

AN ABSTRACT OF THE THESIS OF

Paul Edward Hennon for the degree of Doctor of Philosophy
in Botany and Plant Pathology presented on April 28, 1986.

Title: Pathological and Ecological Aspects of Decline and Mortality of
Chamaecyparis nootkatensis in Southeast Alaska

Abstract approved: .

Redacted for Privacy

Everett M. Hansen

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a valuable tree that is suffering from a serious decline and mortality of unknown cause throughout southeast Alaska. Epidemiological and pathological studies were initiated to determine if a pathogen is the primary cause of this problem. By examining old aerial photographs and by determining the approximate year of death of Alaska-cedar trees that are now in various stages of deterioration, I established that extensive mortality began about 100 years ago. In some areas, the boundary of mortality has advanced, but typically by not more than 100 m. Decline and mortality has apparently not spread to new areas, however, since all sites examined with dying cedars have at least some of the original, 100 year-old mortality present. Maps showing boundaries of mortality at seven sites were made from aerial photographs taken in 1927, 1948, 1965, and 1976 and were supplemented by ground surveys in 1982 and 1983. These data show that local spread has occurred along an ecological gradient from bogs to better drained forest types. Basal scars, common on Alaska-cedar trees in some stands, are caused primarily by brown bears (Ursus arctos), but are not

associated with decline. Reproduction of Alaska-cedar from seeds is failing in most affected stands, but vegetative reproduction by the rooting of lower limbs is succeeding on bog and semi-bog forest types. Because crown symptoms suggest a possible root disease, root systems of 35 healthy and declining Alaska-cedar trees were excavated to study symptoms and to isolate fungi. Symptoms on declining trees included dead fine roots and necrotic lesions on coarse roots and tree boles. Necrotic lesions, similar to those on declining trees, were produced on healthy trees by mechanical wounding without inoculation. More than 50 taxa of fungi were isolated or collected from lesions and other symptomatic tissues; 37 were new reports on Alaska-cedar, but the 12 most common did not kill inoculated seedlings of Alaska-cedar. The possible roles of Armillaria sp., Phytophthora sp., Cylindrocarpon didymum, Mycelium radicis atrovirens, vesicular-arbuscular mycorrhizae, Phloeosinus spp. (bark beetles), and nematodes in decline are discussed. Foliar and soil nutrient analyses support neither nutrient deficiencies nor mineral toxicities as causes of decline. In summary, epidemiological evidence and the lack of aggressive pathogens suggest that biotic agents are not responsible for Alaska-cedar decline and that some abiotic factor(s) is a more likely cause.

Pathological and Ecological Aspects of Decline and Mortality
of Chamaecyparis nootkatensis in Southeast Alaska

by

Paul Edward Hennon

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirement for the
degree of

Doctor of Philosophy

Completed April 28, 1986

Commencement June 1986

APPROVED:

Redacted for Privacy

Professor of Forest Pathology in charge of major

Redacted for Privacy

Chairman of Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented _____ April 28, 1986

Typed by Susan and Paul Hennon for _____ Paul Edward Hennon

ACKNOWLEDGEMENTS

Considering the scope of the cedar project and the degree of support that I received while undertaking field studies in a remote portion of the Alaskan wilderness, the list of people that were of indispensable assistance is rather long. I must first thank collectively all the folks at the Forestry Sciences Laboratory (USFS) in Juneau for their continuing help and good nature: Elaine Loopstra for countless hours of sustaining the field camp and for building the rabbit hutch; Mary Lewis, Dorothy Osborne, and Karen Blankenship for friendly clerical assistance; Tom Laurent, Dick Orchard, and Earl Hubbard for logistical help in setting up the Poison Cove field cabin; Don Smiege and Calvin Bey for administrative support of the cedar project; and, of course, Terry Shaw--who initiated this project and spent countless hours editing my manuscripts. Many people perceive his energy and enthusiasm, but those who work closely with Terry also recognize the size of his heart.

Other help in southeast Alaska made this project possible: Dotsy and other Chatham Area dispatchers put up with regular and sometimes frantic radio messages to keep us in touch with Juneau and the outside world. I especially wish to thank Irene Jimmy for generously allowing us to use her cabin at Poison Cove during four consecutive summers which provided us with the only possible dry research base for miles.

I am especially thankful for the opportunity to study with my major professor, Everett Hansen. I greatly appreciate the high standards and creative, objective thinking that Everett teaches and

exemplifies. Everett teaches the entire range of forest pathology, from swinging a polaski to staining DNA. I also wish to thank Lew Roth for his sage words and assistance during Everett's sabbatical; Don Zobel for help in identifying plants, ideas on nutrient sampling, and thorough manuscript reviews; Gene Newcomb for identifying and quantifying nematodes; Al Funk for identifying several fungi; and John Shoen for providing information on bears. I also wish to thank the brown bears of Baranof and Chichagof Islands who showed as much respect for me as I have for them.

Some of the most valuable education learned while in graduate school at Oregon State University came from discussions with other students. I was lucky to share this experience with Paul Hessburg, Phil Hamm, Keith Reynolds, Borys Tkacz, Pete Angwin, and John Kalafarski. The Botany and Plant Pathology Department is also blessed with several outstanding professors who make learning a passion: Charles Leach, William Denison, and Dallice Mills.

A special thanks goes to two wonderful friends/field workers: Michael McWilliams and Marybetts Sinclair. They cheerfully tolerated a sometimes-grumpy, sometimes-ecstatic graduate student during working conditions that ranged from wet to wetter and only occasionally resorted to mud-wrestling in the muskegs.

Finally, I wish to thank my family: Ed and Betty, my parents, for instilling in me, first, the confidence that I could accomplish whatever in the world I set out to do, and second, the importance of education and learning. I am forever in your debt. There is no person to whom I am more grateful for her continuing love and support than my wife, Susan. It is to you that this work is dedicated. AMEN!

TABLE OF CONTENTS

<u>Chapter</u>	<u>Page</u>
I. INTRODUCTION.....	1
Alaska-cedar: The tree.....	3
Pests of Alaska-Cedar.....	8
History of Alaska-cedar decline.....	10
The setting.....	13
The study.....	16
Literature Cited.....	21
II. DATING THE ONSET OF ALASKA-CEDAR DECLINE.....	24
Abstract.....	24
Introduction.....	25
Materials and Methods.....	27
Results.....	35
1927 Aerial photography.....	35
Released hemlocks.....	37
Rope trees.....	39
Discussion.....	43
Literature Cited.....	49
III. DYNAMICS OF DECLINE AND MORTALITY OF <u>CHAMAECYPARIS</u> <u>NOOTKATENSIS</u> IN SOUTHEAST ALASKA.....	51
Abstract.....	51
Introduction.....	52
Materials and Methods.....	56
Aerial photography.....	56
Forest community associations.....	60
Forest survey.....	62
Snag classes.....	63
Results.....	66
Aerial photography.....	66
Forest community associations.....	72
Distribution of conifers along ecological gradient....	78
Conifers commonly found dead.....	80
Classes of Alaska-cedar snags.....	84
Discussion.....	87
Literature Cited.....	97
IV. FUNGI ON <u>CHAMAECYPARIS NOOTKATENSIS</u>	99
Abstract.....	99
Introduction.....	100
Materials and Methods.....	103
Results.....	103
Discussion.....	122
Literature Cited.....	132

V. ALASKA-CEDAR DECLINE: POTENTIAL PATHOGENIC AGENTS.....	136
Abstract.....	136
Introduction.....	137
Materials and Methods.....	141
Results.....	150
Root and crown symptoms.....	150
Fungal isolations.....	156
Fine root observations.....	162
Sampling for <u>Phytophthora</u> sp.....	162
Nematode sampling.....	165
Pathogenicity testing.....	165
<u>Armillaria</u> inoculations.....	167
Root wounding.....	167
Stem lesions and square patch inoculations.....	167
Discussion.....	171
Literature Cited.....	183
VI. CAUSES OF BASAL SCARS ON ALASKA-CEDAR.....	186
Abstract.....	186
Introduction.....	187
Materials and Methods.....	189
Results.....	191
Occurrence of scars.....	191
Responses to wounding.....	194
Fungi on scars.....	200
Discussion.....	201
Literature Cited.....	210
VII. FOLIAGE AND SOIL NUTRIENT CONCENTRATIONS ASSOCIATED WITH ALASKA-CEDAR DECLINE.....	212
Abstract.....	212
Introduction.....	213
Materials and Methods.....	214
Results.....	219
Foliage nutrients.....	219
Soil nutrients.....	219
Discussion.....	222
Literature Cited.....	225
VIII. REPRODUCTION OF <u>CHAMAECYPARIS NOOTKATENSIS</u> IN SOUTHEAST ALASKA.....	226
Abstract.....	226
Introduction.....	227
Materials and Methods.....	230
Results and Discussion.....	231
Prostrate cedar patches.....	231
Cedar germlings and seedlings.....	236
Possible origins of Alaska-cedar stands.....	242
Literature Cited.....	248
IX. SUMMARY.....	250
Literature Cited.....	266
BIBLIOGRAPHY.....	268

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
Chapter I	
I. 1. Mortality of Alaska-cedar in southeast Alaska.....	2
I. 2. Wood of Alaska-cedar.....	4
I. 3. Map of southeast Alaska.....	14
I. 4. Map of Peril Strait study area.....	17
I. 5. Mortality and field cabin at Poison Cove.....	18
Chapter II	
II. 1. Mortality of Alaska-cedar.....	26
II. 2. Location of study areas.....	29
II. 3. Locations of sites aerial photographs in 1927 and rope tree sampling.....	30
II. 4. Classes of dead Alaska-cedar trees.....	31
II. 5. Released mountain hemlock under dead Alaska-cedar.....	33
II. 6. Alaska-cedar rope tree.....	34
II. 7. 1927 aerial photograph of mortality.....	36
II. 8. Cross section of Alaska-cedar rope tree.....	42
Chapter III	
III. 1. Mortality of Alaska-cedar.....	54
III. 2. Map of locations of ground transects and sites of mapping from aerial photographs.....	57
III. 3. Study sites along Peril Strait.....	58
III. 4. Classes of dead Alaska-cedar trees.....	64
III. 5. Map of mortality boundaries at 7 sites.....	67
III. 6. Intensive map of mortality at Poison Cove.....	71
III. 7. Mortality associated with a long series of bogs.....	73
III. 8. Open bog.....	76
III. 9. Understory vegetation in bog, intermediate type, and on well-drained site.....	77
III.10. Basal area of conifers along bog-drainage gradient.....	79
III.11. Frequency of mortality along bog-drainage gradient.....	81
III.12. Basal area of dead conifers in stands with and without mortality.....	83
III.13. Ordination scores for classes of dead Alaska-cedar trees.....	86
III.14. Ordination scores for classes or rope trees.....	88
III.15. Heights of classes of Alaska-cedar trees along bog-drainage gradient.....	89
III.16. Example of mortality spread from bog to better drainage.....	91

Chapter IV

IV. 1. Microscopic structures of <u>Dermea</u> and <u>Gelatinosporium</u>	125
IV. 2. Microscopic structures of <u>Ceratocystis</u> and <u>Chalara</u>	126
IV. 3. Microscopic structures of <u>Cylindrocarpum</u> and <u>Leptographium</u> ..	127
IV. 4. Microscopic structures of <u>Cryptosporiopsis</u> and <u>Phialophora</u> ..	128
IV. 5. Microscopic structures of <u>Sporidesmium</u> , <u>Pezicula</u> , <u>Apostrasseria</u> , and <u>Seiridium</u>	129
IV. 6. Microscopic structures of <u>Gnomoniella</u> , <u>Dothidea</u> , <u>Herpotrichia</u> , and <u>Ditangium</u>	130
IV. 7. Microscopic structures of VA mycorrhizae and <u>Mycelium</u> <u>radicis atrovirens</u>	131

Chapter V

V. 1. Crown symptoms of dying Alaska-cedar tree.....	139
V. 2. Necrotic lesion on root and bole of dying Alaska-cedar.....	140
V. 3. Method of isolating fungi from bole lesions.....	144
V. 4. Patch inoculation on Alaska-cedar tree.....	149
V. 5. Relationship of condition of crown to root collar and bole..	155
V. 6. Distribution of fungi in necrotic lesions.....	158
V. 7. <u>Armillaria</u> sp. in necrotic lesion.....	160
V. 8. Shoot dieback of regeneratin cedar caused by <u>Apostrasseria</u> ..	161
V. 9. VA mycorrhizae and <u>Mycelium radicis atrovirens</u>	163
V.10. Hyphae of <u>Mycelium radicis atrovirens</u>	163
V.11. Sporangia of <u>Phytophthora</u> sp.	164
V.12. Lesion on roots that were mechanically wounded.....	169

Chapter VI

VI. 1. Old basal scar on Alaska-cedar tree.....	188
VI. 2. Map of study sites.....	190
VI. 3. Frequency distribution of orientation of basal scars.....	192
VI. 4. Frequency distribution of heights of basal scars.....	193
VI. 5. Fresh basal scar on Alaska-cedar tree.....	195
VI. 6. Alaska-cedar tree with numerous basal scars.....	196
VI. 7. Incidence of basal scars on Alaska-cedar along bog-drainage gradient.....	197
VI. 8. Large basal scar caused by humans.....	198
VI. 9. Cross section of Alaska-cedar tree with basal scars.....	199
VI.10. <u>Ceratocystis</u> sp. on recently-caused basal scar.....	202

Chapter VII

VII. 1. Locations for collecting Alaska-cedar foliage.....	215
VII. 2. Locations for collecting Alaska-cedar foliage.....	216

Chapter VIII

VIII. 1. Prostrate patch of Alaska-cedar in a bog.....	229
VIII. 2. Vegetative reproduction from a fallen tree.....	233
VIII. 3. Prostrate patches of Alaska-cedar spreading by layering....	233
VIII. 4. Seedlings of Alaska-cedar from a bog.....	234
VIII. 5. Incidence of prostrate Alaska-cedar along bog-drainage gradient.....	235
VIII. 6. Average number of seedlings of Alaska-cedar along bog-drainage gradient.....	238
VIII. 7. Germling of Alaska-cedar.....	241
VIII. 8. Seedling of Alaska-cedar.....	241
VIII. 9. Sweep in lower bole of Alaska-cedar tree.....	244
VIII. 10. Root system of Alaska-cedar tree.....	245
VIII. 11. Prostrate Alaska-cedar growing into tree-like form.....	246

LIST OF TABLES

<u>Table</u>	<u>Page</u>
Chapter II	
II. 1. Time since release of hemlocks under dead Alaska-cedars.....	38
II. 2. Time since damage of Alaska-cedar rope trees.....	40
II. 3. Differences in time since damage or rope trees at 6 sites...	41
Chapter III	
III. 1. Aerial photographs used to map mortality boundaries.....	59
III. 2. Understory plant taxa used in ordination analysis.....	75
III. 3. Percentage of dead conifer species.....	82
III. 4. Percentage of dead conifer species without long-dead cedar..	85
Chapter IV	
IV. 1. Fungi previously reported on Alaska-cedar.....	101
IV. 2. Fungi sporulating on Alaska-cedar.....	105
IV. 3. Fungi isolated from Alaska-cedar.....	106
IV. 4. Newly compiled list of fungi on Alaska-cedar.....	107
Chapter V	
V. 1. Condition of fine roots on healthy and dying trees.....	152
V. 2. Characteristics of Alaska-cedar study trees.....	154
V. 3. Fungi isolated from symptomatic tissues on dying trees.....	157
V. 4. Pathogenicity testing of fungi isolated from Alaska-cedars..	166
V. 5. Necrotic lesions on roots that developed after wounding....	168
V. 6. Fungi from lesions that developed after wounding.....	170
V. 7. Necrotic lesions that developed from patch inoculations....	172
V. 8. Fungi isolated from lesions from patch inoculations.....	173
Chapter VI	
VI. 1. Fungi on basal scars of Alaska-cedar.....	203
Chapter VII	
VII. 1. Characteristics of sites for foliage sampling.....	217
VII. 2. Nutrient concentrations of Alaska-cedar foliage.....	220
VII. 3. Nutrient concentrations and pH of soil.....	221
Chapter VIII	
VIII. 1. Characteristics of sites with prostrate Alaska-cedar.....	237
VIII. 2. Characteristics of sites with seedlings of Alaska-cedar....	240

PATHOLOGICAL AND ECOLOGICAL ASPECTS OF DECLINE AND MORTALITY
OF CHAMAECYPARIS NOOTKATENSIS IN SOUTHEAST ALASKA

CHAPTER I

INTRODUCTION

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a valuable, long-lived tree species that grows in forests from the Oregon-California border to Prince William Sound in Alaska. It has been suffering from a spectacular decline and mortality problem (Fig. I.1) throughout southeast Alaska for a long, but undetermined span of time. The primary cause of tree death has never been adequately elucidated since this problem has received little previous study; however, several explanations of causes, listed below, have been proposed.

The purpose of this thesis is to evaluate the hypothesis that Alaska-cedar decline, as this forest mortality is now named, is caused by a biotic agent. The alternate hypothesis is that the primary incitant is an abiotic factor. There is only minimal information on decline and mortality, and most ecological aspects of healthy Alaska-cedar (e.g., reproduction and forest community relationships) are poorly understood. Consequently, information was gathered on the ecology of Alaska-cedar forests during the course of these pathological studies.

This chapter reviews previous ecological, silvicultural, and pathological research on Alaska-cedar; outlines the history of



Figure I.1. Mortality of Alaska-cedar at Slocum Arm in southeast Alaska

observations on decline; discusses speculations on possible causes of Alaska-cedar decline; provides information on study areas where I conducted work; and outlines subsequent chapters where study results are provided.

Alaska-cedar: The tree

On a dollar per board foot basis, Alaska-cedar is the most valuable tree species grown in Alaska. Its wood has narrow annual rings, extreme decay resistance, and is bright yellow and aromatic (Fig. I.2) (Harris 1971, Duff et al. 1954). Currently, its wood is used for boat building and other marine uses, interior molding, cabinets, furniture, fence posts, bleacher seats, saunas, musical instruments, carving, and more (Markwardt 1931, Harris 1971, Frear 1982). Some wood is exported to Japan, where it is prized for making ceremonial boxes and is important for the restoration of temples and shrines (Frear 1982).

Alaska-cedar was viewed as the most important tree species in Alaska by the Russians during the 19th Century (Petrof 1880); it was used to construction the hulls of some 20 steamers built in Sitka between 1840 and 1863 (Harris 1970). Also, it was used in the 19th century to line closets and boxes to repel moths (Harris 1971). Native peoples in southeast Alaska and British Columbia used the wood for canoe paddles, totem poles, chests, dishes, and tool handles (Turner 1979). In addition, they used the fibrous inner bark. After soaking it in salt water, pounding, and drying, it was woven into mats, and hats, and used to decorate masks, or prepared with mountain goat wool



Figure I.2. The valuable wood of Alaska-cedar is yellow, aromatic, and decay resistant

and woven into blankets or clothing (Turner 1979). The inner bark was sometimes eaten (Petrof 1880).

Standard common names for this tree species are Alaska-cedar in the United States (Little 1953) and yellow cedar in Canada, but other names are sometimes used: Pacific Coast cypress, Sitka cypress, Pacific Coast cedar, yellow cypress, Alaska yellow-cedar, yellow cypress, Nootka cypress, Nootka Sound cypress, Nootka false-cypress, Alaska ground cypress, Alaska cypress, and canoe cedar (Harris 1971, Viereck and Little 1972).

Alaska-cedar is a member of the Cupressaceae, or cypress family of conifers, that includes the familiar junipers, cedars, and cypresses. This is a large family of 18 genera and over 100 species (Owens and Molder 1984). The common name "cedar" is misleading when applied to trees in this family, because it more accurately applies to the true cedars belonging to the genus Cedrus of the Pinaceae; there are no native species of Cedrus in North America. Almost all species in the Cupressaceae have small, scale-like leaves, and lack distinct buds enclosed by bud scales. Seed cones are usually small and woody, except for Juniperus spp. that have berry-like seed cones. Besides Alaska-cedar, western redcedar (Thuja plicata D. Don) and two junipers (Juniperus communis L. and J. horizontalis Moench) are other species of Cupressaceae native to Alaska (Hulten 1968).

Alaska-cedar is one of only seven species in Chamaecyparis Spach, which literally means false cypress. Three of these species are endemic to North America where they are important commercial forest trees: Port-Orford-cedar (C. lawsoniana (Murr.) Parl.) in southwestern Oregon, Atlantic white cedar (C. thyoides (L.) B.S.P.) in a narrow belt

along the Atlantic and Gulf coasts, and Alaska-cedar. The other four Chamaecyparis species are native to Japan and Taiwan (Owens and Molder 1984).

In general, Alaska-cedar grows in a cool and humid climate, where the growing season is relatively short, but winter temperatures are not severely cold. The natural range of Alaska-cedar extends from Mount Grayback in California, near the Oregon border (Mason 1941), to Port Wells in Prince William Sound in the Gulf of Alaska (Harris 1971). Except for several isolated stands, it grows within 60 km of the Pacific Coast (Harris 1979). In Oregon and most of Washington, Alaska-cedar occurs in the higher elevations (e.g., 600–2300 m (Owens and Molder 1984)) of the Cascade Range. However, Alaska-cedar grows at tidewater from north of Knight Inlet on the mainland in British Columbia (Harris 1971) and from north of Ucluelet or perhaps from Port Renfrew on the west side of Vancouver Island (John Duncan, pers. comm.) in British Columbia to its northernmost extent in Alaska. In southeast Alaska, it occurs from sea level to timberline, sometimes growing in pure stands, but more often as scattered individual trees mixed with western hemlock and Sitka spruce. It is less abundant on well-drained soils, apparently because it cannot compete with the faster growing western hemlock and Sitka spruce (Harris 1971).

Alaska-cedar can be one of the slowest growing trees in North America, but it is among those with the greatest longevity (Harris 1970). Radial growth rates of 2 rings per mm (50 per in) are not uncommon, and 14 rings per mm (360 per in) have been recorded (Harris 1971). Alaska-cedar trees 1000 years old are common (Franklin and Dyrness 1973) and one hollow tree had 1040 rings in the one foot outer

shell (Munday 1931) and had an estimated age of 3500 years (Perry 1954).

Trees in Alaska tend to be somewhat smaller than those in the southern portion of the range (Harris 1970), although relatively large Alaska-cedar trees can be found growing on well-drained soils (Harris 1971). For example, I found one Alaska-cedar tree on such a site in the Peril Strait area that had a dbh of 194 cm and was 44 m tall. The largest known Alaska-cedar was found in Mount Rainier National Park, Washington and had a dbh of 243 cm and was 40.2 m tall (Harris 1970).

The bark of Alaska-cedar is brown or silvery-grey, relatively thin (e.g., 20-30 mm (Bones 1962)), sloughs off in vertical strands, and probably offers little protection from fire (Anderson 1959). Cat faces and dead sides are common on Alaska-cedar in southeast Alaska, but the cause has not been determined (Anderson 1959). Harris (1971) suggested that bears may cause this damage.

Flowering occurs from April to June (Harris 1971). Mature cones are spherical, about 1 cm in diameter, and have spikes. Cones mature in two years (Owens and Molder 1984); thus, both first- and second-year cones may be present on the same branch. Seeds ripen and are wind-disseminated in the autumn of their second year (Harris 1970).

Alaska-cedar can apparently grow on extremely poor soils, so long as abundant moisture is available (Anderson 1959). It is found on heavy, wet azonal organic subalpine soils and on bog (muskeg) soils with deep moss and peat layers. Its best development in Alaska is on thin, organic soils where abundant ground water seeps from higher elevations (Anderson 1959). Neiland (1971) found that Alaska-cedar was

less restricted than other conifers to either bog or forest communities.

