizard (*Phrynosoma douglasii*), Great Basin gopher snake (*Pituophis melanoceucus deserticola*), and Great Basin spadefoot (*Spea intermontana*).

Although the most productive **Great Basin Shrub-Grasslands** have been converted to agriculture, and almost all of the remaining areas have been impacted by livestock grazing, some sizable areas remain. With the exception of Washington state, where Palouse grasslands are now largely limited to the Hanford Military Reservation and tiny Steptoe State Park (Figure 49), other states possessing **Great Basin Shrub-Grassland** contain excellent examples of protected grasslands or areas under special management to preserve their grassland character. Representative areas include the 7,509 ha (18,500 acre) National Bison Range in western Montana, the 21,669 ha (53,544 acre) Craters of the Moon National Monument in south central Idaho, the 74,868 ha (185,000 acre) Malheur National Wildlife Refuge in east central Oregon, and the huge 445,000 ha (1. 4 million acre) Hart Mountain and Charles Sheldon National Wildlife Refuge complex in southeastern Oregon and northern Nevada (Figure 50). Still other fasciations are included in parts of the 7,285 ha (18,000 acre) Arapaho National Wildlife Refuge in north central Colorado; the 92,394 ha (228,000 acre), Long Term Ecological Research Site (LTER 2012), Sevilleta National Wildlife Refuge in central New Mexico; the 14,267 ha (35,254 acre) Wupatki National Monument near Flagstaff, Arizona (Figure 51); and the 37,852 ha (93,533 acre) Petrified Forest National Park near Holbrook, Arizona.

Figure 50. Native Great Basin Shrub-Grassland community of bunchgrasses (*Achnatherum*, *Agropyron*, etc.) mixed with sagebrush and other shrubs in the Trout Creek Mountains, Burns County, Oregon, ca. 2,410 m (7,900 ft). This area had been burned several years previously, which encouraged the grass growth and temporarily set back the sagebrush plants. Undated, D.E.B.

Figure 51. Relict Great Basin Shrub-Grassland near Wupatki National Monument northeast of Flagstaff, Coconino County, Arizona, 1,650 m (5,413 ft). Grasses are native, luxuriant, and diverse in comparison to 47, this site having not been grazed for over 20 years. Black grama (*Bouteloua eriopoda*) and James' galleta (*Hilaria jamesii*) dominate on the cinder soils, along with *Aristida purpurea*, *Eragrostis intermedia*, *Muhlenbergia porteri*, *Setaria leucopila*, and *Sporobolus cryptandrus*. December 2012, E.M.

Oregonian Coastal Grassland

Commonly called "coastal prairie" or "coastal grassland," this cool temperate biotic community occurs discontinuously along the Pacific Coast from Washington state southward to the vicinity of Santa Cruz, California. According to Heady et al. (1977) this grassland is best developed in northwestern California with smaller areas extending as far south as Point Lobos State Reserve in Monterey County. Similar examples are also found on "balds" in the Coastal ranges of northern California and southern Oregon, as well as in the Willamette and other southwestern Oregon valleys. Northward, these grasslands are increasingly confined to coastal headlands where they reach their northern terminus at Quillayute Prairie on the western Olympic Peninsula (Franklin and Dyrness 1973). Too small to depict on the map, nearly all of these grasslands are within 100 km (60 mi) of the coast and below 1,000 m (3,300 ft) elevation.

Although most often noted on level sites, **Oregonian Coastal Grassland** also occupies ridges and south-facing slopes where it alternates with **Oregonian Coastal Conifer Forest** and/or **Oregonian Coastalscrub**. Inland, it most often occurs within **Oregonian Deciduous and Evergreen Forest**, and south of San Francisco Bay, this grassland gradually merges into **California Valley Grassland** with which it shares a number of affinities.

Precipitation can be copious, and annual means may exceed 500 mm (20 in). Although more than 80% of this precipitation is received as rainfall during the winter months (Table 8), the maritime influences of mist and morning dew make for relatively mesic conditions throughout the year. Chilling temperatures are commonplace, especially during the winter months, even though frosts and snowfall are rare.

Historical accounts indicate that **Oregonian Coastal Grassland** could be highly luxuriant, the "prairie" grasses sometimes reaching a height of nearly 2 m (80 in). By way of contrast, headland vegetation populated principally by forbs may never have exceeded 20 cm (8 in). Today, the average height of many of the more heavily grazed sites may be as low as 5 cm (2 in). Heady et al. (1977) reported that moderately grazed heights in one California location averaged 11 cm (4 in), while ungrazed vegetation was about 16.5 cm (7 in) tall. The percent cover ranged from 80 to 95% with annuals comprising from 15 to 32% of the total, the actual composition depending on grazing intensity and history (Figures 52, 53).

Perennial grass dominants may include California danthonia (*Danthonia californica*), Idaho fescue (*Festuca idahoensis*) and red fescue (*F. rubra*). Other species to be expected are bentgrasses (*Agrostis* spp.), bromes (*Bromus* spp.), Pacific reedgrass (*Calamagrostis nutkaensis*), tufted hairgrass (*Deschampsia cespitosa*), blue wildrye (*Elymus glaucus*), mannagrasses (*Glyceria* spp.),

Figure 52. Oregonian Coastal Grassland near Salishan, Oregon, nearly sea level. A "wet meadow" populated mostly be Pacific reedgrass (*Calamagrostis nutkaensis*). May 1974, D.E.B.

meadow barley (*Hordeum brachyantherum*), Junegrass (*Koeleria macrantha*), oniongrasses (*Melica* spp.), dunegrass (*Leymus mollis*), bluegrasses (*Poa* spp.), and various trisetums (*Trisetum* spp.). In addition to these generally northern genera, the warmer, drier sites might have a number of endemics as well as Great Basin and naturalized California species such as silver hairgrass (*Aira caryophyllea*). Also important in the grassland's makeup are such grass-like plants as sedges (*Carex* spp.) and the introduced sweet vernalgrass (*Anthoxanthum odoratum*), while the principal broad-leaved forbs are beach strawberry (*Fragaria chiloensis*), cat's ear (*Hypochaeris radicata*), Douglas' iris (*Iris douglasiana*), brackenfern (*Pteridium aquilinum*), California buttercup (*Ranunculus californicus*), sheep sorrel (*Rumex acetosella*), and blue-eyed grass (*Sisyrinchium bellum*) (Heady et al. 1977).

A study of a "headland prairie" in Oregon showed that the main constituents were primarily a mixture of herbs and shrubs (Franklin and Dyrness 1977). In addition to several species already mentioned, these included common yarrow (*Achillea millefolium*), Idaho bentgrass (*Agrostis idahoensis*), seacoast angelica (*Angelica lucida*), Suksdorf sagebrush (*Artemisia suksdorfii*), Alaska brome (*Bromus sitchensis*), orchardgrass (*Dactylis glomerata*), giant horsetail (*Equisetum telmateia*), bedstraw (*Galium* spp.), common cowparsnip (*Heracleum lanatum*), common velvetgrass (*Holcus lanatus*), seashore lupine (*Lupinus littoralis*), swordfern (*Polystichum munitum*), Western buttercup (*Ranunculus occidentalis*), Nootka rose (*Rosa nutkana*), *Rubus* spp., Canadian goldenrod (*Solidago canadensis*), and Mexican hedgenettle (*Stachys mexicana*). Another study cited by Franklin and Dyrness (1973), this one along the southern Oregon coast, showed more shrubs and herbs to be present than grasses and included such species as woolly goat chicory (*Agoseris abargioides*), harvest brodiaea (*Brodiaea coronaria*), common juniper (*Juniperus communis*), tall coastal plantain (*Plantago subnuda*), dwarf checkerbloom (*Sidalcea malviflora*), and Fremont deathcamas (*Zigadenus fremontii*).

In the Willamette and Rogue River valleys this grassland may take the form of a savanna in which the dominant trees are the winter deciduous oaks - Oregon white oak (*Quercus garryana*) and California black oak (*Q. kelloggii*). The grasses are many of the same species found on the coast but with the addition of taxa more representative of **Great Basin**

Figure 53. Oregonian Coastal Grassland on Cypress Grove Research Center in the Audubon Canyon Ranch Preserve, Marin County, California, ca. 12 m (40 ft). The principal tall grasses according to the Preserve's C. Condeso are *Bromus* spp., *Danthonia californica*, *Deschampsia holciformis*, and *Elymus glaucus*. October 2008, D.E.B.

Table 8. Mean precipitation totals for stations located within or adjacent to Oregonian Coastal Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Oct - Mar	%
Gold Beach R. S., Oregon, USA 42.4° N, 124.4° W	15 (49')	305	262	273	152	97	41	12	30	61	146	321	342	2042 (80.4")	1649	81
Crescent City, California, USA 41.8° N, 124.2° W	12 (40')	251	188	226	117	74	33	10	25	46	124	269	269	1632 (64.3")	1327	81
Eureka, California, USA 40.8° N, 124.2° W	13 (43')	170	140	135	69	56	18	3	3	15	81	117	170	977 (38.4")	813	83
Fort Ross, California, USA 38.5° N, 123.3° W	34 (112')	183	135	135	59	17	6	4	7	18	67	153	154	938 (36.9")	827	88
Half Moon Bay, California, USA 37.5° N, 122.5° W	11 (36')	102	97	105	38	12	6	3	5	11	51	74	106	610 (24.0")	535	88
Santa Cruz, California, USA 37.0° N, 122.0° W	40 (130')	144	125	118	56	10	4	4	3	11	35	112	116	738 (29.0")	650	88
Watsonville, California, USA 36.9° N, 121.8° W	29 (95')	105	87	91	46	7	3	2	2	8	29	81	90	551 (21.7")	483	88

and **California Valley Grasslands.** At least some **Oregonian Coastal Grassland** sites are successional to scrub and/or forest, and most communities are now much altered by grazing. In many cases the new "natives" are primarily perennials such as sweet vernalgrass (*Anthoxanthum odoratum*), common velvetgrass (*Holcus lanatus*), and hairy wallaby grass (*Rytidosperma pilosum*). Annuals may also be conspicuously present and include dogtails (*Cynosurus cristatus*, *C. echinatus*), and brome fescue (*Vulpia bromoides*), with Italian ryegrass (*Lolium perenne* ssp. *multiflorum*) being even more prevalent than in **California Valley Grassland**. Nonetheless, with a return to moderate grazing, most sites will again be dominated by perennials. One vegetative threat, common St. Johnswort (*Hypericum perforatum*), is a large broad-leafed exotic that became established around the turn of the 20th Century. This plant, however, is now much reduced due to the introduction of Klamath weed beetles (*Chrysomela* spp.) after World War II.

The largest grazing animal native to this biotic community is the Roosevelt elk (*Cervus canadensis roosevelti*), which, along with the high rainfall and numerous rodents present, has probably influenced the evolutionary history of this biotic community and its ability to withstand moderate grazing pressures. The most indicative of the rodents is probably the Pacific jumping mouse (*Zapus trinotatus*), other meadow-inhabiting rodents being the the white-footed vole (*Arborimus albipes*), the creeping vole (*Microtus oregoni*), and Townsend vole (*M. townsendii*).

Coastal grassland birds are primarily species of the forest-edge such as the sooty blue grouse (*Dendragapus fuliginosus*), although mountain bluebirds (*Sialia currucoides*) and other open country obligates are also well represented.

Characteristic reptiles and amphibians include the endemic Northwestern garter snake (*Thamnophis ordinoides*) and brown salamander (*Ambystoma gracile gracile*) as well as two other grassland-dwelling salamanders– the black salamander (*Aneides ferreus*) and the California slender salamander (*Batrachoseps attenuatus*).

Representative areas of **Oregonian Coastal Grassland** are contained within several federal preserves including Redwood National Park, Point Reyes National Seashore, and Humboldt Bay National Wildlife Refuge. Some excellent examples, including vernal pools, are also protected within a large series of state parks and reserves that stretch southward from the Oregon coast to Point Lobos, California. Fewer inland sites are in public ownership although some good grassland can be found on the William L. Finley National Wildlife Refuge near Corvallis, Oregon, and in private reserves.

Warm Temperate Grasslands

Warm temperate grasslands are found on six continents and formerly covered sizable areas of southern Eurasia and North America as well as Australia, and include such important regions as the South American "pampas" and South African "veldt." Seasonal drought and drying winds are characteristic climatic features, and periodic long term droughts are to be expected in these landscapes. The mild climate of warm temperate grasslands has always been an attractive feature for agrarian economies even though the incidences of drought make livestock raising erratic and prone to alter these landscapes in several ways.

In North America, warm temperate grasslands are represented by a mostly summer-active **Gulf Coastal Grassland** in southeast Texas and southwest Louisiana, a more or less biseasonal rainfall **Semidesert Grassland** centered in northern Mexico and the American Southwest, and a winter precipitation-summer drought **California Valley Grassland** found in Alta and Baja California and offshore islands. The original grass cover over much of these biotic communities has been considerably reduced, altered and in some cases replaced entirely. Many **Gulf Coastal Grassland** and **Semidesert Grassland** sites, for example, have been invaded almost beyond recognition by woody plants and their grasses replaced by leaf succulents, cacti, or shrubs. **California Valley Grassland**, where this entity remains, is now comprised almost entirely of introduced annuals. Similar displacements have occurred with the native fauna in the above. One herbaceous biotic community, **Southeastern Canebrakes,** formerly an important landscape feature in the southeastern U. S. is now functionally extinct.

Gulf Coastal Grassland

Much of the flat, low-lying coastal plain of Texas and western Louisiana was formerly a tall-grass prairie in which the grasses attained a height of 2 m (80 in) or more by the end of the long May to September growing season. Some of the most prominent species included big bluestem (*Andropogon gerardii*), silver bluestem (*Bothriochloa saccharoides*), Texas wintergrass (*Nassella leucotricha*), switchgrass (*Panicum virgatum*), little bluestem (*Schizachyrium scoparium*), and Indiangrass (*Sorghastrum nutans*). A number of shorter-statured grasses were also present as were a great variety of prairie flowers which often dominated locally. Mottes of wax myrtle (*Myrica cerifera*) and live oaks (*Quercus virginiana*) were generally confined to stream margins and sandy ridges.

Sometimes called "Coastal Prairie" (Tharp 1939), **Gulf Coastal Grassland** formerly extended from 120 km (75 mi) to 150 km (90 mi) inland along the Gulf of Mexico from the vicinity of Matamoros, Mexico, northeastward into southwest Louisiana. Separated from the ocean by extensive coastal strands and coastal marshes, the grassland was bordered on the north and east by **Southeastern Deciduous and Evergreen Forest**. To the west and southwest, **Gulf Coastal Grassland** merged with tropic-subtropic **Tamaulipan Savanna Grassland**, **Tamaulipan Thornscrub**, or **Tamaulipan Semi-deciduous forest**. Today, where not under cultivation or urbanized, this biotic community has been so invaded by trees and shrubs that it is often difficult to interpret as a former grassland. Originally estimated to cover 5.3 million ha (13 million acre), in 1900, approximately 2.4 million ha (6 million acre) remained with less than 2 percent in a recognizable state (Tharp 1939, Shelford 1963, Frye et al. 1984, USDI 1994).

Located primarily on loam and sandy soils as well as some claypans, these grasslands reflected conditions inhibiting tree growth. Wind driven fires undoubtedly played a major role in grassland maintenance as mean monthly wind speeds at climatic stations located in **Gulf Coastal Grassland** exceed those in historic forest communities. Other factors working to maintain a grassland setting in this nearly subtropical biotic community were the hurricanes which periodically visit the region in late summer, and the high incidence of waterlogged soils. Mean annual precipitation is high, if somewhat irregular, with more than 60% of the rain falling during the long April to November growing season (Table 9). Totals range from a mean of 762 mm (30 in) in the south to more than 1,400 mm (55 in) at the prairie's northeastern limits. **Gulf Coastal Grassland** is thus one of the wettest grasslands in the United States.

Numerous grasses, including several endemics, complement the bluestems and other tall dominants. Based on a plant list collected on Attwater Prairie Chicken National

Figure 54. Gulf Coastal Grassland at an altitude of ca. 60 m (200 ft) on Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas. The grass cover is both dense and diverse, and includes such characteristic species as big bluestem (*Andropogon gerardii*), broomsedge bluestem (*Andropogon virginicus*), hairawn muhly (*Muhlenbergia capillaris*), switchgrass (*Panicum virgatum*), little bluestem (*Schizachyrium scoparium*), and Indiangrass (*Sorghastrum nutans*), along with numerous forbs. June 1999, D.E.B.

Wildlife Refuge and other sources, some of the more prevalent species include bushy bluestem (*Andropogon glomeratus*), splitbeard bluestem (*A. ternarius*), broomsedge bluestem (*A. virginicus*), slimspike and other threeawns (*Aristida longespica*, *A. purpurascens et al.),* various lovegrasses (*Eragrostis* spp.), hairy woollygrass (*Erioneuron pilosum*), tanglehead (*Heteropogon contortus*), Gulf or hairawn muhly (*Muhlenbergia capillaris*), several *Panicum*s, gulfdune paspalum (*Paspalum monostachyum*), longspike tridens (*Tridens strictus*), and crinkleawn (*Trachypogon spicatus*) (Frye et al. 1984, USDI 1994) (Figure 54). These grasses are replaced in the wetlands that characterize so much of the region by rough dropseed (*Sporobolus clandestinus*) and other moist soil species.

The number of flowering herbs that can be expected to occur in any given tract of prairie is large, and includes ragweed (*Ambrosia psilostachya*), Indian plantain (*Arnoglossum plantagineum*), butterfly milkweed (*Asclepias tuberosa*), wild indigo (*Baptisia bracteata*), rattlesnake flower (*Brazoria truncata*), winecup (*Callirhoe involucrata*), Indian paintbrush (*Castilleja indivisa*), tickseed (*Coreopsis tinctoria*), Texas croton (*Croton texensis*), hogwort (*C. capitatus*), yankeeweed (*Eupatorium compositifolium*), plains snakecotton (*Froelichia floridana*), lanceleaf blanketflower (*Gaillardia aestivalis*), spiderlily (*Hymenocallis liriosme),* tievine (*Ipomoea cordatotriloba*), blazing star (*Liatris* spp.), *Lupinus subcarnosus* and *L. texensis*, several evening primroses (*Oenothera* spp.), *Phlox* spp., meadow aster (*Symphyotrichum pratensis*), hoarypea (*Tephrosia onobrychoides*), and spiderworts (*Tradescantia* spp.).

Shrubs, both native and introduced are now increasingly common, some of the more ubiquitous being partridge pea (*Cassia fasciculata*), wax myrtle (*Myrica cerifera*), and Macartney rose (*Rosa bracteata*), with prickly-pear (*Opuntia phaeacantha*), and an occasional yucca (*Yucca rupicola*) found in the drier sites. Many areas formerly within **Gulf Coastal Grassland** have now grown up in shrubbery or have been so invaded by trees as to change the plant formation. In the north and east the usurpers are mostly pines and oaks of the **Southeastern Deciduous and Evergreen Forest**, while in the south and west numerous pastures are now so infested with sweet acacia (*Acacia farnesiana*), wait-a-minute bush (*Mimosa aculeaticarpa*), and honey mesquite (*Prosopis glandulosa*), as to be considered "thornscrub" (Figure 55).

Supposedly grazed by bison in historic times, these grasslands were apparently not suited for pronghorn. Although **Gulf Coast Grassland** has been reported to have been a stronghold for the so-called red wolf (*Canis niger*), recent inbreeding suggests that this animal was only a regional race of coyote. Other mammals, with the exception of a few subspecies such as the *subater* race of pygmy mouse (*Baiomys taylori*) and the *ludovicianus* race of prairie vole (*Microtus ochrogaster*), are similar to those present in certain tall-grass communities within **Plains Grassland**.

Birds too, lack much distinction, and except for the poorly differentiated Attwater subspecies of prairie chicken (*Tympanuchus cupido attwateri*), no taxon is restricted to **Gulf Coast Grassland**. Grassland species in general are well represented, however, and the Cassin sparrow (*Aimophila cassinii*), black-throated sparrow (*Amphispiza bilineata*), white-tailed hawk (*Buteo albicaudatus*), lark sparrow (*Chondestes grammacus*), aplomado falcon (*Falco femoralis*), and scissor-tailed flycatcher (*Tyrannus forficatus*) can be considered characteristic breeding birds.

Reptiles and amphibians are better represented, although only a few such as the Gulf Coast toad (*Bufo valliceps*), Texas tortoise (*Gopherus berlandieri*), and northern keeled earless lizard (*Holbrookia propinqua propinqua*) can be considered

Figure 55. Gulf Coastal Grassland in Wharton County, Texas, invaded by brush, in this case, sweet acacia (*Acacia farnesiana*). Elevation 18 m. June 1999, D.E.B.

Table 9. Mean precipitation totals for stations located within or adjacent to Gulf Coastal Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)															Mean Frost Free Days	
		J	F	M	A	M	J	J	A	S	O	N	D	Total	May-Sept	%	> 0° C	MeanWind Speed
Corpus Christi, Texas, USA 27.8° N, 97.5° W	12 (41')	41	39	21	51	77	85	50	89	156	81	39	36	765 (30.2")	457	60	350	19 kph
Victoria, Texas, USA 28.9° N, 96.9° W	32 (104')	47	57	34	66	##	115	66	84	158	84	57	54	936 (36.4")	537	58	361	16 kph
Galveston, Texas, USA 29.3° N, 94.8° W	2 (7')	75	59	53	67	84	88	96	112	148	66	82	92	1022 (40.2")	528	52	345	18 kph
Port Arthur, Texas, USA 29.9° N, 94.0° W	5 (16')	106	94	74	103	##	101	##	138	156	92	110	116	1340 (52.8")	645	48	357	18 kph
Lake Charles, Louisiana, USA 30.1° N, 93.2° W	3 (9')	108	99	77	103	##	106	##	137	132	88	96	129	1347 (53.0")	647	48	356	14 kph

indicator species. Other lizards of **Gulf Coastal Grassland** include the more widely occurring prairie racerunner (*Cnemidophorus sexlineatus viridis*), Texas spotted whiptail (*C. gularis gularis*), southern Prairie skink (*Eumeces septentrionalis obtusirostris*), Western slender grass lizard (*Ophisaurus attenuatus attenuatus*), and Texas horned lizard (*Phrynosoma cornutum*). The snakes too are largely subspecies of species also found in either Plains or Semidesert grasslands– Texas glossy snake (*Arizona elegans arenicola*), Texas scarlet snake (*Cemophora coccinea lineri*), Eastern yellow-bellied racer (*Coluber constrictor flaviventris*), Western diamondback rattlesnake (*Crotalus atrox*), Texas rat snake (*Elaphe obsoleta lindheimeri*), Western coachwhip (*Masticophis flagellum testaceus*), Prairie kingsnake (*Lampropeltis calligaster calligaster*), Plains blind snake (*Lepto-*

typhlops dulcis dulcis), Western smooth green snake (*Opheodrys vernalis*), a bullsnake (*Pituophis melanoleucus sayi*), Massasauga (*Sistrurus catenatus*), the marsh brown snake (*Storeria dekayi limnetes*), Plains black-headed snake (*Tantilla nigriceps fumiceps*), and Western ribbon snake (*Thamnophis proximus orarius*).

Amphibian representatives are also mostly at the subspecies level and include such restricted taxa as the Eastern green toad (*Bufo debilis debilis*) and Hunter's spadefoot (*Scaphiopus holbrooki hunterii*), as well as several chorus frogs having a greater grassland distribution– the spotted chorus frog (*Pseudacris clarkii*), Strecker's chorus frog (*P. streckeri*), and upland chorus frog (*P. triseriata feriarum*).

Because so few plant and animal species are restricted to **Gulf Coastal Grassland**, most recent works regard this biotic community as a fasciation of tall-grass prairie within **Plains Grassland** or ignore it entirely despite its warmer climate (see e.g., Barbour and Billings 1988, 2000). Nonetheless, representative examples of **Gulf Coast Grassland** need to be preserved if the continent's biodiversity is to be retained. This need has been well recognized in Texas where The Nature Conservancy has been instrumental in acquiring approximately 5,460 ha (13,500 acres) of **Gulf Coast Grassland** at six sites intended to be managed by federal and state conservation agencies or TNC itself. Significant areas of this grassland are also protected in the numerous coastal refuges managed by the U. S. Fish and Wildlife Service, and still others are included within state and private refugia. One of the best and largest remaining examples is the 3,238 ha (8,000 acre) Attwater Prairie Chicken National Wildlife Refuge located in Colorado County, TX.

Semidesert Grassland

This large and highly diverse biotic community was originally described and mapped by Forrest Shreve (1917) as a "desert-grassland" transition. Subsequently, ecologists have referred to various portions of **Semidesert Grassland** as "desert savanna" (Shantz and Zon 1924), "mesquite grassland" (Brand 1936, Leopold 1950), "desert plains grassland" (Weaver and Clements 1938, LeSueur 1945), "desert shrub grassland" (Darrow 1944), "grassland transition" (Müeller 1947), and most frequently as "desert grassland" (Nichol 1937, Büechner 1950, Benson and Darrow 1954, Castetter 1956, Humphrey 1958, Lowe 1964, McLaren and Van Devender 1995). In Mexico, these and other grasslands are known collectively as *pastizals* (Rzedowski 1988) while Burgess (1996) proposed the designation "Apacherian shrub-savanna-grassland" despite this biotic community extending far beyond the historic range of these native peoples. We prefer to use the term **Semidesert Grassland** (Little 1950), which, while perhaps less euphonious, is more descriptive from an ecological and geographical perspective. Whatever the terminology, **Semidesert Grassland** is a perennial grass-scrub dominated landscape positioned adjacent to or above desertscrub and below **Plains Grassland**, **Madrean Evergreen Woodland**, or **Interior Chaparral** in which up to 50% of the potential ground cover may be bare ground or occupied by annual and/or herbaceous vegetation. Although **Semidesert Grassland** adjoins the southeastern portions of the Mohave Desert, and abuts the eastern and northern reaches of the Sonoran Desert, the main interactions of this biotic community are with **Chihuahuan Desertscrub**. **Semidesert Grassland** not only surrounds the Chihuahuan Desert, large areas of former grassland within and adjacent to this biotic community have recently been replaced by desert plants along with their animal constituents. Hence, **Semidesert Grassland** is largely a Chihuahuan Semidesert Grassland with fasciations extending westward into west-central Arizona, eastward into Texas, and southward into the Valley of Mexico (Map 1). Expansive and composed of numerous regional fasciations, **Semidesert Grassland** also serves as a biogeographic catch-all for a variety of shrub or "mattoral"-invaded communities situated between desert and grassland.

Extensive areas of **Semidesert Grassland** occurred in the United States in central and southeastern Arizona, in southern New Mexico, and in west Texas where it has expanded diagonally to the northeast toward the Red River and the Oklahoma border (Brown et al. 2007) (Figure 56). In Mexico, this biotic community occupies extensive portions of northeastern Sonora, Chihuahua, Coahuila, Nuevo Leon, San Luis Potosí and Durango before continuing southward on the Central Plateau to the Valley of Mexico after which it

Figure 56. Semidesert Grassland between Lordsburg and Silver City, New Mexico ca. 1,450 m (4,750 ft). These “yucca grasslands” of soaptree yucca or palmilla (*Yucca elata*) cover extensive areas of southeastern Arizona, northern Chihuahua, west Texas, and southern New Mexico, where this plant is the state flower. The bunch grass is sideoats grama (*Bouteloua curtipendula*), drying after an above average monsoon in 2006. The shrubs are mostly creosote (*Larrea tridentata*) with scattered velvet mesquite (*Prosopis velutina*). April 2007, E.M.

Figure 57. Semidesert Grassland near its southern extremity in the vicinity of Perote in the state of Puebla, Mexico, ca. 2,400 m (7,875 ft). Here, on this limestone slope, one encounters many of the same genera if not species of such dry tropic-scrub Semidesert Grassland indicators as *Agave*, *Dasylirion*, *Juniperus*, *Prosopis*, and *Yucca*. The bunchgrasses are also such widely dispersed species as *Bouteloua curtipendula*, with species of *Muhlenbergia* and *Sporobolus* also participating. March 2001, D.E.B.

Figure 58. Semidesert Grassland devolving into Chihuahuan Desertscrub in the San Bernardino Valley, northeastern Sonora, Mexico, ca. 1,125 m (3,700 ft). The replacement of grassland by open communities of such dry-tropic scrub as whitethorn acacia (*Acacia neovernicosa*), tarbush (*Flourensia cernua*), and creosote (*Larrea tridentata*) has transformed large areas of former Semidesert Grassland into matoral or desertscrub due to increasing evapotranspiration rates. March 1993, D.E.B.

reaches its southernmost limits in the vicinity of Tehuacán in northern Puebla and near Nochixtlán in northeastern Oaxaca (Rzedowski 1975, 1988) (Figure 57).

In the northwest and in the northeast, the lower elevation limits of **Semidesert Grassland** may be as low as ca. 1,100 m (3,600 ft). More often, however, the grassland's lower limits are above 1,100 m and below 1,500 m (4,900 ft) where its contact with **Chihuahuan Desertscrub** is complex and manifested in alternating landscape mosaics (Figure 58). Upper elevations are typically between 1,500 and 1,700 m (5,500 ft), reaching altitudes of 2,200 (7,200 ft) to 2,500 m (8,200 ft) in the Valley of Mexico and other southern locales. Within the generally lower **Chihuahuan Desertscrub**, **Semidesert Grassland** also occupies the numerous enclosed drainages and/or alluvial terraces of tobosa grass (*Hilaria mutica*) and sacaton (*Sporobolus wrightii*) (Figures 59, 60).

Most **Semidesert Grassland** locations have a mean annual precipitation of between 300 mm (12 in) and 450 mm (18 in) with the more southerly stations exceeding 600 mm (24 in). More than half of this total falls between August and September, with at least 130 mm (5 in) arriving during the April through August growing season (Table 10). This is important as studies have shown that perennial grass growth depends on the amount and predictability of the rainfall received during this "monsoon" period (Cable 1975). Unlike **Plains Grassland**, which is generally situated northward and above **Semidesert Grassland**, winters are mild and freezing temperatures average less than 150 days a year. Summers are warm to hot with several days over 38° C (100° F) being recorded nearly every year. With the exception of storm periods, relative humidities are low. Winds are prevalent during the late spring and early summer, with another less active period occurring in fall. These winds are, or were, important to the grassland's maintenance, as they carry the lightning-caused fires that historically occurred in **Semidesert Grassland** prior to the onset of the "summer monsoon" (Humphrey 1958, Bahre 1991). As a consequence, this biotic community is best developed in valleys, open hills, slopes, and ridges (Figure 61).

Figure 59. Semidesert Grassland of sacaton (*Sporobolus wrightii*) along the San Pedro River near Lewis Springs in southeastern Arizona ca. 1,260 m (4,130 ft). Sacaton grasslands cover large areas of lower alluvial terrace not previously converted to agriculture. The flowering panicle can reach heights of greater than 2 m (7 ft). August 2001, E.M.