Many horticultural varieties of Alaska-cedar are recognized. The only known hybrid involving Alaska-cedar is intergeneric: Cupressus macrocarpa Hartw. X Chamaecyparis nootkatensis, resulting in a form called Leyland cypress. This hybrid is planted extensively in Great Britain as an ornamental where it is reportedly cold-hardy (Anderson 1959).

Additional information on the biology and silviculture of Alaska-cedar is available in a bibliography with abstracts (Harris 1969).

Pests of Alaska-cedar

Little has changed since Anderson (1959) stated that not much is known of the diseases of Alaska-cedar. Hepting (1971) reported that Alaska-cedar has few diseases, and none are serious. The foliage rust, Gymnosporangium nootkatense Arth., is common on Alaska-cedar (Ziller 1974), but serious damage has not been reported. Phellinus weirii (Murr.) Gilb., an important root disease pathogen of some western conifers (Hadfield 1985), is known on Alaska-cedar only as the cause of a butt-rot (Hepting 1971); it has not been found killing trees in Alaska. Armillaria sp. commonly attacks the roots of Alaska-cedar, but may be unable to successfully attack an unstressed tree (Anderson 1959, Shaw et al. 1985). Two fungi, Gelatinodiscus flavidus Kanouse & Smith (Carpender 1976) and Herpotrichia juniperi (Duby) Petr. (Hepting 1971, Funk 1981), can colonize and kill the foliage of Alaska-cedar while it is underneath snow.

Kabatina thujae Schneider & Arx causes a shoot blight and canker of Alaska-cedar in nurseries in British Columbia (Funk 1981). It has not been found in Alaska. Another shoot blight fungus, Seiridium cardinale (Wagener) Sutton & Gibson, causes a serious disease of Cupressaceae in many parts of the world (Bannister 1962, Funk 1981, Strouts 1973). This fungus is capable of causing an extensive disease in natural forests, but it has not been found in Alaska.

Phytophthora lateralis, the cause of a very destructive root disease of the closely related Port-Orford-cedar (Chamaecyparis lawsoniana) (Roth et al. 1972), has been reported on ornamental Alaska-cedars in British Columbia (Lowe 1981), but has not been reported in Alaska or on Alaska-cedars growing in forests anywhere. Phytophthora diseases can cause large-scale damage. Because symptoms on dying Alaska-cedar trees superficially resemble those caused by Phytophthora spp., study of the role of Phytophthora spp. in Alaska-cedar decline receives special attention in this dissertation.

A bacterial gall disease has been reported on another member of Cupressaceae--Cupressus arizonica Greene (Brown and Evans 1933). The large galls on roots and the root crown of infected trees distinguish this from other root diseases. No other diseases caused by bacteria, viruses, mycoplasma-like organisms, or nematodes have been reported from Alaska-cedar or closely related tree species.

In the only detailed study of fungi isolated from Alaska-cedar, Smith (1970) attempted to determine the cause of black stains in the heartwood of live Alaska-cedar trees. Dark-colored fungi were isolated, and inoculated into wood (several caused stain), but none were identified.

Phloeosinus spp., bark beetles, are among the only insect enemies of Alaska-cedar. Reports of their ability to kill trees range from Phloeosinus attacking and killing large areas of cedar (Downing 1960) to these bark beetles only infesting cedars already dying from some other cause (McCambridge 1954, Anderson 1959, Shaw et al. 1985).

History of Alaska-cedar Decline

The first documented report of Alaska-cedar mortality was made by Sheldon (1912) who, in 1909, observed extensive tree death in Pybus Bay on south Admiralty Island and commented, "Vast areas are rolling swamps with yellow cedar, mostly dead." Dead cedar trees were again reported in 1927, this time by Ranger C. M. Archbold who investigated decline for three hours at Beacon Point on Kupreanof Island (unpublished, on file at Forestry Sciences Laboratory, Juneau, AK). He collected foliage samples from dying Alaska-cedar trees and sent them to J. S. Boyce, Pathologist, USDA Forest Service, Portland, OR. No evidence of insect or disease was detected. The next report of dead cedar trees was made by McCambridge (1954) who found that bark beetles (Phloeosinus sp.) commonly infested dying Alaska-cedars, particularly where those trees were growing on bogs (muskegs) and semi-bog sites. McCambridge, a forest entomologist, concluded that the bark beetles were very rarely the primary cause of tree death. He noted that a high level of mortality occurred throughout southeast Alaska.

Lawrence (1958) attributed the conspicuous number of dead trees in southeast Alaska to be a forest succession of bogs encroaching on forests; on page 117 he states, "Tree crowns grown to enormous size before the moss blanket became so soggy now find themselves too large

to be nourished by receding root systems...because of their usually saturated condition and inadequate aeration, the older trees gradually die and become bleached and stand as a border between forest and muskeg." Neiland (1971) later disputed this reasoning, however, by stating that some trees are dying or dead on steep slopes and that dead and dying trees are interspersed with live, vigorous trees of equal size. Neiland suggested diseases, insects, or fire as potential factors for causing the death of trees.

Anderson (1959) noted extensive mortality in his general treatment on "Silvical characteristics of Alaska-cedar." The extensive death of Alaska-cedar was attributed to winter desiccation during the spring of 1956; he concluded that damage occurred during a bright warm period while the soil was still frozen.

The next mention of cedar mortality was in 1960, when a cedar bark beetle outbreak on Kupreanof and Kuiu Islands was investigated (Downing 1960, 1961). Downing stated that bark beetles were the causal agent of tree death, that more Alaska-cedar died than did western redcedar (Thuja plicata Donn ex D. Don), and that mortality was concentrated on poorly drained slopes and muskegs. Bark beetle activity declined in 1961 (Crosby 1961).

Mortality of cedar was reported in each of the subsequent years by entomologists or pathologists observing the problem during annual insect and disease surveys (Laurent 1982). Often when reporting mortality, no distinction was made between effects on Alaska-cedar or western redcedar. Depending on who was reporting mortality, the primary cause was attributed to bark beetles, root disease, or winter desiccation (Shaw et al. 1985).

My involvement with this forest problem began in 1981, when USDA Forest Service personnel Charles G. Shaw III (Forestry Sciences Laboratory, Juneau, AK), Tom Laurent and Andris Eglitis (Forest Pest Management R-10, Juneau, Alaska), and I initiated investigations on the decline and mortality of Alaska-cedar. Our efforts were directed at describing symptoms of dying cedars, isolating pathogenic fungi, and determining the role of bark beetles. This work culminated in a preliminary report on Alaska-cedar decline (Shaw et al. 1985). A map of sites where cedar mortality had been observed during aerial forest pest detection was constructed. It showed that Alaska-cedar decline is extensive throughout southeast Alaska, except for largely unaffected areas on Admiralty Island and the northern portion of Chichagof Island. We determined that bark beetles were not the primary cause of tree death because most trees died without ever being attacked by beetles and beetles were found only on cedars in late stages of decline. Also, symptoms similar to certain root diseases were found, suggesting that further studies should elucidate their role in decline.

We began more detailed studies in 1982 through a cooperative project with the Forestry Sciences Laboratory in Juneau and the Department of Botany and Plant Pathology at Oregon State University. This project was supported by funds made possible by Alaska National Interest Land Claims Act (ANILCA). In this act, the U.S. Congress provided funds for research dealing with the intensification of timber production and forest management on a shrinking land base (due to the transfer of land to Alaska Native groups, National Monuments, and Wilderness Areas) on the Tongass National Forest in southeast Alaska. Research grants were awarded to projects, such as the present study,

that applied to timber harvesting and forest management on marginally productive lands since some of the future timber harvests will involve these lands. This dissertation reports the findings of this work.

The setting

Southeast Alaska, or the Alaska archipelago, is a strip of coastal mainland and numerous islands that is located east of the 141st meridian and extends about 340 km (540 mi) from Dixon Entrance to Yakutat (Fig. I.3). Although its 7.7 million hectares (19 million acres) of land comprise only 5% of the state, southeast Alaska contains the majority of Alaska's timber resource (Harris and Farr 1974). The Tongass National Forest, established in 1907 and later enlarged to include most of southeast Alaska, is now the largest national forest in the United States.

Southeast Alaska has a cool, wet climate with an annual precipitation of about 150-500 cm (Harris et al. 1974). Winters have relatively moderate temperatures, and summers are cool and wet, without prolonged dry periods. Because of this cool and moist climate, fire is not an important factor in forest succession. Much land is occupied by bogs (muskegs) as a result of high precipitation and low evapotranspiration (Harris et al. 1974). Windthrow and landslides are common disturbances of forests in this region (Harris and Farr 1974). Although the growing season is relatively brief, daylight periods are long in late spring and early summer.

Extensive glaciation during the last ice age has modified the landscape to an obvious extent, creating characteristic U-shaped valleys and serrate ridges. Glaciation and mountain building processes

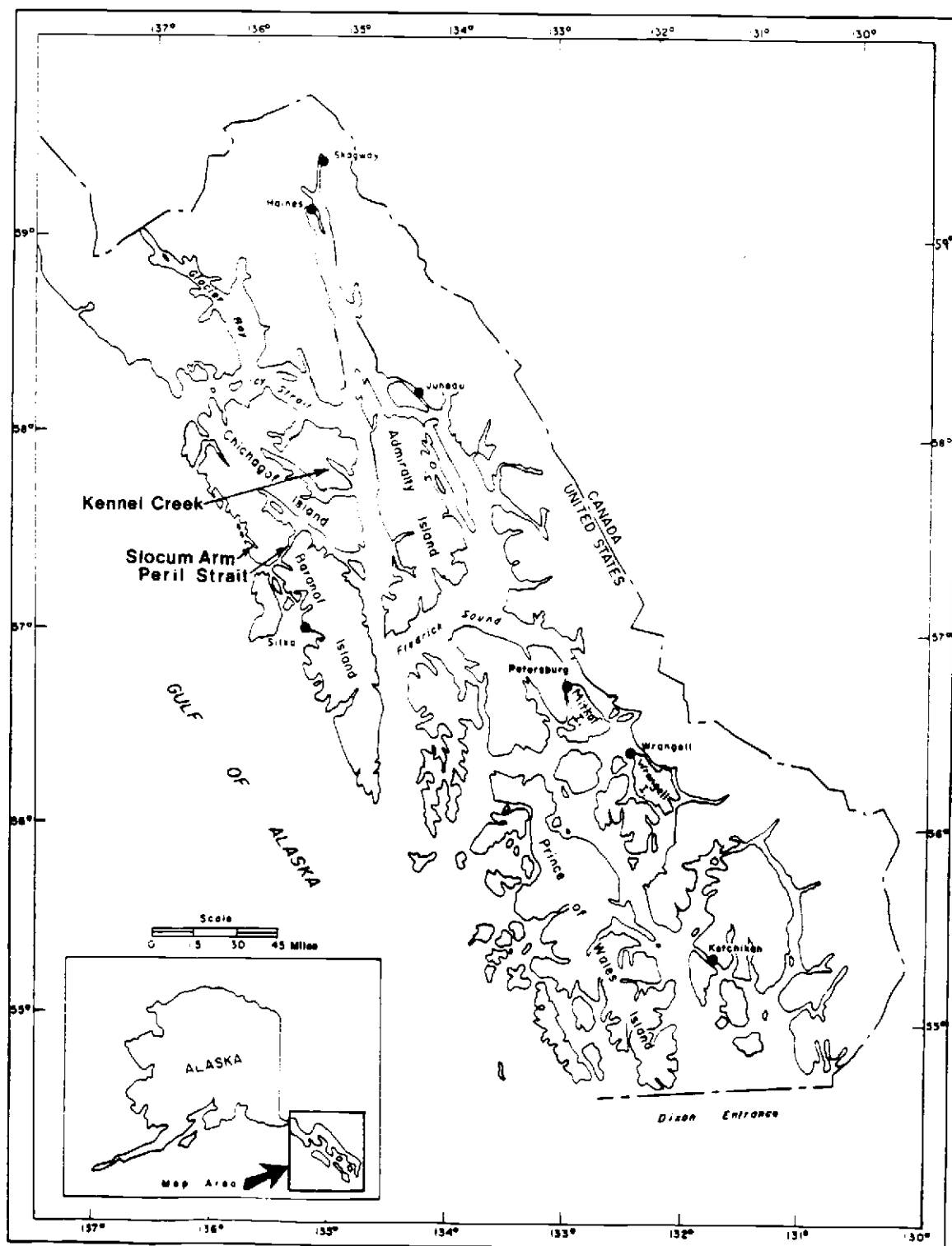


Figure I.3. Map of southeast Alaska

are still active today in the region, but few glaciers are located on the islands where our studies were conducted. The overall geological pattern can be summarized as a northwesterly eugeosyncline with Paleozoic rocks dominating the central lowland areas (Alaback 1982).

Soils in southeast Alaska are young, shallow, and poorly developed (Collins 1974). They are classified as spodosols with thin A2 and B21 horizons (Alaback 1982). Soils with hard intrusive rocks have a high percentage of poorly drained areas and less productive forest vegetation (Collins 1974). The depth of organic matter in these bogs ranges from less than 1 m to greater than 12 m (Harris et al. 1974).

Approximately 60 percent of the land in southeast Alaska is forested; the remainder is alpine, bog (muskeg), and riparian (USDA Forest Service 1978). Forests occur from the ocean shore to timberline, which occurs at about 600 to 800 m. Sitka spruce (Picea sitchensis (Bong.) Carr.) and western hemlock (Tsuga heterophylla (Raf.) Sarg.) are the major commercial tree species. Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) and western redcedar (Thuja plicata Donn ex D. Don) comprise only about five percent of the volume on Tongass National Forest, but the former is the dominant tree species in some areas. Western redcedar grows only to the southern portion of this region, south of about Sumner Strait at 57 degrees N. Mountain hemlock (Tsuga mertensiana (Bong.) Carr.) grows primarily at higher elevations, and shore pine (Pinus contorta Dougl. ex Loud. var contorta) is a non-commercial tree species that occurs primarily in bogs. Two species of Abies occur in southeast Alaska, but neither is common (Hulten 1968).

The study

Most of my research was conducted on Chichagof and Baranof Islands in the Peril Strait area (Fig. I.3), a portion of the Tongass National Forest that is suffering heavy mortality of Alaska-cedar. Parts of some studies (e.g., forest survey and foliage nutrient sampling) were conducted at Slocum Arm and Kennel Creek, elsewhere on Chichagof Island (Fig. I.3). In the Peril Strait area, the majority of work was carried out within 5 miles of Poison Cove (Fig. I.4).

The cabin on the north shore of Poison Cove (Fig. I.5) was used as field headquarters and laboratory. This cabin is owned by Irene Jimmy of Sitka, Alaska; we were fortunate to use this cabin as it was the only structure within miles of this area. The Peril Strait area is roadless; therefore, we used a 16 foot skiff fitted with an outboard motor for daily transportation to and from field sites.

The chapters of this dissertation are organized in the following manner. The objective of Chapter II is to date when extensive mortality began and to determine the time since death for five classes of dead cedar trees. These snag classes are based on the degree of foliage, twigs, and branch retention. Three techniques were used to determine when mortality began and when snags in different stages of deterioration died: 1) inspecting aerial photographs taken in 1927 of sites that now have dead and dying trees, 2) growth ring analysis of smaller hemlocks growing under larger dead Alaska-cedar trees, and 3) counting callus rings on live strips on partially dead Alaska-cedar boles to determine when most of the bole died.

Chapter III, an epidemiological study of Alaska-cedar decline, uses information on when snags in different stages of deterioration died.

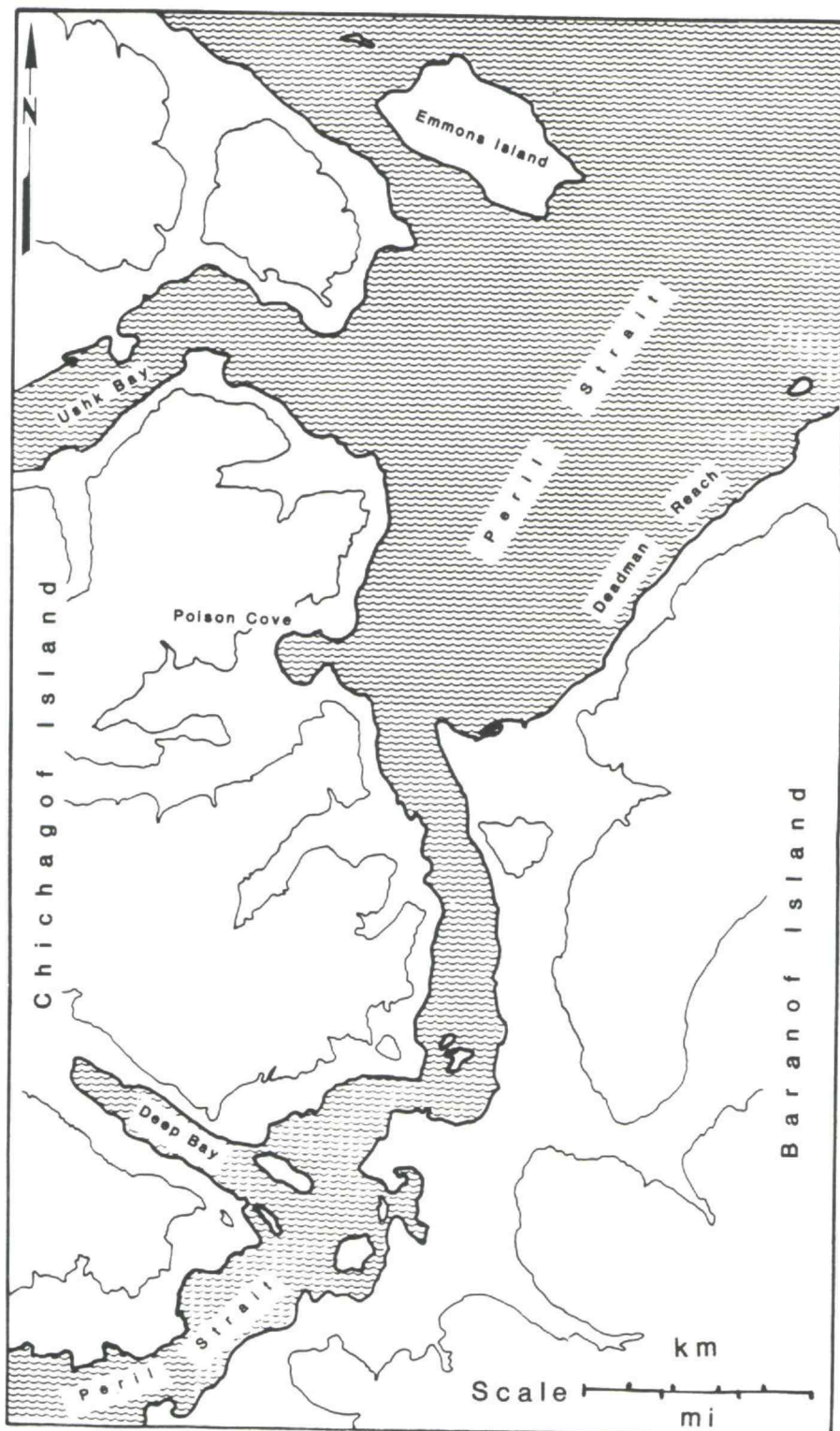


Figure I.4. Map of the Peril Strait area in southeast Alaska



Figure I.5. A) Mortality on the north shore of Poison Cove, Chichagof Island (note the cabin (arrow)), and B) the Poison cove cabin that served as research headquarters and laboratory

In this chapter, aerial photographs taken in 1927, 1948, 1965, and 1976 were used to document spread of mortality. An extensive ground survey was conducted to determine if conifers other than Alaska-cedar are dying, to confirm if most mortality is on unproductive sites, and to determine if intra- or inter-site spread of mortality has occurred.

Of biotic agents capable of killing plants, fungi are the most important pathogens of forest trees; therefore, I devoted a special effort to the study of these organisms. Chapter IV provides a literature review of fungi previously reported on Alaska-cedar and lists the fungi that I isolated and collected from Alaska-cedar. In Chapter V, the roles of these fungi (and nematodes) in Alaska-cedar decline are discussed and symptoms of dying cedars are described. A special effort is made to clarify the role of Phytophthora spp. and Armillaria sp. as incitants of mortality, since Armillaria was previously found on dying cedars (Anderson 1959) and symptoms suggest the possibility of a Phytophthora species as a causal factor (Shaw et al. 1985). Root and lower bole lesions on Alaska-cedar are similar to lesions caused by P. lateralis when it attacks Port-Orford-cedar (Chamaecyparis lawsoniana, a close relative of Alaska-cedar. The pathogenicity of fungi isolated from symptomatic tissues on dying Alaska-cedar trees was tested by inoculating them into healthy cedar seedlings and later observing for mortality or symptoms similar to those on dying trees. I attempted to reproduce symptoms on mature, healthy Alaska-cedars in the forest by mechanically wounding their tissues and by grafting diseased tissues.

Scars on the lower bole of Alaska-cedar trees are common in various parts of southeast Alaska. Chapter VI describes the causes of

these scars, lists fungi on old and recently scarred tissues, discusses decay in wood associated with scars, describes tree response in tissues adjacent to scars, and evaluates the relationship between these scars and Alaska-cedar decline.

Chapter VII evaluates deficient soil nutrients or soil toxins as potential primary incitants of mortality. Foliage from cedars growing in declining and healthy stands was collected, analyzed, and compared for different concentrations of nutrients. Soil adjacent to both live and dead roots was collected, analyzed, and compared for pH and several nutrients.

The reproduction of Alaska-cedar is failing in some areas in southeast Alaska (Shaw et al. 1985); Chapter VIII expands the information on regeneration. Data were collected on Alaska-cedar seedlings and seedlings in the extensive ground survey mentioned above, which allowed me to evaluate the success of reproduction in several different forest community types. In addition, observations made during root excavations of small and large Alaska-cedars aided in our understanding how Alaska-cedar stands regenerate.

Chapter IX is a summary and integrates findings from these studies. Comparisons are made between Alaska-cedar decline and several other forest declines. Future research needs on Alaska-cedar decline are suggested.

These studies increase our understanding of Alaska-cedar decline, and should provide insights into means of managing this important forest tree species and its decline problem.

LITERATURE CITED

- Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63:1932-1948.
- American Forestry Association. 1955. These are the champs. *Amer. For.* 61(9):31-40.
- Anderson, H.E. 1959. Silvicultural characteristics of Alaska-cedar. U.S. For. Serv. Alaska Forest Research Center, Sta. Pap. 11. 10p.
- Bannister, M.H. 1962. Prospects for selection in the cypresses. *New Zealand J. For.* 8:545-559.
- Bones, J.P. 1962. Relating outside- to inside-bark diameter at the top of first 16-foot logs for southeast Alaska. USDA For. Serv. Tech. Note No. 52. Northern For. Exp. Stn., Juneau, AK. 2p.
- Brown J.G. and M.M. Evans. 1933. Crown gall of a conifer. *Phytopathology* 23: 97-101.
- Carpender, S.E. 1976. Taxonomy, morphology, and ontogeny of Gelatinodiscus flavidus. *Mycotaxon* 3:209-232.
- Collins, T.M. 1974. Soils and soil development. pp. 20-23. In: The forest ecosystem of southeast Alaska. I. The setting. Forest Service Gen. Tech. Rep. PNW-12. Pacific Northwest Forest and Range Exp. Sta., Portland, OR.
- Crosby, D. 1962. Forest insect and disease conditions in Alaska. p. 4. In: Forest insect conditions in the United States, 1961. USDA For. Serv.
- Downing, G.L. 1960. A cedar bark beetle outbreak. U.S. For. Serv., Alaska For. Res. Cent., For. Insect Surv. Rep. 6. 2p.
- Downing, G.L. 1961. Forest insect and disease conditions in Alaska. P. 3. In: Forest insect and disease conditions in the United States, 1960. USDA Forest Service.
- Duff, S.R., H. Erdtman, and W.E. Harvey. 1954. The chemistry of the natural order Cupressales. XII. Heartwood constituents of Chamaecyparis nootkatensis (Lamb.) Spach. Nootkatin. *Acta Chem. Scand.* 8(6):1073-1082.
- Duncan, John. Personal communication. Divisional Forester. MacMillan Bloedel. P.O. Box 10. Juskatla, B.C., Canada. VOT 1J0
- Franklin, G. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. Pacific Northwest For. and Range Exp. Sta., Portland, OR. 417p.

- Frear, S.T. 1982. What's killing the Alaska yellow-cedar? *Amer. For.* 88(11):41-43,62-63.
- Funk, A. 1981. Parasitic microfungi of western trees. Can. For. Serv., Pacific Forest Research Centre. BC-X-222. 190p.
- Hadfield, J.S. 1985. Laminated root rot. A guide for reducing and preventing losses in Oregon and Washington. USDA For. Serv. Pacific Northwest Region, Portland, OR. 13p.
- Harris, A.S. 1969. Alaska-cedar. A bibliography with abstracts. USDA For. Serv., Pacific Northwest For. & Range Exp. Sta., Juneau, AK. Res. Pap. PNW-73. 47p.
- Harris, A.S. 1970. The loners of Alaska. *Amer. For.* 76(5): 20-23,55-56.
- Harris, A.S. 1971. Alaska-cedar. USDA For. Serv., American woods-FS 224. 7p.
- Harris, A.S. and W.A. Farr. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. Pacific Northwest Forest and Range Exp. Sta. Portland, OR. Gen. Tech. Rep. PNW-25. 109p.
- Harris, A.S., O.K. Hutchison, W.R. Meehan, D.N. Swanston, A.E. Helmers, J.C. Hendee, and T.M. Collins. 1974. The forest ecosystem of southeast Alaska. 1. The setting. USDA For. Serv. Pacific Northwest Forest and Range Exp. Sta., Portland, OR. Gen. Tech. Rep. PNW-12. 40p.
- Hepting, G.H. 1971. Diseases of forest and shade trees of the United States. USDA For. Serv. Ag. Handb. No. 386. 658p.
- Hulten, E. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press, Stanford, CA. 1008p.
- Laurent, T.H. 1982. Cedar dieback--is it the problem. Pp. 104-107. In: Proceedings of the Second Alaska Integrated Pest Management Conference. Univ. Alaska, Anchorage, AK. Coop. Ext. Serv. 112p.
- Lawrence, D.B. 1958. Glaciers and vegetation in Southeastern Alaska. *American scientist* 46(2):89-122.
- Little, E.L. 1953. Check list of native and naturalized trees of the United States (including Alaska). USDA For. Serv. Ag. Handb. No. 41. Washington D.C. 472p.
- Lowe, D.P. 1981. Check list and host index of bacteria, fungi, and mistletoes of British Columbia. Forest Research Laboratory. Victoria, B.C. Information report BC-X-32. 392.
- Markwardt, L.J. 1931. The distribution and the mechanical properties of Alaska woods. USDA For. Serv., Washington D.C., Tech. Bull. No. 226. 80p.

- Mason, H.L. 1941. The Alaska cedar in California. *Madrono* 6:90.
- McCambridge, W.F. 1954. A summary of forest insect conditions in Alaska, season of 1954. U.S. For. Serv., Alaska For. Res. Cent. 1p.
- Munday, D. 1931. Ancients of the sky lines. *Illus. Canadian forests and outdoors*. November, 1931: 25-27.
- Neiland, B.J. 1971. The forest-bog complex of southeast Alaska. *Vegetatio* 22:1-64.
- Perry, R.S. 1954. Yellow cedar; its characteristics, properties, and uses. Canada Dept. North Aff. and Nat. Resources. Forestry Branch Bull. 114. 119p.
- Petrof, I. 1880. The population and resources of Alaska. In: Committee of military affairs, compilations of narratives, explorations in Alaska. Government Printing Office, Washington D.C. pp. 145-147.
- Roth, L.F., H.H. Bynum, and E.E. Nelson. 1972. Phytophthora root rot of Port-Orford-cedar. USDA For. Serv. For. Pest Leaflet. 131. 7p.
- Shaw, C.G. III, A. Eglitis, T.H. Laurent, and P.E. Hennon. 1985. Decline and mortality of Chamaecyparis nootkatensis in Southeastern Alaska, a problem of long duration but unknown cause. *Plant Dis.* 69:13-17.
- Sheldon, C. 1912. The wilderness of the north Pacific coast islands. Charles Scribner's Sons, New York. 246p.
- Smith, R.S. 1970. Black stain in yellow cedar heartwood. *Can. J. Bot.* 48:1731-1739.
- Strouts, R.G. 1973. Canker of cypresses caused by Coryneum cardinale Wag. in Britian. *Eur. J. For. Pathol.* 3:13-24.
- USDA Forest Service. 1978. Tongass land management plan. United States Forest Service, Alaska Region, Juneau, Alaska.
- USDA Forest Service, 1982. Peeled cedar trees give clues to past. USDA Forest Service, R-6 (Pacific Northwest Region), Greensheet, Sept. 3, 1982. No. 1842. 1 p.
- Viereck, L.A. and E.L. Little Jr. 1972. Alaska trees and shrubs. USDA For. Serv. Ag. Handb. No. 410. Washington D.C. 265p.
- Ziller, W.G. 1974. The tree rusts of Western Canada. *Pacific For. Res. Cen. Can. For. Serv. Dept. of Environ. Publ. No. 1329.* 272p.

CHAPTER II

DATING THE ONSET OF ALASKA-CEDAR DECLINE

ABSTRACT

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a valuable tree species that has been declining and dying for a long, but undetermined, span of time in southeast Alaska. Determining when mortality began and when individual snags died aid in interpreting patterns of mortality spread and in establishing the primary cause of the problem. Aerial photographs showed that mortality was already widespread by 1927. The dates of death for individual Alaska-cedar snags in five stages of deterioration were determined by counting annual rings on: 1) 73 western and mountain hemlocks (released trees) growing beneath larger, dead Alaska-cedars, and 2) callus strips on 46 partially killed Alaska-cedars (rope trees). Average time since death for the five snag classes were: I--dead, foliage retained--4 yrs; II--dead, twigs retained--11 yrs; III--dead, secondary branches retained--31 yrs; IV--dead, only primary branches retained--54 yrs; and V--dead, bole intact but no primary branches retained--81 yrs. Released trees were effective for dating the death of recently killed Alaska-cedars; rope trees were more effective for estimating the time of death of long-dead Alaska-cedars. The longest-dead Alaska-cedars (Class V) that were common and widespread appear to represent the original extensive mortality. Snags in a sixth class with

deteriorating boles were uncommon, not associated with sites of decline, and their death most likely predated extensive mortality. Our analysis indicates that Class V snags died an average of 81 years ago, with some trees having died over 100 years ago. Most of these trees experienced a reduction in radial growth many years prior to death. Thus, these data suggest that extensive mortality began about 1880, and became obvious about 1900-1910, dates supported by historical records.

INTRODUCTION

Decline and mortality of Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is extensive in southeast Alaska (Frear 1982). The problem is primarily associated with bog and semi-bog plant communities (Downing 1960, Chapter III) and affects trees regardless of size (Shaw et al. 1985) (Fig. II.1).

Recent research has investigated the etiology and epidemiology of this problem. The cause of mortality is unknown, but distribution patterns of dead trees imply spread through time. The areas affected have apparently expanded, with dying and recently dead trees surrounding patches of long dead trees (Chapter III), a pattern that suggests a pathogenic agent may be responsible. No pathogen is evident (Shaw et al. 1985, Chapter V), however, and several biotic agents have been eliminated as primary incitants (Shaw et al. 1985, Chapter V). An alternative hypothesis to the biotic cause is that an adverse weather event (Anderson 1959), or some other environmental change, initiated the mortality. Investigations into the distribution and spreading



Figure II.1. Mortality of Alaska-cedar in southeast Alaska

patterns of dying cedars may support or refute my hypothesis of a biotic cause of cedar decline. It is necessary to determine the time of death to interpret mortality patterns and resolve the etiology of this spectacular forest problem. To clarify possible causes of this problem, I attempted to determine the spatial and temporal patterns of mortality (Chapter III). To accomplish this, I needed to determine when mortality began and how long individual trees had been dead.

Alaska-cedar wood is very resistant to decay, and dead trees may persist for long periods of time. Affected Alaska-cedar trees die standing and remain standing, slowly deteriorating for an undetermined number of decades. This has allowed us to reconstruct the patterns of mortality.

The objectives of this study were to determine when extensive mortality in Alaska-cedar began and to determine the time of death for Alaska-cedar snags in various stages of deterioration.

MATERIALS AND METHODS

Three methods were used to estimate the onset of extensive mortality and to determine the time of death for individual Alaska-cedar snags. First, I examined the earliest aerial photographs of southeast Alaska taken in 1926 and 1927. These aerial photographs represent one of the earliest efforts anywhere to photograph large areas of forest (Sargent and Moffit 1929). One vertical and two oblique photographs were taken at each point along flight lines. Study areas were located along Peril Strait, on Chichagof and Baranof Islands

(Fig. II.2) about 50 km northwest of Sitka, Alaska. Thirteen sites (Fig. II.3) were examined using both vertical and oblique photographs for the occurrence and distribution of dead cedar snags in forest stands currently expressing decline and mortality.

For the other two methods, dead Alaska-cedar trees were grouped into one of six snag classes based on degrees of dead foliage, twig, and branch retention (compared to the condition of those tissues in the crown of a live, green cedar) and bole deterioration. Snag classes (Fig. II.4) were:

- I) Foliage retained (at least 10% of total)
- II) Twigs retained (at least 10% of total), most foliage missing
- III) Secondary branches retained (at least 10% of total),
most twigs missing
- IV) Primary branches retained (at least 10% of total), most
secondary branches missing
- V) Most primary branches missing, bole intact to near the top
- VI) Bole broken off and disintegrating

Estimates of the time since death for snags in each class were determined by counting annual rings on trees growing under these snags (released trees) and by counting annual rings in callus growth on partially killed stems of Alaska-cedars (rope trees) that were interspersed among cedar snags.

In the release tree method, 73 western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) or mountain hemlock (*T. mertensiana* (Bong.) Carr.) and 44 Alaska-cedar trees growing beneath previously dominant, but now dead,

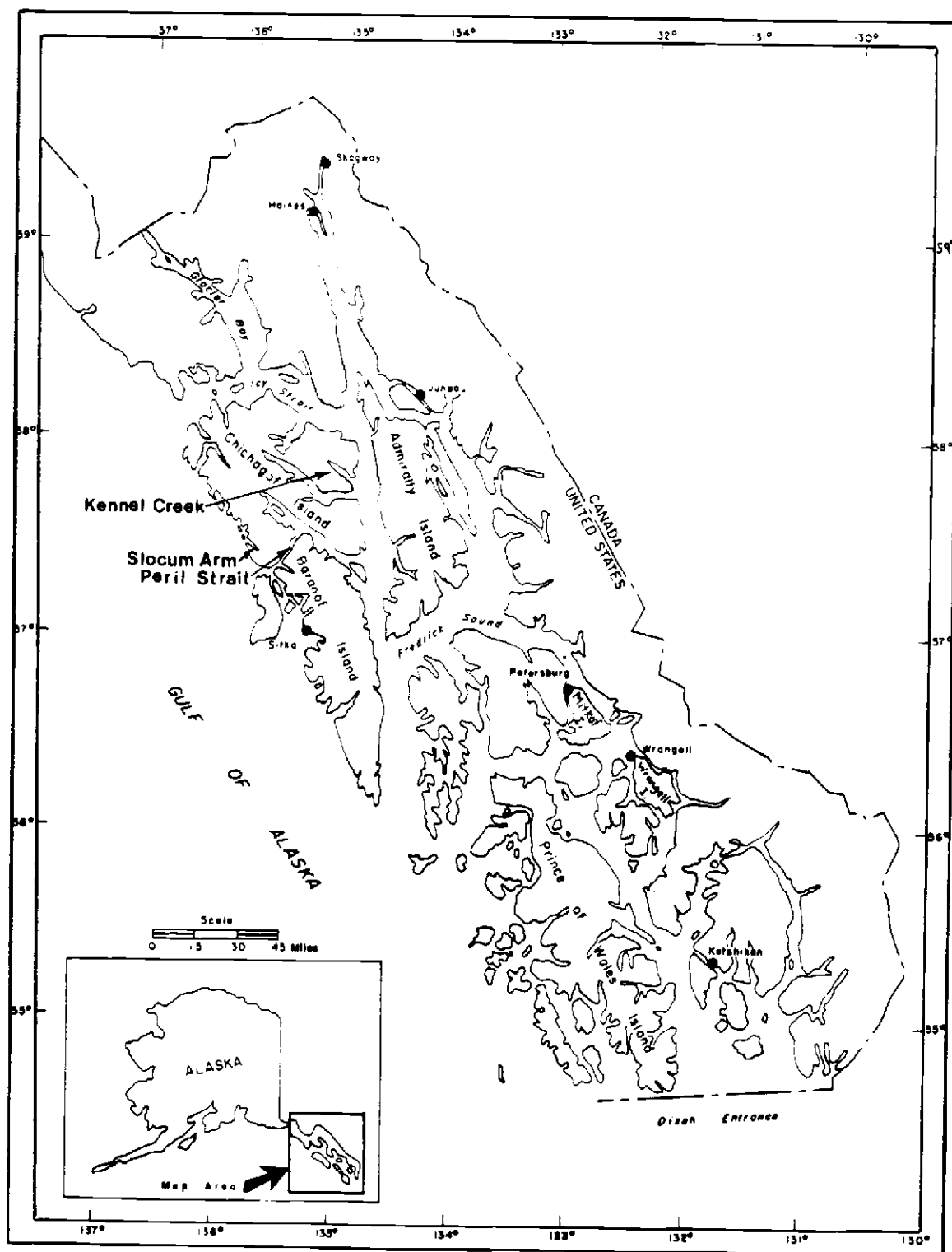


Figure II.2. Location of study area along Peril Strait on Baranof and Chichagof Islands, Alaska

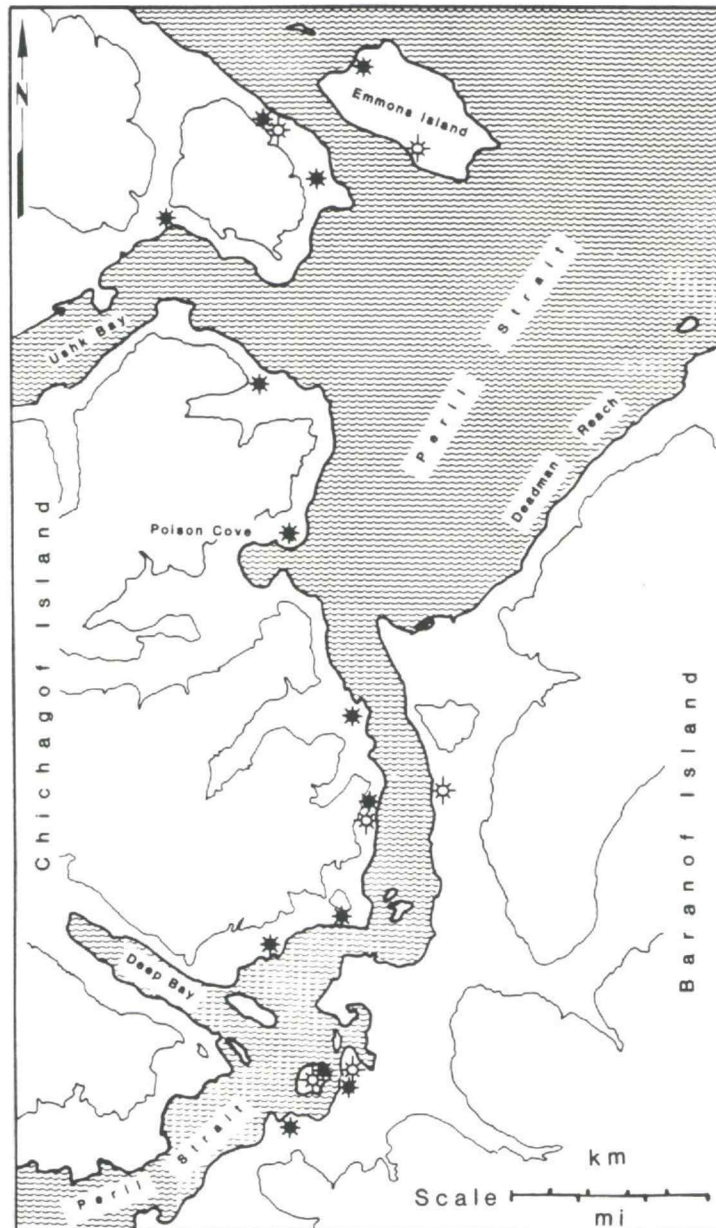


Figure II.3. Map of locations for which mortality was viewed on 1927 aerial photographs (*) and six sampling locations for rope trees (partially killed Alaska-cedars) used to determine the dates of snag death (☼).



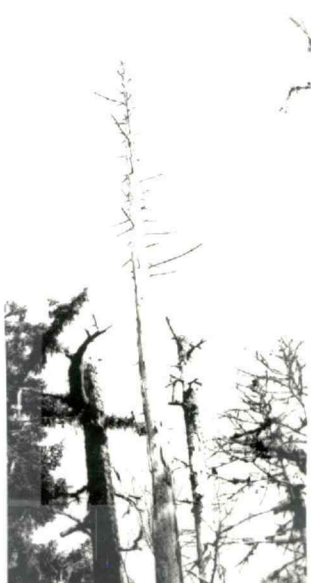
SNAG CLASS I



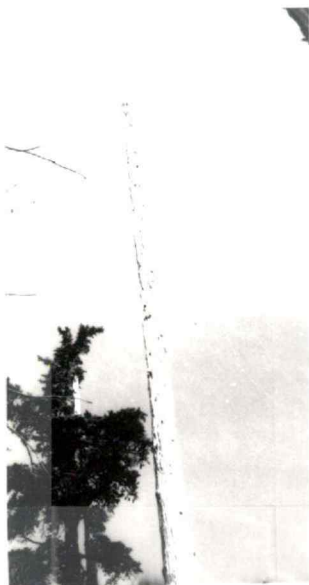
SNAG CLASS II



SNAG CLASS III



SNAG CLASS IV



SNAG CLASS V



SNAG CLASS VI

Figure II.4. Six snag classes for dead Alaska-cedars. Classes are differentiated by degrees of foliage, twig, and branch retention, and bole deterioration.

Alaska-cedar snags were located (Fig. II.5). Only hemlocks or cedars primarily influenced by the death of only one Alaska-cedar were selected. Growth release is more confidently interpreted from trees released by the death of one tree than from trees beneath several overstory trees dying at different times (Lorimer 1985). An additional 17 hemlocks growing beneath live and full-crowned Alaska-cedars were selected as controls. Increment cores were taken from these trees at breast height (1.4 m), shaved with a razor blade, sprayed with water, and viewed at 60x using a dissecting microscope to determine patterns of annual ring growth. A dissecting microscope was used because annual radial growth can be as narrow as 10 rings/mm.

A release event was defined as any five-year sequence of annual growth rings that was approximately twice as wide as that of the previous five-year interval. When release was evident, the number of annual rings formed since release was counted for each released tree, and was associated with the class of Alaska-cedar snag under which the tree was growing. Differences in time since death among the released trees beneath different classes of cedar snags were evaluated by a one-way analysis of variance (ANOVA) and Tukey's multiple comparison test ($p=0.05$).

The other method for determining the time since death for snags in each deterioration class used partially dead Alaska-cedar trees that grew in or near bogs suffering from decline. These trees have a completely dead top (snag class I to V), but one narrow strip of live tissue, consisting of callusing bark and sapwood, connects roots to one live and bushy branch cluster (Fig. II.6). For lack of a better term, these cedars are called "rope trees." The cause of this condition is



Figure II.5. Mountain hemlock (arrow) growing directly beneath a previously dominant, but now dead Alaska-cedar. Growth ring patterns of such released hemlocks were used to determine when the Alaska-cedar died.

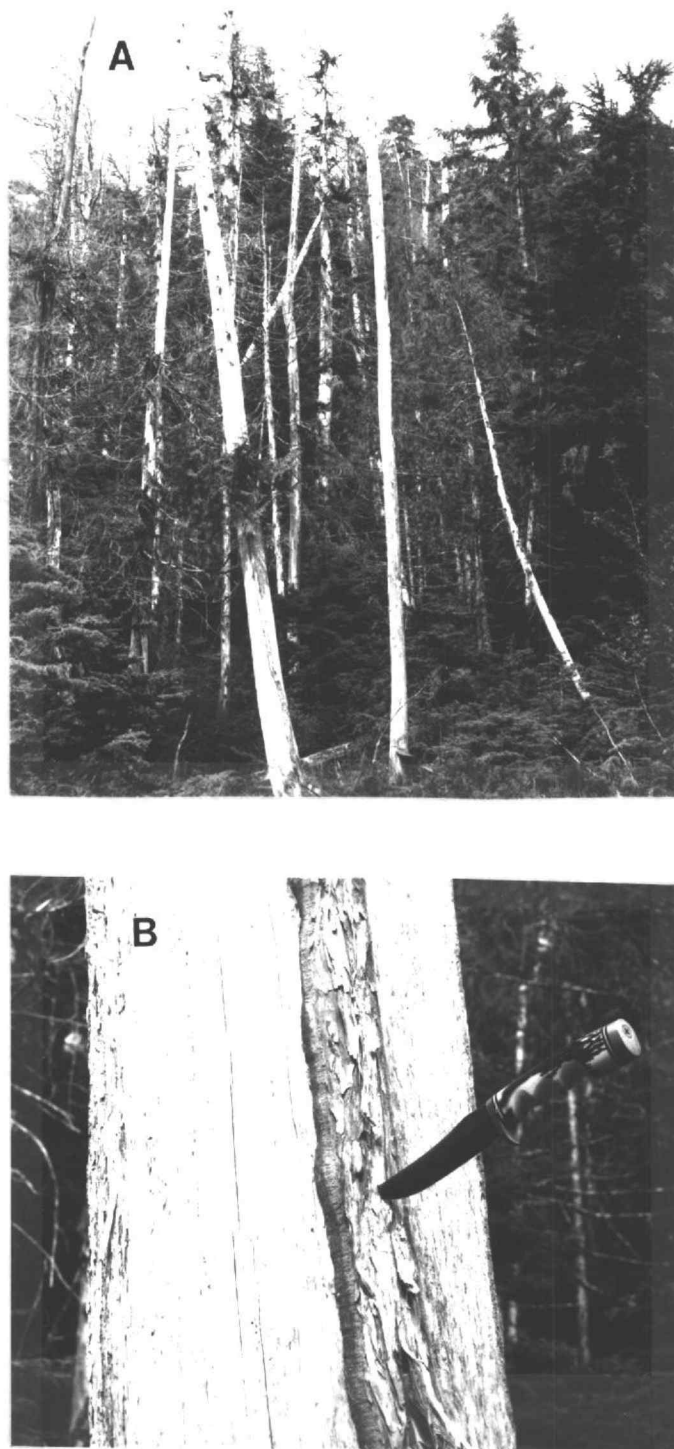


Figure II.6. (A) Alaska-cedar rope tree. These trees have a dead top and dead bole except for a narrow strip of live callusing tissue, (B) that connects roots to one live, bushy branch cluster. Ring counts on strips of callus tissue were used to determine when the main boles died. These results were used to estimate when snags, with tops in a similar stage of deterioration, died.

not known, but we hypothesize that these trees were severely injured, but not completely killed, by whatever caused the more general mortality. Stem discs were removed at approximately 20 cm above the ground from 46 rope trees at six sites. The time since death of the cambium surrounding the live callus was determined by counting annual rings in the callus tissue on the live part of the disc from the present cambium back to where the bole was dead. Each rope tree was placed into one of the snag classes based on the condition of the dead top above the live branch cluster. Differences among the snag classes in time since top and bole death were evaluated by a one-way ANOVA and Tukey's multiple comparison test ($p=0.05$). Width of annual rings before top and bole death was also examined to determine if these trees experienced a growth decline prior to damage.