Figure 60. Semidesert Grassland of tobosa (*Hilaria mutica*) with catclaw (*Acacia greggii*), clock-face prickly-pear (*Opuntia chlorotica*), and snakeweed (*Gutierrezia sarothrae*), between Date Creek and Hillside, Yavapai County, Arizona, ca. 975 m (3,198 ft). This low elevation, northwestern extension of Semidesert Grassland, photographed by R. R. Humphrey in 1950, has been virtually destroyed by the construction of stock tanks, which has led to intensive livestock grazing and soil erosion, causing the grasses to be replaced by creosote and mesquite. Humphrey (1958) was one of the first ecologists to understand that grazing and fire suppression were the primary reasons for brush encroachment in Semidesert Grassland.

Figure 61. Excluded from grazing for perhaps 30 years, this luxuriant and diverse grassland near Ft. Bowie, Cochise County, Arizona ca. 1,500 m (5,000 ft) may represent site potential for Semidesert Grassland communities. Perennials in this photo include southwestern needlegrass (*Achnatherum eminens*), *Aristida* spp., cane beardgrass (*Bothriochloa barbinodis*), a number of gramas (*Bouteloua chondrosioides*, *B. curtipendula*, *B. eriopoda*, *B. gracilis*, *B. hirsuta*, *B. radicosa*, *B. repens*), Arizona cottontop (*Digitaria arizonica*), *Eragrostis* spp., especially *E. intermedia*, wolftail (*Lycurus setosus*), muhlys (*Muhlenbergia arenicola*, *M. porteri*, et al.), burrowgrass (*Scleropogon brevifolius*), and false Rhodes grass (*Trichloris crinita*). Bristlegrass (*Setaria leucopila*) is the conspicuous grass with the spike-like inflorescence. August 2008, E.M.

Figure 62. Semidesert Grassland close to the summit of the Sierra Fra Cristobal, on the border between Sierra and Socorro counties, New Mexico, ca. 1,635 m (5,364 ft). The trees are *Juniperus monosperma* and the principal grasses are New Mexico feathergrass (*Hesperostipa neomexicana*) and curley-mesquite (*Hilaria belangeri*), which are accompanied by yucca and cholla (*Cylindropuntia* spp.). February 1999, D.E.B.

The grasses present were originally mostly bunch-grasses, the bases of the clumps often separated by intervening areas of bare ground and rarely forming a continuous sod cover (Figure 62). Reproduction of these grasses was principally from seed. In areas of heavy to moderate rainfall, livestock grazing reduced these bunch-grasses and encouraged the growth of low-growing sod grasses such as curly mesquite (*Hilaria belangeri*). In lower summer rainfall areas the shift has been from bunch-grasses to annual grasses and/or shrubs. Only where soils are deep, protected from grazing and erosion, and possessed of few shrubs and cacti, do perennial grasses continue to cover extensive landscapes.

Thrifty, extensive grass landscapes stand in marked contrast to the appearance of most **Semidesert Grassland** communities today–especially the lower elevation sites having a history of heavy grazing. More often than not, the original grass cover as well as species composition has been much altered and/or reduced by a wide array of competing shrubs, trees, weeds, and cacti (Figure 63). And despite numerous efforts at range rehabilitation, it remains to be seen whether such areas can be restored to their former character through the use of reduced grazing pressures, brush eradication, and controlled burns. Reseeding alone has generally failed to restore native **Semidesert Grasslands** (Munda and Pater 2003).

Although **Semidesert Grassland** is transitional in the sense of being geographically positioned between **Plains Grassland** and desertscrub, and shares some of the floral and faunal constituents of both, it is a distinctive biotic community in its own right. As such, it is an evolutionary and biogeographic center for a distinguishable array of plant and animal representatives. Many of the grama grasses, for example, sprucetop grama (*B. chondrosioides*), black grama (*B. eriopoda*), hairy grama (*B. hirsuta*), and purple grama (*B. radicans*), maintain a presence from east to west, and from north to south (see Rzedowski 1981). A number of other summer-active perennial grasses, while sometimes local in distribution are even more representative– three-awns (*Aristida divaricata*, *A. purpurea*), slender grama (*B. repens*), gypsum grama (*B. breviseta*), Arizona cottontop (*Digitaria californica*), New Mexico needle-grass (*Hesperostipa neomexicana*), tanglehead (*Heteropogon contortus*), bush muhly (*Muhlenbergia porteri*),

Figure 63. Fall aspect of Semidesert Grassland on Perry Mesa, along the Agua Fria National Monument/Tonto National Forest border, Yavapai County, Arizona, ca. 1,185 m (3,900 ft). The soils are very deep and high in clay, and the grass is almost exclusively tobosa (*Hilaria mutica*) in this photo. Catclaw (*Acacia greggii*), Whipple cholla (*Cylindropuntia whipplei*), bastardsage (*Eriogonum wrightii*), and prickly-pear are also common. November 2009, E.M.

vine mesquite (*Panicum obtusum*), pappus grass (*Pappophorum vaginatum*), desert needle-grass (*Stipa mucronata*), finestem needle-grass (*S. tenuissima*), slim tridens (*Tridens muticus*), and others.

Two especially diagnostic grasses are black grama (*Bouteloua eriopoda*) and tobosa grass (*Hilaria mutica*), the former generally favoring gravelly upland sites, the latter usually found on heavy, lowland soils. Also frequently present, especially at the higher elevations, are any number of **Plains Grassland** grasses–sideoats grama (*Bouteloua curtipendula*), blue grama (*B. gracilis*), buffalo grass (*Büchloe dactyloides*), Plains lovegrass (*Eragrostis intermedia*), wolftail (*Lycurus setosus*), little bluestem (*Schizachyrium scoparium*), bristlegrasses (*Setaria* spp.), and several more–any of which may be intermixed with **Semidesert Grassland** grasses, or even locally dominate. Still other areas may possess regional dominants such as *Stipa ichu* in the Sierra de Catorce, San Luis Potosí, Mexico (Rzedowski 1988). Oftentimes only the less palatable species are present-grasses such as purple threeawn (*Aristida purpurea*), fluffgrass (*Dasyochloa pulchella*), the bottom-dwelling burrograss (*Scleropogon brevifolius,* often persisting in prairie dog communities), and hairy tridens (*Tridens pilosus*). Lehmann's lovegrass (*Eragrostis lehmanniana*), an early "green-up" grass purposely introduced from South Africa, now occupies extensive areas in some northwestern portions of **Semidesert Grassland** and appears to be spreading at the expense of more palatable native grasses, and must now, for better or worse, be considered as part of this biotic community's flora. Generally speaking, as is the case in **Plains Grassland**, the russet-colored grasses provide more nutritious forage to livestock than the lighter, yellowish or "white" species, the former almost always outnumbered by the latter.

Forbs or herbs may be seasonally abundant with different suites of species usually flowering in spring–*Cryptantha* spp., tansy mustards (*Descurainia* spp.), filaree (*Erodium* spp.), lupines (*Lupinus* spp.), pepperweeds (*Lepidium* spp.), and mallows (*Sphaeralcea* spp.) – than during the summer–amaranths (*Amaranthus* spp.), spiderlings (*Boerhaavia* spp.), paintbrush (*Castilleja* spp.), sandmats (*Chamaesyce* spp.), and woolly tidestromia (*Tidestromia lanuginosa*).

And, although the species of shrub, tree, and cacti associates present may appear to vary more than the grasses, many

Figure 64. An open Semidesert Grassland in the state of Durango, Mexico, in which the principal species of dry-tropic scrub is twisted acacia (*Acacia schaffneri*) giving an African savanna aspect to the landscape, ca. 1,980 m (6,355 ft). March 1999, D.E.B.

are more or less found throughout. When present, dry-tropic stem and leaf succulents are especially important in determining the biotic community's composition and landscape character. Examples include the desert spoons or *sotols* (*Dasylirion leiophyllum, D. wheeleri*), beargrasses or *sacahuistas* (*Nolina erumpens, N. microcarpa*, *N. texana*), century-plants and shin-daggers (*Agave lecheguilla*, *A. parryi*, *A. parviflora*, *A. schottii*, etc.), and especially the yuccas (*Yucca baccata*, *Y. decipiens*, *Y. elata*, *Y. faxoniana*, *Y. thompsoniana*, *Y. torreyi*, etc.).

Short leguminous trees, mostly mesquite and acacia or *huisaches* (*Acacia constricta, A. schaffneri*) commonly attain aspect dominance, thus giving the grassland or former grassland an African savanna-like appearance (Figure 64). Other generally or locally important scrubby tree and shrub components, several of which may share or even assume dominance, are catclaw acacia (*Acacia greggii*), Wright's lippia (*Aloysia wrightii*), barberry or *algerita* (*Berberis* spp.), false mesquite (*Calliandra eriophylla*), desert hackberry or *granejo* (*Celtis pallida*), netleaf hackberry (*Celtis reticulata*), Mormon tea (*Ephedra trifurca*), ocotillo (*Fouquieria splendens*), one-seed juniper (*Juniperus monosperma*), allthorn (*Koeberlinia spinosa*), javelina-bush (*Condalia ericoides*), mimosa (*Mimosa aculeaticarpa*, *M. dysocarpa*), little-leaf sumac (*Rhus microphylla*), greythorn (*Zizyphus obtusifolia*), and many others. All of these plants were natural inhabitants of **Semidesert Grassland**, and remain so, albeit now often presenting greater densities than formerly. **Semidesert Grassland** has naturally high shrub diversity, most species being taller than the grasses. The result is therefore often one in which the grass plants are overtopped by their dry-tropic shrub associates, giving a multi-tiered aspect to the landscape physiognomy. Also, such characteristic **Chihuahuan Desertscrub** shrubs as whitethorn acacia (*Acacia constricta, A. neovernicosa*), tarbush (*Flourensia cernua*), and creosote (*Larrea tridentata*) have invaded, and continue to invade, extensive areas of **Semidesert Grassland**, thereby adding to the grassland's broken character (Figure 65). In the north and west, where significantly greater winter precipitation can be expected, smaller invasive shrubs such as turpentine bush (*Ericameria laricifolia*), certain buckwheats (*Eriogonum fasiculatumi*, e.g.), snakeweed (*Gutierrezia sarothrae*), collegeflower (*Hymenopappus flavescens*), burroweed (*Isocoma tenuisecta*), mariola (*Parthenium incanum*), threadleaf groundsel (*Senecio flaccidus*), crownbeards (*Verbesina* spp.), desert zinnia (*Zinnia acerosa*), and herbaceous sages such as *Artemisia ludoviciana* may be present to various degrees, and depending upon location and grazing history, even assume local dominance (Figure 66).

In Mexico, and in parts of Arizona and Texas, it is not unusual for a suite of thornscrub components to be present. Depending upon the location, these may include baby-bonnets (*Coursetia glandulosa*), hopbush (*Dodonaea viscosa*), kidneywood (*Eysenhardtia orthocarpa*), desert cotton or *algodoncillo* (*Gossypium thurberi*), Wright's mock buckthorn (*Sageretia wrightii*), gum bully (*Sideroxylon lanuginosum*), or almost any other species found in Tamaulipan, Sinaloan, or Guerreran thornscrub.

Cacti, while not always conspicuous, are important in the structure and composition of **Semidesert Grassland** (Figure 67**).** Species well represented in this biotic community, include the chollas (e.g., *Cylindropuntia acanthacarpa, C. imbricata*, *C. kleiniae, C. leptocaulis*, *C. spinosior*), several hedgehogs including the rainbow cactus (*Echinocereus rigidissimus*), barrel cactus or *bisnaga* (*Ferocactus pilosus*, *F. wislizenii*, *Thelocactus conothelos*, *T. hexaedrophorus*), the pincushions (*Echinomastus erectocentrus*, *E. intertextus, Mammillaria grahamii, M. heyderi, M. mainiae*, *M. wrightii*) and numerous prickly-pears including *Opuntia chlorotica*, *O. macrocentra*, *O. phaeacantha, O. streptacantha*, etc.

Trees, except for mesquites, acacias and one-seed junipers, are usually restricted to drainageways where one may encounter desert willow (*Chilopsis linearis*), *cumero* (*Celtis reticulata*), Western soapberry (*Sapindus saponaria*), or one of the

Figure 65. Shrub encroachment is extreme and perennial grasses are virtually eliminated in many areas of Semidesert Grassland that were heavily grazed beginning in the early to mid 1800's. Today, the landscape is whitethorn acacia (*Acacia constricta*), tarbush (*Flourensia cernua*), allthorn (*Koeberlinia spinosa*), creosote and mesquite. Photo from near the St. David Cienega, San Pedro Riparian National Conservation Area, Cochise County, Arizona 1,120 m (3,700 ft); Dragoon Mountains in the background. November 2007, E.M.

Figure 66. Overgrazed Semidesert Grassland in the Mule Mountains, Cochise County, Arizona, near the International Border, ca. 1,800 m (5,900 ft) elevation. The area on the left side of the fence has been irreversibly altered due to soil loss and the invasion of turpentine bush (*Ericameria laricifolia*) and mesquite. The less heavily grazed pasture is populated by such grasses as sideoats grama (*Bouteloua curtipendula*), and wolftail (*Lycurus setosus*). The evergreen tree is Emory oak (*Quercus emoryi*), a Madrean species characteristic of the encinal woodland found at elevations higher up in the mountains. June 1995, D.E.B.

oaks from the **Madrean Evergreen Woodland** higher up, e.g. *Quercus chihuahuensis, Q. emoryi*, *Q. grisea*, et al.

Although many **Semidesert Grassland** areas in the north have been subject to investigation, see e.g., the extensive works summarized in McLaran and VanDevender (1995), much less is known about **Semidesert Grassland** communities in central Mexico. Rzedowski (1988) illustrates and briefly describes **Semidesert Grassland** sites near Vallejo, San Luis Potosí inhabited by *Muhlenbergia purpusii*; a halophytic community of *Distichlis spicata* near Coacalco, Mexico; a grassland composed of *Abildgaardia mexicana, Bouteloua radicosa,* and *Hilaria cenchroides*, near Tepotzotlan, Mexico; a *pastizal*

Figure 67. Extreme examples of cactus invasion, especially chollas and prickly-pears can be found in many if not most Semidesert Grassland communities as shown here in southern Zacatecas, Mexico, ca. 2,187 m (7,177 ft). March 1977, D.E.B.

of *Bouteloua*, *Hilaria,* and *Muhlenbergia* with *Acacia schaffneri* near Tepeji del Rio, Hidalgo; a *pastizal* community of *Bouteloua gracilis* (navajita) near Ojuelos, Jalisco; a *pastizal* of *Axonopus* and *Paspalum* near de Lolotla, Hidalgo; a *pastizal* of *Bouteloua*, *Cathestecum* and *Trachypogon* near Iguala, Guerrero and a *pastizal* of *Aristida, Bouteloua*, *Erioneuron,* and *Lycurus*, with *Opuntia streptacantha* (nopal cardón) and *Schinus molle* (pirul) near Tepexpan, Mexico. Of these, only the communities of *Distichlis spicata* and *Bouteloua gracilis* have close counterparts in the U. S. or northern Mexico. One community discussed but not illustrated by Rzedowski (1988), which is composed of *Aristida* spp., *Bouteloua chondrosioides*, and other species of *Bouteloua* is in extreme northeastern Oaxaca between 2,100 and 2,500 m (6,900 and 8,200) elevation. This community is likely the southernmost **Semidesert Grassland** location in North America.

Semidesert Grasslands on Burro Mesa and other sites in west-central Arizona, while formerly populated by perennial warm-season grasses, are today often comprised largely of introduced annuals (Figure 68). Red brome (*Bromus rubens*) may sometimes be the most abundant grass, with wild oats (*Avena*) and bristlegrass (*Setaria*) also prevalant depending on the site and year. Except for the steeper hillsides, the only native grass remaining is often tobosa (*Hilaria mutica*), and these grasslands now have the composition and growth-form appearance of **California Valley Grassland**. Agaves, chollas, palmillas, and sotols, may be lacking as are several characteristic **Semidesert Grassland** animals. Even mesquite, so ubiquitous in so many of these grasslands, is only locally common, and the principal scrub components are acacias (*Acacia* spp.), barberry (*Berberis* spp.), crucifixion thorn (*Canotia holacantha*), one-seed juniper (*Juniperus monsperma*), prickly-pears (*Opuntia* spp.), and scrub oak (*Quercus turbinella).* Annual forbs, both native and alien, are of great importance in the composition, and snakeweed (*Gutierrezia* spp.) is often the most conspicuous perennial.

Mammals indicative or representative of **Semidesert Grassland** include, in the appropriate locations, the Mexican pronghorn (*Antilocapra americana mexicana*), hispid and silky pocket mice (*Chaetodipus hispidus*, *Perognathus flavus*), yellow-faced pocket gopher (*Cratogeomys castanops*), black-tailed prairie dog (*Cynomys ludovicianus*), Merriam, Ord's Phil-

Figure 68. A western fasciation of Semidesert Grassland on Burro Mesa east of the Aquarius Mountains in Yavapai County, Arizona, ca. 1,219 m (4,000 ft). Because of grazing, the original grass cover was much altered when first visited in 1972. Although relatively open, these grasslands were then in a disclimax state and populated mostly by winter-spring annuals—red brome (*Bromus rubens*) and yellow bristlegrass (*Setaria lutescens*), being especially prevalent that year. The principal perennial grass, tobosa (*Hilaria mutica*), was then much reduced and such characteristic Semidesert Grassland grasses as sideoats grama (*Bouteloua curtipendula*), black grama (*B. eriopoda*), and Arizona cottontop (*Digitaria californica*), were confined to rocky hillsides and slopes. This situation was much changed when the same area was visited in 2007 with the annuals much less in evidence and the tobosa grass and other perennial grasses having increased in density. The cacti are Whipple cholla and clock-face prickly-pear (*Opuntia chlorotica*). February 1971, D.E.B.

lip's, and banner-tailed kangaroo rats (*Dipodomys merriami*, *D. ordii*, *D. phillipsii, D. spectabilis*), black-tailed and white-sided jack rabbits (*Lepus californicus, L. callotis*), Southern plains and white-throated wood rats (*Neotoma micropus*, *N. albigula*), Southern grasshopper mouse (*Onychomys torridus*), fulvous harvest mouse (*Reithrodontomys fulvescens*), the cotton rats (*Sigmodon hispidus* and *S. fulviventer*), and Mexican and spotted ground squirrels (*Spermophilis mexicanus S. spilosoma*).

The variety of bird-life is also great, and a list of characteristic nesting species would include the black-throated, Botteri's, Cassin's, and rufous-crowned sparrows (*Amphispiza bilineata*, *A. botterii*, *A. cassinii*, *A. ruficeps*), scaled quail (*Callipepla squamata*), Lucifer's hummingbird (*Calothorax lucifer*), cactus wren (*Campylorhynchus brunneicapillus*), lark sparrow (*Chondestes grammacus*), Chihuahuan raven (*Corvus cryptoleucus*), prairie and aplomado falcons (*Falco mexicanus, F. femoralis*), loggerhead shrike (*Lanius ludovicianus*), savannah sparrow (*Passerculus sandwichensis*), Say's phoebe (*Sayornis saya*), Worthen's sparrow (*Spizella wortheni*), Eastern and Western meadowlarks (*Sturnella magna*, *S. neglecta*), curve-billed thrasher (*Toxostoma curvirostre*), Cassin's kingbird (*Tyrannus vociferans*), and Bell's vireo (*Vireo bellii*).

Reptiles are well represented and include a number of characteristic taxa, especially at the subspecific level. See Appendix 3 for a list from Morafka (1977) and Stebbins (1985) that applies to a variety of habitats within **Semidesert Grassland.** As befits this grassland's generally arid environment, indicative amphibians are less numerous, but include a number of species of more or less regional occurrence. These include the Great Plains toad (*Bufo cognatus*), green toad (*Bufo debilis*), Texas toad (*Bufo speciosus*), Couch's spadefoot (*Scaphiopus couchii*), Plains spadefoot (*Spea bombifrons*), Western spadefoot (*Spea hammondi*), and the New Mexico spadefoot (*Spea multiplicata*).

As is to be expected, many **Semidesert Grassland** species also occur in adjacent scrublands and desertlands, e.g., black-throated sparrow (*Amphispiza bilineata*), Gambel's quail (*Callipepla gambelii*), desert mule deer (*Odocoileus hemionus erimecus*), and Bell's vireo (*Vireo bellii*). Others such as the black-tailed prairie dog (*Cynomys ludovicianus*) and aplomado falcon (*Falco femoralis*), are equally or more representative of other grassland biotic communities, while a few species such as the Oaxaca sparrow (*Aimophila notosticta*) and Worthen's sparrow (*Spizella wortheni*) are endemic to certain communities within **Semidesert Grassland**.

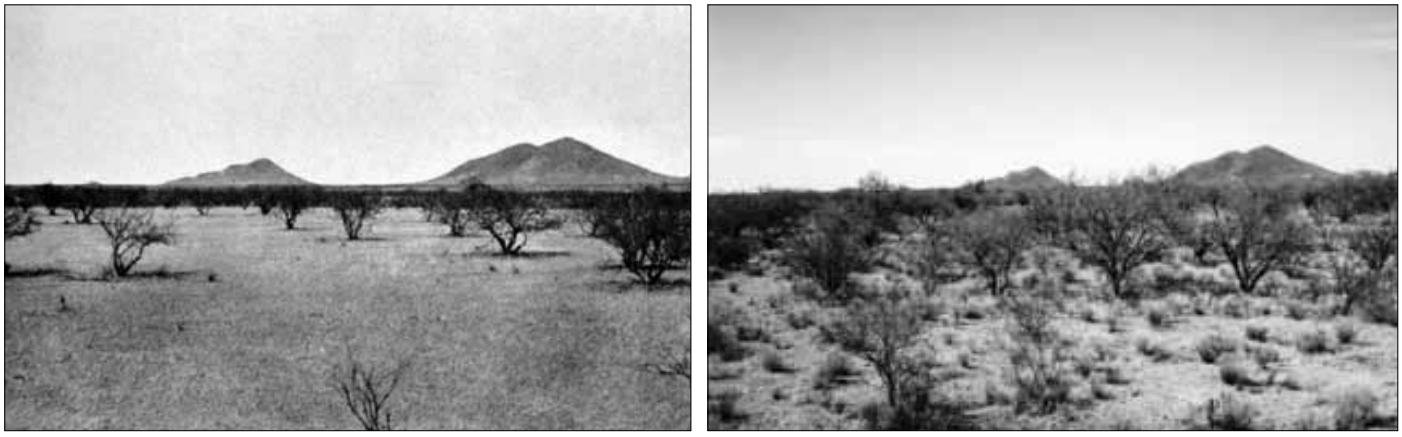
In general, **Semidesert Grassland** and other open landscape-adapted species have fared less well than their scrub-adapted counterparts (see e.g., Brown and Davis 1994). Pronghorn (*Antilocapra americana*), for example, are now absent from large areas of their former range in **Semidesert Grassland** whereas mule deer (*Odocoileus hemionus*) and javelina (*Pecari tajacu*) greatly expanded their ranges during the 20th Century. Such changes in distribution are symptomatic of an increase in the densities of dry-tropic scrub species in this biotic community over the last century. This replacement of marginal grasslands by dense stands of shrubs and trees occurs in a number of ways. Livestock grazing removes the grass cover, thus opening the country to not only erosion but an invasion of desert plants by increasing the evapotranspiration rate, thus decreasing the effective precipitation (desertification). Also, by opening the stands of grass, livestock deposit seeds of mesquite and other shrubs, increasing shrub density. Further, fire suppression allows the establishment of woody plant seedlings. Once begun, this cycle of change is almost irreversible due to changes in surface soil, a lack of fine fuels to carry fire, and the competitive advantage of deep rooted shrubs and trees over shallow-rooted grasses (see e.g. McAullife 1997, McLaren et al. 2003).

Table 10. Mean precipitation totals for stations located within or adjacent to Semidesert Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Apr - Aug	%
Hillside, Arizona, USA 34.5° N, 112.9° W	1012 (3320')	40	38	46	19	9	6	41	62	37	25	39	38	400 (15.8")	137	34
Roswell, New Mexico, USA 33.3° N, 104.5° W	1101 (3649')	9	12	8	12	26	41	43	66	51	27	13	11	319 (12.6")	188	59
Lordsburg, New Mexico, USA 32.3° N, 108.7° W	1324 (4250')	22	15	17	6	7	14	51	53	32	30	18	29	294 (11.6")	131	45
Big Spring, Texas, USA 32.3° N, 101.5° W	762 (2500')	16	20	19	34	71	59	43	52	99	40	20	15	488 (19.2")	259	53
Sasabe, Arizona - Sonora, USA-MEXICO 31.5° N, 111.6° W	1094 (3590')	30	32	26	9	6	7	102	77	50	34	23	47	443 (17.5")	201	45
Fronteras, Sonora, MEXICO 30.9° N, 109.6° W	1136 (3727')	24	11	13	5	3	13	96	87	30	14	12	21	329 (12.9")	204	62
Valentine, Texas, USA 30.5° N, 104.6° W	1347 (4420')	12	11	7	8	19	51	57	74	78	30	15	13	375 (14.8")	209	56
Buenaventura, Chihuahua, MEXICO 29.8° N, 107.5° W	1545 (5069')	8	17	3	12	9	26	89	108	46	29	9	21	377 (14.8")	244	65
Chihuahua, Chihuahua, MEXICO 28.6° N, 106.1° W	1431 (4695')	4	5	8	8	11	25	80	96	95	37	8	21	398 (15.7")	220	55
Sierra Mojada, Coahuila, MEXICO 27.3° N, 103.7° W	1263 (4144')	7	9	8	7	23	46	80	67	84	29	9	14	383 (15.1")	223	58
Monclova, Coahuila, MEXICO 26.9° N, 102.1° W	615 (2018')	13	13	9	18	38	39	47	42	78	32	15	14	358 (14.1")	184	51
El Rodeo, Durango, MEXICO 25.2° N, 104.6° W	1340 (4397')	8	4	2	5	12	48	89	88	81	25	7	9	377 (14.8")	242	64
Cuencame, Durango, MEXICO 24.9° N, 103.7° W	1580 (5183')	10	5	4	6	16	47	75	98	73	26	9	1	370 (14.6")	242	65
Canatlán, Durango, MEXICO 24.5° N, 104.8° W	1950 (6398')	11	4	2	5	9	62	135	133	102	32	7	11	513 (20.2")	344	67
Charcas, San Luis Potosi, MEXICO 23.1° N, 101.1° W	2020 (6628')	11	7	9	12	40	64	59	51	61	39	16	14	383 (15.0")	226	59
Zacatecas, Zacatecas, MEXICO 22.8° N, 102.6° W	2612 (8570')	5	3	2	5	13	49	46	67	51	28	6	12	287 (11.3")	180	63
Leon, Guanajuato, MEXICO 21.1° N, 101.7° W	1809 (5935')	11	7	9	7	29	112	147	134	112	39	13	11	631 (24.8")	429	68
Queretaro, Queretaro, MEXICO 20.6° N, 100.4° W	1813 (5948')	11	5	7	10	44	98	121	103	93	35	9	10	546 (21.5")	376	69
Mixquiahuala, Hidalgo, MEXICO 20.2° N, 99.2° W	2050 (6726')	10	6	13	32	61	83	85	71	72	35	13	9	490 (19.3")	332	68
Distrito Federal Mexico, MEXICO 19.4° N, 99.1° W	2234 (7330')	8	5	12	19	49	106	129	121	110	44	15	7	625 (24.6")	424	68
Tehuacán, Puebla, MEXICO 18.6° N, 97.4° W	1676 (5499')	3	4	18	71	89	76	59	111	38	4	5	2	480 (18.9")	406	85

Grasses in many former areas of **Semidesert Grassland** have been replaced by noxious weeds and woody shrubs and trees, documented by authors such as Leopold (1924), Humphrey (1958), and Martin (1975). Both mesquite and juniper have invaded large areas of former grassland, and a continued increase in shrubbery is indicated by time lapse photography (e.g., Parker and Martin 1952, Hastings and Turner 1965, Turner et al. 2003). Many of these changes are striking, especially in the increase in abundance of certain shrubs and cacti. Less discussed, but of equal or greater importance, is the disappearance and replacement of soil-binding perennial grasses by shallow rooted shrubs and annuals, both native and introduced. Two especially successful native half-shrubs, burroweed (*Isocoma* spp.) and snakeweed (*Gutierrezia* spp.), are now the dominant understory cover over millions of hectares and the only understory indicators of the former presence of a grassland community.

Burroweed may germinate with either fall or spring precipitation, but grows primarily in the spring. And although extensive areas of former **Semidesert Grassland** in Arizona and southwestern New Mexico have been taken over by burrowed, snakeweed (another cool-season germinator), is even more widespread (Martin 1975). Both compete directly with the grasses. For this reason, much of the grassland in these states is now in a disclimax state and has taken on the appearance of an open "soft chaparral" composed of semidesert shrubs and scrub (Figures 69, 70). Eastward, the primary invaders of **Semidesert Grassland** tend to be



Figures 69 and 70. Mesquite Semidesert Grassland community (left) on Rancho Seco in Altar Valley, Pima County, Arizona, ca. 1,139 m (3,750 ft) photographed by David Andrews of the U. S. Geological Survey in 1934 (69). Figure 70 (right) shows the same scene matched and photographed by Ray Turner in 2002. Not only have the mesquites thickened considerably, the grass cover has been largely replaced by snakeweed (*Gutierrezia* sp.) and burroweed (*Isocoma tenuisecta*). Such alterations are occurring today despite the old adage that such landscape changes primarily occurred during the 1880-1910 period.

Chihuahuan Desert species, and much former grassland in southern New Mexico, Texas, and northern Mexico is now populated by *Acacia*, tarbush (*Flourensia cernua*), creosote (*Larrea tridentata*), or mesquite (*Prosopis* sp.), Other areas have been converted to thickets of cacti, *Mimosa*, and other thorny plants where not reduced to bare ground. Other invasions to the south have been equally pervasive, and it is often difficult to accept that much of this change was accomplished within the last 100 years.

Despite its large areal extent and enormous biotic diversity, no national parks have been created to specifically protect **Semidesert Grassland** communities. There are, however, a number of both public and private areas under sustained use management, along with a few areas closed to grazing. One of the largest and best examples of the latter is the 46,540 ha (115,000 acre) Buenos Aires National Wildlife Refuge along the Arizona-Sonora border, which has been protected from grazing since 1985. Other publically managed **Semidesert Grasslands** are contained within the 23,155 ha (57,215 acre) San Andreas National Wildlife Refuge in south-central New Mexico; the 1,436 ha (3,549 acre) San Bernardino N.W.R. in southeastern Arizona; the 18,211 ha (45,000 acre) Las Ciénegas National Conservation Area in southeastern Arizona; and the 28,733 ha (71,000 acre) Agua Fria National Monument in south-central Arizona. Other long standing study areas such as the Sevilleta National Wildlife Refuge in New Mexico and the Jornada and Santa Rita Experimental Ranges in New Mexico and Arizona, while extremely valuable from a rangeland study perspective, have had their **Semidesert Grassland** communities compromised by the introduction of exotic grasses and a long term emphasis on range management and fire suppression (see e.g., McClaren et al. 2003). Still other grasslands such as those present on White Sands Missile Range in New Mexico and Fort Bliss in Texas, while protected from grazing, are subject to anthropomorphic disturbances. There are, unfortunately, no grassland refugia in Mexico, even though a number of conservatively managed sites are worthy of long-term protection.