The six sampling sites for rope trees were located on different islands or, where on the same island, they were separated by several miles (Fig. II.3). This separation allowed us to test by ANOVA ($p=0.05$) whether trees in snag classes from different locations had been dead for similar lengths of time. This test used only rope trees with class IV and V tops, as other classes were relatively uncommon.

RESULTS

1927 Aerial Photography

The 1927 photographs are now of variable quality, but on both vertical and oblique prints with good contrast cedar mortality clearly appears as patches of white snags (Fig. II.7). Mortality of

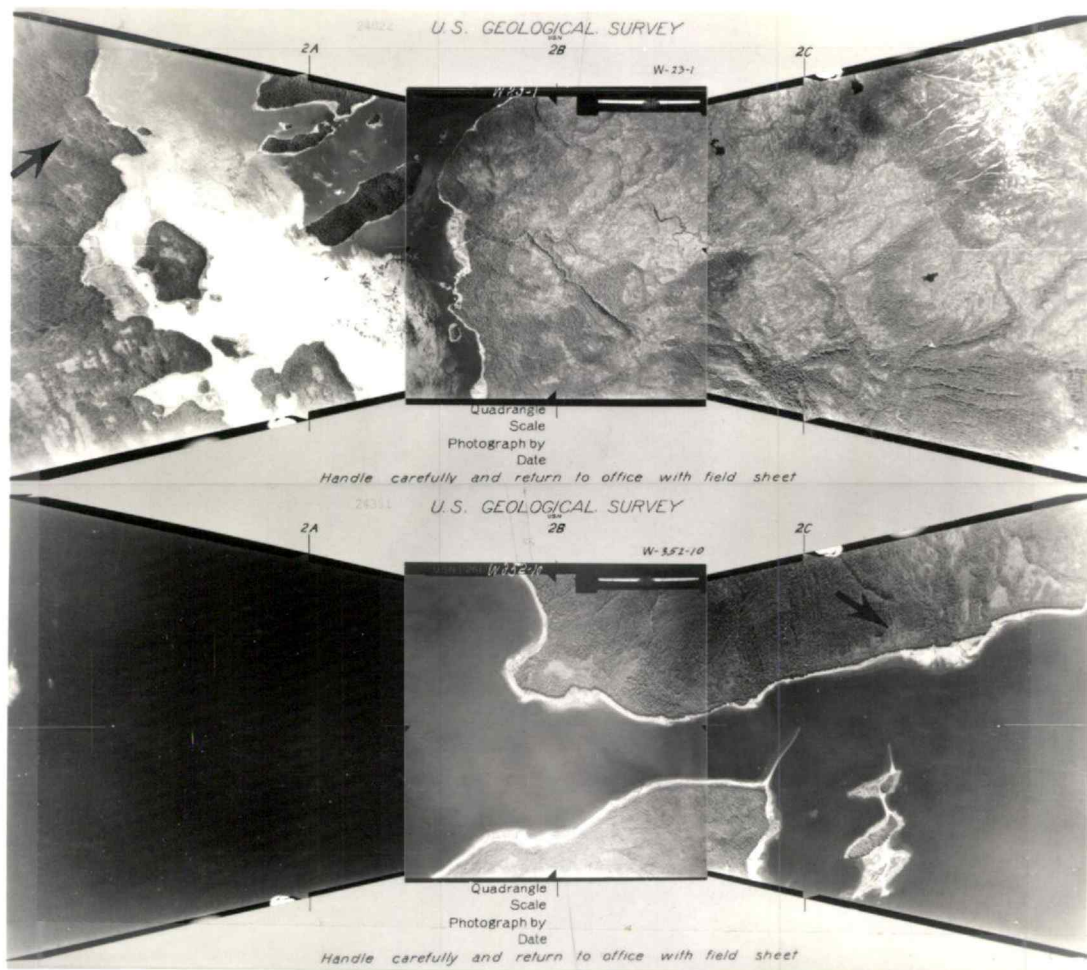


Figure II.7. Aerial photographs taken in 1927 in the Bear Bay portion of Peril Strait (above) and near Vixen Islands on Chichagof Island along Hoonah Sound (below). Note the mortality (arrow).

Alaska-cedar was already widespread in 1927, occurring at all 13 sites with current mortality that were visible on these photographs.

Released Hemlocks

Of the 73 hemlocks that were examined growing beneath dead cedars, 58 (79%) increased on their otherwise relatively constant rate of annual growth, which we interpreted as release. The time of these growth releases differed significantly among snag classes (I-IV) under which the trees grew (Table II.1). Hemlock trees beneath snags in class I released an average of 4 years ago; trees beneath snag class II released an average of 14 years ago, trees beneath snag class III released an average of 26 years ago, and trees beneath snag class IV released an average of 55 years ago.

Not all hemlocks that we examined had a release pattern. Fifteen hemlocks (21%) had no increase in radial growth, even though they were growing beneath large Alaska-cedar snags. Eleven (73%) of the non-released trees were growing under long-dead cedar snags (i.e., class IV and V), although four (27%) were also found beneath snags from each of the more recently dead classes (I-III). Furthermore, five of the 17 (29%) hemlocks that were growing beneath live, full-crowned Alaska-cedars (controls) had unexpected episodes of increased growth—one tree each at 5, 9, 13, 57, and 95 years ago. The remaining hemlocks growing under live Alaska-cedars did not release.

Many Alaska-cedars growing under Alaska-cedar snags also released, but their radial growth fluctuated so much throughout their life that possible times of release, perhaps associated with overstory death, were obscured; thus, Alaska-cedar increments were not analyzed further.

Table II.1. Time since release of previously suppressed western and mountain hemlock trees growing beneath different classes of Alaska-cedar snags. Snag classes are based on degrees of foliage, twig, and branch retention. See Fig. II.4.

Snag class	Hemlocks examined (no.)	Time since release ^{1/} (yrs)	Range (yrs)
I foliage retained	10	3.6 ± 3.2 ^a	0-10
II twigs retained	14	13.6 ± 6.9 ^a	3-24
III secondary branches retained	21	26.2 ± 12.3 ^b	12-52
IV primary branches retained	13	55.4 ± 25.2 ^c	24-100

^{1/} Mean followed by its standard deviation; values followed by different letters differ significantly ($p=0.05$); Tukey's confidence interval = mean ± 11.02.

Rope Trees

Most rope trees were in snag class IV (dead, only primary branches retained) or class V (dead, no branches retained); few rope trees had class I tops (dead, foliage retained). The number of growth rings in callus tissue increased with snag class. Rope trees in Classes II, III, and V differed significantly from one another in number of callus growth rings, and presumably, in time since death of the top and most of the bole (Table II.2). Time since top death for rope trees did not differ significantly among sites for 34 rope trees from either class IV or class V (Table II.3), although tops tended to have died earlier at sites 5 and 6.

Counting rings in callus growth was facilitated by three factors (Fig. II.8). First, a reddish band was common in the annual ring marking the death of the bole and the origin of callus tissue. Second, the first few callus rings of all 46 rope trees grew out radially a few millimeters prior to growing around the dead bole. These first callus rings are considered to represent growth up the side of the then-recently killed bark on the dead bole. Third, surviving sapwood at the time of bole damage has since become heartwood and is decay resistant, while sapwood killed at the time of bole death is stained, decayed, or completely missing.

Stem discs cut from 23 rope trees in snag classes IV and V had clear, sound heartwood and the growth rings prior to bole death were readily measured. The other 18 rope trees had stain or decay that prevented counting rings formed prior to bole death. All 23 rope trees with sound heartwood experienced a growth slow-down many years prior to

Table II.2. Time since callus tissue formation on 46 rope trees (partially living Alaska-cedars). Classes are based on degrees of foliage, twig, and branch retention. See Fig. II.4.

Snag class (above live branch)	Rope trees examined (no.)	Age of callus growth ^{1/} (yrs)	range (yrs)
II twigs retained	2	8.5 ± 0.7 ^a	8-9
III secondary branches retained	3	39.0 ± 15.7 ^b	25-56
IV primary branches retained	13	51.2 ± 18.1 ^b	27-96
V no primary branches retained	28	81.4 ± 22.0 ^c	49-128

^{1/} Mean followed by standard deviation of the mean; values followed by different letters differ significantly (p=0.05); Tukey's confidence interval = mean ± 15.76.

Table II.3. Time (years) since initiation of callus tissue on 34 rope trees (partially live Alaska-cedars) at six separate sites in southeast Alaska.^{1/}

Site (No.)	Location ^{3/}	SNAG CLASS IV		SNAG CLASS V	
		Rope trees examined (no.)	Age of callus growth (yrs) ^{2/}	Rope trees examined (no.)	Age of callus growth (yrs) ^{2/}
1	Emmons Island	0	-	5	78.0 \pm 20.2
2	Roger's Point, Chichagof Island	3	47.7 \pm 3.1	3	73.3 \pm 22.5
3	Susan's Landing, Chichagof Island	2	36.5 \pm 0.7	3	87.7 \pm 18.8
4	Nixon Shoal, Baranof Island	1	48.0	6	66.5 \pm 7.7
5	Bear Bay Island	3	69.0 \pm 32.7	3	101.7 \pm 43.0
6	Bear Bay, Baranof Island	1	62.0	4	94.0 \pm 23.8

^{1/} Class IV rope trees have dead tops with primary branches retained and class V rope trees have dead tops with no primary branches retained, but boles are still intact.

^{2/} Mean followed by standard deviation.

^{3/} see Figure II.3.

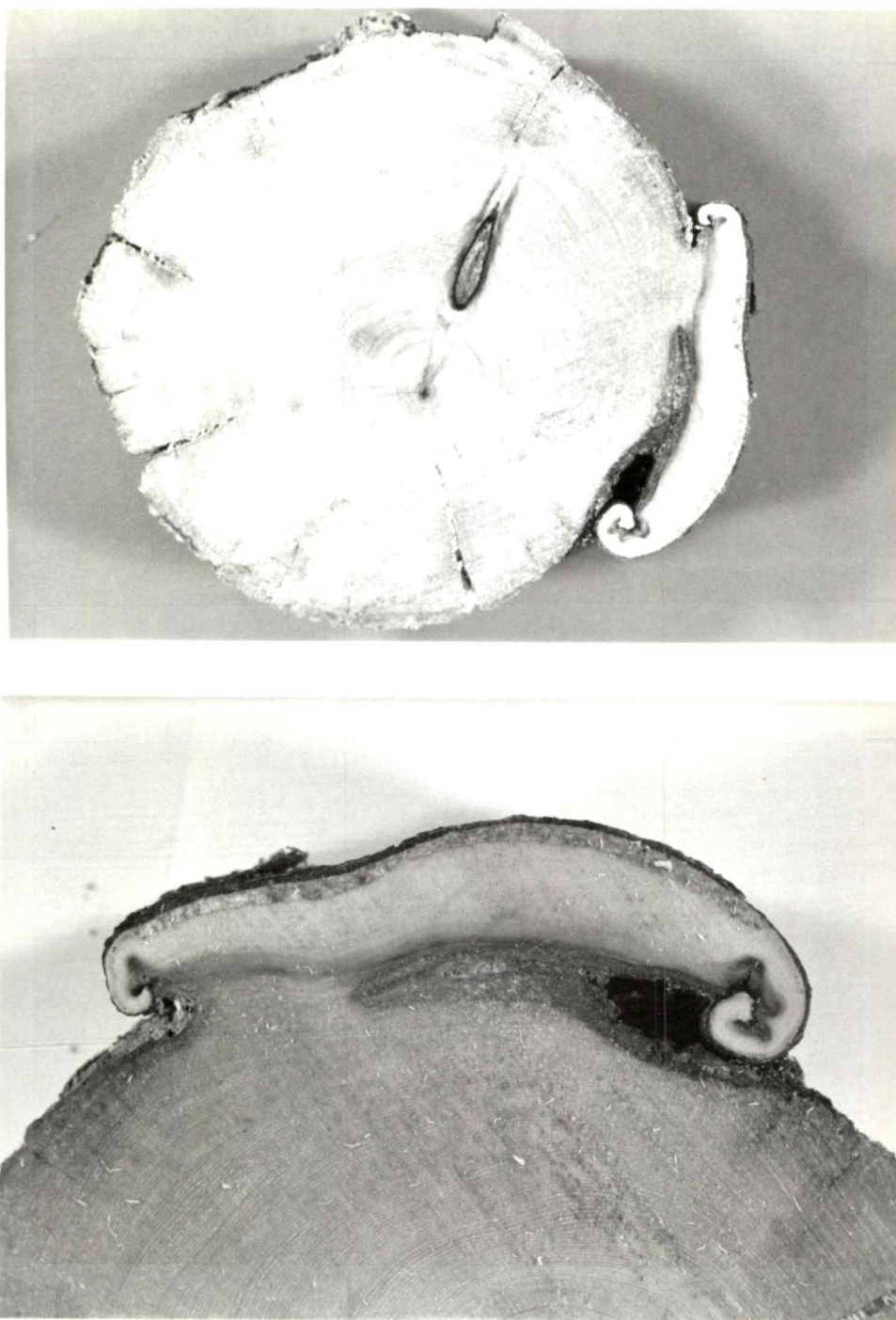


Figure II.8. Cross-section of an Alaska-cedar rope tree (above and below) showing dead bole and callus strip used to date when the top and most of the bole died.

bole death with 10 or more annual rings per millimeter. This growth slow-down began an average of 99 ± 26 years ago for class IV rope trees and 141 ± 30 years ago in class V rope trees. Thus, a reduction in radial growth preceded bole death by an average of 48 and 59 years for rope trees in classes IV and V, respectively. There were no significant differences among sites for the decline in growth for rope trees in class IV or V. Not enough class I-III rope trees were sampled to determine if any growth differences were related to site.

DISCUSSION

Aerial photographs and both methods for dating the death of individual snags were useful in estimating the time of death for snags and for determining when the extensive mortality began. The earliest aerial photographs verified that the problem predates 1927 when numerous and extensively distributed dead trees were already evident. Both the hemlock release and rope tree methods of determining when snags died indicate that snags with more deteriorated crowns died earlier. Yet the estimated times since death for each snag class were not identical for the two methods. The hemlock release method was more reliable in determining time since death of more recently dead snags (i.e., those in classes I, II, and III), but was not useful in determining the time of death for long-dead snags, and hence, when extensive mortality began. Perhaps hemlocks did not release beneath the long-dead snags because many of them occur on bog sites where light may not limit their growth. Rope trees were more reliable in

estimating dates of death for long-dead snags because rope trees usually had class IV and V tops, and thus were the best tool for estimating when extensive mortality began.

Not all hemlocks growing beneath long-dead class IV and V snags showed increased radial growth. Many snags in class IV and V were located on bog and semi-bog sites (Chapter III) where growing conditions may not improve after the overstory dies. Factors responsible for hemlock release were not studied, but changes caused by overstory death such as increased light; nutrient release into the soil from the decomposition of Alaska-cedar roots, mycorrhizae, and foliage; or decreased nutrient competition could contribute to faster radial growth of some hemlocks growing under dead cedars.

Estimating the date of death of overstory snags using release trees is difficult because the two events, overstory death and initiation of increased radial growth of the release tree, may not coincide in time. Some declining Alaska-cedars die slowly with their crowns thinning over a period of years (Shaw et al. 1985), perhaps partially releasing some understory hemlocks one or several years prior to cedar death. However, a lag effect may delay faster radial growth when better conditions develop (e.g., optimal light and moisture) because the optimal conditions of one year influence foliage growth, and consequently radial growth, during the following year (Kramer and Kozlowski 1979). McCaughey and Schmidt (1982) found that suppressed saplings in mixed conifer stands in the Rocky Mountains responded to partial overstory removal with an average 2.5-fold increase in height growth rate, and showed a 4-fold height growth increase in areas where all overstory was removed. Growth was sometimes depressed for one or

two years following cutting as saplings adjusted to the new conditions, but faster growth was underway within two to four years after overstory treatment. Release responses may vary with the shade tolerance of different tree species; hemlock species release well because of their relative shade tolerance.

Rope trees were useful in estimating the time of death for completely dead snags of the same class and, therefore, helped to determine when mortality began. Moreover, they provided clues regarding the potential causes of Alaska-cedar decline. Rope trees shared several characteristics with dead Alaska-cedar snags: 1) rope trees often occurred next to snags with tops in similar stages of deterioration, 2) both experienced a decline in radial growth before death (Shaw et al. 1985), or partial bole death for rope trees, and 3) snag classes of both are similarly associated with particular forest communities (Chapter III). Thus, the cause of damage to rope trees must be considered when evaluating causes for Alaska-cedar decline.

Rope trees were not injured during one sudden incident such as an extreme climatic event; those with the longest-dead (class V) tops had boles that were killed over a long span of time from approximately 50 to 125 years ago. Also, their slow decline in growth many years prior bole death does not support a sudden event as the cause of tree injury.

Rope trees differ from completely dead snags in that there are fewer rope trees with recently killed tops. In an extensive survey of mortality sites (Chapter III), 8% of the Alaska-cedars examined (live and dead) were rope trees. The longer-dead tops predominated on these rope trees as 39% had class V tops and 31% had class IV tops, but only 15% had class III tops, 8% had class II tops, and 7% had class I tops.

Class V rope trees were the most useful in dating the onset of extensive mortality. Whatever caused the onset probably injured and partially killed the cedars that now appear as rope trees. Reasons for why class I, II, and III rope trees are uncommon, even though cedars continue to die, is not understood.

I consider class V snags (boles intact, but no primary limbs retained) to represent the original extensive mortality. These trees died an average of 81 years ago, as estimated by the rope tree method and were present and common at all mortality sites examined (Chapter III). Since some class V snags died before the average of 81 years ago, numerous Alaska-cedars probably began to die before the turn of the century, the best estimate being about about 1880. The early aerial photographs support this date by showing the extensive and widespread occurrence of dead trees in 1927. The more deteriorated snags in class VI with broken off and deteriorated boles were only infrequently encountered and were not associated with distinct mortality sites (Chapter III). These trees died prior to the onset of extensive mortality and may also represent the non-epidemic or background level of mortality. Also, downed cedar logs, which could hypothetically represent an earlier mortality, were not frequently encountered (Chapter III).

The appearance of numerous dead Alaska-cedars around the turn of the century is also suggested by historical observations. Mertens (1827), Rothrock (1868), Dall (1870, observations in 1865), Petrof (1884, observations in 1880), Nelson (1887, observations in 1877-1881), and the Harriman Expedition (Emerson et al. 1904, observations in 1899) all observed Alaska-cedar near Sitka and elsewhere in southeast

Alaska, but none mentioned Alaska-cedar mortality. Sheldon (1912) observed dead Alaska-cedar near Pybus Bay on Admiralty Island in 1909 stating that, "vast areas are rolling swamp, with yellow cedars, mostly dead." Five years later, Anderson (1914) described the size and growth form of Alaska-cedar near Sitka, and his plate XXI shows an "open formation [bog] at 1800 feet." The caption accompanying this photograph reads, "A dying cedar appears on the extreme right..." No further mention of dead or dying Alaska-cedar was made. Subsequent references to dead or dying Alaska-cedar occur from 1927 until the present (Laurent 1982), especially in the Annual Forest Condition Reports for Alaska. Thus, the first historical references of dead or dying Alaska-cedar (1909) seems consistent with our estimates of when a large number of Alaska-cedar snags would have first become obvious in southeast Alaska.

The slow deterioration of Alaska-cedar snags likely results from the species' extreme resistance to decay (Harris 1971), as well as the cool and moist climate of southeast Alaska (Farr and Harris 1979). Sapwood of Alaska-cedars is decayed by a flourishing fungal community following tree death (Chapter IV); however heartwood, even when exposed, is resistant to decay.

Time since death has not previously been estimated for Alaska-cedar snags. In his review on literature of dating tree death in the western United States, Lowery (1982) did not mention Alaska-cedar, but he did place cedars in the class with the most durable wood. Most studies on dating tree death have been on pines and firs and describe characteristics of snags up to ten years after their death. Embry (1963) reported on the state of decomposition of western

redcedar (Thuja plicata Donn ex D. Don) and western hemlock up to nine years after girdling or poisoning in southeast Alaska. Differing methods make comparisons of our results with Embry's difficult, but his results suggest a faster rate of deterioration for western redcedar and especially for western hemlock than for Alaska-cedar.

In conclusion, aerial photographs, the rope tree method of dating cedar death, and historical references all support the suggestion that the onset of extensive mortality of Alaska-cedar began somewhat before the turn of the century (1900).

LITERATURE CITED

- Anderson, H.E. 1959. Silvical characteristics of Alaska-cedar (Chamaecyparis nootkatensis). U.S. Forest Serv. Alaska Forest Res. Center Sta. Paper 11. 10 p.
- Anderson, J.P. 1916. Notes on the flora of Sitka, Alaska. Proceedings of the Iowa Academy of Science. 23:427-482.
- Dall, W.H. 1870. Alaska and its resources. Lee and Shepard, Boston, MA. 627p.
- Downing, G.L. 1960. A cedar bark beetle outbreak. USDA For. Serv., Alaska For. Res. Cent., For. Insect Surv. Rep. 6. 2p.
- Duff, S.R., H. Erdtman, and W.E. Harvey. 1954. The chemistry of the natural order Cupressales. XII. Heartwood constituents of Chamaecyparis nootkatensis (Lamb.) Spach. Nootkatin. Acta Chem. Scand. 8(6):1073-1082.
- Embry, R.S. 1963. Estimating how long western hemlock and western redcedar trees have been dead. USDA For. Serv. Research note NOR-2. 2p.
- Emerson, B.K., C. Palache, W.D. Dall, E.O. Ulrich, and F.H. Knowlton. 1904. Harriman Alaska Expedition. Geology and Paleontology. Vol. IV. Harriman Alaska Series of the Smithsonian Institute. Publication 1993. New York Doubleday Page & Co., New York, NY. 173p.
- Farr, W.A. and A.S. Harris. 1979. Site index of Sitka spruce along the Pacific coast related to latitude and temperatures. For. Sci. 25:145-153.
- Frear, S.T. 1982. What's killing the Alaska yellow cedar? Amer. For. 88(11):41-43, 62-63.
- Harris, A.S. 1971. Alaska-cedar. American Woods-FS 224. USDA Forest Service. 7p.
- Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of woody plants. Academic Press, Orlando, FL. 881p.
- Laurent, T. 1982. Cedar dieback - Is it the problem. Proceedings of the second Alaska Integrated Pest management conference. Univ. of Alaska, Cooperative Extension Service, and USDA Forest Service. pp.104-107.
- Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. Can. J. For. Res. 15:200-213.
- Lowery, D.P. 1982. The dead softwood timber resource and its utilization in the West. USDA For. Serv., Intermountain For. & Range Exp. Sta., Ogden UT. Gen. Tech. Rep. INT-125. 18p.

McCaughey, W.W. and W.C. Schmidt. 1982. Understory tree release following harvest cutting in spruce-fir forests of the Intermountain West. USDA For. Serv. Res. Pap. INT-285.

McGee, C.E. 1981. Response of overtopped white oak to release. U.S. Dep. Agric. For. Serv. Res. Note SO-273.

Mertens, H. 1827. Two scientific notices by the late Dr. Henry Mertens. Botanical Miscellany. 3:1-35.

Nelson, E.W. 1887. Part 1. Birds of Alaska. pp. 19-226. In: Report upon natural history collections made in Alaska between the years 1887 and 1881, by Edward W. Nelson. Arctic series of publications issued in connection with the Signal Service, U. S. Army. No. 3.

Petrof, I. 1880. The population and resources of Alaska. In: Committee of military affairs, Compilations of narratives, explorations in Alaska. Government Printing Office, Washington D.C. pp. 145-147.

Rothrock, J.T. 1867. Sketch of the flora of Alaska. Smithsonian Institute Annual Report 1887:433-463.

Sargent, R.H. and F.H. Moffit. 1929. Aerial photographic surveys in southeastern Alaska. U.S. Geological Survey Bulletin 797-E. GPO. pp. 143-160.

Shaw, C.G. III, A. Eglitis, T.H. Laurent, and P.E. Hennon. 1985. Decline and mortality of Chamaecyparis nootkatensis in Southeastern Alaska, a problem of long duration but unknown cause. Plant Dis. 69:13-17.

Sheldon, C. 1912. The wilderness of the North Pacific Coast islands: a hunter's experience while searching for wapiti, bears, and caribou on the larger islands of British Columbia and Alaska. Scribner's Sons, New York. 246 p.

CHAPTER III

DYNAMICS OF DECLINE AND MORTALITY OF CHAMAECYPARIS NOOTKATENSIS
IN SOUTHEAST ALASKA

ABSTRACT

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a valuable tree species that has been suffering from decline and mortality in southeast Alaska for the last 100 years. Boundaries of mortality at seven sites were mapped using aerial photographs taken in 1927, 1948, 1965, and 1976. Mortality was present at all seven sites in 1927 and its boundaries have expanded. Mortality in 1976, however, typically extended not more than 100 m beyond the 1927 limit. Dead Alaska-cedar trees, classified by their degrees of deterioration (Chapter II), were recorded in 427 plots along 39 ground transects. Fifty-five taxa of understory vegetation were also recorded from 280 plots along 21 transects; variation among vegetation plots was analyzed using Detrended Correspondence Analysis (DECORANA) to produce an ordination. Only one important axis was generated, representing a gradient from bogs to sites with better drainage. These analyses indicate that local spread of cedar decline has occurred along this gradient; plots with more recently killed cedar trees had high average ordination scores (better drainage), and plots with cedars killed long ago had low average scores (boggy). Ordination plot scores from this axis were compared with basal area of live and dead conifer species: Alaska-cedar was less confined than other conifers to either bogs or

the better drained sites and was the dominant tree species in the intermediate (semi-bog) forest type. Alaska-cedar is suffering from a disproportionate level of mortality relative to other conifers, and most mortality is associated with bog and semi-bog sites. Snags that probably date from the onset of extensive mortality (Class V), with all limbs missing but boles intact, were relatively common (at least 8% of all snags) from all 23 sites where intensive mortality was surveyed on the ground. Also, all sites with mortality in southeast Alaska (examined on aerial photographs or observed from the air or ground) have these snags; thus, the problem has probably not spread to new sites since its onset about 100 years ago. Although the decline problem is species-specific and has patterns of local spread, the spread of mortality is along a specific, pre-existing ecological gradient. The apparent lack of any site-to-site spread in the last 100 years suggests that Alaska-cedar decline is not caused by some biotic agent.

INTRODUCTION

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a slow-growing conifer that ranges from Prince William Sound in Alaska, south through British Columbia, to near the Oregon-California border (Harris 1971). Alaska-cedar occurs from sea level to timberline in southeast Alaska (Harris and Farr 1974) where it can grow in nearly pure stands but, more commonly, exists in scattered groups or as individual trees mixed with other conifers (Ruth and Harris 1979). Its

narrow grain, extreme decay resistance, and bright-yellow, aromatic heartwood make Alaska-cedar a useful and valuable timber species (Frear 1982).

Extensive decline and mortality (Fig. III.1) has been occurring for many years in stands of Alaska-cedar throughout southeast Alaska (Laurent 1982, Frear 1982, Shaw et al. 1985). I recently determined that this problem began around 1880 (Chapter II). The primary cause of mortality is unknown; however, no single biotic or abiotic factor appears to be primarily responsible for tree death (Shaw et al. 1985).

Aerial surveys flown to detect forest pests indicate that mortality of Alaska-cedar is extensively distributed throughout southeast Alaska and is most often associated with bog (muskeg) or semi-bog sites (Downing 1960, Laurent 1982). My own aerial observations indicate that dead and dying trees occur in large, expansive areas, as well as smaller, discrete patches. Dying Alaska-cedars sometimes occur on the perimeters of large and small mortality sites, suggesting that the problem may be spreading, although rates of spread are unclear.

Other ecological aspects of Alaska-cedar decline are unknown. For example, the location where trees first began to die has not been determined (Shaw et al. 1985). The influence of slope, drainage patterns, and forest community types on mortality and its possible spread have not been measured. Neiland (1971) reported that Alaska-cedar is less restricted than other conifers to any one of three forest types (bog, forest and an intermediate community), but a detailed description of Alaska-cedar communities or means for distinguishing these community types has not been done.



Figure III.1. Decline mortality of Alaska-cedar at Deadman Reach, Baranof Island, Alaska

The lack of a critical ecological assessment of the mortality problem has limited our understanding of the primary cause of Alaska-cedar decline. Knowledge of which conifer species are affected (i.e., host range of a hypothetical pathogen), where mortality occurs, and when mortality began should help to determine whether the primary cause is biotic or abiotic. If mortality is caused by a pathogen, then patterns of spread should be evident. The patterns of spread should indicate what type of pathogen might be present. Also, examining sites where mortality has occurred for many decades may suggest alternatives for managing affected stands.

The objectives of this paper are: 1) to clarify whether conifer species other than Alaska-cedar are dying in the same areas in large numbers; 2) to determine the occurrence of Alaska-cedar in various forest community types, where it is healthy and also where it is dead and dying; 3) to document whether mortality is spreading over short or long distances, or both; and 4) if mortality is spreading, to describe patterns of spread (i.e., correlations with distance of spread, slope, aspect, and forest community type).

To meet these objectives, aerial photographs taken between 1927 and 1976 were used to document the occurrence and spread of mortality, and surveys were conducted in forest communities expressing varying degrees of mortality. An analysis of understory plant distribution was the basis for an ordination of forest community types.

MATERIALS AND METHODS

Aerial Photographic Analysis of Mortality

Seven areas currently expressing mortality of Alaska-cedar, all on Chichagof and Baranof Islands near Peril Strait (Figs. III.2 and III.3), were examined on aerial photographs taken in 1927, 1948, 1965, and 1976 (Table III.1). All seven sites had some distinct perimeters to the mortality (areas where stands with and without mortality adjoined), but only two sites were discrete patches of mortality completely surrounded by healthy stands or shoreline. The 1976 photographs were in color, the rest were in black and white. The 1927 series consists of one vertical and two oblique photographs taken at each photo point, but only vertical prints were used in mapping. These 1927 photographs are of particular interest since they may represent the earliest photographs anywhere of a large forested area (approximately 10,000 square miles) (Sargent and Moffit 1929). Photographs from some years were not available for all seven sites, but all four serial sets were available for three sites.

Stereopairs (two adjacent and overlapping photographs) of each mortality site from each photographic series were viewed with a stereoscope. Boundary lines were drawn directly onto photographs to delineate the perimeter of mortality at that time. These boundary lines, along with geological details (i.e., beaches, drainages, and ridges) were transposed into maps free of topographic displacement using a radial planimetric plotter (Paine 1981). The four individual maps of each site were combined into one map by using a mapograph machine to bring individual maps to the same scale.

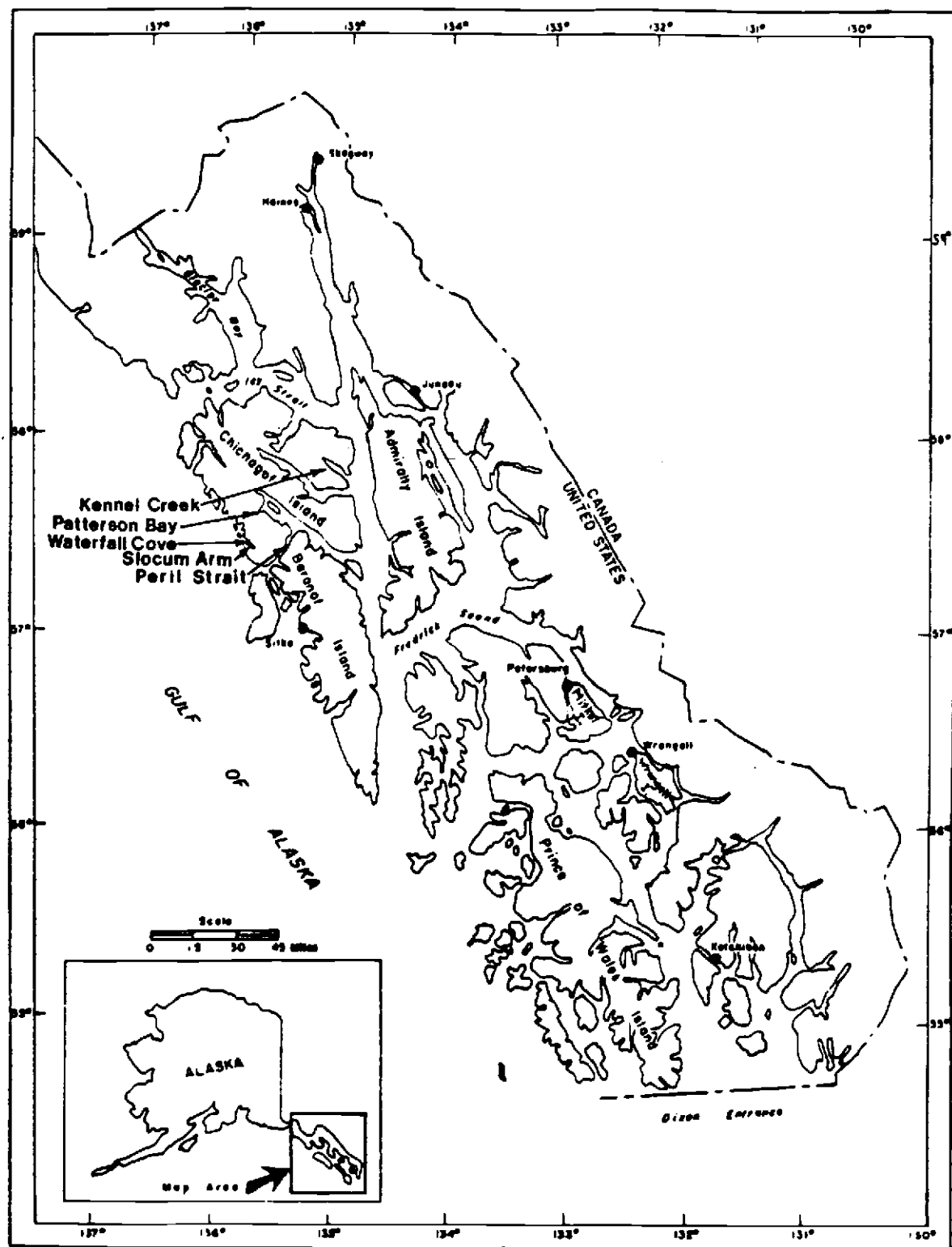


Figure III.2. Location of study sites in southeast Alaska

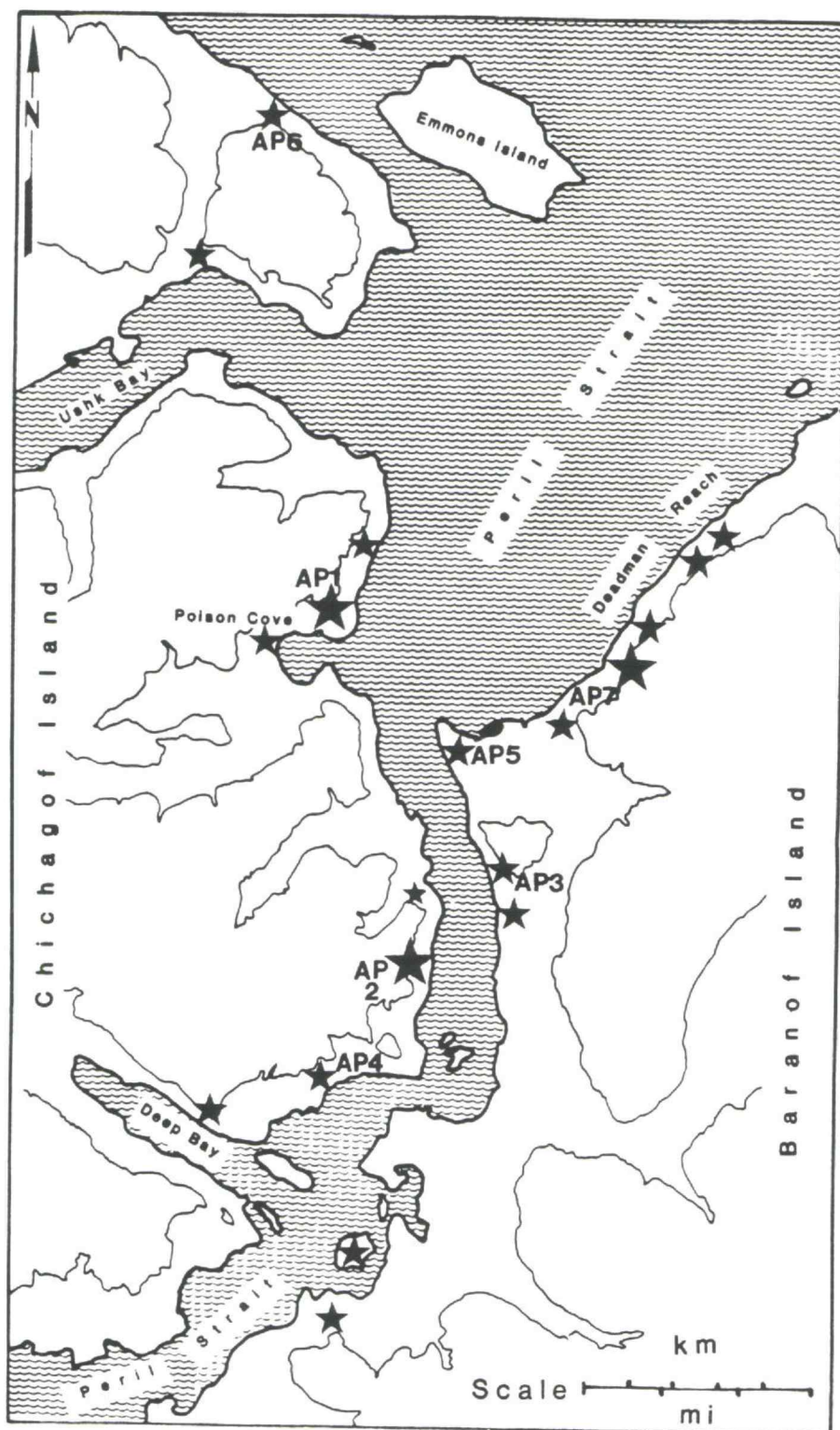


Figure III.3. Map of Peril Strait in southeast Alaska showing extensive ★ and intensive ★ sampling transects and aerial photographic mapping locations (AP).

Table III.1. Aerial photographs used for mapping mortality perimeters (see Fig. III.3). Aerial photographs (1976) used to describe extent of mortality and associations with forest types in the Peril Strait area (below)

<u>Site</u>	<u>1927</u>	<u>1948</u>	<u>1965</u>	<u>1976</u>
1 Poison Cove	W27-2 W29-2	SEA 122L 62 SEA 122L 63	ALP 50A-16 ALP 50A-17	F16CN 25 303 F16CN 25 304
2 Susan's Landing	W22-1 W23-1	SEA 122L-58 SEA 122L-59	ALP 7 17B 30 ALP 7 17B 31	F16CN 26 139 F16CN 26 140
3 Lost Hat	- -	SEA 122R-59 SEA 122R-60	ALP 18-44 ALP 18-45	F16CN 27 198 F16CN 27 199
4 Arthur site	W23-1 W24-1	SEA 122L-58 SEA 122L-59	ALP 51A-2 ALP 51A-3	F16CN 26 141 F16CN 26 142
5 Favorite Anchorage	- -	SEA 122R-60 SEA 122R-61	ALP 17B-34 ALP 17B-35	F16CN 26 137 F16CN 26 138
6 Vixen site	W352-10 W353-10	SEA 122L-68 SEA 122L-69	ALP 50A-26 ALP 50A-27	F16CN 25 298 F16CN 25 299
7 Deadman Reach	- -	SEA 124R-31 SEA 124R-32	ALP 18-47 ALP 18-48	F16CN 27 201 F16CN 27 202

<u>Photographic series</u>	<u>Flight line</u>	<u>Photograph number</u>
F16CN	25	118 - 124
F16CN	25	298 - 312
F16CN	26	130 - 150
F16CN	27	186 - 205
F16CN	28	269 - 280

A map of the Poison Cove site (Fig. III.3) was made more intensively. In addition to mapping boundaries of mortality, the concentration of mortality was visually stratified into four types based on concentrations (or densities) of dead trees: concentrated, moderate, scattered, and background. Intensive maps from 1927, 1948, 1965, and 1976 of Poison Cove were kept separate and not combined into a final map. This allowed for a reconstruction of stand structure and composition before, during, and after the front of dying trees advanced ahead.

In addition, the general distribution of mortality and its association with topographic relief and forest types was examined and described from 75 of the 1976 aerial photographs (Table III.1), which covered most of the forested land (about 22 km²) along Peril Strait (Fig. III.3).

Forest Community Associations

Understory plants were used to determine relationships among forest stands. The presence and abundance of 60 understory plant taxa were recorded from within a 3 m radius of plot centers from the 280 plots described below. Dominance rating included five categories: nearly pure in its layer (>50 percent cover), dominant (25-50 %), common (5-25 %), rare (0-5 %), and absent (0 %). Five rare understory taxa were dropped from the ordination analysis, leaving 55 plant taxa. Understory plant distribution was analyzed by a computer ordination program--DECORANA (Detrended Correspondence Analysis)--which generates axes that represent gradients of plant species' distribution (Hill and Gauch 1980, Gauch 1982). Plot scores and species scores are produced

for all axes. The accuracy of these axes was not subjected to statistical analysis, but was evaluated by examining the relative values of two factors: Eigen values and lengths of gradients: these methods are an aid in interpretation for this type of analysis.

Gauch (1982) recommends graphing environmental parameters (I used coniferous overstory) with axes to see if they have a related distribution that aids in interpretation of gradients. Also, known habitat preferences of species used in the ordination can assist with interpretation of these gradients (Gauch 1982). Therefore, interpretations of these axes were based on field observations of the distribution of these plants and their associated coniferous overstory.

Ordination plot scores along important gradients were grouped into nine equal intervals and class means compared with: mean values for live and dead basal area of each coniferous species, the presence or absence of cedar mortality, classes of cedar snags (see below), and classes of snag tops on cedar rope trees. Rope trees are Alaska-cedars with dead tops and a dead bole except for a narrow strip of live callus tissue connecting a live and bushy branch cluster to roots (Chapter II). Snag classes, and snag classes of the dead tops of rope trees, were related to ordination plot score intervals using a one-way analysis of variance (ANOVA) and Tukey's multiple comparison test ($p=0.05$) to determine if different snag classes were associated with different intervals along the ordination gradient. Live and dead conifer basal area, and incidence of mortality were plotted against ordination gradients and examined visually.

Forest Survey

Survey transects were established through a variety of forest types to evaluate: 1) which tree species were dead or declining, 2) the severity of mortality, 3) the patterns of spread of the mortality, and 4) the general growth habits of Alaska-cedar. A total of 280 plots were established along 21 transect lines at three general locations on Baranof and Chichagof Islands. Sixteen transects were located in forests along Peril Strait, four near Freshwater Bay and one near Slocum Arm (Fig. III.2). All but two transects were at elevations under 300 m. Plots were established every 50 m along transect lines, beginning 25 m from a beach (sea level), and progressed upslope through areas of mortality. Transects ended when two or more consecutive plots contained few, if any, dead trees.

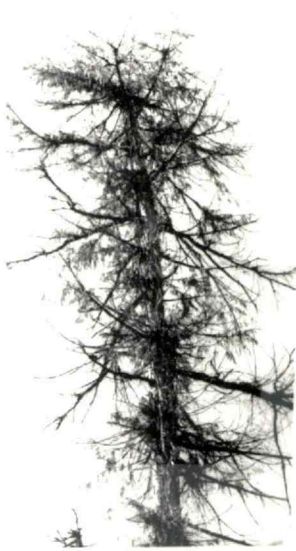
The basal area of live trees and snags (dead trees) was measured for each conifer by using a 3 or 6 m²/ha Basal Area Factor (BAF) wedge prism (Wenger 1984) (13 ft²/ac and 26 ft²/ac, respectively). A 3 m²/ha BAF prism was only used if fewer than ten trees were selected by the 6 m²/ha BAF prism. Snags of Alaska-cedar were easy to distinguish from other species because its aromatic heartwood is detectable even in stems that have been dead for 80 years or more (Chapter II). Snags of other conifers were identified to species by bark or wood characteristics. The two species of hemlock could not be differentiated when dead, and results are expressed as dead hemlock. Some snags could not be identified, except as non-cedars, and were classified as unknown. Tree height, dead or missing tops, epicormic branching, and scars were noted; plot slope, aspect, and elevation were measured; and understory vegetation and conifer reproduction recorded.

More intensive surveys were conducted at three sites along Peril Strait (Fig. III.3). In this survey, a total of 147 plots were sampled along 18 transects; transects at two sites radiated outward from the approximate middle of the somewhat circular patch of dead trees, and on the third site, where dead trees were not grouped in a circular pattern, transects were oriented upslope and parallel to one another. Plot trees were selected with the same prisms described above. Bole diameter at breast height (dbh) was measured for all Alaska-cedar trees, and six places on the cambium around the root collar (60 degrees apart) were examined by removing bark with a knife. These examinations were made to detect necrotic lesions that occur on declining cedars (Shaw et al. 1985) and to correlate their occurrence with azimuth as tested by chi-square analysis ($p=0.05$). Other plot and tree information, except understory plants, was recorded as in the extensive survey.

In the intensive survey, plots were segregated into "mortality" and "relatively healthy" categories based on observations of surrounding portions of the stand. On plots in mortality areas, the proportion that each conifer species contributed to the total basal area of dead conifers and the proportion of dead basal area for each species (from the live + dead basal area of that species) was determined to determine quantitatively which species were dying.