California Valley Grassland

The original nature and composition of California Valley Grassland can only be surmised. Where not under cultivation or urbanized, it is now mostly an annual grassland much disrupted by more than 200 years of grazing, plowing, alien plant introductions, changing fire regimes, and other man-caused disturbances. And although there has been much speculation on the grassland's make-up prior to European settlement, and many investigators believe that the original vegetation was dominated by perennial grasses, historic evidence is meager and the earliest references are to "annual prairies." Whatever the case, today, more than 400 alien forbs and grasses comprise from 50 to 90% of the grassland's vegetative cover (Talbot et al. 1939, Bentley and Talbot 1948, Biswell 1956, Burcham 1956, McNaughton 1968, Heady 1988).

Also called "California annual grassland," "California prairie," "California steppe," and "Valley grassland" (Munz and Keck 1949, Küchler 1964, 1977; Heady 1988), this biotic community is restricted to the Californias where it resides from sea-level to an elevation of ca. 1,200 m (3,950 ft). This grassland formerly occurred throughout California's Central Valley and its surrounding foothills, in coastal valleys, and on coastal mesas and hillsides from the vicinity of San Francisco Bay southward to at least Valle de Trinidad in Baja California Norte. It is also an important vegetation type on southern California's off-shore islands including Isla Guadalupe (Figure 71). **California Valley Grassland** examples can also be found on the east side of the Tehachapi Mountains in portions of Antelope Valley and in other locations on the eastern edge of the Mohave Desert (Figures 72). Parts of the Los Angeles Basin were formerly **California Valley Grassland**, as were portions of the low, interior valley around Riverside, CA, and most of the coastal mesa in Orange County on which Irvine Ranch (now Irvine) is situated. Other southern locales include the Carrizo Plains in San Luis Obispo County, CA; Warner, Ramona, and Coahuila valleys in San Diego County, CA; and Valle San Rafael and Valle del Rodeo in Baja California.

Although the grassland itself has greatly changed, its exterior boundaries appear to remain much the same as when California was acquired from Mexico in the middle of the 19th Century (Heady 1977). Upslope in some valley bottoms, California Valley Grassland commonly grades into California Evergreen Woodland where it may form savannas with California buckeye (*Aesculus californica*), California walnut (*Juglans californica*), blue oak (*Quercus douglasii*), valley oak (*Q. lobata*), or other overstory trees. In the south, and near the coast, it often occurs with **California Coastalscrub** at lower elevations and with **California Chaparral** in higher locations (Figure 73).

Figure 71. Disclimax California Valley Grassland on the northeastern portion of Guadalupe Island 250 km (160 mi) off the Pacific coast of Baja California. Here as elsewhere in this biotic community the native grassland flora has given way to adventive annuals; in this case and year (1979), wild oats (*Avena fatua*) was the grassland's principal participant. April 1979, D.E.B.

Figure 72. California Valley Grassland and tule elk (*Cervus canadensis nannodes*) on Wind Wolves Preserve, San Luis Obispo County, California, ca. 1,155 m (3,790 ft). The residual brown colored grasses are probably perennial species of needlegrasses (*Achnatherum* spp., *Nassella* spp.) whereas the new flush of green vegetation is mostly composed of Mediterranean annuals. January 2004, Kevin Clark.

Figure 73. California Valley Grassland mixed with saltbush (*Atriplex polycarpa*) looking toward Bitter Creek National Wildlife Refuge southwestern San Joaquin Valley foothills of Kern County, south of Maricopa, California, ca. 304 m (1,000 ft). January 2004, D.E.B.

Formerly, the grassland graded into marshlands in the lower valley locations, and where perennial or near perennial streams drain the valleys, a narrow band of riparian deciduous forest or woodland may be present. Vernal pools or "hog wallows," small, hardpan floor depressions that fill with water during the wet winter months, were formally unique wetland features of many **California Valley Grasslands**, especially in the Central Valley (Holland and Jain 1977) (Figure 74).

The climate is warm-temperate Mediterranean characterized by mild, moderately wet winters with warm to hot, dry summers. The growing season is from seven to 11 months with 200 to 325 frost-free days (Munz and Keck 1949). Annual rainfall averages range from as low as 120 mm (5 in) on the Carrizo Plain to more than 500 mm (20 in) in some northern coastal locations with more than 80% of the total falling during the October through March period (Table 11). Summer temperatures frequently exceed 41 degrees C (105 F), and while winter temperatures rarely drop below -4 °C (25 F), winter frosts may be heavy (Biswell 1956).

After studying **California Valley Grassland** for more than 25 years and examining a number of relict sites, Heady (1977) concluded that the original vegetation was dominated by perennial bunch-grasses. Of these, the principal species were thought to be needlegrasses – primarily foothill needlegrass and purple needlegrass (*Nassella lepida, N. pulchra*) with nodding needlegrass (*N. cernua*) more prevalent in the south and desert needlegrass (*Pappostipa speciosa*) in Antelope Valley. Other perennial grasses included spidergrass (*Aristida ternipes*), squirreltail (*Elymus elymoides*), blue wildrye (*Elymus glaucus*), Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria macrantha*), beardless wildrye (*Leymus triticoides*), California melicgrass (*Melica californica*), smallflower melicgrass (*M. imperfecta*), and Sandberg bluegrass (*Poa secunda*). Interspersed among these bunchgrasses were a number of native annuals including such grass species as prairie threeawn (*Aristida oligantha*), annual hairgrass (*Deschampsia danthonioides*), several Orcutt grasses (*Orcuttia* spp.), rat-tail fescue (*Vulpia myuros*), and Pacific fescue (*Vulpia microstachys*). A number of broadleaf herbs, many having bulbs, were also present and included both annuals and perennials (Heady 1977, Sawyer and Keebler-Wolf 1995).

Because purple needlegrass often comes in after burning, this perennial is thought to have occupied extensive

Figure 74. California Valley Grassland on Cosumnes River Preserve, Sacramento County, California, ca. 15 m (50 ft). The trees in background along the drainage are valley oaks (*Quercus lobata*). Note the vernal pool in left center of photo. 1995, Ron Cole.

areas prior to fire suppression (Biswell 1956). Certainly the absence of large herbivores other than tule elk (*Cervus canadensis nannodes*), and the periodic fires set by Native Americans prior to the introduction of livestock permitted this possibility.

Whatever the pre-European vegetation, **California Valley Grassland** is now largely annual grassland composed of "alien" forbs and grasses (Figure 75). The changes that have occurred appear to be irreversible, and both the annual and alien aspects of the vegetation are now permanent characteristics of this biotic community save a few relatively mesic and protected sites (Figures 76, 77). Several studies, including one on the San Joaquin Experimental Range in the western Sierra Nevada foothills, which was in an area that had been protected from grazing for more than 50 years, showed virtually no return to a "native prairie." Although none of the native bunchgrasses have been entirely eliminated, these species are now confined to relict areas and dominate only locally (Sawyer and Keeler-Wolf 1995). Indeed, one wonders if large areas of **California Valley Grassland** may not have always been populated principally by annuals.

Today the principal introduced annuals according to Heady (1977) are silver hairgrass (*Aira caryophyllea*), slender oat (*Avena barbata*), wild oats (*A. fatua*), ripgut brome (*Bromus diandrus*), soft brome (*B. hordeaceus*), compact brome (*B. madritensis*), several ryegrasses (*Lolium* spp.), and rat-tail fescue (*Vulpia myuros*). Forbs commonly present include mustards (*Brassica* spp.), owl's clover (*Castilleja exserta* et al.), star-thistles (*Centaurea* spp.), stork's bill (*Erodium botrys*), filaree (*E. cicutarium*), the native California poppy (*Eschscholzia californica*), California goldfields (*Lasthenia californica*), lupines (*Lupinus bicolor,* et al.), and johnny-tuck (*Triphysaria eriantha*). These forbs, together with the grasses, often occur within a diverse environment and it is not uncommon for 50 or more species to be present in a relatively small area.

Not all of the introduced species arrived at the same time. Early alien arrivals prior to the California Gold Rush included *Erodium cicutarium, Hordeum murinum*, *Lolium perenne, Poa annua, Rumex crispus*, and *Sonchus asper*. The following years probably saw the most significant period of change, and ubiquitous species as *Avena fatua* and *Brassica nigra* were well established by the Civil War. Since then, *Aira caryophyllea, Aegilops triuncialis*, *Brachypodium distachyon*, *Bromus rubens*, *Centaurea melitensis*, *Chondrilla juncea*, *Gastridium phleoides*,

Figure 75. Spring aspect of California Valley Grassland on Potrero Mesa north of Mystic Lake Wildlife Area, Riverside County, California, ca. 600 m (1,970 ft). A former test site for Lockheed Aircraft, this grassland community is composed primarily of spring annuals, many of them introduced forbs such as filaree (*Erodium cicutarium*), which turns brown during the summer months and constitutes a fire hazard that prevents this biotic community from becoming California Coastalscrub. Undated, D.E. B.

Figure 76. Spring aspect of California Valley Grassland showing both annual forbs and perennial grasses on Jepson Prairie Preserve, Solano, County, California, ca. 23 m (75 ft). 1995, Ron Cole.

Table 11. Mean precipitation totals for stations located within or adjacent to California Valley Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)													
		J	F	M	A	M	J	J	A	S	O	N	D	Total	% Oct - Mar
Willows, California, USA															
39.5° N, 122.3° W	71 (233')	79	71	61	25	10	8	3	5	10	25	74	145	516 (20.2")	88
Fairfield, California, USA															
38.3° N, 122.1° W	12 (40')	122	84	81	33	8	3	< 1	3	8	36	81	84	543 (21.4")	90
Stockton, California, USA															
38.0° N, 121.3° W	4 (12')	71	51	56	28	8	3	3	3	10	20	56	53	362 (14.3")	85
Newark, California, USA															
37.5° N, 122.0° W	3 (10')	73	53	53	28	5	< 1	< 1	3	5	23	53	51	347 (13.7")	88
Merced, California, USA															
37.3° N, 120.5° W	47 (153')	53	53	51	28	8	3	< 1	< 1	5	18	48	43	310 (12.3")	85
Fresno, California, USA															
36.8° N, 119.7° W	102 (336')	51	46	41	25	8	3	< 1	< 1	5	13	36	36	264 (10.5")	84
Salinas, California, USA															
36.7° N, 121.6° W	21 (69')	58	51	53	28	5	3	< 1	3	5	15	46	51	318 (12.5")	86
Coalinga, California, USA															
36.2° N, 120.4° W	204 (670')	38	41	28	15	5	< 1	< 1	< 1	8	10	25	30	200 (7.9")	86
Buttonwillow, California, USA															
35.4° N, 119.5° W	82 (269')	25	28	23	13	5	3	< 1	< 1	5	8	15	15	140 (5.5")	82
Tustin - Irvine Ranch, California, USA															
33.7° N, 117.8° W	36 (118')	56	56	53	23	5	< 1	< 1	3	10	8	41	43	298 (11.8")	86
Warner Springs, California, USA															
33.3° N, 116.6° W	969 (3179	66	80	64	44	6	2	13	26	9	19	32	79	440 (17.3")	77

Hordeum murinum, and several *Sisymbrium* species have all become established, some like *Bromus hordeaceus* becoming important grassland constituents. Most of the alien species are from southern Europe and the Middle East with Spain being heavily represented (Heady 1977).

Grazing appears to favor some forbs over grasses and other herbs, and fields of filaree are indicators of heavy grazing and are probably successional to the grasses. Tall species such as *Avena fatua* and *Bromus hordeaceus* prosper best under light grazing. Some species also mature and set seed earlier in the year than others–*Agoseris heterophylla*, *Castilleja* spp., *Hypochoeris radicata*, *Lasthenia californica*, *Lotus* spp., and *Trifolium* spp. Others tend to flower and set seed during the summer months– *Aristida oligantha*, *Croton setigerus*, *Gastridium phleoides*, and *Madia* spp. (Heady 1977).

Unlike the also-warm temperate **Semidesert** and **Gulf Coastal** grasslands, shrubs are not usually important landscape features of **California Valley Grassland**. The exceptions are mostly in the more arid south where allscale (*Atriplex polycarpa*), sages including big sage (*Artemisia tridentata*), and goldenweed (*Pyrrocoma racemosa*) may be present along with any of a suite of coastalscrub shrubs (Heady 1977).

According to Philbrick and Haller (1977) the grasslands of the Channel Islands are somewhat different from those on the mainland in that such non-grass associates as yarrow (*Achillea millifolium*), bluedicks (*Dichelostemma capitatum*), California buttercup (*Ranunculus californicus*), and Western blue-eyed grass (*Sisyrinchium bellum*) are likely to be present. Perhaps because of its status as a gunnery range and grazing refugium, San Clemente Island contains impressive areas of needlegrass (*Nassella* spp.) grassland.

The slogan to keep "California Green and Golden" is an appropriate moniker for **California Valley Grassland**. Most of the annuals germinate with the first significant rains in early fall, gradually turning the landscape into a soft green carpet (Heady 1977). Growth through the winter is slow due to the cool temperatures, but greatly accelerates with the coming of spring, most plants maturing between April and early June. The composition, height, and character of the grassland thus changes not only annually but throughout the year, and depends on precipitation amounts and chronology, temperatures, grazing history and intensity, relative humidity and other factors. In some serendipitous years, especially those following copious fall rains, a great show of wildflowers may present a brief mosaic of oranges, yellows, and purple with the appearance of California poppies, lupines, owl's clover, etc. (Figure 77). Herbs may dominate in some years, grasses in others. By the end of June, however, the countryside is a golden brown and will remain so until the rains come and the cycle begins anew. Most of the seeds remain through the summer, some remaining viable for years.

Only recently have a few areas of **California Valley Grassland** received what will hopefully be long term protection, and even now, the number of reserves and protected areas containing this biotic community are few. Some nota-

Figure 77. Lupines (*Lupinus*) and poppies (*Eschscholzia*) in The Wildlands Conservancy at Wind Wolves Preserve, San Luis Obispo County, California; Undated, David Clendenen.

ble exceptions are the Hastings Reservation in Carmel Valley managed by the University of California, and the U. S. Forest Service's San Joaquin Experimental Range on the west slopes of the Sierra Nevada. There are also a number of excellent county parks, and growing number of private, state, and Federal reserves: The Wind Wolves Preserve (Figures 72, 77), 38,445 ha (95,000 acre) managed by the California non-profit Wildlands Conservancy; the 58, 276 ha (144,000 acre) Carrizo Plains National Monument, and the 52,000 ha (70,000 acre) Cache Creek Natural Area, both managed by the Bureau of Land Management. A limited number of state and private reserves also protect vernal pools and other grassland features such as the small but noteworthy 500 ha (1250 acre) Colusa Bypass Wildlife Area managed by the California Department of Fish and Game.

As befits a relatively recent evolutionary history, the number of endemic mammals in **California Valley Grassland** are few and these limited to the San Joaquin/Nelson's antelope squirrel (*Ammospermophilus nelsoni*), San Joaquin Pocket mouse (*Perognathus inornatus*), the California ground squirrel (*Spermophilus beecheyi*), and San Joaquin kit fox (*Vulpes velox mutica*). Otherwise, the mammal constituents are chiefly those open country species of more general distribution such as and the recently re-introduced tule elk and pronghorn antelope.

Birds too, with the exception of the California condor (*Gymnogyps californianus*) and yellow-billed magpie (*Pica nuttalli*) and are principally those of more general grassland distribution– the rufous-crowned sparrow (*Aimophila ruficeps*), grasshopper sparrow (*Ammodramus savannarum*), burrowing owl (*Athene cunicularia*), white-tailed kite (*Elanus leucurus*), prairie falcon (*Falco mexicanus*), and savannah sparrow (*Passerculus sandwichensis*). Reptiles and amphibians in **California Valley Grassland** are also mostly "generalists" with the exception of such "California" species as the California (Western) whiptail (*Aspidoscelis tigris*), California toad (*Bufo boreas halophilus*), Western yellow-bellied racer (*Coluber constrictor mormon*), the Southern and Northern Pacific rattlesnakes (*Crotalus oreganus helleri*, *C. o. oreganus*), coast horned lizard (*Phrynosoma coronatum*), and Western spadefoot (*Spea hammondii*).

Neotropical Savanna Grasslands

"Savanna," or *sabaña*, is a designation to describe any Neotropical biotic community dominated by grasses, sedges, or forbs and in which only scattered trees and/or large shrubs participate. Beard (1953), who was much interested in the formation and characteristics of Neotropical grasslands, concluded that the savanna term was an AmerIndian word used in Cuba and Haiti to describe a treeless plain, and thus considered this to be the origin of the term rather than the Spanish *sabaña* or blanket. Although the term is also commonly used to describe grasslands in Africa, and even certain Nearctic communities (e.g., McPherson 1977, Burgess 1995), we retain Beard's original concept limiting savannas to Neotropical America and limit this designation to describe grasslands in Florida, the Caribbean Islands, Mexico, and Central America.

As the equatorial region is approached, increasingly warmer winters, coupled with increasingly longer and wetter growing seasons, tends to favor a gradual transition from scrub and grassland to forest. Perennial grasses and woody plants become antagonists, and natural grasslands occur mostly on shallow stony or sandy soils receiving between 100 and 400 mm (4 -16 in) of precipitation. Grasses predominate over woody plants on the finer soil types only when certain edaphic and fire-favoring factors intervene, thereby restricting grasslands mostly to valley bottoms and level plains if they occur at all. Moreover, grasses have fibrous, deep (intensive) root systems in contrast to the less fibrous, shallower, (extensive) roots of most woody plants so that their removal by excessive numbers of grazing animals or mechanical disturbance often results in transpiration loss at or close to the soil surface. A succession to scrub or brush encroachment then begins, and even if the grasses are no longer grazed, erratic precipitation patterns, a lower frequency of fire, and the increasing germination rate of thorny plants conspire against them. Grazing not only disseminates viable seeds of woody species, the breaking up of the soil surface by hoof action encourages scrub invasion. As if these biases against grassland reestablishment were not enough of a detriment to their existence, the level or gentle terrain that characterizes most savannas facilitates their conversion to farmland and/or intensively managed pastures planted with exotic species.

Not all savannas are found in arid and semi-arid areas. Beard (1944, 1953), for example, pointed out that savanna conditions are controlled by edaphics, sweeping fires, and less importantly, climate. Wet savannas in particular, he observed, were often without a true water table and alternately experienced water-logging and desiccation. He also noted that many savannas occurred on permeable soil horizons that overlaid an impermeable basin, and that this lack of drainage retarded tree growth. Wagner (1964) thought that even dry savannas were edaphically controlled in part, and that their occurrence in northwest Costa Rica and southwest Nicaragua was abetted by the ashy volcanic substrate in these areas, which when wet, formed an impenetrable mass to seedling tree roots. Wagner also recognized the importance of fire, offering that fire maintained and perhaps created the original savannas, which he observed to favor volcanic slopes near the coast where offshore winds were a communicating force. Wagner also believed that wet savannas were subject to both periodic flooding and burning, and that edaphic conditions were responsible for the maintenance of pine and palm savannas along the wet Atlantic coast of Central America.

Savannas were undoubtedly more extensive historically than at present (Belt 1888) with most of western Nicaragua being savanna and the forests largely restricted to drainages, mountains, and the eastern portions of the country. The continual invasion of large areas of former savanna by trees and other woody vegetation, coupled with the observation that forests typically replace natural and man-caused openings without continued clearing and burning, has even raised the question whether Neotropical savannas are natural vegetative communities. In support of this proposition is the fact that large native herbivores are almost totally lacking in the savanna grasslands of tropical North America. There are other explanations for this phenomenon, however, including not only a general absence of extensive tropical grasslands north of the Isthmus of Panama until Holocene times, but the lack of large grassland mammals available to occupy such habitats in recent times (see e.g., Betancourt et al. 1990, McClaran and Van Devender (1995).

But even though it is true that no large herbivores are found in North America's Neotropical grasslands, a similar statement can also be made for the adjacent forests where few large ground mammals are present. Such animals as the white-tailed deer are successional species and are neither forest nor savanna obligates, but persist in both. Moreover,

there are a number of smaller forms, principally birds such as the bobwhite quail (*Colinus virginianus*), which are well adapted to savanna grasslands. This latter observation especially, argues that these biotic communities, while having a relatively short evolutionary history, are naturally occurring entities.

Savannas are complex ecosystems, and owe their origins and presence to a combination of topographic, climatic, edaphic, and biotic factors. The result has been a long history of discussions as to how savannas originate and how they are maintained. Although some investigators have claimed that a pronounced dry season is a prerequisite to savanna formation, most ecologists are of the opinion that there is no such thing as a savanna climate *per se*. Instead, they argue that savannas occur under a variety of climatic conditions, ranging from a mean annual precipitation of less than 500 mm (20 in) to more than 2,500 mm (100 in). Similarly, drought periods, which facilitate savanna maintenance, may range from nearly negligible in duration to up to seven months. That savannas typically share the same climate as adjacent tropical deciduous forests and other woody formation-classes caused Beard (1944, 1953, 1955) to conclude that the reason that most savannas are located on flat, level areas is because savannas were primarily edaphic in nature and that these areas had dense, compacted soils unfavorable to tree growth.

Most ecologists, while recognizing the particular soil characteristics of savannas, consider savannas largely successional in nature, owing their existence to either naturally occurring or anthropomorphic fires (Humphrey 1958, Brown 1994). Although hurricanes and other disturbance factors may simulate the role of fire, all grasslands are probably maintained by burning, whether from lightning or human caused fires. Without a 3 to 10 year burning regime, savanna grasslands devolve into thornscrub, forests, or even desertscrub depending upon the moisture regime.

Wet savannas, while requiring a burning regime, are somewhat different from drier, upland savannas in that these communities almost invariably possess a hard lens substrate that separates a fine-soiled surface from the more porous subsoil. This edaphic character allows the upper strata to alternately become saturated during the wet season or dry out during the dry season, thus facilitating both the growing and burning of herbaceous vegetation. As a result, unless located immediately offshore where periodic hurricanes discourage the encroachment of forests, wet savannas are typically limited to flat depressions or *llanos*, many of which are actually seasonal wetlands in which sawgrasses, rushes, and other semi-aquatic plants dominate, e.g., the Everglades of southern Florida. Upland or "dry savannas," on the other hand, may occupy *cerros*, *lomas*, *mesas*, and other features of moderate relief in addition to *llanos*. Although most commonly encountered on open plains, dry savannas may occur on nearly any terrain subject to periodic fires driven by dry season winds. Wind is therefore a factor common to all grasslands as it serves to drive both lightning-caused natural fires and anthropomorphic fires. Where grazing is prohibited, as at Masaya Volcana National Park in Nicaragua, savanna vegetation predominates on slopes subject to lightning strikes and the seasonal winds that precede the rainy season. These fires, consuming dried grasses and other herbaceous fuels, if unregulated, are frequent enough to maintain a grassland, albeit one in a constant state of succession. Indeed, were it not for the combination of abundant fine fuel, fires, and wind, the Park's **Central American Savanna Grassland** would give way to the tropical deciduous forest and other formations that comprise the dominant vegetation throughout most of this part of Nicaragua. As it is, the Park's vegetation is largely a *zacatonal* grassland where not interrupted by post-successional communities of deciduous forest or thornscrub.

Savannas are most extensive in North America within the Central American Biotic Province, but have been reported in all Neotropical biotic provinces (Beard 1953, Brown et al. 1998). Beard (1953) described both natural and anthropogenic savannas occurring in Puerto Rico, Cuba, Hispaniola, the Lesser Antilles, Honduras, Nicaragua, Guatemala, Belize, and El Salvador; while Porter (1973) and Jantzen (1983) reported savannas in Costa Rica and Panama, respectively. In Mexico, Rzedowski (1988) describes and illustrates savannas in the Campeche, Veracruz, and Guerreran biotic provinces, and reports others in the Tamaulipan, Yucatán, and Sinaloan biotic provinces. All of these savannas are more or less successional in nature and subject to a variety of influences. Some of these communities, particularly those in the most mesic and driest sites may even be described as ephemeral rather than successional.

Central American Savanna Grassland

Central America's savannas have been described by Carr (1950), Beard (1953), Parsons (1955), Taylor (1962, 1963), Alexander (1973), Mueller-Dombois and Ellenberg (1974), Davidse (1985), and most recently by Hartshorn (2000), who defined this biotic community as an area of nearly continuous grass cover with trees forming up to 30% of the cover. Because these grasslands occur in areas having sufficient precipitation to support forests, there has been much interpretation as to what factors determine a savanna, which savannas are natural, and which ones are anthropogenic (Beard 1953, Bennet 1968, Kellerman 1984). Again, although there does not appear to be a "savanna climate" *per se*, other than a recognizable dry season (*verano*) that allows for periodic burning, there seems to be an edaphic commonality of shallow soils overlaying an impervious substratum.

The number of associations represented within the various savannas is large, most investigators differentiating between the "wet savannas" on the Atlantic Coast of northern Nicaragua, Honduras, and Belize, and the somewhat drier savannas found in the western portions of Panama, Costa Rica, Nicaragua, ,and El Salvador. Hence, it may be prudent to separate **Central American Savanna Grassland** into eastern and western biotic communities based on differences in both total and seasonal precipitation amounts- the Atlantic coast savannas generally having annual precipitation amounts exceeding 2,000 mm (79 in) and a less pronounced dry season than savannas in western Central America (Table 12).

Perhaps the most well known Central American savannas are the lowland pine savannas found on the plains of northeastern Nicaragua, eastern Honduras, the Petén region of Guatemala, and northeast-central Belize (Standley and Steyermark 1945; Carr 1950; Beard 1953; Parsons 1955; Taylor 1962, 1963; and Alexander 1973). Punctuated by 25 m (82 ft) tall *Pinus caribaea*, and often accompanied by palms such as *Acoelorrhaphe wrightii*, these grasslands commonly receive annual rainfall amounts between 1,000 and 2,500 mm (extremes to 3,500 mm, 138 in), and occur primarily on level plains having clay or sand soils over an impermeable limestone or hard clay base (Figure 78). A four month long dry season, in which less than 100 mm (4 in) falls during any one month, facilitates both natural and man-made fires, and unlike some Pacific coast savannas, which require almost annual ignition, the pine savannas appear to be natural communities maintained by seasonally high water tables, seasonal desiccation, periodic fires (every one to three years), and infertile soils (Beard 1953, Taylor 1963, Hartshorn 2000).

Western **Central American Savanna Grassland** shares some of the same characteristics and plant species as the

Table 12. Mean precipitation totals for stations located within or adjacent to Central American Savanna Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	May-Oct	%
Savannah, BELIZE[1]																
16.5°N, 88.5°W	6 (20')	128	67	66	55	131	307	350	293	327	301	101	145	2360 (92.9")	1709	72
Punto Cabezas, NICARAGUA[1]																
14.1° N, 83.4° W	< 100 (325')	182	78	57	57	207	423	407	359	344	354	309	247	3024 (119.1")	2094	69
Puerto Lempira, NICARAGUA[1]																
15.2° N, 83.8° W	< 100 (325')	192	138	70	78	217	384	432	353	317	460	413	293	3347 (131.7")	2163	65
Limbaika, NICARAGUA[1]																
13.5° N, 84.1° W	< 200 (656')	132	51	68	85	219	373	452	361	229	266	225	147	2608 (102.7")	1900	73
Lovago, NICARAGUA[2]																
12.0° N, 85.2° W	ca. 200	28	13	6	19	109	255	170	172	245	262	87	34	1400 (55.1")	1213	87
Managua (Las Mercedes) NICARAGUA[2]																
12.1° N, 86.2° W	54 (177')	2	3	4	3	136	237	132	121	213	315	42	10	1218 (47.9")	1154	95
Borrell, NICARAGUA[2]																
12.5° N, 87.1° W	25 (82')	0	0	1	5	195	345	202	257	374	420	78	3	1880 (73.9")	1793	95
Sabanagrande, HONDURAS[2]																
13.8° N, 87.3° W	959 (3146')	3	5	9	50	249	250	84	123	350	209	34	1	1367 (53.8")	1265	93
Valle San Juan, EL SALVADOR[2]																
13.3° N, 88.6° W	50 (164')	3	7	6	31	167	324	340	311	400	383	61	3	2036 (80.1")	1925	95
San Salvador, EL SALVADOR[2]																
13.7° N, 89.2° W	699 (2293')	7	7	13	53	179	315	312	307	317	230	40	12	1792 (70.6")	1660	93
David, PANAMA[2]																
8.4° N, 82.4° W	29 (95')	29	23	43	96	286	348	235	333	435	359	294	63	2544 (100.1")	1996	78

[1] Atlantic watershed
[2] Pacific watershed

wetter Atlantic savannas including the presence of such savanna tree indicators as *Byrsonima crassifolia*, *jicaro* or cannonball tree (*Crescentia alata*), *chaparo* or sandpaper tree (*Curatella americana*), *Haematoxylum* spp., and *roble* (*Quercus oleoides*), over a coarse grass or sedge understory (Figures 79, 80, 81). These trees, depending on the location, may be replaced or augmented by a number of others including, *Acacia farnesiana*, *A. costaricensis*, *Clethra hondurensis*, *Guazuma ulmifolia*, *Pithecellobium dulce, Tabebuia heterophylla,* and various palms, which like other woody species, may occur as individuals or in mottes. Mean annual rainfall, while somewhat drier than in the pine savannas, is still high, and may range anywhere between 1,000 to 2,500 mm (39 -98 in) with a four to seven month dry season, thus facilitating burns nearly every year.

Some grasslands in western Central America, besides being generally drier and lacking pines, are characterized by the palm *Acrocomia aculeata,* as well as such locally dominant trees as wild cashew (*Anacardium occidentale*), *Nectandra* spp., *Psidium guajava, Xylopia aromatica*, and *X. frutescens* (Bennet 1968). Prominent shrubs may include *Calliandra houstoniana*, *Henriettella seemannii*, *Miconia* spp., and *Psidium* spp., particularly in those savannas that have not burned in several years.

The grass cover is typically 30-80 cm (12-31 in) in most **Central American Savanna Grassland** communities, and even when found on gentle slopes and bald hills, contains some of the same grasses and sedges as on level ground and in pine savannas. Native grasses are often mixed with introductions and include *Andropogon bicornis, Aristida* spp., *Arundinella deppeana, Axonopus aureus, A. centralis, Eragrostis ciliaris, E. geniculata, Leptocoryphium* spp., *Muhlenbergia implicata, Panicum purpurascens, P. rudgei, Paspalum virgatum, P. humboldtianum*, *Pennisetum bambusiforme, P. setosum, Pereilema crinitum, Sacciolepis striata, Schizachyrium brevifolium, S. condensatum, Setaria* spp., *Sporobolus indicus, Trachypogon angustifolius,* and *T. spicatus* (Taylor 1963, Porter 1973, Davidse 1985). In the wetter areas, tall (2m, 79 in) tussocks of *Paspalum virgatum* may form nearly pure stands, while on the drier slopes one may encounter *Aristida ternipes, Bouteloua alamosana*, and *B. disticha.* Important sedges are *Fimbristylis annua*, and *Rhynchospora mexicana.* Herbs are numerous and in some western locales in El Salvador, the *jicama* (*Pachyrhizus erosus*) is an important food crop (Beard 1953).

The most commonly cultivated grass in much of Central America is *jaraguá* (*Hyparrhenia rufa*), which grows up to 2m (7 ft). This and other mostly African imports such as *Cynodon dactylon*, *C. nlemfuensis*, *Digitaria eriantha,* Guinea grass (*Panicum maximum*), and *Urochloa mutica*, are grown in pastures up to 900 m (2,950 ft) in elevation (Jantzen 1983). Unless burned annually, however, these pastures soon give way to more conventional savanna inhabitants including scattered patches of *jicaro* (*Crescentia alata*), and such fire-resistant trees as *nance* (*Byrsonima crassifolia*), and *chaparro* (*Curatella americana*) (Figure 82).

As previously stated, large wild herbivores are essentially lacking in Central America's savannas, the one exception being the nearly extinct giant anteater (*Myrmecophaga tridac-*

Figure 78 (left). A representative of Central American Savanna Grassland containing Caribbean pine (*Pinus caribaea*) and roble (*Quercus oleoides*). These "pine savannas" are some of the wettest grasslands in North America and are driven by edaphic conditions, namely a permeable layer of soil overlaying a hard pan of clay, serpentine, or other impermeable material. March 1987, D.E.B. Figure 79 (right). A Central American Savanna Grassland composed of a periodically flooded "wet savanna" community on Crooked Tree Wildlife Sanctuary in Belize. The principal trees are logwood (*Haematoxylum campechianum*). March 1987, D.E.B.

Figure 80. A *jicaro* or cannonball tree, *Crescentia alata*, in an overgrazed Central American Savanna Grassland in Managua Province, Nicaragua, ca. 60 m (200 ft) elevation. Typical "savanna indicators" are one or more of three short trees—nance (*Byrsonima crassifolia*), chaparo, or sandpaper tree (*Curatella americana*), and *jicaro*. March 1998, D.E.B.

Figure 81. Short grass Central American Savanna Grassland on Isla de Ometepe in Lake Nicaragua, Volcán Concepción in background. The tree in this artificially maintained grassland is a nance (*Byrsonima crassifolia*). March 1998, D.E.B.

tyla), which reaches its northern limits in Honduras. Indeed, the only mammal that could be considered a savanna obligate is the more widely distributed hispid cotton rat (*Sigmodon hispidus*). Otherwise, mammal representatives of **Central American Savanna Grassland** are those species of wider distribution that also frequent ecotones and successional habitats such as the southern pygmy mouse (*Baiomys musculus*), northern naked-tailed armadillo (*Cabassous centralis*), least shrew (*Cryptotis parva*), dusky rice rat (*Melanomys caliginosus*), white-tailed deer (*Odocoileus virginianus*), northern pygmy rice rat (*Oligoryzomys fulvescens*), and common cane mouse (*Zygodontomys brevicauda*). Ground squirrels and prairie dogs are lacking, the biomass being made up by harvest mice such as *Reithrodontomys darienensis, R. fulvous,* and *R. gracilis*, with the more arid-adapted *R. brevirostris* and *R. paradoxus* occuring in dry savannas as well as in **Central American Dry Forest** (Hall and Kelson 1959, Reid 1997). Introduced cattle and horses, more than make up for any loss of herbivory, however, and **Central American Savanna Grassland** is an important and invaluable vegetation type to Central America's rural economy. Partially because of its depredations on livestock, the vampire bat (*Desmodus rotundus*) is therefore the most well known of the many bats that use this biotic community as foraging habitat.

Birds are a different story. In addition to such temperate grassland species as the Western meadowlark (*Sturnella neglecta*), one may find in the appropriate locations such widespread savanna obligates as Botteri's sparrow (*Aimophila botteri*), the white-tailed hawk (*Buteo albicaudatus*), double-striped thick-knee (*Burhinus bistriatus*), plain-breasted ground dove (*Columbina minuta*), pale-vented pigeon (*Patagioenas cayennensis*), stripe-headed sparrow (*Peucaea ruficauda*), striped owl (*Pseudoscops clamator*), the variable, yellow-bellied, and white-collared seed-eaters (*Sporophila aurita, S. nigricollis, S. torqueola*), yellow-faced grassquit (*Tiaris olivacea*), fork-tailed flycatcher (*Tyrannus savana*), and blue-black grassquit (*Volatinia jacarina*) (see e.g., Ridgely 1976, Stiles and Skutch 1989, Howell and Webb 1995).

Figure 82. Central American Savanna Grassland within Santa Rosa National Park, Guanacaste Province, Costa Rica. The principal grass is said to be *jaragua* (*Hyparrhenia rufa*), a pasture grass introduced from Africa. The debate over whether these grassland communities are "natural" or anthropogenic is now largely moot given the widespread and frequent presence of such identities and the occurrence of both natural and man-made fires. March 1984, D.E.B.

Unfortunately, the habitat affiliations of Central America's herpetofauna have yet to be adequately investigated and no summary of their affiliations is presently practical. This situation will undoubtedly soon change as some examples of **Central American Savanna Grassland** are protected for study in the numerous national parks located in Costa Rica, and in selected preserves in Belize, Honduras, Nicaragua and Panama.

Guatemalan-Guerrean Savanna Grassland

Miranda (1952), Breedlove (1973) and Gomez-Pompo et al. (1964) describe "short-tree savannas" on the Pacific coastal plain of Guatemala and Chiapas, as well as in the Rio Papaloápan drainage, that extend northward into southern Mexico to Oaxaca, and Guerrero with smaller savanna examples being reported in Colima, Nayarit and southern Sinaloa (Rzedowski 1975, Rzedowski and MacVaugh 1966) (Figure 83). Although most of these grasslands are positioned fairly close to the Pacific Ocean, other savannas, thought to be of anthropomorphic origin also occur in the interior valleys of Chiapas (Breedlove 1973). Recognized on the basis of such widely occurring savanna trees as *nance* (*Byrsonima crassifolia*), *jicaro* (*Crescentia alata C. cujete*,) and *raspa viejo* (*Curatella americana*), these tropical savannas are generally drier, smaller, and more discontinuous than those on the Atlantic and Gulf coasts. The above trees may be joined or locally replaced by thickets or individuals of *Acacia pennatula*, *Alvaradoa amorphoides*, *Mimosa tenuifolia*, or *Piscidia piscipula*, as well as such palms such as *Attalea* spp., and sombrero palm (*Brahea dulcis*) (Figure 84). Most of the trees however, are typically gnarled and low, usually between 3 and 6 m (10-20 ft) tall, a few sometimes attaining a height of 20 m (66 ft). Although typically well spaced, the trees also occur in mottes or *bosquetes* when the savanna has not been regularly burned, and as in **Central American Savanna Grassland**, those pastures having individual *Ceiba* spp., or *Enterolobium cyclocarpum* trees can be identified as man-made savannas derived from dry or semievergreen forest (Miranda 1952).

According to Buller et al. (1960), the principal grasses are *Bouteloua dimorpha*, *B. repens*, *B. curtipendula*, *Cathestecum erectum*, *C. multifidum*, *Elionurus tripsacoides, Heteropogon contortus*, *Hilaria cenchroides, H. semplei*, and several species of *Panicum*, *Paspalum* and *Tripsacum*.

Usuallly located on deep, poorly drained soils on flat plains or on gradual slopes, elevations range from slightly above sea-level to ca. 900 m (2,950 ft). Some savannas are found on metamorphic rock hillsides, and Rzedowski (1981) questioned whether these grasslands might not all be anthropomorphic in origin. Drier than the savannas on the Gulf Coast, annual rainfall ranges between 600 and 1,000 mm (24-39 in) with more than 90% of the total occurring between May and October (Table 13). Therefore, the November-April winter period constitutes a pronounced dry season, and this is the time when most fires occur, naturally or otherwise.

Centered in southeastern Guerrero and southern Oaxaca and Chiapas, these grasslands appear to support relatively few endemics. Most investigators, however, consider these fire- maintained savannas as more or less natural, while similar grasslands located inland in the central depression of Chiapas are thought to be anthropomorphic in origin

Figure 83. Guatemalan-Guerreran Savanna Grassland 3 km (1.9 mi) inland from Salina Cruz, Oaxaca, Mexico. This is the grassland habitat of the Tehuantepec jackrabbit (*Lepus flavigularis*) and such tropical savanna birds as the double-striped thick-knee (*Burhinus bistriatus*) and bobwhite (*Colinus virginianus coylocos*). Note the presence of *Crescentia alata*. Elevation 15 m (49 ft). February 2011, Randall D. Babb.

Table 13. Mean precipitation totals for stations located within or adjacent to Guatemalan-Guerreran Savanna Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	May-Oct	%
Ixtepec, Oaxaca, MEXICO 16.6° N, 95.1° W	1200 (3937')	4	6	3	5	48	200	129	155	217	67	18	4	857 (33.7")	816	95
Chicapa, Oaxaca, MEXICO 16.4° N, 94.8° W	30 (98')	3	3	5	6	62	221	154	150	236	74	16	4	931 (38.7")	897	96
La Trinitaria, Chiapas, MEXICO 16.1° N, 92.1° W	1530 (5020')	7	14	11	34	94	209	128	132	213	112	27	14	994 (39.1")	888	89
Pochutla, Oaxaca, MEXICO 15.8° N, 96.5° W	160 (525')	2	4	2	5	54	184	142	164	247	66	25	3	898 (35.3")	857	95

Figure 84. Guatemalan-Guerreran Savanna off Mexican Highway 190 near Huajuapan de León, Oaxaca, Mexico. The mostly less than 5 m (16 ft) trees in this upland dry savanna site are sombrero palms (*Brahea dulcis*) with some shrubby nances and *raspa viejo* trees (*Curatella americana*) present. The area had recently burned, replenishing such native grasses as *Bouteloua*, *Paspalum*, and *Setaria*. March 1992, Louella Brown.

(Breedlove 1973). Only a few vertebrate species such as the stripe-headed sparrow (*Aimophila ruficauda*) and giant pocket gopher (*Orthogeomys grandis*) might qualify as savanna endemics despite the adjacent **Guerreran Thornscrub** and **Gurreran Deciduous Forest** being relatively rich in endemic species (Reid 1997, Howell and Webb 1995). None of these savannas is within a park or preserve created especially for their protection.

Campechian-Veracruz Savanna Grassland

The largest savannas in Mexico are those situated inland from the Gulf Coast from Campeche northward through Tabasco to southern Veracruz (Miranda 1952, Vasquez 1963, West 1966, Sousa 1968, León and Gómez-Pompo 1970, Puig 1972, Gómez-Pompo 1973, Rzedowski 1988). These mostly wet *sabanas*, which generally reside on seasonally flooded, ash derived soils above an impermeable clay hardpan, are found mostly below an elevation of 150 m (492 ft). Two major tropical savanna communities have been recognized—a lowland, wet savanna, and a saline coastal grassland, the latter usuually merging into a maritime wetland (see e.g., Gómez-Pompo 1973). (Figure 85).

The lowland savannas are populated primarily by grasses and sedges between 80 and 100 cm (31- 39 in) tall. Where native grasses still dominate, more than 90% are species of tropical affinity-- *Andropogon bicornis*, *A. glomeratus*, *Bothriochloa alta*, *Bouteloua dimorpha, Cathestecum*, *Ctenium*, *Diectomis*, *Digitaria insularis, D. leucites*, *Elionurus tripsacoides, Eragrostis, Imperata*, *Lasiacis, Leptocoryphium*, *Mesosetum*, *Muhlenbergia*, *Oplismenus, Orthoclada laxa*, *Panicum repens*, *Paspalum conjugatum, P. notatum*, *P. pectinatum*, *P. plicatulum*, *P. virgatum*, *Pennisetum*, *Setaria parviflora*, *Soderstromia*, and *Trachypogon* (see e.g., Miranda 1958 and Gómez-Pompo 1970). Grasses having a more northern distribution, namely *Aristida* spp., *Bouteloua repens*, *B. curtipendula*, *Heteropogon contortus* and *Hilaria* spp., are relatively infrequent, and generally restricted to sandy plains and dunes (Miranda 1952, Gómez-Pompa 1973). More often, however, the native grasses have been replaced by improved pastures of Guinea grass (*Panicum maximum*) imported from Africa. As one goes closer to the sea the more saline tolerant grasses and sedges increasingly dominate the savanna—*Andropogon glomeratus*, *Distichlis spicata*, *Spartina alterniflora*, *S. spartinae*—until the savanna takes on the characteristics of an herbaceous wetland. Herbs such as *Hibiscus costatus* may be profuse or scarce depending on location, grazing history, and successional stage (Miranda 1952).

Most of the natural savannas are recognizable to the casual observer by their wooded component of fire resistant savanna trees and palmettos— *Byrsonima crassifolia*, *Coccoloba barbadensis*, *Cocos regia*, *Crescentia cujete*, *Curatella americana*, *Mimosa tenuifolia*, *Psidium guajave*, *Quercus oleoides*, *Sabal mexicana*, and species of *Clethra, Clidemia*, *Conostegia*, *Dodonaea*, *Miconia*, *Vitex* and *Waltheria* (Miranda 1952, Miranda 1958, Gómez-Pompo 1973) (Figure 86). In the interior sites, such as in northern Chiapas, *Haematoxylum campechianum* may be found along with islands of *palma tasiste* (*Acoelorrhaphe wrightii*).

Maintained by periodic burning and a difficult to penetrate hardpan, these savannas are more mesic than most of Mexico's savannas, receiving between 1,000 and 2,000 mm (39-79

Figure 85. Typical Campechian-Veracruz Savanna Grassland in the lowlands of Tabasco, Mexico. Such “wet savanna” communities are composed of tropical grasses and sedges punctuated by *Crescentia* and other fire-adapted trees. These associations are a function of seasonal flooding, impervious substrates, contrasting wet and dry seasons, offshore winds, episodic hurricanes, periodic fires, and human history. March 1992, D.E.B.

Figure 86. A recently burned and flooded Campechian-Veracruz Savanna Grassland near the Campeche-Tabasco border. Note the dense semi-evergreen forest on the rise in background. The tree is *Sabal mexicana*, a common savanna participant. March 1992, D.E.B.

Table 14. Mean precipitation totals for stations located within or adjacent to Campechian-Veracruz Savanna Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Nov - Apr	%
Veracruz, Veracruz, MEXICO 19.1° N, 96.1° W	16 (52')	35	15	14	17	37	344	376	343	358	134	68	24	1765 (69.5")	173	10
El Palmar, Veracruz, MEXICO 18.5° N, 96.8° W	180 (591')	50	42	52	65	147	464	559	529	536	262	90	52	2847 (112.1")	351	12
Coatzacoalcos, Veracruz, MEXICO 18.2° N, 94.4°W	23 (75')	121	80	54	63	124	222	238	266	484	448	237	198	2536 (99.8")	753	30

Figure 87. Campechian-Veracruz Savanna Grassland community similar to that shown in Figure 86 but with a longer fire history interval. The trees are rapidly crowding out the grasses and the community is well along in its succession to tropical semi-evergreen forest. March 1992, D.E.B.

in) of precipitation a year, 75% of which falls between May and October (Table 14). Hurricanes and torrential rains are relatively common and the mean annual precipitation in some sites may even exceed 3,000 mm (118 in). Most of the burning therefore takes place at the end of the short April-May dry season (Figure 87).

Campechian-Veracruz Savanna Grassland harbors a number of savanna species of more general disturibution such as the double-striped thick-knee (*Burhinus bistriatus*), plain-breasted ground dove (*Columbiana minuta interrupta*), hispid pocket gopher (*Orthogeomys grandis*), striped owl (*Pseudoscops clamator*), hispid cotton rat (*Sigmodon hispidus*), and fork-tailed flycatcher (*Tyrannus savana*). But these wet savannas are also home to endemics such as the pale-vented pigeon (*Patagioenas cayennensis*). Few if any of these savannas are contained within a national park or nature reserve.

Tamaulipan Savanna Grassland

The shrinking and replacement of grasslands in the Tamaulipan Biotic Province and their replacement by chaparral has been well documented by Clover (1937), Johnston (1963), Gonzalez-Medrano (1992), Schmidley (2002), and others. As recently as the 1950s, Martin (1958) reported "a thorn savanna on an uninhabited rolling plain ca. 30 kms (18 mi) east of Llera at the base of the Sierra de Tamaulipas that was covered with a dense grass sward with yuccas and populated by the tree *Piscidia communis*." Once occupying extensive regions inland from the Gulf of Mexico between parallels 23°N and 29°N, these so-called "mesquite prairies" containing grasses about 60 cm (24 in) tall have now been reduced to remnants and supplanted by **Tamaulipan Thornscrub**, farms, and/or pastureland, or simply paved over.

Elevations are relatively low—mostly between sea level and ca. 500 m (1,640 ft), and the annual rainfall is sparse, between 400 and 700 mm (16-28 in) with about 75% or more falling during the April to October period (Table 15). Freezing temperatures are unusual to non-existent, being restricted to the rare *nortes* and then only lasting of short duration. More common are hurricanes and offshore winds, as most of the savannas reside within 100 km of the Gulf Coast.

To consider **Tamaulipan Savanna Grassland** a formerly open prairie is probably an exaggeration as areas of thornscrub and individual woody plants appear to always have been present, the grasslands tending to favor the sandier soils (Johnston 1963) (Figure 88). That the brush species advanced and thickened after the advent of livestock grazing and a reduction in the incidence of fires cannot be denied, however. The most common of these woody shrubs and small trees was mesquite (*Prosopis glandulosa*), followed by the prickly-pear (*Opuntia lindheimeri*), and such thornscrub species as *granejo* (*Celtis pallida*) (Figure 89). The variety of woody plants increases southward with mottes of live oaks (*Quercus oleoides*, *Q. virginiana*) sparingly found throughout.

Johnston (1963) made an extensive survey of Tamaulipan grassland remnants, reporting on the character and constituents of this biotic community in three general areas—34 black clay sites in Kleberg County, Texas, several loose sand sites in Kenedy County and at the edge of the "Wild Horse Desert" in Texas, and on 20 reddish sandy loam sites near Loreto in Tamaulipas, Mexico. He found that the grasses varied considerably with temperate- species such as buffalograss (*Buchloe dactyloides*) and little bluestem (*Schizachyrium scoparium*) being more common in Texas, and species of *Bouteloua*, especially *B. radicosa* dominating some Tamaulipan sites. Other prevalent grasses reported by Johnston (1963) indicated the composition of **Tamaulipan Savanna Grassland** to be a mixture of both temperate and tropical species

Figure 88. Tamaulipan Savanna Grassland northeast of the Calles railroad station in Tamaulipas, Mexico, ca. 400 m (1,312 ft). The tall trees are *Sabal mexicana* and the principal grass a species of *Cynodon*. Note the abundance of shrubs and forbs. June 1998, D.E.B.

Table 15. Mean precipitation totals for stations located within or adjacent to Tamaulipan Savanna Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Apr - Oct	%
Padilla, Tamaulipas, MEXICO 24.0° N, 98.8° W	153 (502')	19	19	22	45	104	91	50	74	143	75	24	21	687 (27.1")	582	85
Sabinas, Coahuila, MEXICO 27.9° N, 101.1° W	335 (1099')	14	16	11	35	69	64	29	57	86	48	17	14	460 (18.1")	388	85
Cotulla, Texas, USA 28.4° N, 99.3° W	132 (433')	25	36	21	52	71	57	27	46	82	56	27	27	527 (20.7")	391	74
Crystal City, Texas, USA 28.7° N, 99.8° W	177 (580')	24	33	22	42	88	58	90	62	82	63	24	20	608 (23.9")	485	80

Figure 89. Tamaulipan Savanna Grassland near Crystal City, Texas, in the process of becoming thornscrub. The principal invading trees and shrubs are *Condalia* sp., honey mesquite (*Prosopis glandulosa*), *granejo* (*Celtis pallida*), and prickly-pear (*Opuntia* spp.). Sufficient temperate and tropical grasses and forbs nonetheless probably remain to regain dominance should the site be burned or cleared. June 1998, D.E.B.

such as *Aristida purpurea*, *Bouteloua hirsuta*, *Cenchrus spinifex*, *Chloris* spp, *Eragrostis* spp., *Hilaria belangeri*, *Panicum hallii, P. virgatum*, *Paspalum setaceum*, *Schedonnardus paniculatus*, *Tridens muticus*, and *Urochloa ciliatissima* among others. Forbs, especially in the more heavily grazed areas, commonly outnumbered the grasses, and were represented by such perennials as *Boerhavia coccinea*, *Cassia* spp., *Evolvulus* spp., *Heliotropium confertifolium*, *Oxalis frutescens*, *Polygala alba*, *Rhynchosia americana*, as well as a plethora of seasonal annuals. Saline depressions and areas close to the Gulf are often dominated by salt tolerant grass species such as *Distichlis, Spartina spartinae*, and *Sporobolus cryptandrus*. A number of stem succulents and short-statured shrubs such as *Calliandra conferta*, *Chamaecrista greggii, Coursetia axillaris*, *Krameria ramosissima*, and *Lippia graveolens* complete the assemblage (Johnston 1963).

None of the areas visited by Johnston (1963) covered more than a few hundred acres and no areas of **Tamaulipan Savanna Grassland** are known to be reserved for the purpose of grassland preservation and maintenance. This is unfortunate as this biotic community, along with **Gulf Coastal Grassland**, represents the northern nesting sites for a number of neotropical birds such as Botteri's sparrow (*Aimophila botterii*), the white-tailed hawk (*Buteo albicaudatus*), and aplomado falcon (*Falco femoralis*). It is also the northernmost habitat for several other species, and is the distributional center for the Texas tortoise (*Gopherus berlandieri*).

Sonoran Savanna Grassland

Never extensive, seral fire-adapted savannas once occupied edaphically favorable sites within Sinaloan Thornscrub and the Sonoran Desert in Sonora and southern Arizona between 90 and 1,000 m (295-3,280 ft) elevation (Figure 90). Such areas included the *llanos* within Shreve's (1951) Plains of Sonora and Foothills of Sonora subdivisions of the Sonoran Desert as well as certain lands in the lower Santa Cruz River watershed and adjacent areas in southern Arizona (Brown 1994). Restricted to fine textured sand and clay soils on level plains receiving a mean annual precipitaion ranging from between ca. 275 and 525 mm (11-21"). (>60% of which falls between July and September), these fire-climax communities were so ephemeral that no sites exist in an unaltered state today (Figures 91, 92). Indeed, most sites are so lacking in either perennial or annual grass cover, that some biologists have questioned the existence of this biotic community (e.g. Van Devender 1995) despite the successful conversion of many former grassland sites in Sonora to buffelgrass (*Pennisetum ciliare*) pastures.

J. T. Wright, who collected the savanna-affiliated masked bobwhite at Rancho Noria de Pesqueira, Sonora, in 1931, told Tomlinson (1972) "the country at that time consisted of wide, grass-covered valleys with certain grasses reaching over the heads of the native white-tailed deer." Brand (1936) mapped large areas in central and eastern Sonora as *Sonoran mesquite-grassland*, and Shreve (1951) in a desciption of certain areas in the central portion of his *Plains of Sonora* states, "Grasses often form as much as 75% of this cover, which gives an aspect of abundant verdure after the period of summer rain." But, because of heavy grazing of livestock and the resulting reduction of fires, most of these grasslands were greatly altered by 1900 in southern Arizona and after 1940 in Sonora (Tomlinson 1972, Brown 1977, Bahre 1985, Brown et al. 2012). Whatever the present situation, these habitats are physiographically and floristically considered **Sonoran Savanna Grassland** (Figures 93, 94).

Past accounts and more recent investigations of these relict *llanos* indicate that the principal grasses were summer-active annuals and root perennials averaging some 60 cm (24 in) in height (see appendix 2 for list of SSG species)

Species most commonly encountered included Rothrock grama (*Bouteloua rothrockii*) and three-awns (*Aristida purpurea*, *A. ternipes*, etc.). Other tropic-subtropic species included *Bouteloua aristidoides*, *B. barbata*, *B. parryi*, *B. radicosa*, *B. repens* along with windmill grasses (*Chloris* spp), false grama (*Cathestecum erectum*), and tanglehead (*Heteropogon contortus*). Sod-forming or grasses more typical of **Semidesert Grassland** tended to be restricted to more mesic sites along drainages and ungrazed slopes; e.g., curley mesquite (*Hilaria belangeri*) and vine mesquite (*Panicum obtusum*). Forbs were always impor-

Figure 90. Sonoran Savanna Grassland near Carbo, Sonora, as it appeared during March 1984. The principal trees in the background are mesquite (*Prosopis velutina*), foothill paloverde (*Parkinsonia microphylla*) and ironwood (*Olneya tesota*). The grasses are mostly Rothrock grama (*Bouteloua rothrockii*), three-awns (*Aristida* spp.) and Arizona cottontop (*Digitaria californica*). This area has since been planted to buffelgrass (*Pennisetum ciliare*) pasture. March 1984, D.E.B.

Figure 91. Sonoran Savanna Grassland south of Benjamin Hill, Sonora during the summer of 1964, in the process of converting to thornscrub. A plethora of thorny shrubs and trees are replacing the native bunchgrasses, which regularly burned prior to being grazed by cattle. This is the area where and when the masked bobwhite (*Colinus virginianus ridgwayi*) was "rediscovered" by Jim (pictured here) and Seymour Levy. Neither the grassland nor the bird can be found there now. Summer 1964, Steve Gallizioli, Arizona Department of Game and Fish (AZGF).

tant participants and included pigweed (*Amaranthus palmeri*), ragweed (*Ambrosia* spp.), spiderling (*Boerhavia* spp.), croton (*Croton* spp.), spurge (*Euphorbia* spp.), and purslane (*Portulaca* spp.).

Tree and shub components are almost always present, varying in composition from north to south, and in density from site to site. At the northern extremities, mesquite (*Prosopis velutina*) is often the only arborial constituent (Figure 95). Ironwood (*Olneya tesota*) was a close second, however, and other important tree and tall shrub species noted were the acacias (*Acacia angustissima*, *A. farnesiana*, *A. greggi*, and others), *Atamisquea emarginata*, the paloverdes

Figure 92. Former Sonoran Savanna Grassland ca. 1915 near Casa Grande, Arizona, 423 m (1400 ft). Photo courtesy of Casa Grande Valley Historical Society. The species of grass are unknown but appear perennial in nature as do grasses shown in other historic photos taken before the drilling of wells and universal livestock grazing.

Figure 93. Sonoran Savanna Grassland of annual grasses and mesquite within the Sonoran Desert being maintained through fire, Santa Rosa District of Papago Indian Reservation, ca. 675 m (2,215 ft). February 1969, Charles H. Lowe, Jr.

(*Parkinsonia aculeata, P. florida, P. microphylla, P. praecox*,), *jito* (*Forchammeria watsonii*), and *guayacán* (*Guaiacum coulteri*) (Figure 96). Depending upon location, the following plants may be important in a sparse shrub/scrub layer protruding above the grasses: *Caesalpinia* spp., desert hackberry (*Celtis pallida*), babybonnets (*Coursetia glandulosa*), brittlebush (*Encelia farinosa*), kidneywood (*Eysenhardtia orthocarpa*), tree ocotillo (*Fouquieria macdougalii*), janusia (*Janusia gracilis*), sangre de christo (*Jatropha cardiophylla*), and *Lycium* spp. Dense mottes or thickets of shrubs and trees, often festooned with tangles of vines, are generally confined to the drainages. Large cacti, while commonly present, are not ubiquitous, and typically

Table 16. Precipitation data for stations located within or adjacent to Sonoran Savanna Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	July-Sept.	%
Punta de Agua, Sonora, MEXICO 28.25° N, 110.25° W 220	220	26	9	5	6	t	13.7	107	124	59	43	7	30	431	290	67
Suaqui, Sonora, MEXICO 29.11° N, 109.41° W	250	31	16	11	5	3	27	163	141	53	27	12	30	519	356	69
La Colorado, Sonora, MEXICO 29.48° N, 110.35° W	390	22	15	5	1	1	14	106	112	36	10	9	26	357	255	71
Mazatán, Sonora, MEXICO 29.00° N, 110.09° W	550	28	18	9	2	0	37	150	182	7	26	7	36	502	339	69
Rancho Carizzo, Sonora, MEXICO[1] 30.03° N, 111.15° W	732	16	7	8	2	t	7	96	121	43	14	8	21	344	260	76
Bacoachi, Sonora, MEXICO 30.30° N, 109.58° W	1050	7	19	13	5	3	19	132	112	34	24	16	29	436	279	64
Tumacacori, Arizona, USA 31.34° N, 111.03° W	996	21	15	17	6	3	10	101	92	34	18	15	30	361	226	63

[1] Data from Tomlinson (1972)

Figure 94. Re-created Sonoran Savanna Grassland in Avra Valley, Arizona, ca. 600 m (2,000 ft), as it appeared during the fall of 2010. Former farmland purchased by the City of Tucson for the water rights, this parcel has been uncultivated and ungrazed for ca. 10 years. As a consequence the field is now occupied by a successional grassland dominated by *Bouteloua rothrockii*, which will eventually be replaced by mesquite and other shrubbery unless burned or cleared. Fall 2010, D.E.B.

Figure 95. Vernal pools within Sonoran Savanna Grassland along the lower Santa Cruz River, Pinal County Arizona. Spring aspect. The mesquite have shed their leaves and the annual forbs are dotting the landscape. Mustards and other greenery persist in this low spot. April 2012, D.E.B.

include one of four species of cholla (*Cylindropuntia arbuscula, C. fulgida*, *C. leptocaulis, C. thurberi*,) senita (*Pachycereus schottii*), *Stenocereus alamosensis*, *pitahaya* or organpipe cactus (*S. thurberi*), or an infrequent saguaro (*Carnegiea gigantea*).

Monthly and seasonal precipitation for seven locations within or adjacent to historic **Sonoran Savanna Grassland** sites are summarized in Table 16. Mean annual precipitation ranges from 260 to 520 mm (10-20 in), with 160 to 350 mm (6-14 in) falling during the July to September monsoon season. Freezes, while possible during any winter are never of long duration and rarely drop below -4°C. Killing frosts are therefore a rare occurrence.