Snag Classes

Each dead Alaska-cedar was placed into one of six snag classes, based on degrees of foliage, twig, or branch retention, and deterioration of its bole (Fig. III.4). Time since death has been



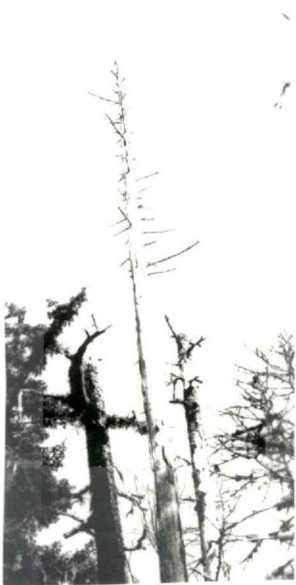
SNAG CLASS I
most foliage
retained;
dead \bar{x} = 3 yrs



SNAG CLASS II
most twigs
retained;
dead \bar{x} = 11 yrs



SNAG CLASS III
most secondary
branches retained;
dead \bar{x} = 31 yrs



SNAG CLASS IV
most primary
branches;
dead \bar{x} = 54 yrs



SNAG CLASS V
no primary
branches retained;
bole intact
dead \bar{x} = 81 yrs



SNAG CLASS VI
no primary
branches retained,
bole deteriorated;
death not dated

Figure III.4. Snag classification system for dead Alaska-cedar trees.

estimated for five of these snag classes (Chapter II). From those data we calculated the mean time since death for snag classes to be:

Class I -- dead, foliage retained.....dead \bar{x} = 3 yrs
 Class II -- dead, twigs retained.....dead \bar{x} =11 yrs
 Class III-- dead, secondary branches retained...dead \bar{x} =31 yrs
 Class IV -- dead, primary branches retained.....dead \bar{x} =54 yrs
 Class V -- dead, no branches retained.....dead \bar{x} =81 yrs
 Class VI -- dead, bole broken and deteriorated..death not dated

A modal snag class was determined for each plot. The mode, rather than mean, is a better indicator of the condition of most snags since mean values could represent a snag class not present on a plot by averaging long dead and more recently killed snags. Plots lacking Alaska-cedar trees were rated zero. Plots with two-thirds or more live symptomless cedars were rated healthy. Plots with one-third or more dead or dying cedar were assigned either a rating equal to the modal snag class in that plot (i.e., I, II, III, IV, V, or VI) or as dying. Plots were designated "dying" if cedars with live but thinning or off-color crowns were more common than any snag class. In the unusual case of ties, plots were assigned a snag rating equal to the longer-dead (higher-number) class, which best reflects when mortality began.

RESULTS

Analysis of Mortality on Aerial Photographs

Maps delineating the extent of mortality made from aerial photographs taken in 1927, 1948, 1965, and 1976 clearly show that peripheral boundaries of mortality have expanded at all seven sites (Figs. III.5a-d). In 1927, however, mortality was apparent on each site and covered a large portion of the area where trees are now dead and dying. Subsequent mortality has rarely extended more than 100m beyond the boundary apparent in 1927. Additional mortality has occurred upslope, along the contour, and downslope; however, mortality encroached upslope most commonly.

On the site mapped intensively at Poison Cove (Fig. III.6), the edge of mortality appears to have progressed slowly outward with a scattering of trees dying ahead of others, rather than advancing as a narrow band of dying Alaska-cedars. Within this zone of scattered dead trees, mortality intensified as more trees died. The central area with the greatest density of snags in 1927 had only scattered, recent mortality in 1976. This central area appeared on photographs as a green region contrasting with the grey of peripheral regions with heavy mortality. Mortality fronts stopped at shorelines or obvious and abrupt changes in forest type.

In addition to detailed mapping, 1976 aerial photographs were used to determine the extent and distribution of cedar mortality along Peril Strait. Mortality appeared to be associated with the edges of nearly all open bogs. Some bogs extend, contiguously or in chains, for several miles along fairly flat terrain at lower elevations (Fig.

SITE 1: POISON COVE

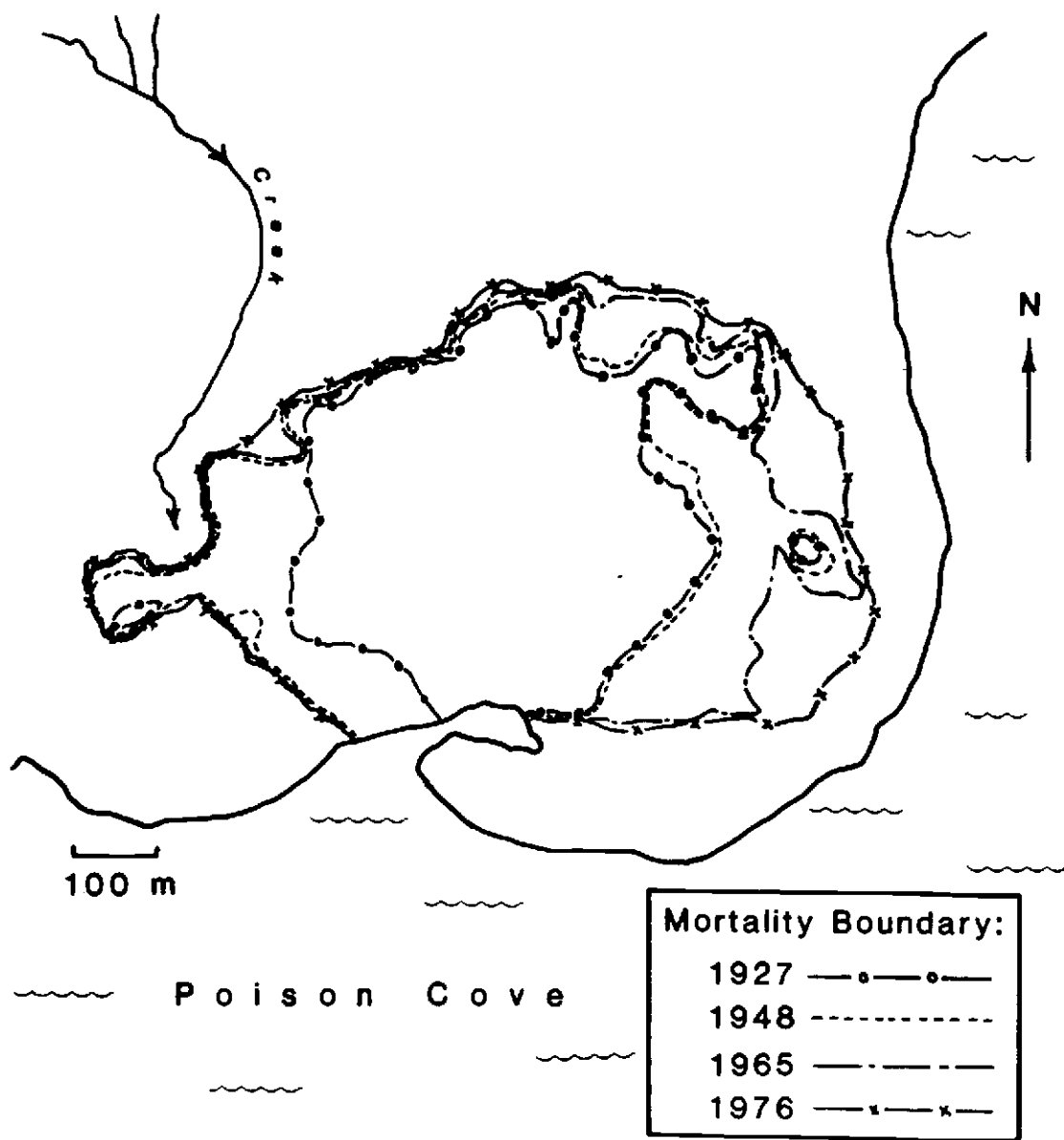
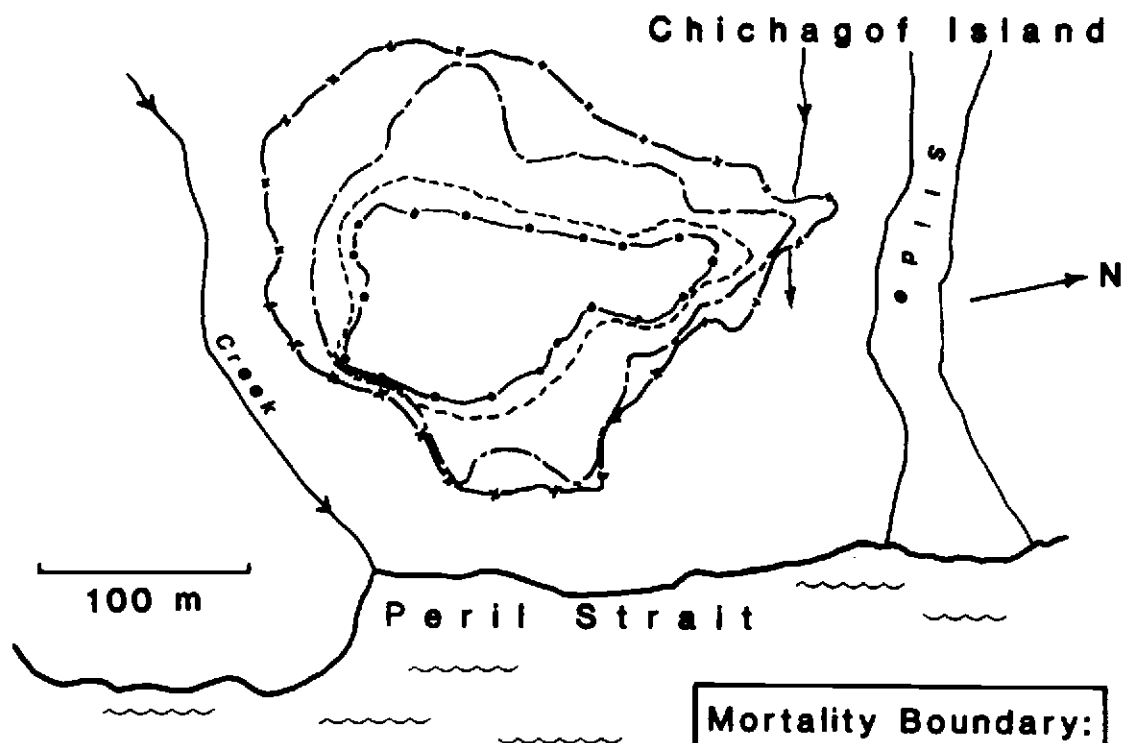


Figure III.5a. Mortality at Poison Cove showing the perimeters of dead and dying trees in 1927, 1948, 1965, and 1976. Maps made from aerial photographs taken in each year.

SITE 2: SUSAN'S LANDING



SITE 3: LOST HAT

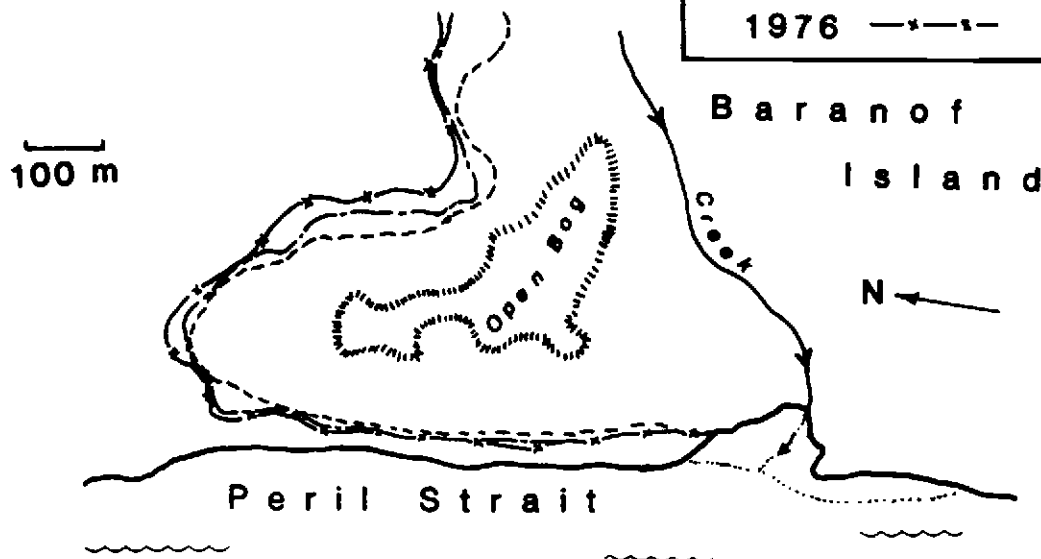
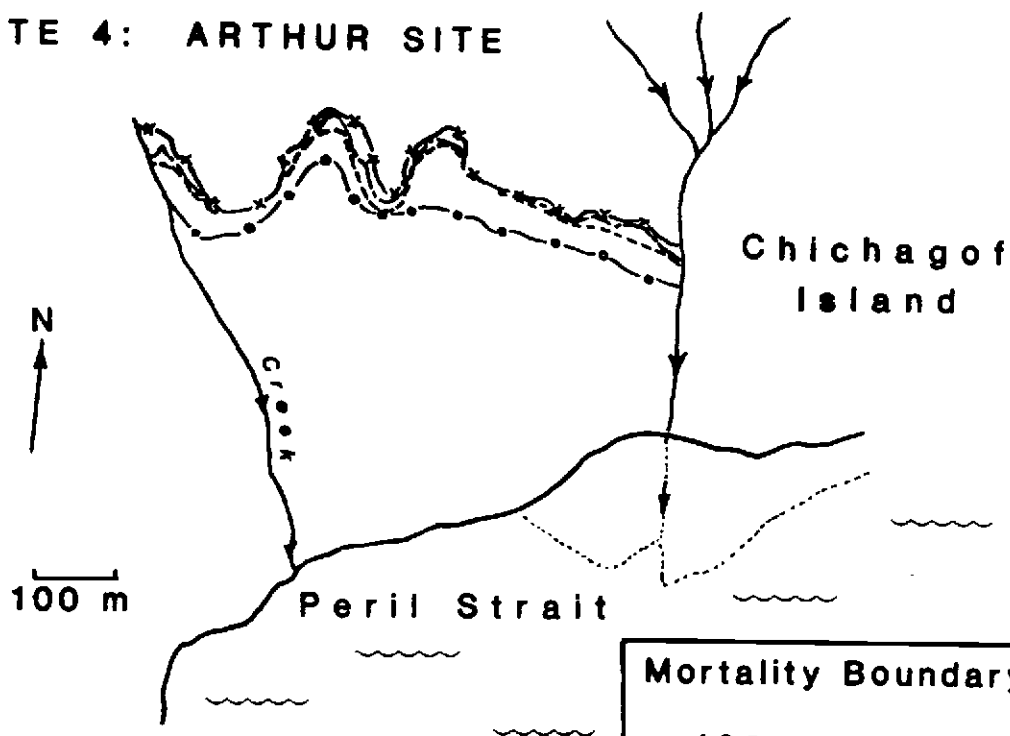


Figure III.5b. Mortality at Susan's Landing and Lost Hat showing the perimeters of dead and dying trees in 1927, 1948, 1965, and 1976. Maps made from aerial photographs taken in each year.

SITE 4: ARTHUR SITE



SITE 5: FAVORITE ANCHORAGE

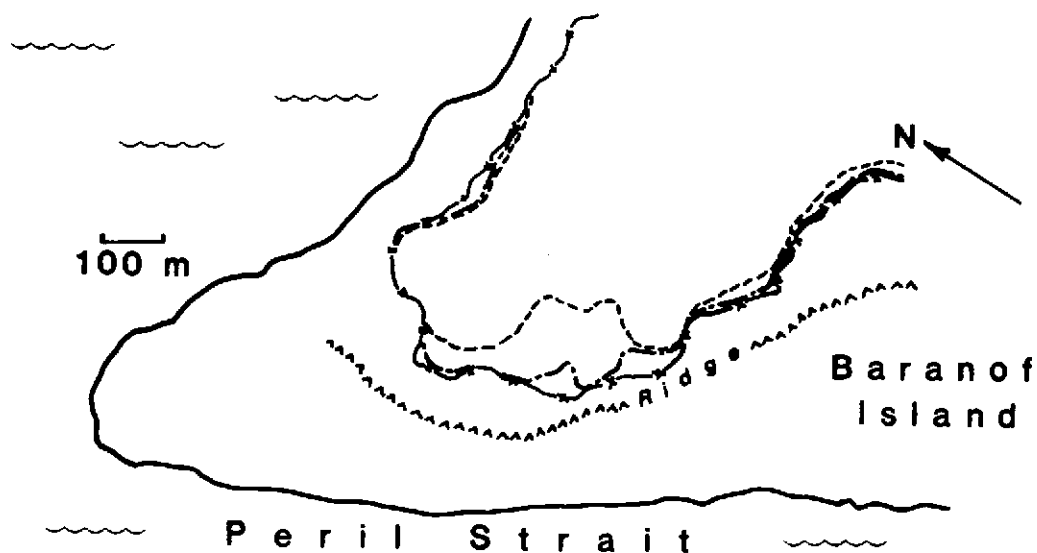
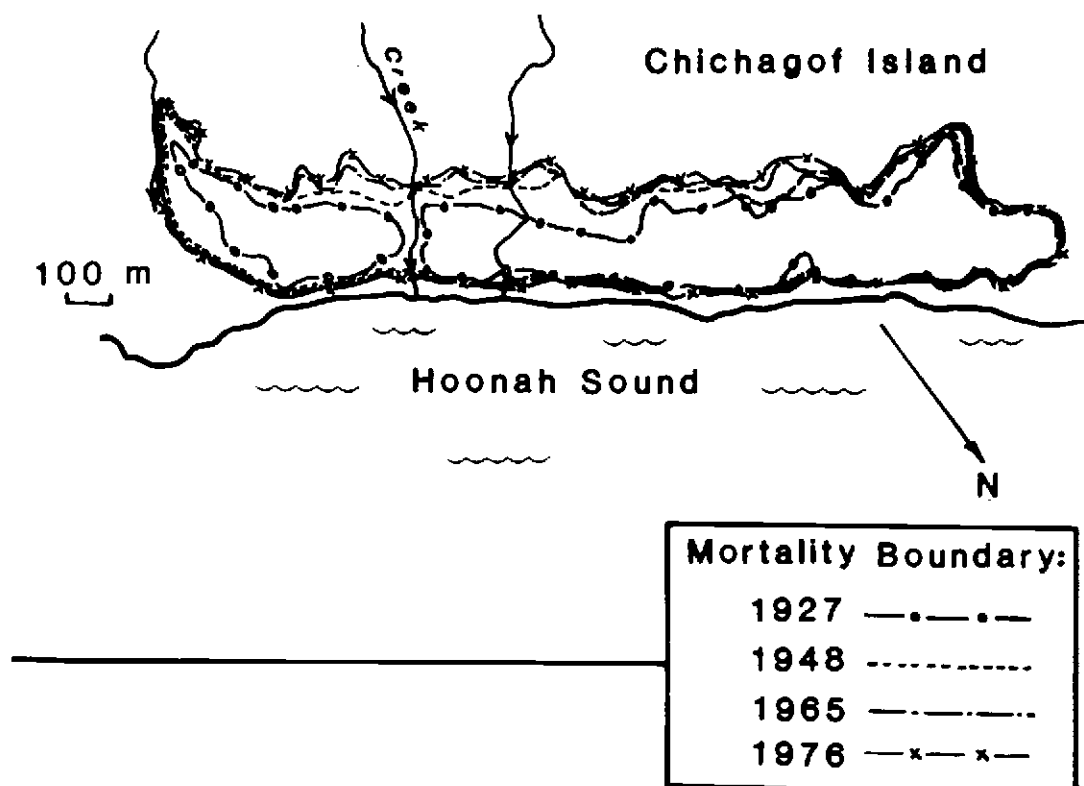


Figure III.5c. Mortality at Arthur Island site and Favorite Anchorage showing the perimeters of dead and dying trees in 1927, 1948, 1965, and 1976. Maps made from aerial photographs taken in each year.

SITE 6: VIXEN SITE



SITE 7: DEADMAN REACH

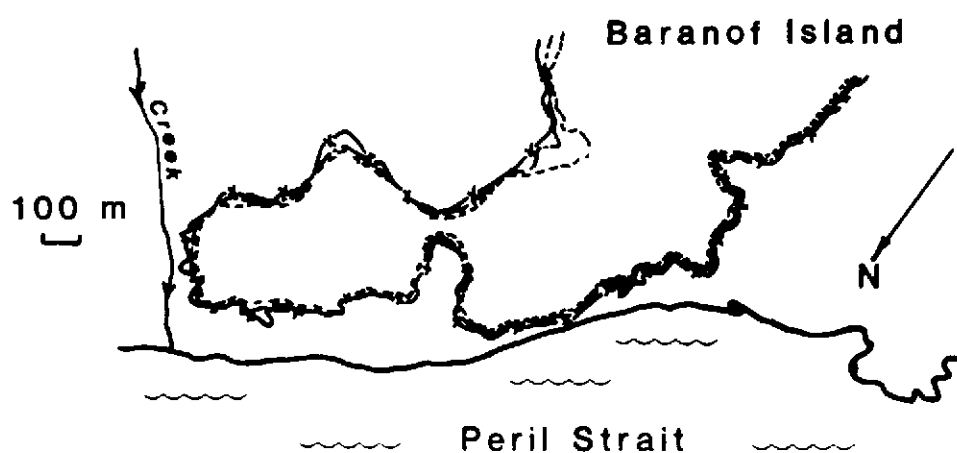


Figure III.5d. Mortality at Vixen Island site and Deadman Reach showing the perimeters of dead and dying trees in 1927, 1948, 1965, and 1976. Maps made from aerial photographs taken in each year.