From November to the abrupt onset of the summer rains the following year, the landscape becomes increasingly desolate. Cattle and aridity have eaten or withered the grasses, and except for the woody plants, many of which are now also bare, the groundcover may appear nonexistent. But by late June afternoon temperatures commonly exceed 38ºC and the humidity rises. Usually the summer rains begin by the first half of July and last through September. If enough moisture is received, a rapid forb/grass growth springs up, and trees renew their leaves. (Figures 97, 98). Forbs erupt as if by magic and develop rapidly while the trees and shrubs renew their leaves. Species of plants that have not bloomed the previous spring now do so. Greenery may now dominate the landscape, the amount of herbaceous growth being determined by the generosity of the rains, little or no growth occuring should they fail. However, should residual herbaceous growth be lacking, or lightning strikes fail to ignite the cured grasses prior to the monsoons, the woody and thorny components will reclaim landscape dominance within a remarkably short time—10 years or less.

One former area of Sonoran Savanna Grassland deserved of special attention is the outwash plains along the lower Santa Cruz River and its tributaries in Arizona. Known as the Santa Cruz Flats, this area of alternating clay pans and sandy plains from Altar Valley downsteam to the Pima Indian villages was historically a tropic-subtropic grassland of some importance to travelers and their livestock as well as grassland associated wildlife including pronghorn (Brown 2009). Maintained at its lower elevations by periodic flooding, the Santa Cruz Flats today, because of prolonged graz-

Figure 96. Sonoran Savanna Grassland being invaded by *Cercidium sonorae* in the Valle de Agua Caliente on Yaqui Indian land, Sonora, Mexico. The principal grass here at ca. 500 m (1,600 ft) is Rothrock grama (*Bouteloua rothrockii*). June 2012, Anibella Flores.

Figure 97. Late summer aspect of Sonoran Savanna Grassland on the Santa Cruz Flats, Pinal County, Arizona. Elevation ca. 510 m (1,670 ft). Velvet mesquite (*Prosopis velutina*) with a flush of herbaceous layer after the commencement of the summer rains. September 2010, D.E.B.

Figure 98. A weedy *bajio* in Sonoran Savanna Grassland within the Valle de Agua Caliente. These edaphic herblands of mostly annual plants such as *Amaranthus palmeri* were formerly choice masked bobwhite haunts. Today, these habitats, where they exist at all, are heavily impacted by livestock, in this case, horses. June 2012, Anibella Flores.

ing, are largely barren of vegetation save velvet mesquite, and in a few favored areas, annual weeds. Its fine surface soils washed away in floods and blown away by winds, these former edaphic grasslands have devolved into mesquite-annual savannas, barren sand wastes, and clay bottomed *playacitas* (see Figure 95)

The transformation of these short-term savannas to what is now considered thornscrub or desertscrub has resulted in the displacement of an interesting subtropical grassland fauna that included a number of invertebrates. Although these changes may have benifited certain animals such as the caracara (*Caracara cheriway*), javelina (*Pecari tajacu*), other, more open country adapted species appear to have been negatively affected, e.g., the white-tailed hawk (*Buteo albicaudatus*) and antelope jackrabbit (*Lepus alleni*). The numbers and distributions of several endemics such as the Sonoran green toad (*Bufo retiformis*) and rufous-winged sparrow (*Peucaea carpalis*), have also been greatly reduced. And the native masked bobwhite (*Colinus virginianus ridgwayi*) is now faced with extinction in the wild.

Caribbean Savanna Grassland

Beard (1953) determined that naturally occurring savannas were restricted in the Greater Antilles to Cuba and Hispaniola, and in the Lesser Antilles to only Barbuda. He found no savannas on Jamaica, and those grasslands he found on Puerto Rico he considered domestic pastures derived from dry forest communities (Figure 99). Despite the widespread occurrence of savannas on Cuba and Hispaniola, he thought that many of these pastures, like those on Dominica, and Antigua, were artificial and dependant on human burning and clearing for their existence. Whatever their origin, there are nonetheless savannas on several Caribbean islands, and whether natural or man-made, these areas support a number of grassland endemics.

The largest savannas in the Caribbean are on Cuba, this biotic community now occupying more than one third of the island's natural vegetation in the plains and low country where there is a significant dry season from November through April (Seifriz 1943, Beard 1953) (Table 17). An exception to the low relief was in the Sierra de Nipe, and savannas existed in areas having from 500 mm (20 in) of precipitation and a 7-8 month dry season to areas having 2,500 mm (98 in) of rainfall and only a short dry period (Beard 1953). Whatever the location, natural savannas are nearly always synonymous with certain edaphic conditions, the grasslands being invariably found on clay or sand surfaces laid over a chalk, limestone, serpentine, or some other impermeable formation. As elsewhere, Beard (1953) divided true savannas into orchard savannas (mostly on sandy soils), palm savannas (mostly on clay soils), and pine savannas or *pinas* (mostly on limonite).

The prominent savanna grasses reported by Beard (1953) were *Andropogon virginicus* and *Sporobolus indicus*, both locally accompanied or replaced by *Arundinella deppeana*, *Ichnanthus* spp., *Imperata brasiliensis*, *Lasiacis* spp. *Lithacne* spp., *Panicum tenerum*, and *Sorghastrum stipoides*. A number of sedges including *Bulbostylis paradoxa*, *Rhynchospora globosa*, and *Scleria* spp. may also be present. Typical trees in these "orchard savannas" varied from place to place but included *Byrsonima* spp., and *Curatella americana*, as well as such forest trees as *Anacardium occidentale, Brya ebenus*, *Bucida buceras*, *Guapira fragrans, Guettarda scabra*, *Quercus oleoides, Rondeletia cornifolia*, *Tabebuia lepidophylla*, *T. pallida*, and *Xylopia grandiflora*. Other wetter savannas also had the introduced logwood, *Haematoxylum campechianum*.

Beard (1953) also noted a number of palm savanna communities, especially in Holguin Province. The palms and palmettos inhabiting these savannas were variable and included *Acoelorraphe wrightii, Coccothrinax garciana*, *C. yuraguana, Copernicia yarey*, *C. glabrescens*, and *Sabal maritima*. The dicots were represented by the ubiquitous

Figure 99. Caribbean Savanna Grassland in Mayaguez District, Puerto Rico. The trees are mostly mesquite in this artificially maintained grassland, which is periodically burned and the trees thinned (Beard 1953). March 1986, D.E.B

Byrsonima crassifolia. Principal grasses were several species of *Paspalum*, tussock grasses with cutting leaves, along with *Andropogon glomeratus*, *A. gracilis*, *A. virginicus*, *Aristida refracta*, *A. neglecta*, *Bothriochloa saccharoides*, *Cenchrus distichophyllus*, *Hymenachne condensate, Hypogynium virgatum*, *Imperata brasiliensis*, *Leptocoryphium lanatum*, *Sporobolus purpurascens*, *S. indicus*, and *Trachypogon filifolius*. Sedges such as *Dichromena ciliata,* and *Rhynchospora globosa* were also much in evidence as were numerous forbs and the shrubs *Malpighia glabra* and *Stigmaphyllon diversifolium*. Artificial savannas were usually dominated by cultivated species of *Panicum*, sometimes punctuated by the trees *Acacia nilotica* or *Prosopis chilensis*.

Also found in the hills of the Sierra de los Organos of Cuba was a savanna association of *Quercus virginiana* and *Pinus tropicalis*, in which the dominant grass was *Sorghastrum stipoides*. Other associations were populated by *Byrsonima*, and *Curatella*, with *Arundinella deppeana* as the dominant grass. Endless savanna variations were also reported to occur on the Isle of Pines (now the Isle of Youth) including pine savannas of the 15-25 m (49-82 ft) tall *Pinus cubensis* between 400 and 600 m (1,312-1,970 ft) elevation, overtopping a grass layer about 45 cm (18 in) tall that included several species of *Panicum*.

Beard (1944, 1953) also thought that Cuba's savannas were of varied origin and much influenced by anthropological disturbance as well as such natural forces as climate, geology, drainage, soil-type, fire and grazing. When it came to assigning origins to Cuba's savannas, however, he was even

Figure 100. Caribbean Savanna Grassland in Pinar del Rio province, Cuba. A wet savanna of mostly introduced African grasses, this savanna is maintained as a pasture within semi-evergreen forest by burning. June 2001, D.E.B.

Figure 101. Artificially maintained palm savanna near Havana, Cuba. Determining whether Caribbean Savanna Grassland was originally savanna or tropical semi-evergreen forest is often moot due to the region's long fire history, both natural and anthropological. June 2001, D.E.B.

more conservative than Seifriz (1943), considering only 5-8% of the island's grasslands to be natural instead of Seifriz's 25-30% (Figure 100). He also considered fire to be a modifying agent rather than a controlling factor, as he determined that Cuba's grasslands could neither be induced nor maintained by fire. Of the island's several savanna types, Beard only recognized those savannas residing on alluvial soils under a dry climate with 300 to 600 mm (12-24 in) of annual precipitation and a 9-10 month dry season to be entirely natural. The others he considered as being either controlled by unfavorable water drainage and experiencing drastic changes in water tables such as the wetland savannas of the Florida Everglades and the Zapata Swamp of Cuba; or semi-anthropomorphic in that they had to be maintained by fire or other human interventions such as logging, grazing and planting of exotic grasses (Figure 101). Nor did he apparently recognize lightning-caused fires, winds or hurricanes as naturally enabling factors.

Beard (1953) also described savanna communities on Hispaniola's plains and plateaus, noting that this formation occurred from the coastal plain to up to about 520 m (1,700 ft) elevation. The mean annual precipitation in these areas was from about 1,100 to1,200 mm (43-47 in) with a dry season that extended from November through April when the total amount of rain falling in any given month was less than 10 cm (4 in) (Table 17).

The most interesting of these communities consisted of pure stands of grass on a treeless plain with *Themeda quadrivalvis* as the principal species, occurring as a pure stands or with *Abildgaardia monostachya*, *Andropogon bicornis*, *Aristida refracta*, *A. tener*, *Fimbristylis diphylla, Paspalum densum*, *P. millegrana*, *P. plicatulum*, and *Sorghastrum parviflorum*. Major herbs present included *Crotalaria* spp., *Euphorbia prostrata*, *Lobelia aquatica*, *Polygala* spp., *Stigmatophyllon* spp. and *Zephyranthes citrina*.

Another savanna type described by Beard (1953) in Hispaniola was an "orchard" community found in the lowlands and foothills where *Pinus occidentalis* participated along with such typical savanna trees as *Anacardium*, *Byrsonima*, and *Curatella*, on rolling and broken ground. Again, *Andropogon* and *Themeda* were important grasses as were the palms *Coccoloba rotundifolia* and *Coccothrinax argentea*. Other tree participants included *Acacia skleroxyla*, *Comocladia* spp., *Chrysophyllum oliviforme*, *Eugenia* spp., and *Pisonia* spp.

The above communities contrasted sharply with a "dry savanna" found on nearly soil-less limestone on level plains

Table 17. Monthly precipitation totals for locations within or adjacent to Caribbean Savanna Grassland.

Location - Lat./Long.	Altitude (m)	Precipitation (mm)														
		J	F	M	A	M	J	J	A	S	O	N	D	Total	Dec-Mar	%
Cienfuégos, CUBA 22.2° N, 80.4° W	< 60 (<200')	19	26	30	39	110	162	114	184	205	175	34	20	1118 (44.0")	95	8
Caibarien, CUBA 22.5° N, 79.5° W		37	29	26	60	166	196	128	150	207	208	74	41	1322 (52.0")	133	10
Moron, CUBA 22.1° N, 78.6° W	<76 (250')	36	30	39	86	186	226	158	171	221	184	77	30	1443 (56.8")	135	9
Jatibonico, CUBA 21.9° N, 79.2° W	98 (322')	26	21	44	77	199	235	178	182	181	186	42	22	1393 (54.8")	113	8
Florida, CUBA 21.5° N, 78.2° W	<300 (1000')	29	34	36	62	193	235	167	185	209	205	55	32	1441 (56.7")	131	9
Francisco, CUBA 20.8° N, 77.6° W	<300 (1000')	20	21	31	90	206	235	182	188	187	176	48	19	1404 (55.3")	91	6
Victoria de las Tunas, CUBA 21.0° N, 77.0° W	76-300 (250-1000')	17	23	28	48	130	168	134	137	166	152	62	20	1085 (42.7")	88	8
San Juan de la Mag., DOMINICAN REPUBLIC 18.8° N, 71.3° W	415 (1362')	11	14	27	75	125	97	109	124	143	150	59	36	968 (38.1")	88	9

near the ocean in which the annual rainfall was only between 500 mm and 760 mm (20 – 30 in), and subject to a severe dry season. Here the principal grass present was often *Uniola virgata,* alone, or mixed in with *Bouteloua repens* and the leaf-succulent *Agave antillarum*. Oftentimes too, the epiphytic orchid, *Tetramicra ekmanii* was present on the *Uniola* clumps, while such shrubs as *Jacquinia berteroi, Maytenus buxifolia*, *Plumeria alba*, and *Schaefferia ephedroides*, gave the landscape a semidesert grassland aspect. This community too was considered to be "natural" by Beard (1953).

Except for the white-tailed deer (*Odocoileus virginianus*), which was introduced in Cuba in the 1930s, savanna inhabiting mammals in the Caribbean islands mainly consist of domestic livestock. The number of birds associated with palm and other savanna habitats is relatively large, however, and include such endemics as Fernandina's flicker (*Colaptes fernandinae*) of Cuba, the palmchat (*Dulus dominicus*) of Hispaniola, and the black-faced grassquit (*Tiaris bicolor*) of Cuba; as well as more marginal savanna species including the tawny-shouldered blackbird (*Agelaius humeralis*) of Cuba and Hispaniola, the yellow-shouldered blackbird (*A. xanthomas*) of Puerto Rico, and the zapata sparrow (*Torreornis inexpectata*) of Cuba. Most savanna affiliates, however, while limited to one or two islands in the Greater Antilles, are also found on the mainland and include such widespread species as the grasshopper sparrow (*Ammodramus savannarum*), limpkin (*Aramus guarauna*), burrowing owl (*Athene cunicularia*), double-striped thick-knee (*Burhinus bistriatus*), crested caracara (*Caracara cheriway*), marsh harrier (*Circus cyaneus*), bobwhite (*Colinus virginianus*, Cuba only), common ground dove (*Columbina passerina*), smooth-billed ani (*Crotophaga ani*), kestrel (*Falco sparverius*), Western meadowlark (*Sturnella neglecta*), and yellow-faced grassquit (*Tiaris olivacea*), and sandhill crane (*Grus canadensis*). Other savanna-dwelling birds have either been introduced or recently arrived on their own, a testament to the expansion of savanna communities since the arrival of Europeans. Included among the former are the lesser goldfinch (*Carduelis psaltria*) to Cuba; the guineafowl (*Numida meleagris*), introduced to the Greater Antilles from Africa; the village weaver (*Ploceus cucullatus*) to Hispaniola from Africa; and the orange-cheeked waxbill (*Estrilda melpoda*) and hooded weaver (*Lonchura cucullata*)—both imports to Puerto Rico from Africa. Species arriving from South America to the Lesser Antilles on their own include the glossy cowbird (*Molothrus bonariensis*), saffron finch (*Sicalis flaveola*), and grassland yellow finch (*S. luteola*) (Bond 1961).

Savanna-dwelling reptiles such as Hispaniola's pigmy blue-tailed ameiva (*Ameiva lineolata*) and Haitian striped curly-tailed lizard (*Leiocephalus pratensis*), attest to the long term presence of savanna habitats in the Greater Antilles; while the grassland status of the grass coqui (*Eleutherodactylus brittoni*) found in Puerto Rico's savannas, is more problematic (Schwartz & Henderson 1991).

Other Neotropical Savannas

There are other savanna communities in North America's Neotropics that have been identified but not described in this text. As stated previously, **Central American Savanna Grassland** might be better served by dividing this biotic community into a wetter, Atlantic coast subdivision and a drier Pacific coast subdivision. Rzedowski (1988) makes reference to grasslands on the west coast of Mexico from Colima to Sinaloa, which might indicate the presence of a **Nayarit-Sinaloan Savanna Grassland.** Lundell (1934) and Miranda (1958) describe savannas within the Yucatán peninsula which might warrant separation from similar appearing communities in the Central American and Campechian-Veracruz biotic provinces. Gentry (1946a) describes a *savanilla* taking up a brief expanse on the north side of the Sierra Tacuichamona in central Sinaloa between *encinal* and short-tree forest (**Sinaloan Deciduous Forest**) communities, which was characterized by "open areas of turf-like grasses alternating with shrubs and trees." The grasses were identified as *Bouteloua eludens* and *Cathesticum* spp. In addition to oaks (*Quercus* spp.), *quebracho* (*Lysiloma divaricatum*), and *amapa* (*Handroanthus impetiginosus*), the savanilla's trees and woody shrubs contained such typical savanna species as *Byrsonima crassifolia*, *Mimosa palmeri*, and *Piscidium mollis* along with an occasional cacti (*Lemaireocereus* spp.). A similar savanilla was also described as occurring in the nearby Sierra Surutato (Gentry 1946b) in what might constitute a **Sinaloan Savanna Grassland**.

Figure 101. In the tablelands and basins of south-central Mexico, in Morelos, eastern Michoacan and northern Guerrero, one encounters subclimax Guerreran Savanna Grassland communities anthropomorphically maintained by long histories of clearing, prescribed burning and cultivation. Richly clothed in both native and introduced tropical grasses, the savanna aspect is maintained by such trees as cultivated guamuchils (*Pithecellobium dulce*) and such thorny Guerreran Thornscrub species as *Acacia farenesia*. At right-center is an arborescent *Opuntia* sp. D. E. B.

Concluding Remarks

Grasslands are some of our most productive ecosystems as well as among the most critically endangered due to conversion to croplands and other anthropogenic uses. Nearly 99% of pre-settlement, North American tall grass prairie is lost –probably forever, and similar stories play out across the globe. Because so few intact grasslands remain, conservation must be a priority, yet current high corn and soy bean prices, driven by the biofuel industry, have accelerated their conversion. A recent study mapping the absolute change in the Western Corn Belt grasslands to corn or soybeans shows approximately 528,000 ha (1.3 million acres) lost from 2006 to 2011 (Wright & Wimberly 2013).

In the United States, Federal programs to mitigate risks associated with farming such as disaster relief and crop insurance, coupled with the high prices for soy and corn commodities, have created incentives to cultivate those grasslands that were heretofore unsuitable. Poorly drained and/or shallow soils, wetlands, drought-prone, and marginal grasslands with high erosion potential continue to be converted for short-term profitability. The impacts of this loss of grassland habitat are numerous and disturbing. Populations of grassland-nesting birds are declining faster than any other group of North American birds (Stephens, et al. 2008). The wetlands of the Prairie Pothole Region, one of the most important breeding grounds for North American migratory waterfowl, continue to be drained and converted. The impacts on grassland mammals, reptiles, and invertebrates, while less monitored, accelerate annually.

The consequences of present day agricultural practices are, of course, not limited to wildlife issues. Soil carbon sequestration is significantly reduced in grassland conversion with long-term implications regarding global climate change. Loss of wetland-grassland associations has negative impacts on water tables and purification cycles. Grassland conversions, especially on lands vulnerable to erosion, have cascading effects on soil quality, crop yields, net productivity, flooding, and water storage (Wright & Wimberly 2013). With respect to biofuel development, Tilman et al. (2005) point out that present biofuel strategies based on corn ethanol and soy are not properly aligned with deliverable benefits, and may indeed be suboptimal in terms of net energy and carbon balances in addition to being detrimental to the ecosystems involved.

This manuscript, however, is not a grassland obituary. Rather, it is an inventory of what we have with eventual, if partial, restoration in mind. Science may inform us of our options and the consequences of our actions, but it is up to policy makers, institutions, and individuals to make the decisions that will affect what remains of our grassland resources. But our window of opportunity for reversing the trend is closing. In order to preserve these remarkable ecosystems, environmental policy that weighs the balance of short-term economic gain against long-term loss needs to be reconsidered. Support for grassland preserves must be maintained and accelerated, and remnant expanses increased and set aside. Grassland restoration and preservation is needed in order to continue to enjoy their bounty, and mandatory for the well-being of our planet.

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Appendix I. Worldwide Grasslands

Figure 1. Mongolian Steppe at 1,500 m (4,921) elevation near Rashaant in Khovsgol Aimag, Mongolia. It is autumn and the bunch-grasses and forbs have cured and the plants are prepared for the winter dormant period in this arctic-boreal environment that experiences a mean annual rainfall between 200 -270 mm/year. September 2008, Aimee Kessler.

Figure 2. Eurasian Meadow Steppe at elevation 2,180 m near Kemin, Kyrgyz Republic (Kyrgyzstan) dominated by *Brachypodium pinnatum, Festuca valesiaca, Helictotrichon tianschanicum, Hypericum scabrum,* and *Stipa capillata*. Mean annual temperature is 32.5° F. This cold temperate biotic community is a prime example of a "continental climate" and is a Palearctic analog to the Nearctic's Plains Grassland. The mean annual rainfall is 375 mm (15 in) with most falling during the growing season. July 2000, John B. Taft.

Figure 3. Mongolian Shrug-steppe (Desert-grassland) by Lake Issyk-Kul, Kyrgyz Republic at an elevation of 1,725 m (5659 ft). The mean annual precipitation here is only 125 mm and the principal shrubs are *Artemisia* sp., *Caragana kirgisorum*, *Ephedra intermedia,* and *Kochia prostrata* mixed in with a thin cover of *Stipa bungeana*, *S. orientalis*, and other xeric adapted plants. July 1999, John B. Taft.

Figure 4. *Stipa capulata*-dominated steppe grassland – Tien Shan, Kyrgyzstan, from an expedition with Nikolai Friesen, Herbert Hurka, Gregori Lazkov, and Barbara Neuffer. July 2004, Barbara Neuffer (University of Osnabrueck).

Figure 5. East African Savanna Grassland. Zebras on the floor of the Ngorongoro Crater, Tanzania. This part of the Serengeti is referred to locally as the "short grass plains" elevation ca. 1,676 m. September 1973, David and Nancy Pearson.

Figure 6. South African Highveld southwest of Johannesburg in Natal Province, elevation ca. 1,700 m (5,300 ft). The mean annual rainfall is ca. 713 mm (28 in), most of which falls during the summer period of October through March. The whitish colored grasses (*Eragrostis* spp.) in this warm-temperate biotic community are said to be indicative of a low nutritional content, the reddish, rooigrass (*Themeda triandra*) being more valuable as livestock forage. The occasional trees are lance-leaf sumac (*Rhus lancea*). April 1987, David E. Brown.

Figure 7. Subtropical Australian Spinifex (hummock) Grassland at an elevation of ca. 250 m (780 ft) in Kennedy Range National Park, Western Australia, ca. 60 km (36 mi) east of Gascoyne Junction. The mean annual rainfall in this area is ca. 214 mm (8 in), which falls mostly in late summer (January-July) with March thunderstorms being of sporadic importance. The dominant grasses are *Triodia basedowii,* and *T. pungens*. Winter 2008, John Alcock.

Figure 8. South American Pampas in the southeastern corner of the Oriente Province of Buenos Aires, Argentina, near the Atlantic Ocean. Present is a mixture of the genera *Avena*, *Lolium*, and *Nassella*. November 2008, Fernando Zuloaga.

Figure 9. Patagonian Tussock Grassland (Udvard 1975 a,b), Chubut Province of Argentina with mostly *Festuca* and *Poa*. October 2008, Fernando Zuloaga.

Figure 10. Insulantarctican Tussock Grassland (Udvard 1975 a,b), Steeple Jason Island, Falkland Islands, Argentina. Native tussock-grass (*Poa flabellata*) can reach heights of greater than 3 m. Tussocks are coastal areas on the mainland and small offshore islands below 200 m influenced by wave-splash and sea-spray. This vegetation is often associated with seabird colonies, especially penguin rookeries [http://herbaria.plants.ox.ac.uk/bol/falklands/]. January 2008, Dave and Nancy Pearson.

Appendix II. Matrix of plants referenced in text with the grassland type in which each occurs.

Family	Scientific name	Common name	ROCKY MOUNTAIN ALPINE AND SUBALPINE	CASCADE-SIERRAN SUBALPINE	TRANSVOLCANIC ALPINE AND SUBALPINE	ROCKY MOUNTAIN MONTANE	CASCADE-SIERRAN MONTANE	MADREAN MONTANE	PLAINS	GREAT BASIN	OREGONIAN COASTAL	GULF COASTAL	SEMIDESERT	CALIFORNIA VALLEY	CENTRAL AMERICAN SAVANNA	GUATEMALAN-GUERREAN SAVANNA	CAMPECHIAN-VERACRUZ SAVANNA	TAMAULIPAN SAVANNA	SONORAN SAVANNA	CARIBBEAN SAVANNA	other	
Aceraceae	Acer negundo	box elder							x													
Agavaceae	Agave	agave											x									
Agavaceae	Agave antillarum																			x		
Agavaceae	Agave lecheguilla	lechuguilla											x									
Agavaceae	Agave parryi	Parry's agave											x									
Agavaceae	Agave parviflora	smallflower century plant											x									
Agavaceae	Agave schottii	Schott's century plant											x									
Agavaceae	Dasylirion	sotol											x									
Agavaceae	Dasylirion leiophyllum	green sotol											x									
Agavaceae	Dasylirion wheeleri	desert spoon, common sotol											x									
Agavaceae	Furcraea parmentieri				x																	
Agavaceae	Nolina erumpens	foothill beargrass											x									
Agavaceae	Nolina microcarpa	sacahuista											x									
Agavaceae	Nolina texana	Texas sacahuista											x									
Agavaceae	Yucca	yucca							x				x									
Agavaceae	Yucca angustissima	narrowleaf yucca								x												
Agavaceae	Yucca baccata	banana yucca											x									
Agavaceae	Yucca decipiens												x									
Agavaceae	Yucca elata	soaptree yucca, palmilla											x									
Agavaceae	Yucca faxoniana	Eve's needle											x									
Agavaceae	Yucca glauca	soapweed yucca							x	x			x									
Agavaceae	Yucca rupicola	Texas yucca										x										
Agavaceae	Yucca thompsoniana	Thompson's yucca											x									
Agavaceae	Yucca torreyi	Torrey's yucca											x									

Amaranthaceae	Amaranthus	amaranth							x				x									
Amaranthaceae	Froelichia floridana	plains snakecotton										x										
Amaranthaceae	Tidestromia lanuginosa	woolly tidestromia											x									
Anacardiaceae	Anacardium occidentale	cashew													x					x		
Anacardiaceae	Comocladia																			x		
Anacardiaceae	Rhus aromatica	fragrant sumac							x													
Anacardiaceae	Rhus glabra	smooth sumac								x												
Anacardiaceae	Rhus microphylla	littleleaf sumac											x									
Anacardiaceae	Schinus molle	pirul											x									
Annonaceae	Xylopia aromatica	monkey pepper													x							
Annonaceae	Xylopia frutescens	Malagueto													x							
Annonaceae	Xylopia grandiflora																			x		
Apiaceae	Angelica lucida	seacoast angelica									x											
Apiaceae	Eryngium				x																	
Apiaceae	Eryngium yuccifolium	button eryngo							x													
Apiaceae	Heracleum maximum	cow parsnip		x							x											
Apiaceae	Ligusticum grayi	Gray's licorice-root		x																		
Apiaceae	Lomatium martindalei	Cascade parsley	x	x																		
Apiaceae	Pseudocymopterus	false springparsley				x																
Apocynaceae	Plumeria alba																			x		
Arecaceae	Acoelorrhaphe wrightii	Everglades palm, palma tasiste													x		x			x		
Arecaceae	Acrocomia aculeata														x							
Arecaceae	Attalea															x						
Arecaceae	Brahea dulcis	sombrero palm														x						
Arecaceae	Coccoloba rotundifolia																			x		
Arecaceae	Coccothrinax argentea																			x		
Arecaceae	Coccothrinax garciana																			x		
Arecaceae	Coccothrinax yuraguana																			x		
Arecaceae	Cocos regia	palmita															x					
Arecaceae	Copernicia glabrescens																			x		
Arecaceae	Copernicia yarey																			x		
Arecaceae	Sabal maritima																			x		
Arecaceae	Sabal mexicana																x	x				
Asclepiadaceae	Asclepias tuberosa	butterfly milkweed										x										
Asclepiadaceae	Oxylobus				x																	
Asteraceae	Achillea millefolium	common yarrow	x	x						x	x			x								
Asteraceae	Agoseris	agoseris	x	x						x												
Asteraceae	Agoseris apargioides	woolly goat chicory									x											
Asteraceae	Agoseris glauca	pale agoseris		x																		
Asteraceae	Agoseris heterophylla	annual agoseris												x								
Asteraceae	Ambrosia	ragweed																	x			
Asteraceae	Ambrosia psilostachya	Cuman ragweed							x			x										
Asteraceae	Antennaria	pussytoes							x													
Asteraceae	Antennaria parvifolia	small leaf pussytoes								x												
Asteraceae	Arnoglossum plantagineum	Indian plantain										x										
Asteraceae	Artemisia	sagebrush	x			x			x	x	x			x								
Asteraceae	Artemisia arbuscula	little sagebrush		x			x			x												
Asteraceae	Artemisia arctica	boreal sagebrush					x															
Asteraceae	Artemisia bigelovii	Bigelow sage								x												
Asteraceae	Artemisia cana	silver sagebrush								x												
Asteraceae	Artemisia dracunculus	tarragon							x													
Asteraceae	Artemisia filifolia	sandsage							x													