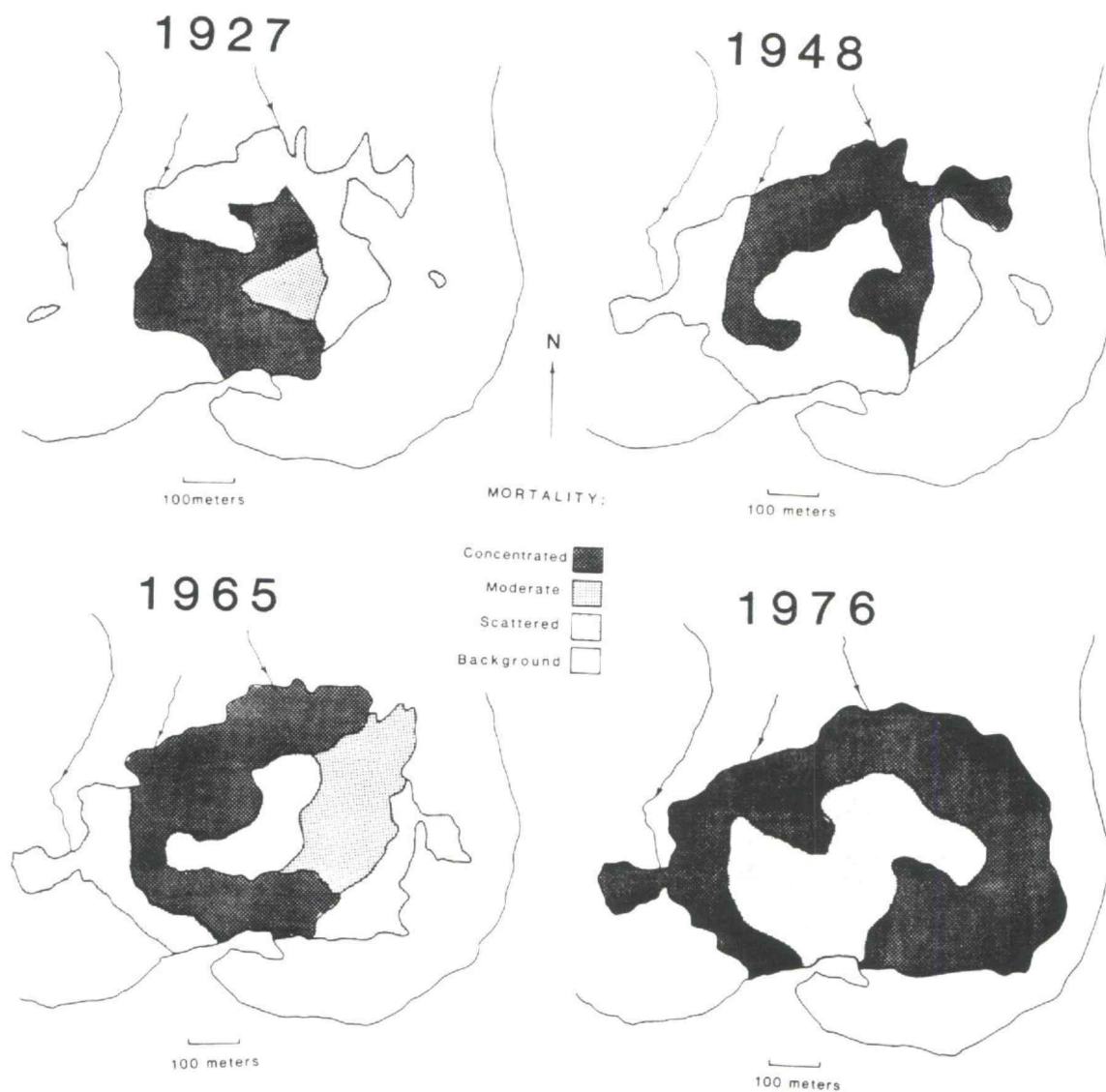


Figure III.6. Maps of mortality of Poison Cove mortality made from 1927, 1948, 1965, and 1976 aerial photographs. Severity of mortality was placed into four categories based on densities of dead trees.

III.7). Mortality was consistently associated with the edges of these bogs, as viewed from 1976 aerial photographs. One long series of bogs extends for about 7 km (4 mi) from the drainages connecting Ushk Bay to Deep Bay (Fig. III.3) and has extensive mortality on the bog edges along the entire distance. Another long, unbroken stretch of dead trees occurs on Baranof Island at low elevations from just south of Deadman Reach for 9 km (6 mi) to Fish Bay (Fig. III.7). Large areas without mortality generally lack bogs.

Only four bogs found on the aerial photographs in the Peril Strait area lacked mortality; all four sites were above 150 m elevation and between 450 and 1200 m from the ocean. Subsequent ground examinations substantiated the lack of mortality around these bogs even though Alaska-cedar predominated in these surrounding stands at all four sites.

Mortality extends above 150 m elevation at some sites, however. One location, near Waterfall Cove at Slocum Arm, was observed from an airplane (Fig. II.1.) to have mortality extending from sea level to above 300 m (1000') elevation in a contiguous area of dead and dying trees. Another site, west of Poison Cove, was surveyed and had mortality extending up to 238 m (780') elevation.

Forest Community Associations

Data for understory plant taxa were analyzed to determine in which plant communities Alaska-cedar grew and in which the mortality occurred to better understand cedar autecology and possible reasons for tree decline. Ordination analysis (DECORANA) of the 55 understory plant taxa from 280 plots produced only one important axis. Only axis I is



Figure III.7. Mortality associated with a long series of bogs along Peril Strait on Baranof Island, Alaska.

considered to be important because values for both measures of axis importance, Eigen values and gradient lengths, fell off sharply and stabilized for the second and subsequent axes:

Axis I	Eigen value = 0.412	gradient length = 2.70
Axis II	Eigen value = 0.123	gradient length = 1.74
Axis III	Eigen value = 0.101	gradient length = 1.33
Axis IV	Eigen value = 0.082	gradient length = 1.09

Because DECORANA produces ordination scores for each species, plant taxa can be ordered along this first axis to assist in its interpretation. Understory plant taxa are ranked (Table III.2) according to their ordination scores from the first axis. The distribution of these species suggests that this first axis represents a gradient from bog communities to those with better drainage. Taxa with the lowest ordination scores were only observed growing on open bogs (Fig. III.8). For example, two species with extremely low ordination scores, Vaccinium uliginosum and Drosera rotundifolia, occurred predominantly on the edges of pools of water in open bogs (Fig. III.9a). Many taxa with intermediate scores were common along a wide range of the gradient (e.g., Cornus canadensis and Coptis trifolia). Other taxa with intermediate scores were confined to a specific intermediate position along the vegetative gradient (e.g., Fauria crista-galli (Fig. III.9b) and Cladothamnus pyrolaeiflorus). Understory plants with high ordination scores occurred only on the sites with better drainage away from bogs (e.g., Maianthemum dilatatum and Moneses uniflora) (Fig. III.9c). Thus, the position on the axis of

Table III.2. Understory plant taxa used in DECORANA ordination analysis. Taxa are ranked by their ordination scores for the first and only important axis from 280 plots. Plants with low scores occurred on bogs, those with high scores occurred on sites with better drainage.

Understory Plant Species	Species Ordination Score
<i>Vaccinium uliginosum</i> L.....	0
<i>Tofieldia glutinosa</i> (Michx.) Pers. subsp. <i>brevistyla</i> Hitchc.....	2
<i>Drosera rotundifolia</i> L.....	3
<i>Pinus contorta</i> Dougl. ex Loud subsp. <i>contorta</i> seedling.....	4
<i>Ledum palustre</i> L. subsp. <i>groenlandicum</i> (Oeder) Hult.....	7
<i>Kalmia polifolia</i> Wang.....	8
<i>Sanguisorba stipulata</i> Raf.....	14
<i>Empetrum nigrum</i> L.....	15
<i>Gentiana douglasiana</i> Bong.....	15
<i>Vaccinium caespitosum</i> L.....	17
<i>Pteridium aquilinum</i> (L.) Kuhn subsp. <i>langinosum</i> (Bong.) Hult.....	17
<i>Geum calthifolium</i> Menzies.....	17
<i>Dodecatheon jeffreyi</i> Van Houte.....	22
<i>Carex</i> spp., grasses.....	24
<i>Erigeron peregrinus</i> (Pursh) Green.....	25
<i>Phyllodoce aleutica</i> (Spreng.) Heller Love & Love subsp. <i>glanduliflora</i> (Hook.) Hult.....	25
<i>Equisetum</i> spp.....	27
<i>Fauria crista-galli</i> (Menzies) Makino.....	28
<i>Cladothamnus pyrolaeiflorus</i> Bong.....	29
<i>Vaccinium vitis-idaea</i> L.....	29
<i>Plantanthera dilatata</i> (Pursh) Lindl.....	31
<i>Coptis trifolia</i> (L.) Salisb.....	33
<i>Sphagnum</i> spp.....	35
<i>Tsuga mertensiana</i> (Bong.) Sarg. (seedling).....	37
<i>Chamaecyparis nootkatensis</i> (D. Don) Spach (seedling).....	37
<i>Linnaea borealis</i> L. subsp. <i>longiflora</i> (Torr.) Hult.....	38
<i>Lysichiton americanum</i> Hult. & St. John.....	41
<i>Veratrum viride</i> (Alt.) Pursh subsp. <i>sinuata</i> (Regel) Hult.....	42
<i>Lycopodium</i> spp.....	43
<i>Cornus canadensis</i> L.....	50
<i>Picea sitchensis</i> (Bong.) Carr (seedling).....	51
<i>Menziesia ferruginea</i> Sm.....	55
<i>Vaccinium alaskensis</i> How.....	57
<i>Coptis asplenifolia</i> Salisb.....	57
<i>Tsuga heterophylla</i> (Raf.) Sarg. (seedling).....	64
<i>Blechnum spicant</i> (L.) Roth.....	64
<i>Rubus pedatus</i> Sm.....	65
<i>Tiarella trifoliata</i> L.....	65
<i>Vaccinium parvifolium</i> Sm.....	65
<i>Athyrium felix-femina</i> (L.) Roth subsp. <i>cyclosorum</i> (Rupr.) Christens.....	68
<i>Listera</i> sp.....	76
<i>Rubus spectabilis</i> Pursh.....	78
<i>Streptopus streptopoides</i> (Ledeb.) Fry & Rigg.....	79
<i>Prenanthes alata</i> (Hook.) Dietr.....	80
<i>Thelypteris phegopteris</i> (L.) Slosson.....	81
<i>Streptopus amplexifolius</i> (L.) DC.....	82
<i>Dryopteris dilatata</i> (Hoffm.) Gray subsp. <i>americana</i> (Fisch.) Hult.....	83
<i>Echinopanax horridum</i> (Sm.) Decne. & Planch.....	89
<i>Streptopus roseus</i> Michx. subsp. <i>curvipes</i> (Vail) Hult.....	89
<i>Pyrola secunda</i> L. subsp. <i>secunda</i>	92
<i>Gymnocarpium dryopteris</i> (L.) Newm.....	94
<i>Maianthemum dilatatum</i> (How.) Nels. & Macbr.....	94
<i>Moneses uniflora</i> (L.) Gray.....	97
<i>Coralorrhiza maculata</i> Raf. subsp. <i>mertensiana</i> (Bong.) Calder & Taylor.....	100



Figure III.8. Open bog (muskeg) in southeast Alaska with mortality in surrounding stands

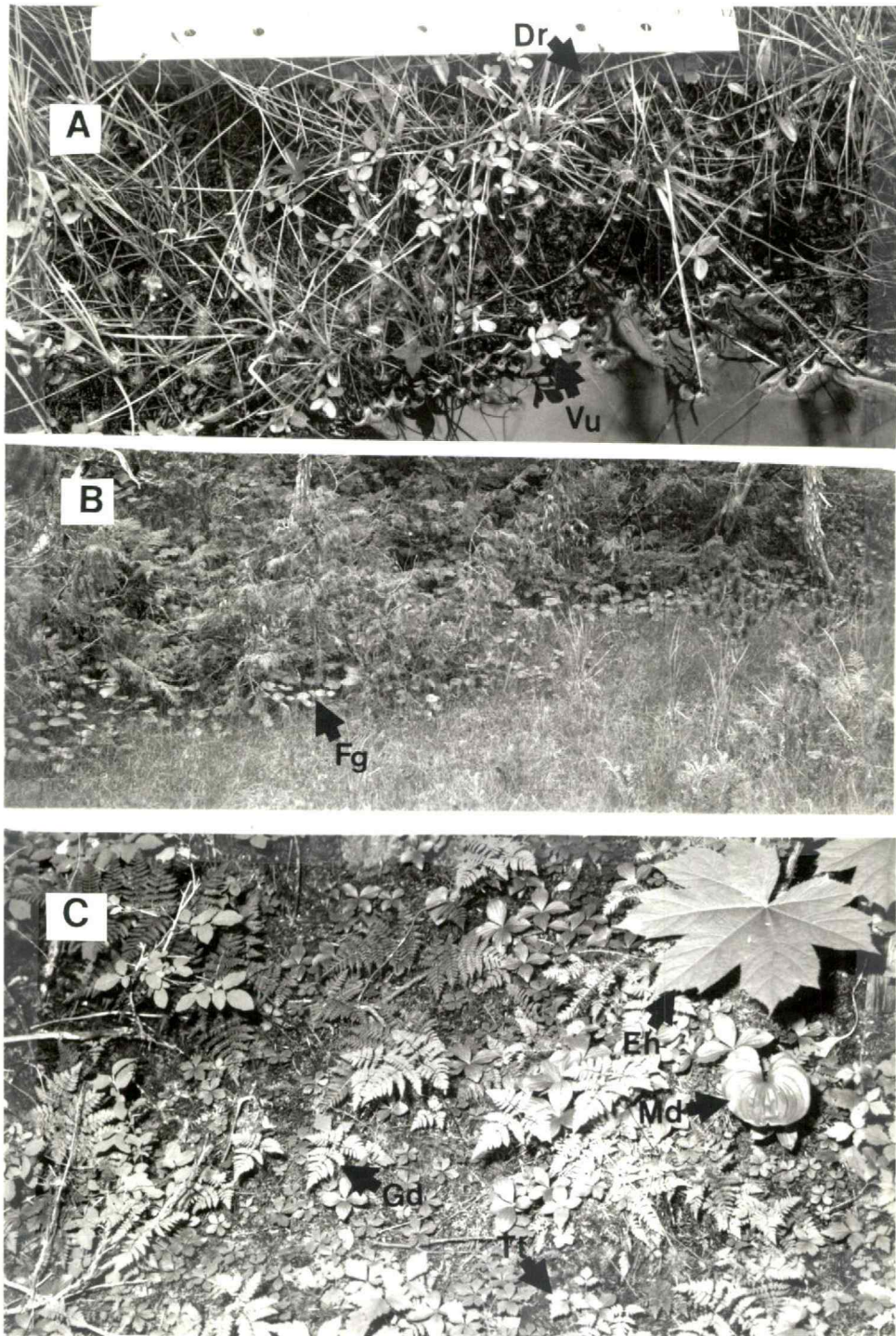


Figure III.9. A) Bog vegetation near pond: Vaccinium uliginosum (Vu) and Drosera rotundifolia (Dr); B) Fauria crista-galli (Fg) often occupies an intermediate position inbetween bogs and sites with better drainage; and C) vegetation on a better drained site: Gymnocarpium dryopteris (Gd), Maianthemum dilatatum (Md), Echinopanax horridum (Eh), and Tiarella trifoliata (Tt).

these understory species helps to substantiate the interpretation of the primary ordination axis.

Distribution of Conifers Along the Gradient from Bog to Better Drainage

DECORANA also produced plot ordination scores representing the same gradient from bog (low scores) to better drainage (high scores). Plot ordination scores were compared with data recorded from the 280 survey plots (e.g., live and dead tree basal area and cedar snag classes).

Based on average basal areas of live trees, Alaska-cedar was the dominant component along most of the vegetation gradient (Fig. III.10). Shore pine (Pinus contorta Dougl. ex Loud. var contorta) was common in the open bogs where total conifer basal area was at a minimum. At the other extreme (better drainage), western hemlock (Tsuga heterophylla (Raf.) Sarg.) was predominant, Alaska-cedar decreased, and shore pine was absent. Sitka spruce (Picea sitchensis (Bong.) Carr.) also had its greatest basal area on the better drained sites but was less common than western hemlock. Mountain hemlock (T. mertensiana (Bong.) Carr.) had much the same trend as Alaska-cedar but was not a dominant component at lower elevations where most of our sampling was conducted. Near timberline, mountain hemlock is the only tree-like species.

Alaska-cedar was rarely missing from plots along the middle portion of the gradient, but cedar trees were often absent in bogs or on the well drained sites. Prostrate Alaska-cedar (e.g., 0.5 to 1 m tall), not recorded in the basal area data, were common in bogs and semi-bogs in the Peril Strait area (Chapter VIII), even though upright

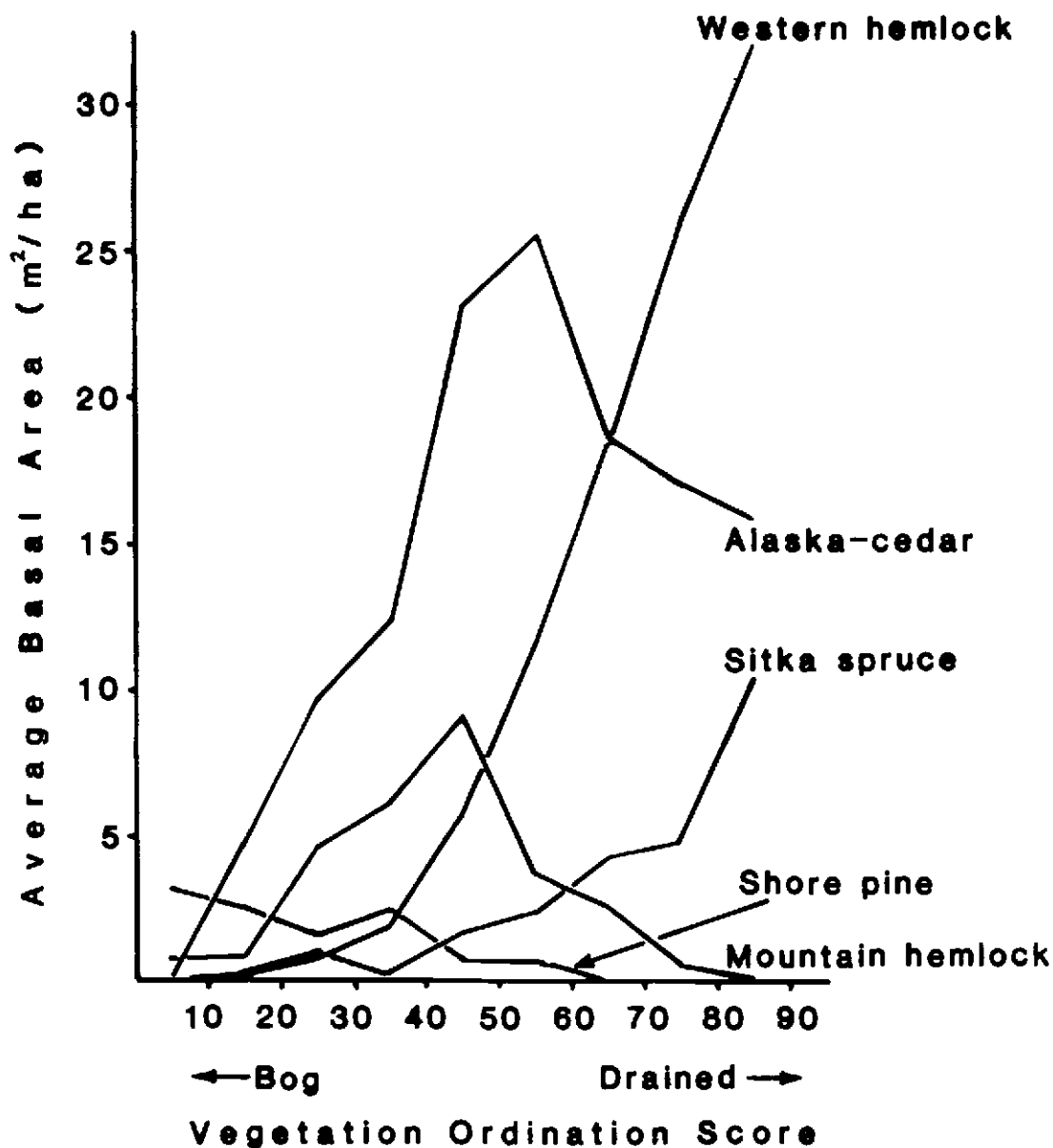


Figure III.10. Average basal area of live conifers along the vegetation gradient from bogs to sites with better drainage. Ordination scores resulted from a DECORANA analysis of occurrence and distribution of understory species on 280 plots. Mean basal area is plotted for 9 equal intervals along the gradient.

Alaska-cedar trees may be uncommon on these boggy sites. The prostrate form was absent on well drained sites.

Conifers Commonly Found Dead

Mortality was primarily associated with bog and semi-bog forest types (Fig. III.11). Alaska-cedar was the principal dead species in stands with a high proportion of mortality, accounting for 74% of the dead basal area (Table III.3). The level of dead Alaska-cedar in stands not affected by decline (about 23% of the basal area of Alaska-cedar) was similar to that of other species (Fig. III.12). Dead hemlock accounted for 16.8% of the mortality in declining stands, with other species only having negligible dead basal area. Since Alaska-cedar predominated in many of these stands, the percent basal area dead for each species provided a better measure of which species were affected. Sixty-five percent of Alaska-cedar basal area was dead in these stands, nearly twice the percentage of any other species. Mountain hemlocks were rarely dying. A fairly high percentage of spruce was dead (34.8%), but spruce was not common in mortality areas, and is probably poorly adapted to the boggy conditions where most mortality occurs. Western hemlock was more common than Sitka spruce in mortality areas. Since dead western and mountain hemlock could not be distinguished, evaluation of their condition in mortality sites was difficult. Even if all dead hemlock, and all the dead unknown group were classified as dead western hemlock, only 36% of western hemlock basal area would be dead, markedly less than the 65% for Alaska-cedar (Table III.3).

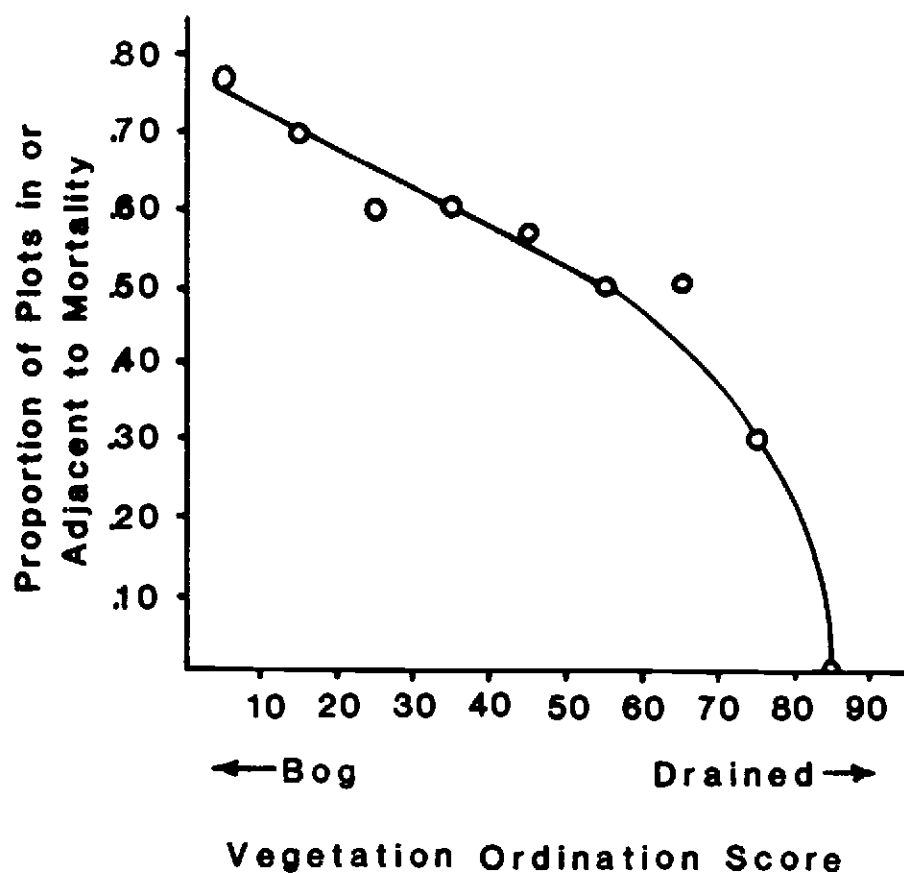


Figure III.11. Frequency of Alaska-cedar mortality along 9 intervals of the vegetation gradient from bog to better drainage. Each of 280 plots was designated as within or outside of mortality perimeters based on field observations.

Table III.3. Percentage that each conifer species contributed to total basal area of dead conifers and percent of basal area dead for each conifer species^{1/}.