Family	Scientific name	Common name	ROCKY MOUNTAIN ALPINE AND SUBALPINE	CASCADE-SIERRAN SUBALPINE	TRANSVOLCANIC ALPINE AND SUBALPINE	ROCKY MOUNTAIN MONTANE	CASCADE-SIERRAN MONTANE	MADREAN MONTANE	PLAINS	GREAT BASIN	OREGONIAN COASTAL	GULF COASTAL	SEMIDESERT	CALIFORNIA VALLEY	CENTRAL AMERICAN SAVANNA	GUATEMALAN-GUERREAN SAVANNA	CAMPECHIAN-VERACRUZ SAVANNA	TAMAULIPAN SAVANNA	SONORAN SAVANNA	CARIBBEAN SAVANNA	other	
Asteraceae	Artemisia frigida	prairie sagewort	x			x	x		x	x												
Asteraceae	Artemisia ludoviciana	white sagebrush					x															
Asteraceae	Artemisia rigida	scabland sagebrush								x												
Asteraceae	Artemisia suksdorfii	Suksdorf sagebrush									x											
Asteraceae	Artemisia tridentata	big sagebrush		x			x			x				x								
Asteraceae	Artemisia tripartita	threetip sagebrush		x			x			x												
Asteraceae	Balsamorhiza sagittata	arrowleaf balsamroot		x																		
Asteraceae	Bidens muelleri				x																	
Asteraceae	Bidens triplinervia				x																	
Asteraceae	Centaurea	knapweed, star-thistle								x				x								
Asteraceae	Chondrilla juncea	rush skeletonweed												x								
Asteraceae	Chrysothamnus	rabbitbrush				x																
Asteraceae	Chrysothamnus pulchellus	Southwestern rabbitbrush								x												
Asteraceae	Chrysothamnus viscidiflorus	yellow rabbitbrush								x												
Asteraceae	Cirsium	thistle			x				x													
Asteraceae	Coreopsis tinctoria	tickseed										x										
Asteraceae	Crepis occidentalis	largeflower hawksbeard								x												
Asteraceae	Echinacea angustifolia	blacksamson echinacea							x													
Asteraceae	Echinacea pallida	pale purple coneflower							x													
Asteraceae	Encelia farinosa	brittlebush																	x			
Asteraceae	Ericameria laricifolia	turpentine bush											x									
Asteraceae	Ericameria nauseosa	rubber rabbitbrush								x												
Asteraceae	Erigeron	fleabane	x	x		x																
Asteraceae	Erigeron algidus	talus fleabane		x																		
Asteraceae	Erigeron breweri	Brewer's fleabane		x																		
Asteraceae	Erigeron peregrinus	subalpine fleabane		x																		
Asteraceae	Erigeron speciosus	aspen fleabane		x																		
Asteraceae	Erigeron strigosus	prairie fleabane							x													
Asteraceae	Eriophyllum lanatum	woolly sunflower		x																		
Asteraceae	Eucephalus ledophyllus	Cascade aster		x			x			x												
Asteraceae	Eupatorium compositifolium	yankeeweed										x										
Asteraceae	Flourensia cernua	tarbush											x									
Asteraceae	Gaillardia aestivalis	lanceleaf blanketflower										x										
Asteraceae	Gnaphalium				x																	
Asteraceae	Gnaphalium oxyphyllum				x																	
Asteraceae	Gnaphalium salicifolium				x																	
Asteraceae	Gnaphalium seemannii				x																	
Asteraceae	Gutierrezia	snakeweed						x	x	x			x									
Asteraceae	Gutierrezia sarothrae	snakeweed								x			x									

Asteraceae	Haplopappus stolonifer				x																	
Asteraceae	Helenium bigelovii	Bigelow's sneezeweed		x																		
Asteraceae	Helianthella quinquenervis	fivenerve helianthella						x														
Asteraceae	Helianthella uniflora	sunflower		x																		
Asteraceae	Helianthus	sunflower				x				x												
Asteraceae	Helianthus pauciflorus	stiff sunflower							x													
Asteraceae	Helianthus petiolaris	Prairie sunflower							x													
Asteraceae	Hieracium	hawkweed		x																		
Asteraceae	Hymenopappus flavescens	collegeflower											x									
Asteraceae	Hypochaeris radicata	cat's ear									x			x								
Asteraceae	Ionactis linariifolia	flaxleaf whitetop aster							x													
Asteraceae	Isocoma tenuisecta	burroweed								x			x									
Asteraceae	Laennecia schiedeana				x																	
Asteraceae	Lasthenia californica	California goldfields												x								
Asteraceae	Liatris	blazing star							x			x										
Asteraceae	Liatris punctata	dotted blazing star							x													
Asteraceae	Lygodesmia juncea	rush skeletonplant							x													
Asteraceae	Madia	tarweed												x								
Asteraceae	Oreostemma alpigenum	tundra aster		x																		
Asteraceae	Packera streptanthifolia	Rocky Mountain groundsel				x			x													
Asteraceae	Parthenium incanum	mariola											x									
Asteraceae	Parthenium integrifolium	wild quinine	x						x													
Asteraceae	Pleiacanthus spinosus	skeletonweed		x																		
Asteraceae	Pyrrocoma racemosa	goldenweed												x								
Asteraceae	Raillardella argentea	silky raillardella		x																		
Asteraceae	Ratibida pinnata	pinnate prairie coneflower							x													
Asteraceae	Rudbeckia hirta	blackeyed Susan				x																
Asteraceae	Saussurea americana	American saw-wort		x																		
Asteraceae	Senecio				x	x																
Asteraceae	Senecio angulifolius				x																	
Asteraceae	Senecio flaccidus	threadleaf groundsel											x									
Asteraceae	Senecio scalaris				x																	
Asteraceae	Senecio triangularis	arrowleaf ragwort					x															
Asteraceae	Solidago	goldenrod	x	x		x																
Asteraceae	Solidago canadensis	Canadian goldenrod					x		x		x											
Asteraceae	Solidago missouriensis	Missouri goldenrod							x	x			x									
Asteraceae	Sonchus asper	spiny sowthistle												x								
Asteraceae	Symphyotrichum ericoides	white heath aster							x													
Asteraceae	Symphyotrichum pratensis	meadow aster										x										
Asteraceae	Taraxacum	dandelion	x																			
Asteraceae	Tetradymia canescens	spineless horsebrush								x												
Asteraceae	Verbesina	crownbeard											x									
Asteraceae	Vernonia baldwinii	Baldwin's ironweed							x													
Asteraceae	Werneria nubigena				x																	
Asteraceae	Wyethia	mule ears								x												
Asteraceae	Zinnia acerosa	desert zinnia											x									
Berberidaceae	Berberis	barberry, algerita											x									
Bignoniaceae	Chilopsis linearis	desert willow											x									
Bignoniaceae	Crescentia alata	cannonball tree, jicaro													x	x						
Bignoniaceae	Crescentia cujete	jicaro														x	x					
Bignoniaceae	Handroanthus impetiginosus	amapa																			x	
Bignoniaceae	Tabebuia heterophylla	white cedar													x							
Bignoniaceae	Tabebuia lepidophylla																			x		

Family	Scientific name	Common name	ROCKY MOUNTAIN ALPINE AND SUBALPINE	CASCADE-SIERRAN SUBALPINE	TRANSVOLCANIC ALPINE AND SUBALPINE	ROCKY MOUNTAIN MONTANE	CASCADE-SIERRAN MONTANE	MADREAN MONTANE	PLAINS	GREAT BASIN	OREGONIAN COASTAL	GULF COASTAL	SEMIDESERT	CALIFORNIA VALLEY	CENTRAL AMERICAN SAVANNA	GUATEMALAN-GUERREAN SAVANNA	CAMPECHIAN-VERACRUZ SAVANNA	TAMAULIPAN SAVANNA	SONORAN SAVANNA	CARIBBEAN SAVANNA	other	
Bignoniaceae	Tabebuia pallida																			x		
Boraginaceae	Amsinckia menziesii	Menzies' fiddleneck								x												
Boraginaceae	Cryptantha	cryptantha											x									
Boraginaceae	Heliotropium confertifolium	leafy heliotrope																x				
Boraginaceae	Lithospermum caroliniense	Carolina puccoon							x													
Boraginaceae	Lithospermum ruderale	Western stoneseed								x												
Brassicaceae	Brassica													x								
Brassicaceae	Brassica nigra	black mustard												x								
Brassicaceae	Descurainia	tansymustard											x									
Brassicaceae	Descurainia impatiens				x																	
Brassicaceae	Descurainia pinnata	Western tansymustard								x												
Brassicaceae	Draba				x																	
Brassicaceae	Draba jorullensis				x																	
Brassicaceae	Draba volcanica				x																	
Brassicaceae	Isatis tinctoria	Dyer's woad								x												
Brassicaceae	Lepidium	pepperweed											x									
Brassicaceae	Sisymbrium													x								
Brassicaceae	Sisymbrium altissimum	tumblemustard								x												
Cactaceae	Carnegiea gigantea	saguaro																	x			
Cactaceae	Coryphantha vivipara	spinystar							x													
Cactaceae	Cylindropuntia acanthocarpa	buckhorn cholla											x									
Cactaceae	Cylindropuntia arbuscula	pencil cholla																	x			
Cactaceae	Cylindropuntia imbricata	tree cholla							x	x			x									
Cactaceae	Cylindropuntia kleiniae	candle cholla											x									
Cactaceae	Cylindropuntia leptocaulis	Christmas cholla											x									
Cactaceae	Cylindropuntia spinosior	cane cholla											x									
Cactaceae	Cylindropuntia thurberi																		x			
Cactaceae	Cylindropuntia whipplei	Whipple cholla											x									
Cactaceae	Echinocactus horizonthalonius	Turk's head											x									
Cactaceae	Echinocereus rigidissimus	rainbow hedgehog cactus											x									
Cactaceae	Echinocereus viridiflorus	nylon hedgehog cactus							x													
Cactaceae	Echinomastus erectocentrus	redspine fishhook cactus											x									
Cactaceae	Echinomastus intertextus	white fishhook cactus											x									
Cactaceae	Ferocactus pilosus	Mexican lime cactus											x									
Cactaceae	Ferocactus wislezeni	barrelcactus											x									
Cactaceae	Mammillaria grahamii	Graham's nipple cactus											x									
Cactaceae	Mammillaria heyderi	little nipple cactus											x									
Cactaceae	Mammillaria mainiae	counterclockwise nipple cactus											x									
Cactaceae	Mammillaria wrightii	Wright's nipple cactus											x									

Cactaceae	Opuntia	prickly-pear							x	x			x									
Cactaceae	Opuntia chlorotica	clock face prickly-pear											x									
Cactaceae	Opuntia engelmannii	Engelmann's prickly-pear											x									
Cactaceae	Opuntia fragilis	brittle prickly-pear							x													
Cactaceae	Opuntia humifusa	devil's-tongue							x													
Cactaceae	Opuntia lindheimeri	Texas pricklypear																x				
Cactaceae	Opuntia macrocentra	purple prickly-pear											x									
Cactaceae	Opuntia macrorhiza	twistspine prickly-pear							x	x			x									
Cactaceae	Opuntia phaeacantha	tulip prickly-pear										x	x									
Cactaceae	Opuntia polyacantha	Plains prickly-pear							x	x												
Cactaceae	Opuntia streptacantha	nopal cardón											x									
Cactaceae	Pachycereus schottii	senita																	x			
Cactaceae	Stenocereus alamosensis																		x			
Cactaceae	Stenocereus thurberi	organpipe cactus, pitahaya																	x			
Cactaceae	Thelocactus conothelos												x									
Cactaceae	Thelocactus hexaedrophorus												x									
Campanulaceae	Campanula					x																
Campanulaceae	Campanula rotundifolia	bellflower	x																			
Campanulaceae	Lobelia aquatica																			x		
Campanulaceae	Lobelia nana				x																	
Capparaceae	Atamisquea emarginata	vomitbush																	x			
Capparaceae	Forchammeria watsonii	jito																	x			
Capparaceae	Koeberlinia spinosa	allthorn											x									
Caprifoliaceae	Symphoricarpos albus	common snowberry		x																		
Caprifoliaceae	Symphoricarpos microphylla				x																	
Caprifoliaceae	Symphoricarpos occidentalis	Western snowberry							x													
Caryophyllaceae	Arenaria	sandwort		x	x																	
Caryophyllaceae	Arenaria bryoides				x																	
Caryophyllaceae	Arenaria capillaris ssp. americana	fescue sandwort		x																		
Caryophyllaceae	Arenaria pumicola	Crater Lake sandwort		x																		
Caryophyllaceae	Cerastium				x																	
Celastraceae	Canotia holacantha	crucifixion thorn											x									
Celastraceae	Maytenus buxifolia																			x		
Celastraceae	Schaefferia ephedroides																			x		
Chenopodiaceae	Atriplex canescens	fourwing saltbush								x												
Chenopodiaceae	Atriplex polycarpa	allscale												x								
Chenopodiaceae	Chenopodium	goosefoot							x													
Chenopodiaceae	Grayia spinosa	hopsage								x												
Chenopodiaceae	Krascheninnikovia lanata	winter fat								x												
Chenopodiaceae	Salsola tragus	Russian thistle							x	x			x									
Chenopodiaceae	Sarcobatus vermiculatus	greasewood								x												
Clethraceae	Clethra																x					
Clethraceae	Clethra hondurensis														x							
Clusiaceae	Hypericum perforatum	common St. Johnswort									x											
Combretaceae	Bucida buceras	gregorywood																		x		
Commelinaceae	Commelina	dayflower							x													
Commelinaceae	Commelina alpestris				x																	
Commelinaceae	Tradescantia	spiderwort										x										
Commelinaceae	Tradescantia occidentalis	prairie spiderwort							x													
Commelinaceae	Weldenia candida				x																	
Convolvulaceae	Evolvulus																	x				

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Convolvulaceae	Ipomoea cordatotriloba	tievine										x										
Convolvulaceae	Ipomoea decasperma							x														
Cucurbitaceae	Sicyos parviflorus	smallflower bur cucumber			x																	
Cupressaceae	Juniperus	juniper											x									
Cupressaceae	Juniperus communis	common juniper	x								x											
Cupressaceae	Juniperus deppeana	alligator juniper						x														
Cupressaceae	Juniperus monosperma	oneseed juniper							x	x			x									
Cupressaceae	Juniperus monticola	mountain juniper			x																	
Cupressaceae	Juniperus occidentalis	Western juniper		x																		
Cupressaceae	Juniperus scopulorum	Rocky Mountain juniper								x												
Cupressaceae	Juniperus standleyi				x																	
Cupressaceae	Juniperus virginiana	Eastern redcedar							x													
Cyperaceae	Abildgaardia mexicana												x									
Cyperaceae	Abildgaardia monostachya																			x		
Cyperaceae	Bulbostylis paradoxa																			x		
Cyperaceae	Carex	sedge	x	x	x	x	x															
Cyperaceae	Carex albonigra	blackandwhite sedge		x																		
Cyperaceae	Carex atherodes	wheat sedge							x													
Cyperaceae	Carex breweri	Brewer's sedge		x																		
Cyperaceae	Carex filifolia	threadleaf sedge		x					x													
Cyperaceae	Carex gravida	heavy sedge							x													
Cyperaceae	Carex microptera	sawmill sedge		x																		
Cyperaceae	Carex obtusata	obtuse sedge							x													
Cyperaceae	Carex pensylvanica	Pennsylvania sedge							x													
Cyperaceae	Carex rostrata	beaked sedge							x													
Cyperaceae	Carex scopulorum	mountain sedge		x																		
Cyperaceae	Carex utriculata	Northwest Territory sedge		x																		
Cyperaceae	Cyperus	flatsedge				x	x															
Cyperaceae	Cyperus fendlerianus	Fendler's flatsedge						x														
Cyperaceae	Cyperus schweinitzii	Schweinitz's flatsedge							x													
Cyperaceae	Dichromena ciliata																			x		
Cyperaceae	Eleocharis	spike rush	x	x		x																
Cyperaceae	Eleocharis quinqueflora	fewflower spikerush		x																		
Cyperaceae	Fimbristylis annua													x								
Cyperaceae	Fimbristylis diphylla																			x		
Cyperaceae	Rhynchospora globosa																			x		
Cyperaceae	Rhynchospora mexicana													x								
Cyperaceae	Scleria																			x		
Dilleniaceae	Curatella americana	chaparo, raspa viejo, sandpaper tree												x	x	x				x		

Dryopteridaceae	Polystichum munitum	swordfern									x											
Ebenaceae	Diospyros virginiana	persimmon							x													
Elaeagnaceae	Elaeagnus commutata	silverberry	x																			
Elaeagnaceae	Shepherdia	buffaloberry							x	x												
Elaeagnaceae	Shepherdia argentea	buffaloberry	x																			
Ephedraceae	Ephedra	joint fir, Mormon tea								x												
Ephedraceae	Ephedra torreyana	Torrey's jointfir								x												
Ephedraceae	Ephedra trifurca	Mormon tea											x									
Equisetaceae	Equisetum telmateia	giant horsetail									x											
Ericaceae	Arctostaphylos uva-ursi	kinnikinnick					x															
Ericaceae	Cassiope mertensiana	Western moss heather		x																		
Ericaceae	Gaultheria humifusa	alpine spicywintergreen	x																			
Ericaceae	Kalmia microphylla	alpine laurel		x																		
Ericaceae	Kalmia polifolia	bog laurel	x				x															
Ericaceae	Pernettya prostrata				x																	
Ericaceae	Phyllodoce	mountainheath		x																		
Ericaceae	Phyllodoce empetriformis	pink mountainheath		x																		
Ericaceae	Vaccinium	blueberry		x			x															
Ericaceae	Vaccinium cespitosum	dwarf bilberry	x	x																		
Ericaceae	Vaccinium myrtillus	whortleberry	x																			
Euphorbiaceae	Chamaesyce	sandmat											x						x			
Euphorbiaceae	Croton	croton																	x			
Euphorbiaceae	Croton capitatus	hogwort										x										
Euphorbiaceae	Croton setigerus	dove weed												x								
Euphorbiaceae	Croton texensis	Texas croton										x										
Euphorbiaceae	Euphorbia	spurge																	x			
Euphorbiaceae	Euphorbia prostrata	prostrate sandmat																		x		
Euphorbiaceae	Jatropha cardiophylla	sangre de Christo																	x			
Euphorbiaceae	Stillingia sylvatica	queen's-delight							x													
Fabaceae	Acacia angustissima	prairie acacia																	x			
Fabaceae	Acacia constricta	white thorn acacia											x									
Fabaceae	Acacia costaricensis														x							
Fabaceae	Acacia farnesiana	sweet acacia										x			x				x			
Fabaceae	Acacia greggii	catclaw											x						x			
Fabaceae	Acacia neovernicosa	viscid acacia, whitethorn acacia											x									
Fabaceae	Acacia nilotica																			x		
Fabaceae	Acacia pennatula															x						
Fabaceae	Acacia schaffneri	twisted acacia											x									
Fabaceae	Acacia skleroxyla																			x		
Fabaceae	American snoutbean	American snoutbean																x				
Fabaceae	Amorpha canescens	leadplant							x													
Fabaceae	Astragalus					x			x													
Fabaceae	Astragalus arrectus	Palouse milkvetch		x																		
Fabaceae	Astragalus micranthus				x																	
Fabaceae	Baptisia bracteata	wild indigo										x										
Fabaceae	Brya ebenus	ebony coccuswood																		x		
Fabaceae	Caesalpinia																		x			
Fabaceae	Calliandra conferta	Rio Grande stickpea																x				
Fabaceae	Calliandra eriophylla	mesquite											x									
Fabaceae	Calliandra houstoniana														x							
Fabaceae	Cassia																	x				

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Fabaceae	Cercidium praecox	palo brea							x									x				
Fabaceae	Chamaecrista fasciculata	partridge pea							x													
Fabaceae	Chamaecrista greggii	Gregg's sensitive pea																x				
Fabaceae	Coursetia axillaris	Texas babybonnets																x				
Fabaceae	Coursetia glandulosa	babybonnets											x						x			
Fabaceae	Enterolobium cyclocarpum														x							
Fabaceae	Erythrina montana							x														
Fabaceae	Eysenhardtia orthocarpa	kidneywood											x						x			
Fabaceae	Haematoxylum brasiletto	Brazilwood													x							
Fabaceae	Haematoxylum campechianum	logwood													x		x			x		
Fabaceae	Lathyrus					x																
Fabaceae	Lathyrus nevadensis	Sierra Nevada pea		x																		
Fabaceae	Lotus	trefoil		x		x								x								
Fabaceae	Lotus oblongifolius	bird's-foot trefoil		x																		
Fabaceae	Lupinus	lupine	x	x	x	x																
Fabaceae	Lupinus aridus	desert lupine		x																		
Fabaceae	Lupinus bicolor	miniature lupine												x								
Fabaceae	Lupinus breweri	Brewer's lupine		x																		
Fabaceae	Lupinus cacuminis				x																	
Fabaceae	Lupinus latifolius	broadleaf lupine		x			x															
Fabaceae	Lupinus leucophyllus	velvet lupine		x																		
Fabaceae	Lupinus littoralis	seashore lupine									x			x								
Fabaceae	Lupinus montanus				x																	
Fabaceae	Lupinus sericeus	silky lupine		x																		
Fabaceae	Lupinus subcarnosus	Texas bluebonnet										x										
Fabaceae	Lupinus texensis	Texas lupine										x										
Fabaceae	Lysiloma divaricatum	quebracho																				
Fabaceae	Mimosa aculeaticarpa	wait-a-minute bush										x	x									
Fabaceae	Mimosa dysocarpa	velvetpod mimosa											x									
Fabaceae	Mimosa tenuifolia														x	x						
Fabaceae	Olneya tesota	ironwood																	x			
Fabaceae	Pachyrhizus erosus	jicama												x								
Fabaceae	Parkinsonia aculeata	Mexican palo verde																	x			
Fabaceae	Parkinsonia florida	blue paloverde																	x			
Fabaceae	Parkinsonia microphylla	foothill paloverde																	x			
Fabaceae	Piscidia communis																	x				
Fabaceae	Piscidia piscipula														x							
Fabaceae	Pithecellobium dulce													x								
Fabaceae	Prosopis	mesquite							x				x						x	x		

Fabaceae	Prosopis chilensis	Chilean mesquite																		x		
Fabaceae	Prosopis glandulosa	honey mesquite							x			x						x					
Fabaceae	Prosopis velutina	velvet mesquite											x						x				
Fabaceae	Psoralidium	scurfpea							x														
Fabaceae	Psoralidium lanceolatum	lemon scurfpea								x													
Fabaceae	Psoralidium tenuiflorum	slimflower scurfpea							x														
Fabaceae	Tephrosia onobrychoides	hoarypea										x											
Fabaceae	Tephrosia virginiana	Virginia tephrosia							x														
Fabaceae	Trifolium	clover	x	x										x									
Fabaceae	Vicia	vetch	x			x			x														
Fagaceae	Quercus chihuahuensis	Chihuahuan oak											x										
Fagaceae	Quercus douglasii	blue oak												x									
Fagaceae	Quercus emoryi	Emory oak											x										
Fagaceae	Quercus garryana	Oregon white oak									x												
Fagaceae	Quercus grisea	grey oak											x										
Fagaceae	Quercus havardii	shinnery oak							x														
Fagaceae	Quercus kelloggii	California black oak									x												
Fagaceae	Quercus lobata	valley oak												x									
Fagaceae	Quercus macrocarpa	bur oak							x														
Fagaceae	Quercus marilandica	blackjack oak							x														
Fagaceae	Quercus oleoides	roble													x		x	x		x			
Fagaceae	Quercus rubra	red oak							x														
Fagaceae	Quercus stellata	post oak							x														
Fagaceae	Quercus turbinella	scrub oak											x										
Fagaceae	Quercus virginiana	live oak										x						x		x			
Fouquieriaceae	Fouquieria macdougalii	tree ocotillo																	x				
Fouquieriaceae	Fouquieria splendens	ocotillo											x										
Gentianaceae	Gentiana pumilio				x																		
Geraniaceae	Erodium botrys	stork's bill												x									
Geraniaceae	Erodium cicutarium	filaree											x	x									
Geraniaceae	Geranium potentillaefolium				x																		
Geraniaceae	Geranium viscosissimum	sticky geranium		x																			
Grimmiaceae	Racomitrium crispulum				x																		
Grossulariaceae	Ribes	currant		x																			
Hippocastanaceae	Aesculus californica	California buckeye												x									
Hydrangeaceae	Philadelphus lewisii	Lewis mockorange								x													
Hydrophyllaceae	Phacelia				x																		
Iridaceae	Iris douglasiana	Douglas' iris									x												
Iridaceae	Iris missouriensis	Rocky Mountain iris	x			x																	
Iridaceae	Sisyrinchium bellum	Western blue-eyed grass									x			x									
Juglandaceae	Carya	hickory							x														
Juglandaceae	Juglans californica	California walnut												x									
Juglandaceae	Juglans nigra	black walnut							x														
Juncaceae	Juncus	rush	x	x		x	x																
Juncaceae	Luzula	woodrush			x																		
Juncaceae	Luzula racemosa				x																		
Krameriaceae	Krameria ramosissima	manystem ratany																x					
Lamiaceae	Agastache urticifolia	nettleleaf giant hyssop		x			x																
Lamiaceae	Brazoria truncata	rattlesnake flower										x											
Lamiaceae	Hedeoma piperita				x																		
Lamiaceae	Salvia				x																		

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Lamiaceae	Salvia aethiopis	Mediterranean sage								x												
Lamiaceae	Salvia azurea	azure blue sage							x													
Lamiaceae	Stachys mexicana	Mexican hedgenettle									x											
Lamiaceae	Vitex															x						
Liliaceae	Allium validum	Pacific onion, swamp onion		x																		
Liliaceae	Brodiaea	brodiaea								x												
Liliaceae	Brodiaea coronaria	crown brodiea									x											
Liliaceae	Calochortus	mariposa lily							x	x												
Liliaceae	Calochortus macrocarpus	sagebrush mariposa lily								x												
Liliaceae	Camassia scilloides	Atlantic camas							x													
Liliaceae	Dichelostemma capitatum	bluedicks												x								
Liliaceae	Erythronium	fawnweed		x																		
Liliaceae	Erythronium grandiflorum	yellow avalanche-lily					x															
Liliaceae	Hymenocallis liriosme	spiderlily										x										
Liliaceae	Nothoscordum bivalve	crowpoison							x													
Liliaceae	Veratrum californicum	corn-lily				x																
Liliaceae	Veratrum viride	hellebore		x																		
Liliaceae	Zephyranthes citrina																			x		
Liliaceae	Zigadenus fremontii	Fremont deathcamus									x											
Malpighiaceae	Byrsonima																			x		
Malpighiaceae	Byrsonima crassifolia	nance												x	x	x						
Malpighiaceae	Janusia gracilis	janusia																	x			
Malpighiaceae	Malpighia glabra																			x		
Malpighiaceae	Stigmaphyllon diversifolium																			x		
Malpighiaceae	Stigmatophyllon																			x		
Malvaceae	Callirhoe involucrata	winecup										x										
Malvaceae	Gossypium thurberi	desert cotton											x									
Malvaceae	Guazuma ulmifolia													x								
Malvaceae	Hibiscus costatus															x						
Malvaceae	Sidalcea malviflora	dwarf checkerbloom									x											
Malvaceae	Sidalcea reptans	Sierra checkerbloom		x																		
Malvaceae	Sphaeralcea	mallow				x							x									
Malvaceae	Sphaeralcea coccinea	scarlet globemallow							x													
Malvaceae	Triumfetta chihuahuensis							x														
Malvaceae	Waltheria															x						
Martyniaceae	Martynia	devil's claw											x									
Melastomataceae	Clidemia															x						
Melastomataceae	Conostegia															x						
Melastomataceae	Henriettella seemannii													x								

Melastomataceae	Miconia																x					
Myricaceae	Myrica cerifera	wax myrtle										x										
Myrtaceae	Eugenia																			x		
Myrtaceae	Psidium guajava	guava													x		x					
Nyctaginaceae	Boerhavia	spiderling											x						x			
Nyctaginaceae	Boerhavia coccinea	scarlet spiderling																x				
Nyctaginaceae	Guapira																			x		
Nyctaginaceae	Mirabilis	four o'clock							x													
Nyctaginaceae	Pisonia																			x		
Oleaceae	Fraxinus pennsylvanica	green ash							x													
Onagraceae	Camissonia tanacetifolia	tansyleaf evening primrose								x												
Onagraceae	Chamerion angustifolium	fireweed		x			x															
Onagraceae	Gaura coccinea	scarlet gaura							x													
Onagraceae	Oenothera	primrose										x										
Onagraceae	Oenothera rhombipetala	fourpoint evening primrose							x													
Orchidaceae	Spiranthes romanzoffiana	hooded lady's tresses		x																		
Orchidaceae	Tetramicra ekmanii																			x		
Oxalidaceae	Oxalis				x																	
Oxalidaceae	Oxalis frutescens	shrubby woodsorrel																x				
Papaveraceae	Eschscholzia californica	California poppy												x								
Pinaceae	Abies amabilis	Pacific silver fir		x																		
Pinaceae	Abies lasiocarpa	subalpine fir, corkbark fir	x	x																		
Pinaceae	Larix lyalli	subalpine larch		x																		
Pinaceae	Picea engelmannii	Engelmann spruce	x	x																		
Pinaceae	Picea glauca	blue spruce	x			x																
Pinaceae	Pinus albicaulis	whitebark pine		x																		
Pinaceae	Pinus caribaea	Caribbean pine													x							
Pinaceae	Pinus contorta	lodgepole pine		x																		
Pinaceae	Pinus cubensis	Cuban pine																		x		
Pinaceae	Pinus culminicola	Potosi pinyon			x																	
Pinaceae	Pinus edulis	two needle pinyon				x		x	x	x			x									
Pinaceae	Pinus hartwegii	Hartweg pine			x																	
Pinaceae	Pinus jefferyi	Jeffrey pine		x			x															
Pinaceae	Pinus montezumae	Montezuma pine			x																	
Pinaceae	Pinus occidentalis	Hispaniolan pine																		x		
Pinaceae	Pinus ponderosa	Ponderosa pine	x	x		x	x	x	x													
Pinaceae	Pinus tropicalis	tropical pine																		x		
Pinaceae	Tsuga mertensiana	mountain hemlock		x																		
Plantaginaceae	Plantago	plantain			x																	
Plantaginaceae	Plantago patagonica	woolly plantain								x												
Plantaginaceae	Plantago subnuda	tall coastal plantain									x											
Plantaginaceae	Sibthorpia repens				x																	
Poaceae	Achnatherum		x						x	x												
Poaceae	Achnatherum aridum	Mormon needlegrass								x												
Poaceae	Achnatherum eminens	Southwestern needlegrass											x									
Poaceae	Achnatherum hymenoides	Indian ricegrass					x			x												
Poaceae	Achnatherum lettermanii	Letterman's needlegrass		x																		
Poaceae	Achnatherum nelsonii	Columbia needlegrass								x												
Poaceae	Achnatherum occidentale	Western needlegrass		x						x												
Poaceae	Achnatherum thurberianum	Thurber's needlegrass					x			x												
Poaceae	Aegilops cylindrica	jointed goatgrass	x							x												

Family	Scientific name	Common name	ROCKY MOUNTAIN ALPINE AND SUBALPINE	CASCADE-SIERRAN SUBALPINE	TRANSVOLCANIC ALPINE AND SUBALPINE	ROCKY MOUNTAIN MONTANE	CASCADE-SIERRAN MONTANE	MADREAN MONTANE	PLAINS	GREAT BASIN	OREGONIAN COASTAL	GULF COASTAL	SEMIDESERT	CALIFORNIA VALLEY	CENTRAL AMERICAN SAVANNA	GUATEMALAN-GUERREAN SAVANNA	CAMPECHIAN-VERACRUZ SAVANNA	TAMAULIPAN SAVANNA	SONORAN SAVANNA	CARIBBEAN SAVANNA	other	
Poaceae	Aegilops triuncialis	barbed goatgrass												x								
Poaceae	Agropyron		x	x		x			x	x												
Poaceae	Agropyron cristatum	crested wheatgrass					x															
Poaceae	Agrostis	bentgrass	x						x		x											
Poaceae	Agrostis idahoensis	Idaho bentgrass									x											
Poaceae	Agrostis rossiae	Ross' bentgrass		x																		
Poaceae	Aira caryophyllea	silver hairgrass									x			x								
Poaceae	Andropogon	bluestem						x	x													
Poaceae	Andropogon bicornis														x		x			x		
Poaceae	Andropogon gerardii	big bluestem							x			x										
Poaceae	Andropogon glomeratus	bushy bluestem															x			x		
Poaceae	Andropogon gracilis																			x		
Poaceae	Andropogon hallii	sand bluestem							x													
Poaceae	Andropogon tener		x																	x		
Poaceae	Andropogon ternarius	splitbeard bluestem										x										
Poaceae	Andropogon virginicus	broomsedge bluestem										x								x		
Poaceae	Anthoxanthum odoratum	sweet vernalgrass									x											
Poaceae	Aristida adscensionis	sixweeks threeawn							x	x		x	x	x	x			x	x	x		
Poaceae	Aristida californica	California threeawn																	x			
Poaceae	Aristida divaricata	poverty threeawn											x									
Poaceae	Aristida longespica	slimspike threeawn										x										
Poaceae	Aristida neglecta																			x		
Poaceae	Aristida oligantha	Prairie threeawn												x								
Poaceae	Aristida purpurascens	arrowfeather threeawn										x										
Poaceae	Aristida purpurea	purple threeawn							x	x			x					x	x			
Poaceae	Aristida refracta																			x		
Poaceae	Aristida schiedeana	single threeawn						x														
Poaceae	Aristida ternipes	spidergrass												x	x				x			
Poaceae	Arundinella deppeana														x					x		
Poaceae	Avena barbata	slender oat												x								
Poaceae	Avena fatua	wild oats												x								
Poaceae	Axonopus												x									
Poaceae	Axonopus aureus														x							
Poaceae	Axonopus fissifolius																x					
Poaceae	Blepharoneuron tricholepis	pine dropseed	x					x														
Poaceae	Bothriochloa alta																x					
Poaceae	Bothriochloa barbinodis	cane beardgrass											x						x			
Poaceae	Bothriochloa saccharoides	silver bluestem										x								x		
Poaceae	Bouteloua							x	x													

Poaceae	Bouteloua alamosana	Alamos grama													x							
Poaceae	Bouteloua aristidoides	needle grama																	x			
Poaceae	Bouteloua barbata	sixweeks grama																	x			
Poaceae	Bouteloua breviseta	gypsum grama											x									
Poaceae	Bouteloua chondrosioides	sprucetop grama											x									
Poaceae	Bouteloua curtipendula	sideoats grama							x				x			x	x		x			
Poaceae	Bouteloua dactyloides	buffalograss							x									x				
Poaceae	Bouteloua dimorpha															x	x					
Poaceae	Bouteloua disticha														x							
Poaceae	Bouteloua eludens	Santa Rita Mountain grama																			x	
Poaceae	Bouteloua eriopoda	black grama								x			x									
Poaceae	Bouteloua gracilis	blue grama				x		x	x	x			x									
Poaceae	Bouteloua hirsuta	hairy grama							x	x			x					x				
Poaceae	Bouteloua parryi	Parry's grama																	x			
Poaceae	Bouteloua radicosa	purple grama											x					x	x			
Poaceae	Bouteloua repens	slender grama											x			x	x		x	x		
Poaceae	Bouteloua rothrockii	Rothrock grama																	x			
Poaceae	Brachypodium distachyon	purple brome												x								
Poaceae	Briza rotunda				x																	
Poaceae	Bromus	brome						x	x		x											
Poaceae	Bromus carinatus	California brome		x																		
Poaceae	Bromus ciliatus	fringed brome						x														
Poaceae	Bromus diandrus	ripgut brome												x								
Poaceae	Bromus hordeaceus	soft brome												x								
Poaceae	Bromus inermis	smooth brome							x													
Poaceae	Bromus madritensis	compact brome												x								
Poaceae	Bromus rubens	red brome											x									
Poaceae	Bromus sitchensis	Alaska brome									x											
Poaceae	Bromus tectorum	cheatgrass					x			x												
Poaceae	Buchloe dactyloides	buffalograss							x													
Poaceae	Calamagrostis breweri	reedgrass		x			x															
Poaceae	Calamagrostis canadensis	bluejoint panicgrass	x																			
Poaceae	Calamagrostis nutkaensis	Pacific reedgrass									x											
Poaceae	Calamagrostis rubescens						x															
Poaceae	Calamagrostis tolucensis	Toluca reedgrass			x																	
Poaceae	Calamagrostis vulcanica				x																	
Poaceae	Calamovilfa longifolia	prairie sandreed							x													
Poaceae	Cathestecum	false grama											x				x					
Poaceae	Cathestecum erectum															x			x			
Poaceae	Cathestecum multifidum															x						
Poaceae	Cenchrus distichophyllus																			x		
Poaceae	Cenchrus spinifex	sand bur																x				
Poaceae	Chloris	fingergrass							x									x	x			
Poaceae	Chloris virgata	feather fingergrass																	x			
Poaceae	Ctenium	toothache grass															x					
Poaceae	Cynodon														x			x				
Poaceae	Cynodon dactylon	Bermudagrass							x													
Poaceae	Cynodon nlemfuensis														x							
Poaceae	Cynosurus cristatus	crested dogstail grass									x											
Poaceae	Cynosurus echinatus	bristly dogstail grass									x											
Poaceae	Dactylis glomerata	orchardgrass				x			x		x											

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Poaceae	Danthonia	oatgrass	x																			
Poaceae	Danthonia californica	California oatgrass									x											
Poaceae	Danthonia intermedia	timber oatgrass							x													
Poaceae	Danthonia parryi	Parry's oatgrass							x													
Poaceae	Danthonia unispicata	onespike oatgrass								x												
Poaceae	Dasyochloa pulchella	fluffgrass											x									
Poaceae	Deschampsia							x	x													
Poaceae	Deschampsia caespitosa	tufted hairgrass	x								x											
Poaceae	Deschampsia danthonioides	annual hairgrass												x								
Poaceae	Deschampsia holciformis	Pacific hairgrass									x											
Poaceae	Dichanthelium villosissimum	whitehair rosette grass							x													
Poaceae	Diectomis																x					
Poaceae	Digitaria californica	Arizona cottontop											x						x			
Poaceae	Digitaria eriantha	digitgrass													x							
Poaceae	Digitaria insularis	sourgrass															x					
Poaceae	Digitaria leucites																x					
Poaceae	Distichlis																	x				
Poaceae	Distichlis spicata	saltgrass								x			x				x					
Poaceae	Elionurus tripsacoides															x	x					
Poaceae	Elymus		x																			
Poaceae	Elymus canadensis	Canada wildrye					x		x													
Poaceae	Elymus caninus	bearded wheatgrass		x																		
Poaceae	Elymus elymoides	squirreltail		x			x		x	x			x	x								
Poaceae	Elymus flavescens	yellow wildrye								x												
Poaceae	Elymus glaucus	blue wildrye		x							x			x								
Poaceae	Elymus lanceolatus	thickspike wheatgrass								x												
Poaceae	Elymus trachycaulus	slender wheatgrass							x													
Poaceae	Enteropogon chlorideus	umbrellagrass																	x			
Poaceae	Eragrostis								x			x	x				x	x				
Poaceae	Eragrostis ciliaris	gophertail lovegrass													x							
Poaceae	Eragrostis geniculata														x							
Poaceae	Eragrostis intermedia	plains lovegrass								x			x									
Poaceae	Eragrostis lehmanniana	Lehmann's lovegrass											x									
Poaceae	Erioneuron pilosum	hairy woollygrass										x										
Poaceae	Festuca		x	x					x													
Poaceae	Festuca amplissima				x			x														
Poaceae	Festuca arizonica	Arizona fescue	x																			
Poaceae	Festuca campestris	rough fescue		x			x			x												
Poaceae	Festuca hallii	Plains rough fescue	x																			

Poaceae	Festuca idahoensis	Idahoe fescue	x	x		x	x		x	x	x			x								
Poaceae	Festuca livida				x																	
Poaceae	Festuca ovina	sheep fescue							x													
Poaceae	Festuca rosei				x																	
Poaceae	Festuca rubra	red fescue									x											
Poaceae	Festuca thurberi	Thurber's fescue	x																			
Poaceae	Festuca tolucensis	Toluca fescue			x																	
Poaceae	Festuca viridula	greenleaf fescue		x																		
Poaceae	Gastridium phleoides	nit grass												x								
Poaceae	Glyceria	mannagrass									x											
Poaceae	Hesperostipa		x						x													
Poaceae	Hesperostipa comata	needle and thread					x		x	x												
Poaceae	Hesperostipa curtiseta	shortbristle needle and thread							x													
Poaceae	Hesperostipa neomexicana	New Mexico needle-grass											x									
Poaceae	Hesperostipa spartea	porcupinegrass	x						x													
Poaceae	Heteropogon contortus	tanglehead										x	x			x	x		x			
Poaceae	Hilaria							x									x					
Poaceae	Hilaria belangeri	curly mesquite							x				x						x			
Poaceae	Hilaria cenchroides															x						
Poaceae	Hilaria jamesii	James' galleta							x	x												
Poaceae	Hilaria mutica	tobosa grass											x									
Poaceae	Hilaria semplei															x						
Poaceae	Holcus lanatus	common velvetgrass									x											
Poaceae	Hordeum								x													
Poaceae	Hordeum brachyantherum	meadow barley									x											
Poaceae	Hordeum murinum	mouse barley												x								
Poaceae	Hymenachne condensata																			x		
Poaceae	Hyparrhenia rufa	jaragua													x							
Poaceae	Hypogynium virgatum																			x		
Poaceae	Ichnanthus	bedgrass																		x		
Poaceae	Imperata																x					
Poaceae	Imperata brasiliensis	Brazilian satintail																		x		
Poaceae	Koeleria macrantha	Junegrass	x	x		x	x	x	x	x	x			x								
Poaceae	Lasiacis																x			x		
Poaceae	Leptochloa fusca ssp. uninervia	Mexican sprangletop																	x			
Poaceae	Leptocoryphium														x		x					
Poaceae	Leptocoryphium lanatum																			x		
Poaceae	Leucopoa kingii	spike fescue	x																			
Poaceae	Leymus								x													
Poaceae	Leymus cinereus	Basin wildrye								x												
Poaceae	Leymus mollis	dunegrass									x											
Poaceae	Leymus triticoides	beardless wildrye								x				x								
Poaceae	Lithachne	diente de perro																		x		
Poaceae	Lolium perenne ssp. multiflorum	Italian ryegrass									x			x								
Poaceae	Lycurus setosus	wolftail											x									
Poaceae	Melica	oniongrass									x											
Poaceae	Melica bulbosa	oniongrass		x																		
Poaceae	Melica californica	California melicgrass												x								
Poaceae	Melica imperfecta	smallflower melicgrass												x								
Poaceae	Mesosetum																x					
Poaceae	Muhlenbergia		x						x				x				x					

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Poaceae	Muhlenbergia arenicola	sand muhly											x									
Poaceae	Muhlenbergia capillaris	hairawn muhly										x										
Poaceae	Muhlenbergia emersleyi	bullgrass						x														
Poaceae	Muhlenbergia gigantea				x																	
Poaceae	Muhlenbergia implicata													x								
Poaceae	Muhlenbergia macroura				x			x														
Poaceae	Muhlenbergia montana	mountain muhly				x																
Poaceae	Muhlenbergia porteri	bush muhly								x			x						x			
Poaceae	Muhlenbergia pungens	sandhill muhly							x													
Poaceae	Muhlenbergia purpusii												x									
Poaceae	Muhlenbergia pusilla				x																	
Poaceae	Muhlenbergia quadridentata				x																	
Poaceae	Muhlenbergia rigida	purple muhly						x														
Poaceae	Muhlenbergia robusta				x																	
Poaceae	Muhlenbergia torreyi	ring muhly							x	x												
Poaceae	Muhlenbergia wrightii	spike muhly	x																			
Poaceae	Nassella cernua	nodding needlegrass												x								
Poaceae	Nassella lepida	foothill needlegrass												x								
Poaceae	Nassella leucotricha	Texas wintergrass										x										
Poaceae	Nassella pulchra	purple needlegrass												x								
Poaceae	Nassella viridula	green needlegrass							x													
Poaceae	Oplismenus															x						
Poaceae	Orcuttia	Orcutt grass												x								
Poaceae	Orthoclada laxa															x						
Poaceae	Panicum capillare	witchgrass																	x			
Poaceae	Panicum hallii	tumblegrass																x				
Poaceae	Panicum maximum	Guinea grass													x		x					
Poaceae	Panicum obtusum	vine mesquite											x						x			
Poaceae	Panicum purpurascens													x								
Poaceae	Panicum repens															x						
Poaceae	Panicum rudgei													x								
Poaceae	Panicum tenerum	bluejoint panicgrass																		x		
Poaceae	Panicum virgatum	switchgrass							x			x						x				
Poaceae	Pappophorum vaginatum	whiplash pappusgrass																	x			
Poaceae	Pappostipa speciosa	desert needlegrass								x			x	x								
Poaceae	Pascopyrum smithii	Western wheatgrass	x			x			x	x												
Poaceae	Paspalum								x				x							x		
Poaceae	Paspalum conjugatum															x						
Poaceae	Paspalum densum																			x		

Poaceae	Paspalum humboldtianum														x							
Poaceae	Paspalum millegrana																			x		
Poaceae	Paspalum monostachyum	gulfdune paspalum										x										
Poaceae	Paspalum notatum																x					
Poaceae	Paspalum pectinatum																x					
Poaceae	Paspalum plicatulum																x			x		
Poaceae	Paspalum setaceum	thin paspalum																x				
Poaceae	Paspalum virgatum	talquezal													x		x					
Poaceae	Pennisetum bambusiforme														x							
Poaceae	Pennisetum ciliare	buffelgrass																	x			
Poaceae	Pennisetum setosum														x							
Poaceae	Pereilema crinitum														x							
Poaceae	Phleum alpinum	alpine timothy	x	x																		
Poaceae	Piptochaetium virescens				x																	
Poaceae	Poa	bluegrass	x	x					x		x											
Poaceae	Poa annua	annual bluegrass			x																	
Poaceae	Poa arida	Plains bluegrass							x													
Poaceae	Poa cusickii	Cusick's bluegrass								x												
Poaceae	Poa fendleriana	muttongrass	x																			
Poaceae	Poa nemoralis	inland bluegrass	x																			
Poaceae	Poa pratensis	Kentucky bluegrass				x	x		x	x												
Poaceae	Poa reflexa	nodding bluegrass	x																			
Poaceae	Poa secunda	Sandberg bluegrass		x					x	x				x								
Poaceae	Pseudoroegneria spicata	bluebunch wheatgrass		x			x		x	x												
Poaceae	Ptilagrostis kingii	Sierra needlgrass		x																		
Poaceae	Rytidosperma pilosum	hairy wallaby grass									x											
Poaceae	Sacciolepis striata														x							
Poaceae	Schedonnardus paniculatus	tumblegrass	x															x				
Poaceae	Schizachyrium brevifolium	serillo dulce													x							
Poaceae	Schizachyrium condensatum	Colombian bluestem													x							
Poaceae	Schizachyrium scoparium	little bluestem							x			x	x					x				
Poaceae	Scleropogon brevifolius	burrograss							x	x			x									
Poaceae	Scolochloa festucacea	common rivergrass							x													
Poaceae	Setaria								x						x							
Poaceae	Setaria parviflora	marsh bristlegrass															x					
Poaceae	Setaria leucopila	bristlegrass								x			x									
Poaceae	Setaria lutescens	yellow bristlegrass											x									
Poaceae	Sorghastrum nutans	Indiangrass							x			x										
Poaceae	Sorghastrum parviflorum																			x		
Poaceae	Sorghastrum stipoides	needle Indiangrass																		x		
Poaceae	Spartina alterniflora																x					
Poaceae	Spartina gracilis	alkali cordgrass							x													
Poaceae	Spartina spartinae	gulf cordgrass															x	x				
Poaceae	Sporobolus	dropseed							x				x									
Poaceae	Sporobolus airoides	alkali sacaton							x	x									x			
Poaceae	Sporobolus clandestinus	rough dropseed										x										
Poaceae	Sporobolus compositus var. drum	Drummond's dropseed							x													
Poaceae	Sporobolus contractus	spike dropseed																	x			
Poaceae	Sporobolus cryptandrus	sand dropseed							x	x			x					x	x			
Poaceae	Sporobolus heterolepis	Prairie dropseed							x													
Poaceae	Sporobolus indicus	smut grass													x					x		

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Poaceae	Sporobolus purpurea																			x		
Poaceae	Sporobolus wrightii	sacaton											x									
Poaceae	Stipa							x	x													
Poaceae	Stipa ichu	Peruvian feathergrass			x								x									
Poaceae	Stipa mucronata	desert needlegrass											x									
Poaceae	Stipa tenuissima	finestem needle-grass											x									
Poaceae	Taeniatherum caput-medusae	Medusahead								x												
Poaceae	Themeda quadrivalvis																			x		
Poaceae	Trachypogon							x									x					
Poaceae	Trachypogon angustifolius													x								
Poaceae	Trachypogon filifolius																			x		
Poaceae	Trachypogon spicatus	crinkleawn										x	x		x							
Poaceae	Trichloris crinita	false Rhodes grass											x									
Poaceae	Tridens muticus	slim tridens											x									
Poaceae	Tridens pilosus	hairy tridens											x									
Poaceae	Tridens strictus	longspike tridens										x										
Poaceae	Trisetum							x			x											
Poaceae	Trisetum irazuense				x																	
Poaceae	Trisetum spicatum	spike trisetum		x	x																	
Poaceae	Triticum								x													
Poaceae	Uniola virgata	limestone grass																		x		
Poaceae	Urochloa ciliatissima	tumblegrass																x				
Poaceae	Urochloa mutica													x								
Poaceae	Vulpia bromoides	brome fescue									x											
Poaceae	Vulpia microstachys var. pauciflo	Pacific fescue												x								
Poaceae	Vulpia myuros	rat-tail fescue			x									x								
Polemoniaceae	Gilia nuttallii	Nuttall gilia		x																		
Polemoniaceae	Ipomopsis	skyrocket	x			x																
Polemoniaceae	Ipomopsis aggregata	scarlet gilia		x																		
Polemoniaceae	Phlox			x								x										
Polemoniaceae	Phlox diffusa	spreading phlox					x															
Polemoniaceae	Phlox longifolia	longleaf phlox								x												
Polemoniaceae	Polemonium	Jacob's-ladder		x																		
Polygalaceae	Polygala																			x		
Polygalaceae	Polygala alba	white milkwort																x				
Polygonaceae	Coccoloba barbadensis																x					
Polygonaceae	Eriogonum	buckwheat		x						x												
Polygonaceae	Eriogonum flavum	alpine golden buckwheat		x																		
Polygonaceae	Eriogonum heracleoides	parsnipflower buckwheat		x																		

Polygonaceae	Eriogonum marifolium	marumleaf buckwheat		x																		
Polygonaceae	Eriogonum nudum	naked buckwheat		x																		
Polygonaceae	Eriogonum pyrolifolium	Shasta buckwheat		x																		
Polygonaceae	Eriogonum wrightii	bastardsage											x									
Polygonaceae	Polygonum	knotweed		x																		
Polygonaceae	Polygonum bistortoides	American bistort	x																			
Polygonaceae	Polygonum davisiae	Davis' knotweed		x																		
Polygonaceae	Rumex	dock								x												
Polygonaceae	Rumex acetosella	sheep sorrel									x											
Portulacaceae	Cistanthe umbellata	Mt. Hood pussypaws		x																		
Portulacaceae	Claytonia lanceolata	lanceleaf springbeauty		x			x															
Portulacaceae	Portulaca	purselane																	x			
Primulaceae	Jacquinia berteroi																			x		
Pteridaceae	Pteridium aquilinum	brackenfern				x					x											
Ranunculaceae	Caltha leptosepala	marsh marigold	x																			
Ranunculaceae	Delphinium	larkspur	x	x						x												
Ranunculaceae	Pulsatilla	pasqueflower							x													
Ranunculaceae	Pulsatilla occidentalis	Western pasqueflower		x																		
Ranunculaceae	Ranunculus	buttercup		x	x																	
Ranunculaceae	Ranunculus californicus	California buttercup									x			x								
Ranunculaceae	Ranunculus occidentalis	Western buttercup									x											
Resedaceae	Reseda luteola				x																	
Rhamnaceae	Ceanothus velutinus	snowbrush ceanothus					x															
Rhamnaceae	Cercocarpus ledifolius	curl-leaf mountain mahogany					x															
Rhamnaceae	Condalia	condalia							x									x				
Rhamnaceae	Condalia ericoides	javelina bush											x									
Rhamnaceae	Sageretia wrightii	Wright's mock buckthorn											x									
Rhamnaceae	Zizyphus obtusifolia	greythorn											x									
Rosaceae	Alchemilla pinnata				x																	
Rosaceae	Alchemilla procumbens				x																	
Rosaceae	Amelanchier	serviceberry								x												
Rosaceae	Coleogyne ramosissima	blackbrush								x												
Rosaceae	Crataegus	hawthorn								x												
Rosaceae	Crataegus douglasii	black hawthorn		x																		
Rosaceae	Fragaria chiloensis	beach strawberry									x											
Rosaceae	Geum triflorum	old man’s whiskers		x																		
Rosaceae	Potentilla	cinquefoil	x	x	x																	
Rosaceae	Potentilla candicans				x																	
Rosaceae	Potentilla flabellifolia	high mountain cinquefoil					x															
Rosaceae	Potentilla glandulosa	yellow cinquefoil		x																		
Rosaceae	Potentilla gracilis	slender cinquefoil		x																		
Rosaceae	Potentilla heterosepala				x																	
Rosaceae	Potentilla hippiana	woolly cinquefoil	x																			
Rosaceae	Potentilla leonine				x																	
Rosaceae	Potentilla staminea				x																	
Rosaceae	Prunus angustifolia	Chickasaw plum							x													
Rosaceae	Prunus emarginata	bitter cherry					x															
Rosaceae	Prunus virginiana	chokecherry	x	x					x	x												
Rosaceae	Purshia tridentata	bitterbrush		x			x			x												
Rosaceae	Rosa bracteata	Macartney rose										x										
Rosaceae	Rosa nutkana	Nutka rose		x			x			x	x											

Family	Scientific name	Common name	ROCKY MOUNTAIN ALPINE AND SUBALPINE	CASCADE-SIERRAN SUBALPINE	TRANSVOLCANIC ALPINE AND SUBALPINE	ROCKY MOUNTAIN MONTANE	CASCADE-SIERRAN MONTANE	MADREAN MONTANE	PLAINS	GREAT BASIN	OREGONIAN COASTAL	GULF COASTAL	SEMIDESERT	CALIFORNIA VALLEY	CENTRAL AMERICAN SAVANNA	GUATEMALAN-GUERREAN SAVANNA	CAMPECHIAN-VERACRUZ SAVANNA	TAMAULIPAN SAVANNA	SONORAN SAVANNA	CARIBBEAN SAVANNA	other	
Rosaceae	Rubus										x											
Rosaceae	Rubus parviflorus	thimbleberry					x															
Rubiaceae	Galium	bedstraw									x											
Rubiaceae	Guettarda scabra	wild guave																		x		
Rubiaceae	Rondeletia cornifolia																			x		
Salicaceae	Populus	cottonwood							x													
Salicaceae	Populus balsamifera	black cottonwood		x																		
Salicaceae	Populus tremuloides	aspen	x																			
Salicaceae	Salix	willow		x					x													
Salicaceae	Salix scouleriana	Scouler's willow					x															
Sapindaceae	Dodonaea															x						
Sapindaceae	Dodonaea viscosa	hopbush											x									
Sapindaceae	Sapindus saponaria	Western soapberry											x									
Sapotaceae	Chrysophyllum oliviforme																			x		
Sapotaceae	Sideroxylon lanuginosum	gum bully											x									
Saxifragaceae	Heuchera micrantha	alumroot		x																		
Saxifragaceae	Lithophragma glabrum	woodland-star								x												
Saxifragaceae	Mitella breweri	Brewer's miterwort		x																		
Scrophulariaceae	Castilleja	paintbrush											x									
Scrophulariaceae	Castilleja arachnoidea	cobwebby Indian paintbrush		x																		
Scrophulariaceae	Castilleja bella				x																	
Scrophulariaceae	Castilleja exserta	owl's clover												x								
Scrophulariaceae	Castilleja lutescens	yellow paintbrush		x																		
Scrophulariaceae	Castilleja parviflora	mountain Indian paintbrush		x			x															
Scrophulariaceae	Mimulus	monkeyflower				x																
Scrophulariaceae	Mimulus lewisii	purple monkeyflower		x			x															
Scrophulariaceae	Nuttallanthus canadensis	Canada toadflax							x													
Scrophulariaceae	Pedicularis orizabae				x																	
Scrophulariaceae	Penstemon	beardtongue		x		x				x												
Scrophulariaceae	Penstemon gentianoides				x																	
Scrophulariaceae	Penstemon heterodoxus	Sierra beardtongue		x																		
Scrophulariaceae	Penstemon procerus	littleflower penstemon		x																		
Scrophulariaceae	Penstemon rydbergii	Rydberg's penstemon		x																		
Scrophulariaceae	Triphysaria eriantha	Johnny-tuck												x								
Scrophulariaceae	Verbascum thapsus					x																
Simaroubaceae	Alvaradoa amorphoides														x							
Solanaceae	Lycium																		x			
Sphagnaceae	Sphagnum	sphagnum	x																			
Tiliaceae	Tilia americana	American basswood							x													

Ulmaceae	Celtis occidentalis	common hackberry							x													
Ulmaceae	Celtis pallida	desert hackberry, granejo							x				x					x	x			
Ulmaceae	Celtis reticulata	netleaf hackberry											x									
Ulmaceae	Ulmus americana	American elm							x													
Ulmaceae	Ulmus rubra	slippery elm							x													
Valerianaceae	Valeriana sitchensis	Sitka valerian		x																		
Verbenaceae	Aloysia wrightii	Wright's lippia											x									
Verbenaceae	Glandularia bipinnatifida	Dakota mock vervain						x														
Verbenaceae	Lippia graveolens	Mexican oregano																x				
Verbenaceae	Verbena stricta	hoary verbena							x													
Violaceae	Viola	violet				x																
Violaceae	Viola nannei				x																	
Zygophyllaceae	Guaiacum coulteri	guayacán																	x			
Zygophyllaceae	Larrea tridentata	creosote											x									

Appendix III. Matrix of animals referenced in text with the grassland type in which each occurs.

Class	Order	Family	Scientific name	Common name	ROCKY MOUNTAIN ALPINE AND SUBALPINE	CASCADE-SIERRAN SUBALPINE	TRANSVOLCANIC ALPINE AND SUBALPINE	ROCKY MOUNTAIN MONTANE	CASCADE-SIERRAN MONTANE	MADREAN MONTANE	PLAINS	GREAT BASIN	OREGONIAN COASTAL	GULF COASTAL	SEMIDESERT	CALIFORNIA VALLEY	CENTRAL AMERICAN SAVANNA	GUATEMALAN-GUERREAN SAVANNA	CAMPECHIAN-VERACRUZ SAVANNA	TAMAULIPAN SAVANNA	SONORAN SAVANNA	CARIBBEAN SAVANNA
Amphibia	Anura	Bufonidae	Bufo boreas	Western toad	x																	
Amphibia	Anura	Bufonidae	Bufo boreas halophilus	California toad											x							
Amphibia	Anura	Bufonidae	Bufo cognatus	Great Plains toad							x			x								
Amphibia	Anura	Bufonidae	Bufo debilis	green toad									x	x								
Amphibia	Anura	Bufonidae	Bufo retiformis	Sonoran green toad																	x	
Amphibia	Anura	Bufonidae	Bufo speciosus	Texas toad										x								
Amphibia	Anura	Bufonidae	Bufo valliceps	Gulf Coast toad									x									
Amphibia	Anura	Bufonidae	Bufo woodhousii	Woodhouse's toad							x											
Amphibia	Anura	Hylidae	Pseudacris clarkii	spotted chorus frog							x		x									
Amphibia	Anura	Hylidae	Pseudacris streckeri	Strecker's chorus frog							x		x									
Amphibia	Anura	Hylidae	Pseudacris triseriata	Western chorus frog	x			x			x		x									
Amphibia	Anura	Leptodactylidae	Eleutherodactylus brittoni	grass coqui																		x
Amphibia	Anura	Pelobatidae	Scaphiopus couchii	Couch's spadefoot toad										x								
Amphibia	Anura	Pelobatidae	Scaphiopus holbrookii	Eastern spadefoot toad									x									
Amphibia	Anura	Pelobatidae	Spea bombifrons	spadefoot toad							x			x								
Amphibia	Anura	Pelobatidae	Spea hammondi	Western spadefoot toad										x	x							
Amphibia	Anura	Pelobatidae	Spea intermontana	Great Basin spadefoot toad								x										
Amphibia	Anura	Pelobatidae	Spea multiplicata	New Mexico spadefoot toad										x								
Amphibia	Anura	Ranidae	Rana pipiens	Northern leopard frog				x														
Amphibia	Caudata	Ambystomatidae	Ambystoma gracile gracile	brown salamander									x									
Amphibia	Caudata	Ambystomatidae	Ambystoma tigrinum	Eastern tiger salamander	x			x														
Amphibia	Caudata	Ambystomatidae	Aneides ferreus	black salamander									x									
Amphibia	Caudata	Ambystomatidae	Batrachoseps attenuatus	California slender salamander									x									
Aves	Apodiformes	Trochilidae	Calothorax lucifer	Lucifer's hummingbird										x								
Aves	Caprimulgiformes	Caprimulgidae	Chordeiles minor	common nighthawk	x						x				x							

Aves	Charadriiformes	Burhinidae	Burhinus bistriatus	double-striped thick-knee													x	x	x			x	
Aves	Charadriiformes	Charadriidae	Charadrius montanus	mountain plover							x												
Aves	Charadriiformes	Scolopacidae	Bartramia longicauda	upland plover	x						x												
Aves	Charadriiformes	Scolopacidae	Calidris fuscicollis	white-rumped sandpiper	x																		
Aves	Charadriiformes	Scolopacidae	Limosa fedoa	marbled godwit	x																		
Aves	Charadriiformes	Scolopacidae	Numenius americanus	long-billed curlew	x						x												
Aves	Charadriiformes	Scolopacidae	Tryngites subruficollis	buff-breasted sandpiper							x												
Aves	Columbiformes	Columbidae	Columbina minuta interrupta	plain-breasted ground dove													x		x				
Aves	Columbiformes	Columbidae	Columbina passerina	common ground dove																		x	
Aves	Columbiformes	Columbidae	Patagioenas cayennensis	pale-vented pigeon													x		x				
Aves	Cuculiformes	Cuculidae	Crotophaga ani	smooth-billed ani																		x	
Aves	Falconiformes	Accipitridae	Buteo albicaudatus	white-tailed hawk										x			x			x	x		
Aves	Falconiformes	Accipitridae	Buteo jamaicensis	red-tailed hawk	x																		
Aves	Falconiformes	Accipitridae	Buteo lagopus	rough-legged hawk	x																		
Aves	Falconiformes	Accipitridae	Buteo regalis	ferruginous hawk	x						x	x											
Aves	Falconiformes	Accipitridae	Buteo swainsoni	Swainson's hawk	x						x				x								
Aves	Falconiformes	Accipitridae	Circus cyaneus	marsh harrier																		x	
Aves	Falconiformes	Accipitridae	Elanus leucurus	white-tailed kite												x							
Aves	Falconiformes	Cathartidae	Gymnogyps californianus	California condor												x							
Aves	Falconiformes	Falconidae	Caracara cheriway	caracara																	x	x	
Aves	Falconiformes	Falconidae	Falco femoralis	aplomado falcon										x	x					x			
Aves	Falconiformes	Falconidae	Falco mexicanus	Prairie falcon							x	x			x	x							
Aves	Falconiformes	Falconidae	Falco sparverius	American kestrel	x			x														x	
Aves	Galliformes	Meleagridinae	Meleagris gallopavo	wild turkey				x															
Aves	Galliformes	Numididae	Numida meleagris	guineafowl																		x	
Aves	Galliformes	Odontophoridae	Callipepla gambelii	Gambel's quail											x								
Aves	Galliformes	Odontophoridae	Callipepla squamata	scaled quail											x								
Aves	Galliformes	Odontophoridae	Colinus virginianus	bobwhite														x				x	
Aves	Galliformes	Odontophoridae	Colinus virginianus ridgwayi	masked bobwhite																	x		
Aves	Galliformes	Phasianidae	Alectoris graeca	rock partridge								x											
Aves	Galliformes	Phasianidae	Centrocercus urophasianus	sage grouse								x											
Aves	Galliformes	Phasianidae	Dendragapus fuliginosus	sooty grouse									x										
Aves	Galliformes	Phasianidae	Dendragapus obscurus	dusky grouse	x	x																	
Aves	Galliformes	Phasianidae	Dendragapus obscurus sierra	Sierra blue grouse		x																	
Aves	Galliformes	Phasianidae	Tympanuchus cupido	greater Prairie chicken							x												
Aves	Galliformes	Phasianidae	Tympanuchus cupido attwateri	Attwater Prairie chicken										x									
Aves	Galliformes	Phasianidae	Tympanuchus pallidicinctus	lesser Prairie chicken							x												
Aves	Galliformes	Phasianidae	Tympanuchus phasianellus	sharp-tailed grouse							x												
Aves	Galliformes	Phasianidae	T. phasianellus columbianus	Columbian sharp-tail grouse								x											
Aves	Gruiformes	Aramidae	Aramus guarauna	limpkin																		x	
Aves	Gruiformes	Gruidae	Grus canadensis	sandhill crane																		x	
Aves	Passeriformes	Alaudidae	Eremophila alpestris	horned lark	x			x			x	x											
Aves	Passeriformes	Calcariidae	Calcarius ornatus	chestnut-collared longspur							x												
Aves	Passeriformes	Calcariidae	Rhynchophanes mccownii	McCown's longspur							x												
Aves	Passeriformes	Cardinalidae	Spiza americana	dickcissel							x												
Aves	Passeriformes	Corvidae	Corvus corax	common raven	x			x															
Aves	Passeriformes	Corvidae	Corvus cryptoleucus	Chihuahuan raven											x								
Aves	Passeriformes	Corvidae	Nucifraga columbiana	Clark's nutcracker		x																	
Aves	Passeriformes	Corvidae	Pica nuttalli	yellow-billed magpie												x							
Aves	Passeriformes	Corvidae	Pica pica	common magpie								x											
Aves	Passeriformes	Dulidae	Dulus dominicus	palmchat																		x	
Aves	Passeriformes	Emberizidae	Aimophila botterii	Botteri's sparrow											x		x			x			
Aves	Passeriformes	Emberizidae	Aimophila notosticta	Oaxaca sparrow											x								
Aves	Passeriformes	Emberizidae	Aimophila ruficauda	stripe-headed sparrow														x					
Aves	Passeriformes	Emberizidae	Aimophila ruficeps	rufus-crowned sparrow											x	x							
Aves	Passeriformes	Emberizidae	Ammodramus bairdii	Baird's sparrow							x												
Aves	Passeriformes	Emberizidae	Ammodramus henslowii	Henslow's sparrow							x												
Aves	Passeriformes	Emberizidae	Ammodramus savannarum	grasshopper sparrow							x	x							x			x	
Aves	Passeriformes	Emberizidae	Amphispiza bilineata	black-throated sparrow										x	x								

Class	Order	Family	Scientific name	Common name	ROCKY MOUNTAIN ALPINE AND SUBALPINE	CASCADE-SIERRAN SUBALPINE	TRANSVOLCANIC ALPINE AND SUBALPINE	ROCKY MOUNTAIN MONTANE	CASCADE-SIERRAN MONTANE	MADREAN MONTANE	PLAINS	GREAT BASIN	OREGONIAN COASTAL	GULF COASTAL	SEMIDESERT	CALIFORNIA VALLEY	CENTRAL AMERICAN SAVANNA	GUATEMALAN-GUERREAN SAVANNA	CAMPECHIAN-VERACRUZ SAVANNA	TAMAULIPAN SAVANNA	SONORAN SAVANNA	CARIBBEAN SAVANNA
Aves	Passeriformes	Emberizidae	Artemisiospiza belli	sage sparrow								x										
Aves	Passeriformes	Emberizidae	Calamospiza melanocorys	lark bunting							x											
Aves	Passeriformes	Emberizidae	Chondestes grammacus	lark sparrow							x	x		x	x							
Aves	Passeriformes	Emberizidae	Passerculus sandwichensis	savanna sparrow	x						x	x			x	x						
Aves	Passeriformes	Emberizidae	Peucaea carpalis	rufous-winged sparrow																	x	
Aves	Passeriformes	Emberizidae	Peucaea cassinii	Cassin's sparrow							x			x	x							
Aves	Passeriformes	Emberizidae	Peucaea ruficauda	stripe-headed sparrow													x	x				
Aves	Passeriformes	Emberizidae	Pooecetes gramineus	vesper sparrow							x	x										
Aves	Passeriformes	Emberizidae	Spizella breweri	Brewer's sparrow								x										
Aves	Passeriformes	Emberizidae	Spizella pallida	clay-colored sparrow							x											
Aves	Passeriformes	Emberizidae	Spizella pusilla	field sparrow							x											
Aves	Passeriformes	Emberizidae	Spizella wortheni	Worthen's sparrow											x							
Aves	Passeriformes	Emberizidae	Torreornis inexpectata	zapata sparrow																		x
Aves	Passeriformes	Emberizidae	Volatinia jacarina	blue-black grassquit													x					
Aves	Passeriformes	Emberizidae	Xenospiza baileyi	Sierra Madre sparrow			x			x												
Aves	Passeriformes	Fringillidae	Carduelis psaltria	lesser goldfinch																		x
Aves	Passeriformes	Icteridae	Agelaius humeralis	tawny-shouldered blackbird																		x
Aves	Passeriformes	Icteridae	Agelaius xanthomus	yellow-shouldered blackbird																		x
Aves	Passeriformes	Icteridae	Dolichonyx oryzivorus	bobolink							x											
Aves	Passeriformes	Icteridae	Molothrus bonariensis	glossy cowbird																		x
Aves	Passeriformes	Icteridae	Sturnella magna	Eastern meadowlark				x			x				x							
Aves	Passeriformes	Icteridae	Sturnella neglecta	Western meadowlark				x			x				x		x					x
Aves	Passeriformes	Laniidae	Lanius excubitor	Northern shrike								x										
Aves	Passeriformes	Laniidae	Lanius ludovicianus	loggerhead shrike											x							
Aves	Passeriformes	Mimidae	Oreoscoptes montanus	sage thrasher								x										
Aves	Passeriformes	Mimidae	Toxostoma curvirostre	curve-billed thrasher											x							
Aves	Passeriformes	Motacillidae	Anthus spragueii	Sprague's pipit							x											
Aves	Passeriformes	Parulidae	Setophaga coronata	yellow-rumped warbler							x											
Aves	Passeriformes	Ploceidae	Estrilda melpoda	orange-cheeked waxbill																		x
Aves	Passeriformes	Ploceidae	Lonchura cucullata	hooded weaver																		x
Aves	Passeriformes	Ploceidae	Ploceus cucullatus	village weaver																		x
Aves	Passeriformes	Thraupidae	Sicalis luteola	grassland yellow finch																		x
Aves	Passeriformes	Thraupidae	Sporophila aurita	variable seedeater													x					
Aves	Passeriformes	Thraupidae	Sporophila nigricollis	yellow-bellied seedeater													x					
Aves	Passeriformes	Thraupidae	Sporophila torqueola	white-collared seedeater													x					
Aves	Passeriformes	Thraupidae	Tiaris bicolor	black-faced grassquit																		x
Aves	Passeriformes	Thraupidae	Tiaris olivaceus	yellow-faced grassquit													x					x
Aves	Passeriformes	Troglodytidae	Campylorhynchus brunneicapillus	cactus wren											x							
Aves	Passeriformes	Turdidae	Sialia currucoides	mountain bluebird	x			x	x				x									
Aves	Passeriformes	Turdidae	Sialia mexicana	Western bluebird				x														
Aves	Passeriformes	Turdidae	Turdus migratorius	American robin	x																	
Aves	Passeriformes	Tyrannidae	Sayornis saya	Say's phoebe											x							
Aves	Passeriformes	Tyrannidae	Tyrannus forficatus	scissor-tailed flycather										x								
Aves	Passeriformes	Tyrannidae	Tyrannus savana	fork-tailed flycatcher													x		x			
Aves	Passeriformes	Tyrannidae	Tyrannus vociferans	Cassin's kingbird											x							
Aves	Passeriformes	Vireonidae	Vireo bellii	Bell's vireo											x							
Aves	Piciformes	Picidae	Colaptes fernandinae	Fernandina's flicker																		x
Aves	Strigiformes	Strigidae	Athene cunicularia	burrowing owl							x								x			x

Aves	Strigiformes	Strigidae	Pseudoscops clamator	striped owl												x		x				
Mammalia	Artiodactyla	Antilocapridae	Antilocapra americana	pronghorn	x			x			x	x				x						
Mammalia	Artiodactyla	Antilocapridae	Antilocapra americana mexicana	Mexican pronghorn											x							
Mammalia	Artiodactyla	Antilocapridae	Antilocapra americana sonoriensis	Sonoran pronghorn																	x	
Mammalia	Artiodactyla	Bovidae	Bison bison	bison	x						x	x		x								
Mammalia	Artiodactyla	Bovidae	Bison bison athabascae	wood bison								x										
Mammalia	Artiodactyla	Bovidae	Ovis canadensis	bighorn sheep	x				x													
Mammalia	Artiodactyla	Bovidae	Ovis canadensis californiana	California bighorn sheep		x			x													
Mammalia	Artiodactyla	Cervidae	Cervus canadensis nannodes	tule elk												x						
Mammalia	Artiodactyla	Cervidae	Cervus canadensis roosevelti	Roosevelt elk									x									
Mammalia	Artiodactyla	Cervidae	Cervus elaphus	elk	x			x			x											
Mammalia	Artiodactyla	Cervidae	Odocoileus hemionus	mule deer	x																	
Mammalia	Artiodactyla	Cervidae	Odocoileus hemionus erimecus	desert mule deer											x							
Mammalia	Artiodactyla	Cervidae	Odocoileus virginianus	white-tailed deer	x	x		x	x													x
Mammalia	Artiodactyla	Tayassuidae	Pecari tajacu	javelina											x						x	
Mammalia	Carnivora	Canidae	Canis canis	red wolf										x								
Mammalia	Carnivora	Canidae	Canis latrans	coyote	x																	
Mammalia	Carnivora	Canidae	Canis lupus	grey wolf	x																	
Mammalia	Carnivora	Canidae	Vulpes velox	swift fox							x					x						
Mammalia	Carnivora	Canidae	Vulpes vulpes	red fox	x																	
Mammalia	Carnivora	Mustelidae	Mustela erminea	ermine	x																	
Mammalia	Carnivora	Mustelidae	Mustela frenata	long-tailed weasel	x																	
Mammalia	Carnivora	Mustelidae	Mustela nigripes	black-footed ferret							x											
Mammalia	Carnivora	Mustelidae	Taxidea taxus	American badger	x						x				x							
Mammalia	Carnivora	Ursidae	Ursus arctos	grizzly bear	x																	
Mammalia	Chiroptera	Phyllostomidae	Desmodus rotundus	vampire bat													x					
Mammalia	Chiroptera	Vespertilionidae	Lasionycteris noctivagans	silver-haired bat	x																	
Mammalia	Chiroptera	Vespertilionidae	Lasiurus cinereus	hoary bat	x																	
Mammalia	Chiroptera	Vespertilionidae	Myotis volans	long-legged myotis	x																	
Mammalia	Cingulata	Dasypodidae	Cabassous centralis	Northern naked-tailed aramadillo													x					
Mammalia	Edentata	Myrmecophagidae	Myrmecophaga tridactyla	giant anteater													x					
Mammalia	Insectovora	Soricidae	Cryptotis goldmani alticola	goldman's broad-clawed shr.			x															
Mammalia	Insectovora	Soricidae	Cryptotis parva	North American least shrew													x					
Mammalia	Insectovora	Soricidae	Sorex cinereus	masked shrew	x																	
Mammalia	Insectovora	Soricidae	Sorex nanus	dwarf shrew	x																	
Mammalia	Insectovora	Soricidae	Sorex obscurus	dusky shrew	x																	
Mammalia	Insectovora	Soricidae	Sorex vagrans	vagrant shrew	x		x															
Mammalia	Lagomorpha	Leporidae	Brachylagus idahoensis	pygmy rabbit								x										
Mammalia	Lagomorpha	Leporidae	Lepus alleni	antelope jackrabbit																	x	
Mammalia	Lagomorpha	Leporidae	Lepus americanus	snowshoe hare	x																	
Mammalia	Lagomorpha	Leporidae	Lepus californicus	black-tailed jackrabbit											x							
Mammalia	Lagomorpha	Leporidae	Lepus callotis	white-sided jack-rabbit						x					x							
Mammalia	Lagomorpha	Leporidae	Lepus flavigularis	Tehuantepec jackrabbit														x				
Mammalia	Lagomorpha	Leporidae	Lepus townsendii	white-tailed jackrabbit	x						x	x										
Mammalia	Rodentia	Cricetidae	Melanomys caliginosus	dusky rice rat													x					
Mammalia	Rodentia	Cricetidae	Oligoryzomys fulvescens	Northern pygmy rice rat													x					
Mammalia	Rodentia	Cricetidae	Zygodontomys brevicauda	common cane mouse													x					
Mammalia	Rodentia	Dipodidae	Zapus hudsonius	meadow jumping mouse							x											
Mammalia	Rodentia	Dipodidae	Zapus princeps	Western jumping mouse	x							x										
Mammalia	Rodentia	Dipodidae	Zapus trinotatus	Pacific jumping mouse									x									
Mammalia	Rodentia	Erethizontidae	Erethizon dorsatum	porcupine	x	x			x													
Mammalia	Rodentia	Geomyidae	Cratogeomys castanops	yellow-faced pocket gopher											x							
Mammalia	Rodentia	Geomyidae	Geomys bursarius	plains pocket gopher							x											
Mammalia	Rodentia	Geomyidae	Orthogeomys grandis	giant pocket gopher														x	x			
Mammalia	Rodentia	Geomyidae	Thomomys	pocket gopher	x	x																
Mammalia	Rodentia	Geomyidae	Thomomys bottae	Botta's pocket gopher	x			x														
Mammalia	Rodentia	Geomyidae	Thomomys talpoides	Northern pocket gopher																		
Mammalia	Rodentia	Heteromyidae	Chaetodipus hispidus	hispid pocket mouse											x							

Class	Order	Family	Scientific name	Common name	ROCKY MOUNTAIN ALPINE AND SUBALPINE	CASCADE-SIERRAN SUBALPINE	TRANSVOLCANIC ALPINE AND SUBALPINE	ROCKY MOUNTAIN MONTANE	CASCADE-SIERRAN MONTANE	MADREAN MONTANE	PLAINS	GREAT BASIN	OREGONIAN COASTAL	GULF COASTAL	SEMIDESERT	CALIFORNIA VALLEY	CENTRAL AMERICAN SAVANNA	GUATEMALAN-GUERREAN SAVANNA	CAMPECHIAN-VERACRUZ SAVANNA	TAMAULIPAN SAVANNA	SONORAN SAVANNA	CARIBBEAN SAVANNA
Mammalia	Rodentia	Heteromyidae	Dipodomys merriami	Merriam's kangaroo rat										x								
Mammalia	Rodentia	Heteromyidae	Dipodomys ordii	Ord's kangaroo rat										x								
Mammalia	Rodentia	Heteromyidae	Dipodomys phillipsii	Phillip's kangaroo rat										x								
Mammalia	Rodentia	Heteromyidae	Dipodomys spectabilis	banner-tailed kangaroo rat										x								
Mammalia	Rodentia	Heteromyidae	Perognathus fasciatus	olive-backed pocket mouse							x											
Mammalia	Rodentia	Heteromyidae	Perognathus flavescens	plains pocket mouse							x											
Mammalia	Rodentia	Heteromyidae	Perognathus flavus	silky pocket mouse										x								
Mammalia	Rodentia	Heteromyidae	Perognathus inornatus	San Joaquin pocket mouse											x							
Mammalia	Rodentia	Heteromyidae	Perognathus parvus	Great Basin gophersnake																		
Mammalia	Rodentia	Leporidae	Romerolagus diazi	volcano rabbit			x															
Mammalia	Rodentia	Muridae	Arborimus albipes	white-footed vole									x									
Mammalia	Rodentia	Muridae	Baiomys musculus	Southern pygmy mouse												x						
Mammalia	Rodentia	Muridae	Baiomys taylori	pygmy mouse									x									
Mammalia	Rodentia	Muridae	Lemmiscus curtatus	sagebrush vole								x										
Mammalia	Rodentia	Muridae	Microtus californicus	California vole				x														
Mammalia	Rodentia	Muridae	Microtus longicaudus	Long-tailed vole	x																	
Mammalia	Rodentia	Muridae	Microtus mexicanus	Mexican vole	x			x														
Mammalia	Rodentia	Muridae	Microtus montanus	montane vole	x																	
Mammalia	Rodentia	Muridae	Microtus ochrogaster	Prairie vole							x		x									
Mammalia	Rodentia	Muridae	Microtus oregoni	creeping vole								x										
Mammalia	Rodentia	Muridae	Microtus pennsylvanicus	meadow vole	x																	
Mammalia	Rodentia	Muridae	Microtus townsendii	Townsend's vole								x										
Mammalia	Rodentia	Muridae	Neotoma albigula	white-throated woodrat										x								
Mammalia	Rodentia	Muridae	Neotoma micropus	Southern Plains woodrat										x								
Mammalia	Rodentia	Muridae	Neotomodon alstoni	Mexican volcano mouse			x															
Mammalia	Rodentia	Muridae	Onychomys leucogaster	Northern grasshopper mouse							x	x										
Mammalia	Rodentia	Muridae	Onychomys torridus	Southern grasshopper mouse										x								
Mammalia	Rodentia	Muridae	Peromyscus maniculatus	deer mouse	x																	
Mammalia	Rodentia	Muridae	Phenacomys intermedius	heather vole	x																	
Mammalia	Rodentia	Muridae	Reithrodontomys brevirostris	short-nosed harvest mouse												x						
Mammalia	Rodentia	Muridae	Reithrodontomys darienensis	Darien harvest mouse												x						
Mammalia	Rodentia	Muridae	Reithrodontomys fulvescens	fulvous harvest mouse										x		x						
Mammalia	Rodentia	Muridae	Reithrodontomys gracilis	slender harvest mouse												x						
Mammalia	Rodentia	Muridae	Reithrodontomys megalotis	Western harvest mouse							x	x										
Mammalia	Rodentia	Muridae	Reithrodontomys montanus	plains harvest mouse							x			x								
Mammalia	Rodentia	Muridae	Reithrodontomys paradoxus	Nicaraguan harvest mouse												x						
Mammalia	Rodentia	Muridae	Sigmodon fulviventer	tawny-bellied cotton rat										x								
Mammalia	Rodentia	Muridae	Sigmodon hispidus	hispid cotton rat										x		x		x				
Mammalia	Rodentia	Sciuridae	Ammospermophilus nelsoni	Nelson's antelope squirrel											x							
Mammalia	Rodentia	Sciuridae	Callospermophilus madrensis	Sierra Madre ground squirrel						x												
Mammalia	Rodentia	Sciuridae	Cynomys gunnisoni	Gunnison's prairie dog								x										
Mammalia	Rodentia	Sciuridae	Cynomys leucurus	white-tailed prairie dog								x										
Mammalia	Rodentia	Sciuridae	Cynomys ludovicianus	black-tailed prairie dog							x			x								
Mammalia	Rodentia	Sciuridae	Cynomys parvidens	Utah prairie dog								x										
Mammalia	Rodentia	Sciuridae	Marmota caligata	hoary marmot		x																
Mammalia	Rodentia	Sciuridae	Marmota flaviventris	yellow-bellied marmot	x	x																
Mammalia	Rodentia	Sciuridae	Spermophilus beecheyi	California ground squirrel											x							
Mammalia	Rodentia	Sciuridae	Spermophilus beldingi	Belding's ground squirrel					x													

Mammalia	Rodentia	Sciuridae	Spermophilus columbianus	Columbian ground squirrel		x			x													
Mammalia	Rodentia	Sciuridae	Spermophilus franklinii	Franklin's ground squirrel							x											
Mammalia	Rodentia	Sciuridae	Spermophilus lateralis	golden-mantled ground squ.	x	x																
Mammalia	Rodentia	Sciuridae	Spermophilus mexicanus	Mexican ground squirell											x							
Mammalia	Rodentia	Sciuridae	Spermophilus richardsonii	Richardson's ground squirrel	x						x											
Mammalia	Rodentia	Sciuridae	Spermophilus saturatus	Cascade gold-mantled gr.squ.		x			x													
Mammalia	Rodentia	Sciuridae	Spermophilus spilosoma	spotted ground squirell											x							
Mammalia	Rodentia	Sciuridae	Spermophilus washingtoni	Washington ground squirrel								x										
Mammalia	Rodentia	Sciuridae	Tamias cinereicollis	gray-collared chipmunk	x																	
Mammalia	Rodentia	Sciuridae	Tamias minimus	least chipmunk	x							x										
Reptilia	Squamata	Anguidae	Ophisaurus attenuatus attenuatus	Western slender glass lizard							x			x								
Reptilia	Squamata	Colubridae	Arizona elegans arenicola	Texas glossy snake										x								
Reptilia	Squamata	Colubridae	Arizona elegans elegans	Kansas glossy snake							x											
Reptilia	Squamata	Colubridae	Cemophora coccinea lineri	Texas scarlet snake										x								
Reptilia	Squamata	Colubridae	Coluber constrictor flaviventris	Eastern yellow-bellied racer							x			x								
Reptilia	Squamata	Colubridae	Coluber constrictor mormon	Western yellow-bellied racer								x				x						
Reptilia	Squamata	Colubridae	Diadophis punctatus arnyi	Prairie ringneck snake							x											
Reptilia	Squamata	Colubridae	Elaphe obsoleta lindheimeri	Texas rat snake										x								
Reptilia	Squamata	Colubridae	Gyalopion canum	Western hooknose snake											x							
Reptilia	Squamata	Colubridae	Heterodon nasicus gloydi	dusky hognose snake							x											
Reptilia	Squamata	Colubridae	Heterodon nasicus kennerlyi	Kennerly's hognose snake											x							
Reptilia	Squamata	Colubridae	Heterodon nasicus nasicus	Plains hognose snake							x											
Reptilia	Squamata	Colubridae	Hypsiglena torquata jani	Texas night snake											x							
Reptilia	Squamata	Colubridae	Lampropeltis calligaster calligaster	Prairie Kingsnake							x			x								
Reptilia	Squamata	Colubridae	Masticophis flagellum testaceus	Western coachwhip							x			x	x							
Reptilia	Squamata	Colubridae	Masticophis taeniatus	striped whipsnake								x			x							
Reptilia	Squamata	Colubridae	Opheodrys vernalis	smooth green snake										x								
Reptilia	Squamata	Colubridae	Opheodrys vernalis blanchardi	Western smooth green snake							x											
Reptilia	Squamata	Colubridae	Pantherophis guttatus emoryi	Great Plains rat snake							x											
Reptilia	Squamata	Colubridae	Pantherophis obsoleta	Western rat snake										x								
Reptilia	Squamata	Colubridae	Pituophis melanoleucus	gophersnake	x																	
Reptilia	Squamata	Colubridae	Pituophis melanoleucus deserticola	Great Basin gophersnake								x										
Reptilia	Squamata	Colubridae	Pituophis melanoleucus sayi	bullsnake							x			x								
Reptilia	Squamata	Colubridae	Rhinocheilus lecontei tessellatus	Texas long-nosed snake											x							
Reptilia	Squamata	Colubridae	Salvadora grahamiae	mountain patch-nosed snake											x							
Reptilia	Squamata	Colubridae	Salvadora hexalepis	Western patch-nosed snake											x							
Reptilia	Squamata	Colubridae	Sonora semiannulata	ground snake											x							
Reptilia	Squamata	Colubridae	Storeria dekayi limnetes	marsh brown snake										x								
Reptilia	Squamata	Colubridae	Tantilla nigriceps	Plains blackhead snake							x				x							
Reptilia	Squamata	Colubridae	Tantilla nigriceps fumiceps	Plains blackhead snake										x								
Reptilia	Squamata	Colubridae	Tantilla wilcoxi	Chihuahuan black-headed sn.											x							
Reptilia	Squamata	Colubridae	Thamnophis elegans	Western terrestrial garter sn.	x			x														
Reptilia	Squamata	Colubridae	Thamnophis marcianus	checkered garter snake							x											
Reptilia	Squamata	Colubridae	Thamnophis ordinoides	Northwestern garter snake									x									
Reptilia	Squamata	Colubridae	Thamnophis proximus orarius	Texas ribbon snake										x								
Reptilia	Squamata	Colubridae	Thamnophis radix	Plains garter snake							x											
Reptilia	Squamata	Colubridae	Tropidoclonion lineatum	lined snake							x											
Reptilia	Squamata	Leiocephalidae	Leiocephalus pratensis	Haitian striped curly-tailed liz.																		x
Reptilia	Squamata	Leptotyphlopidae	Leptotyphlops dulcis dissectus	New Mexico blind snake											x							
Reptilia	Squamata	Leptotyphlopidae	Leptotyphlops dulcis dulcis	Prairie racerunner										x	x							
Reptilia	Squamata	Leptotyphlopidae	Leptotyphlops humilis segregus	Trans-Pecos blind snake											x							
Reptilia	Squamata	Phrynosomatidae	Cophosaurus texanus	Texas greater earless liz.							x				x							
Reptilia	Squamata	Phrynosomatidae	Holbrookia maculata	lesser earless lizard							x											
Reptilia	Squamata	Phrynosomatidae	Holbrookia maculata approximans	speckled earless Lizard											x							
Reptilia	Squamata	Phrynosomatidae	Holbrookia maculata perspicua	Prairie earless Lizard							x											
Reptilia	Squamata	Phrynosomatidae	Holbrookia propinqua propinqua	Northern keeled earless liz.										x								
Reptilia	Squamata	Phrynosomatidae	Phrynosoma cornutum	Texas horned Lizard							x			x	x	x						
Reptilia	Squamata	Phrynosomatidae	Phrynosoma coronatum	coast horned lizard												x						

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Reptilia	Squamata	Phrynosomatidae	Phrynosoma douglasii	short-horned lizard	x						x	x										
Reptilia	Squamata	Phrynosomatidae	Phrynosoma modestum	round-tailed horned lizard											x							
Reptilia	Squamata	Phrynosomatidae	Sceloporus poinsettii	crevice spiny lizard											x							
Reptilia	Squamata	Phrynosomatidae	Sceloporus undulatus	Eastern fence lizard							x				x							
Reptilia	Squamata	Phrynosomatidae	Uta stansburiana	desert side-blotched lizard											x							
Reptilia	Squamata	Scincidae	Eumeces multivirgatus multivirgatus	many-lined skink							x											
Reptilia	Squamata	Scincidae	Eumeces obsoletus	Great Plains skink							x											
Reptilia	Squamata	Scincidae	Eumeces septentrionalis	Northern Prairie skink							x											
Reptilia	Squamata	Scincidae	E. septentrionalis obtusirostris	Southern Prairie skink							x			x								
Reptilia	Squamata	Scincidae	Eumeces skiltonianus	Western skink					x													
Reptilia	Squamata	Scincidae	Eumeces skiltonianus skiltonianus	Western skink					x													
Reptilia	Squamata	Teiidae	Ameiva lineolata	pigmy blue-tailed ameiva																		x
Reptilia	Squamata	Teiidae	Aspidoscelis tigris	California whiptail												x						
Reptilia	Squamata	Teiidae	Aspidoscelis uniparens	desert grassland whiptail											x							
Reptilia	Squamata	Teiidae	Cnemidophorus exsanguis	Chihuahuan spotted whiptail											x							
Reptilia	Squamata	Teiidae	Cnemidophorus gularis gularis	Texas spotted whiptail							x			x	x							
Reptilia	Squamata	Teiidae	Cnemidophorus inornatus	little striped whiptail											x							
Reptilia	Squamata	Teiidae	Cnemidophorus neomexicanus	New Mexico whiptail											x							
Reptilia	Squamata	Teiidae	Cnemidophorus sexlineatus viridis	Prairie racerunner							x			x								
Reptilia	Squamata	Viperidae	Crotalus atrox	Western diamondback rattle.										x	x							
Reptilia	Squamata	Viperidae	Crotalus lepidus	rock rattlesnake											x							
Reptilia	Squamata	Viperidae	Crotalus molossus	black-tailed rattlesnake											x							
Reptilia	Squamata	Viperidae	Crotalus oreganus helleri	Southern Pacific rattlesnake												x						
Reptilia	Squamata	Viperidae	Crotalus oreganus oreganus	Northern Pacific rattlesnake												x						
Reptilia	Squamata	Viperidae	Crotalus scutulatus	Mohave rattlesnake											x							
Reptilia	Squamata	Viperidae	Crotalus viridis viridis	Prairie rattlesnake							x											
Reptilia	Squamata	Viperidae	Sistrurus catenatus	Massasauga rattlesnake										x								
Reptilia	Squamata	Viperidae	Sistrurus catenatus tergeminus	Western Massasauga							x				x							
Reptilia	Testudines	Emydidae	Gopherus berlandieri	Texas tortoise										x						x		
Reptilia	Testudines	Emydidae	Gopherus flavomarginatus	Bolson tortoise											x							
Reptilia	Testudines	Emydidae	Terrapene ornata luteola	desert box turtle											x							
Reptilia	Testudines	Emydidae	Terrapene ornata ornata	ornate box turtle							x				x