Tree species	Total basal dead area (%) (from all species)	Basal area dead ^{3/} (%) (within each species)
Sitka spruce	2.7	34.8
Hemlock ^{2/}	16.8	22.3 ^{4/} , 29.7 ^{5/}
Shore pine	0.2	5.9
Alaska-cedar	74.4	65.3
Unknown	5.9	-
Total 100		

^{1/} Data from 92 plots expressing mortality at 3 sites

^{2/} Snags of western and mountain hemlock snags could not be distinguished and are grouped as dead hemlock.

^{3/} Percent dead basal area (BA) = (dead BA / total BA) X 100

^{4/} Percent dead hemlock = (dead hemlock BA / total hemlock BA) X 100

^{5/} Percent dead western hemlock = (dead hemlock BA) / (dead hemlock BA + live western hemlock BA) X 100 (this assumes that all dead hemlock is western hemlock)

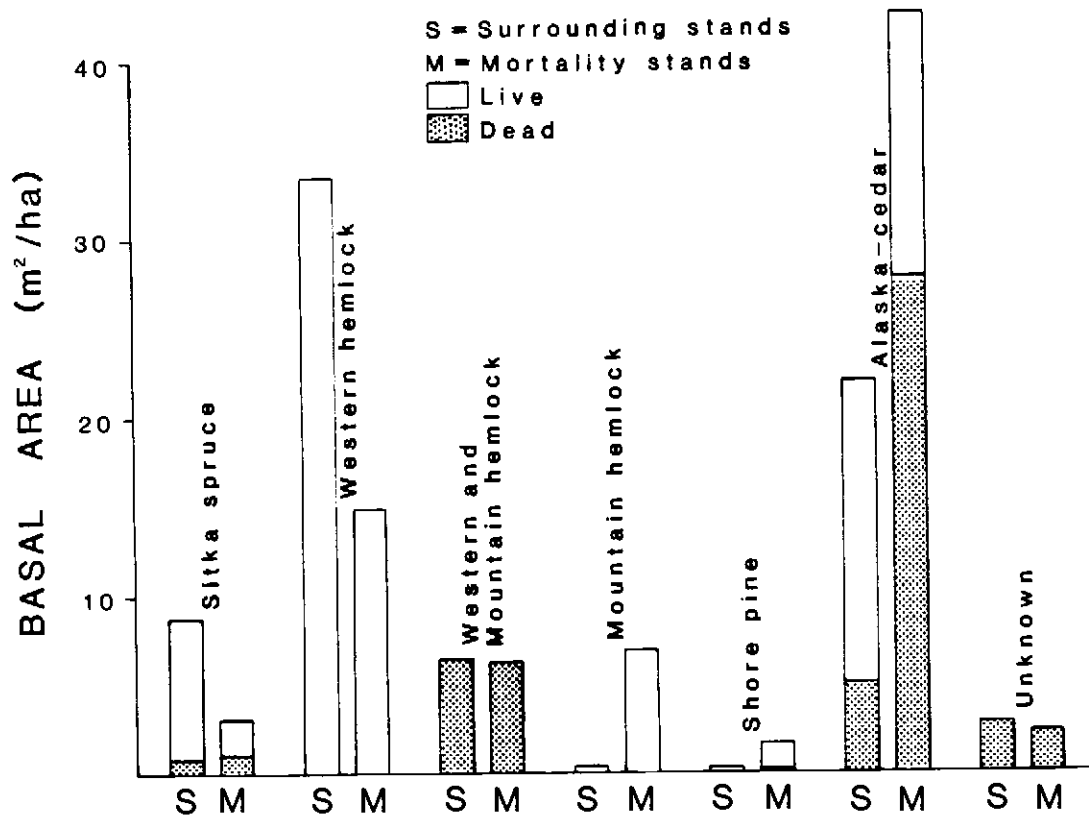


Figure III.12. Proportion of basal area that was live and dead in stands suffering from decline and in surrounding stands not suffering decline. Based on 147 prism plots. Dead hemlock trees could not be identified to species. Some trees ("Unknown") could not be identified to species, except that they were not Alaska-cedar.

Neiland (1971) suggested that Alaska-cedar trees decay and deteriorate more slowly and consequently, more dead Alaska-cedar might accumulate as other tree species deteriorate beyond recognition. In Table III.4, the Classes IV, V, and VI (dead for 40 years or more) are excluded from the basal area of dead Alaska-cedar to make data more comparable with the less decay-resistant species. Even with this portion of dead Alaska-cedar excluded from analysis, a higher proportion of Alaska-cedar (55%) was dead.

The frequency of root collar lesions on Alaska-cedar trees was not significantly correlated with azimuth or aspect, but these lesions were more common on cedars with dying crowns (46%) than for cedars with full, green crowns (11%).

Classes of Alaska-cedar Snags

Snags lacking limbs (Class V) were present on all sites with dead Alaska-cedar and comprised at least 8% (range=8-60%) of all snags on 23 sites with heavy mortality. More recently killed snags (i.e., Classes I-IV) were also present at all transects, indicating that the mortality has continued at all locations since initiation. Our general reconnaissance revealed only one site, at Patterson Bay (Fig. III.2), that had only long-dead Class IV and V snags and lacked recent mortality. No sites, however, have recently killed trees in the absence of long-dead snags.

Comparing modal snag classes with vegetation ordination scores for each plot indicated that different snag classes were associated with different intervals along the gradient from bog to better drainage (Fig. III.13). Snags with no limbs (Class V) predominated in bog plant

Table III.4. Percent basal area dead for each tree species in stands suffering mortality. Long-dead Alaska-cedar trees (in Classes VI, VII, and VIII) were not included in order to make data more comparable to the other, less decay resistant tree species.^{1/}

Tree species ^{2/}	Basal Area Dead (%)
Sitka spruce	36
Hemlock ^{3/}	25
Shore pine	0
Alaska-cedar	55

^{1/} Data from 92 plots expressing mortality at 3 sites

^{2/} 2% of the total dead basal area was long-dead and beyond identification except that it was not Alaska-cedar

^{3/} Snags of western and mountain hemlock snags could not be distinguished and are grouped as dead hemlock.

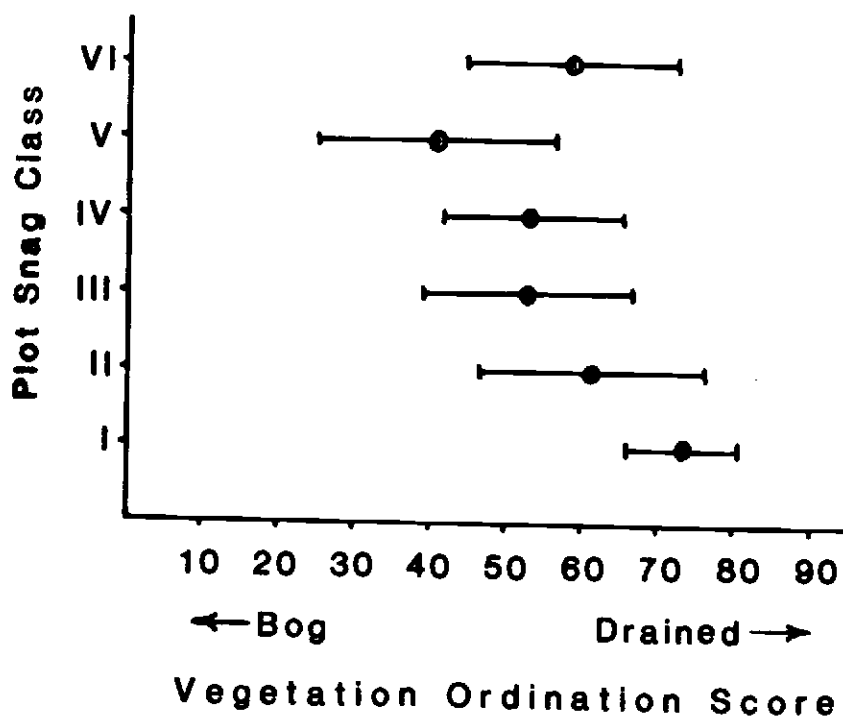


Figure III.13. Average ordination scores (\pm standard deviation) of plots assigned modal snag classes along the gradient from bog to better drainage. Modal snag classes were the most commonly occurring snag class on each plot. Snag classes were based on degrees of foliage, twig, and branch retention. Ordination by DECORANA based on understory from 280 plots.

communities. Plots with more recently killed snags (Classes IV, III, II, and I) supported progressively better drained plant communities; snags in Classes I, III, and V differed significantly in their plot ordination scores. Plots with the longest-dead trees (Class VI, with deteriorating boles) were uncommon, not associated with severe mortality, and were not confined to bogs, as were Class V snags.

Rope trees, Alaska-cedars trees with a dead top and dead bole, except for a thin strip of callus tissue connecting one live branch cluster to roots, followed the same trend (Fig. III.14). Those rope trees that had dead tops without limbs (Class V) occurred with bog understory plants, while those with more recently killed tops occurred on sites with better drained plant communities (Chapter II).

Average heights of dominant and codominant Alaska-cedar trees (dead and live) tended to be greater on plots with primarily healthy trees. There was a trend toward shorter trees on plots where long-dead snags (Classes III-V) predominated, especially on plots with Class V snags (no limbs retained) (Fig. III.15).

DISCUSSION

Mortality of Alaska-cedar began on bog sites in southeast Alaska around 1880 (Chapter II). Subsequent spread of mortality onto better drained sites is confirmed by our aerial photographic analysis and survey results. The latter showed that long-dead, Class V snags were primarily associated with bog understory plants, more shore pine and mountain hemlock, less total conifer basal area, rope trees, and

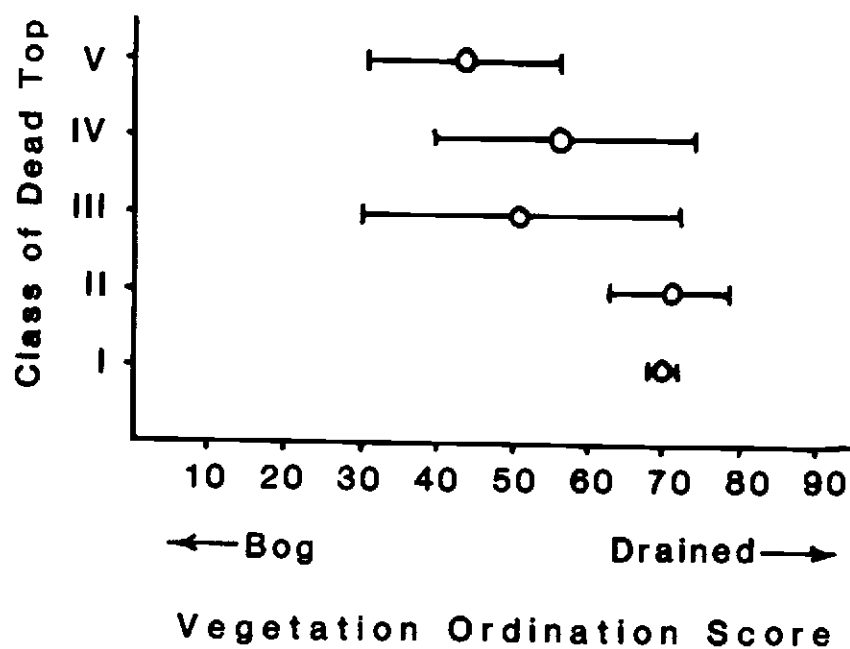


Figure III.14. Average ordination scores (\pm standard deviation) for plots with rope trees that have different classes of dead tops. Understory ordination by DECORANA based on 280 plots. Rope trees are Alaska-cedars with dead tops and dead boles except a narrow, vertical strip of callus tissue connecting roots to a single live branch cluster (see Fig. II.6).

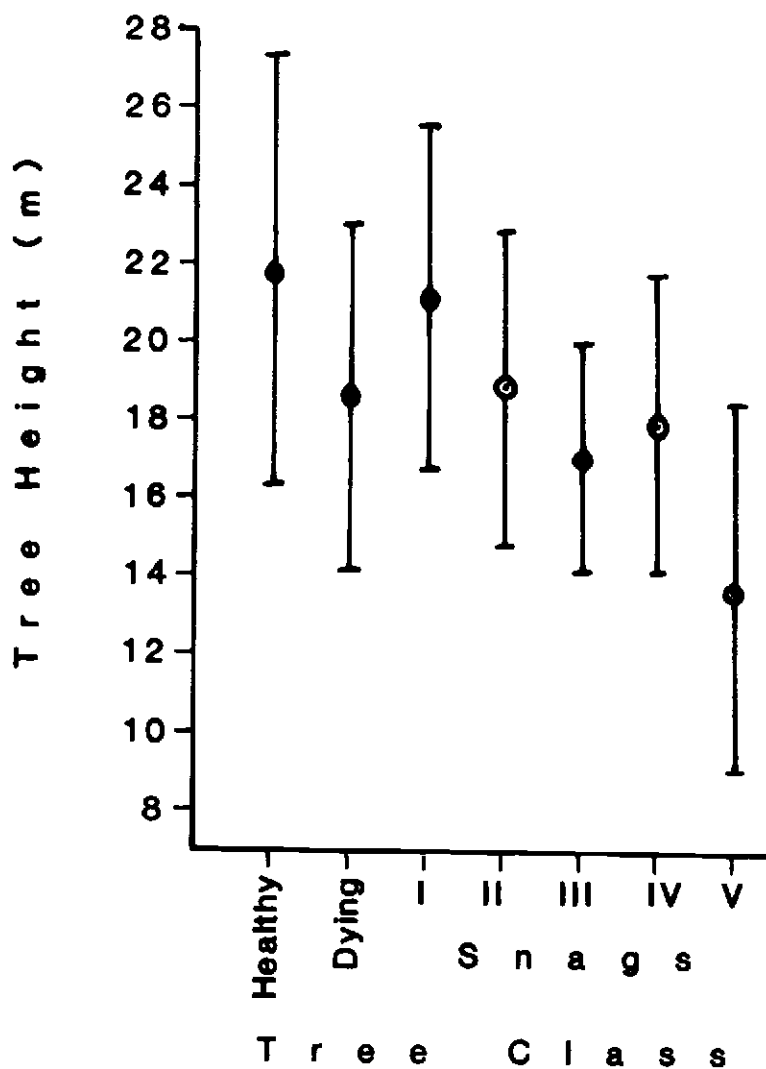


Figure III.15. Average heights (\pm standard deviation) of Alaska-cedar trees (dominant and codominant) on plots with live, dying, or dead trees. Plots with dead trees were grouped into classes according to the most common snag type (see Fig. III.4).

shorter Alaska-cedar trees--all of which are characteristics of bogs and semi-bogs. These snags were Alaska-cedar trees killed in the initial occurrence of this extensive mortality. More deteriorated snags in Class VI predate the onset of extensive mortality (Chapter II), and their occurrence is unassociated with sites having large numbers of dead and dying trees. More recently killed trees (Classes I-IV) were associated with understory communities having better drainage, more western hemlock, more total conifer basal area, and taller Alaska-cedar trees, confirming the spread into forest types with better drainage.

Sites with a gradient from bog to better drainage usually had a corresponding gradient of snag Classes from V to I, respectively, which represents spread of mortality through time (Fig. III.16). Spread of mortality within any one site occurs as a slow advance along an established ecological gradient. The gradient from bog to better drainage was often related to slope, with better drained communities occurring upslope from bogs. The common upslope spread of mortality is explained by mortality originating in bogs and spreading upslope along the gradient to better drainage communities. The downslope change to better drained hemlock-spruce types was often abrupt.

Spreading patterns were not, however, apparent on all sites expressing mortality. Some stands had an abrupt transition from open bog to better drainage and lacked spread. Other sites (e.g., Slocum Arm, Fig. II.1) lacked overall spreading patterns because initial mortality was extensive and occurred within a mosaic of overlapping bog and semi-bog types. Some areas occur as elongated series of bogs that have a long band of mortality parallel and upslope from the bogs.

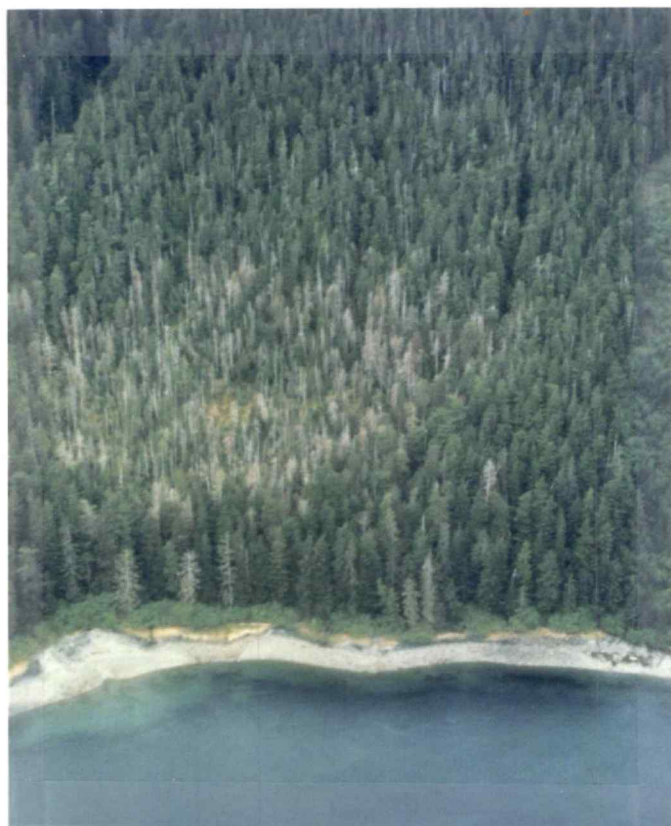


Figure III.16. Example of the spread of mortality from a small bog to surrounding stands (Susan's Landing Site--see Fig. III.5).

Thus, mortality consistently started in bogs and on bog edges, regardless of bog shape or size, and subsequently spread to forest communities with better drainage.

One site, near Patterson Bay (Chichagof Island), was an anomaly with many large Class V Alaska-cedar snags, but no subsequent mortality has occurred among the old snags nor has mortality spread out into adjacent stands. A dense growth of vigorous, pole sized Alaska-cedars comprised the majority of the live stand. Understory plants were not sampled, but bog plants were absent. Perhaps this site had a change in drainage patterns, which may have improved soil conditions for surviving cedars resulting in less mortality and increased growth.

The clearly defined trends in amounts of conifer basal area substantiate our interpretation of the first ordination axis as a bog to better drainage gradient since we already have an indication of the distribution of these tree species. Shore pine is primarily a bog species (Harris and Farr 1974); western hemlock and Sitka spruce have their best development on the best drained sites (Ruth and Harris 1979).

Several forms of error are potentially associated with mapping perimeters of mortality from aerial photographs. The 1948 photographs were of a small scale, and any errors in mapping would be intensified when bringing them to a common, larger scale with the other maps. Also, the more recent aerial photographs were of better quality and thus helped to increase accuracy in locating the actual perimeters of mortality. In particular, locations of mortality perimeters on the 1976 color photographs are more accurate than from the previous black and white photography. One could argue that the greater extent of

mortality on maps made from more recent aerial photographs is a result of more accurately discerning the scattered dead trees at the mortality edge; however, my survey data and field observations provide corroborating evidence that maps made from aerial photographs accurately represent spread of the mortality.

The patterns of mortality spread contrast with those reported for other conifers declines. Sprugel (1976) reported waves of Abies balsamea mortality in the eastern U.S. with well-defined, moving fronts. Apparently, this mortality did not spread along a vegetational gradient as shown for Alaska-cedar in this study. Also, Abies successfully reproduced from seed, and another wave of mortality might be expected by the time the regenerated stand was 100 yrs old (Sprugel 1976). Alaska-cedar, on the other hand, is not establishing by seedlings, although it reproduces vegetatively by the rooting of lower branches (Chapter VIII) in many mortality areas. The cause of the Abies mortality is unknown, but spread rates were associated with wind patterns and ice glaze or winter desiccation. Circular, expanding patterns of mortality and subsequent conifer regeneration are the result of the root rot fungus, Phellinus weirii (Murr.) Gilb., in mountain hemlock stands in Oregon (McCauley and Cook 1980). The spread of mortality in neither of these studies was shown to follow forest community gradients that existed prior to the mortality, as I have shown in the present study.

I suggest that mortality in Alaska-cedar spread along a pre-existing environmental and vegetational gradient. The forest community gradient (bog to better drainage) could be a result of extensive mortality of Alaska-cedar, the principle overstory tree along

the gradient. Understory plant communities may have been changed dramatically during the 80 to 100 years following the death of the cedars. Such an event might explain the association of bog plants with the long-dead Class V snags. My data, however, suggest that bogs, and therefore bog plant communities, were in place well before the onset of Alaska-cedar decline. Most forest trees, and all Alaska-cedars larger than seedlings, were older than 100 years. Their distribution (i.e., pines associated with bogs and western hemlock with better drainage) and heights of Alaska-cedars (shorter in bog stands) are evidence that sites were already bogs or semi-bogs before extensive mortality began to occur some 80 to 100 years ago. Furthermore, the few bogs with Alaska-cedar, but without cedar mortality, had the same species of bog plants.

Different forest conditions occur where the long-dead (Class V) snags stand, behind the moving front of Alaska-cedar mortality. A new stand of vigorous-appearing trees sometimes grew up beneath the bark-free, white snags. Alaska-cedar, western hemlock, and to some extent mountain hemlock, were the dominant tree species in these areas and appeared as a green zone from a distance or on color aerial photographs. Most or all of these trees were older than 100 years (Hennon, unpublished data) and were probably present as understory conifers during the initial mortality. The Alaska-cedar component of these new stands probably reproduced vegetatively (Chapter VIII). In other stands with long-dead snags, continued mortality of smaller Alaska-cedar trees has apparently prevented development of this green zone. Reasons for the reoccurrence of mortality in some stands but not in others is not clear. On extremely boggy sites, release of live

trees after old mortality has not occurred, perhaps because factors suppressing the growth of live trees (e.g., anaerobic soils) were not improved by the death of Alaska-cedars (Chapter II).

The development from forest to bog requires the waterlogging of the forest floor which results from the proliferation of Sphagnum moss, the development of poor drainage, or both. This process, paludification (Noble et al. 1984), may lead to the death of forest trees as sufficient oxygen or nutrients become less available in the wet soil. Whether there is a general successional direction for forests in southeast Alaska, whether from forest to bog or bog to forest, is presently unresolved. Dachnowski-Stokes (1941) showed evidence that forests encroach on bogs. Lawrence (1958) interpreted buried logs as evidence of change from forest to bog. Neiland (1971) reported floristic evidence that forest-bog transitions are proceeding in both directions.

Understanding the process of paludification has a direct bearing on determining the cause of Alaska-cedar decline. In this paper, I determined that cedars are dying primarily in bog and semi-bog plant communities. Elsewhere (Chapters V and IV), I determined that biotic factors are probably not primarily responsible for the widespread mortality--suggesting an abiotic cause. One abiotic hypothesis for tree death is that bogs, for climatic or other reasons, are advancing on the semi-bog sites where so many trees are dying. My observations, however, suggest that if bogs are advancing on forests, then the rate of advancement is imperceivable. Bogs observable on the 1927 aerial photography have not noticeably expanded. One might expect to see more evidence of rapidly expanding sphagnum mats or invasion of other bog

plants into forests if there have been drastic changes in bog size in the last 100 years since the onset of extensive mortality. Thus, if bogs are expanding, then the rate of bog expansion is probably too slow to provide a simple explanation for the widespread decline. Also, the relatively high rate of mortality for Alaska-cedar, probably one of the conifers best adapted to growing in bogs, compared to a lower incidence of mortality for other conifers is not explained by the hypothesis of expanding bogs. Nonetheless, it is clear that a better understanding of the development and chemistry of bog soils, along with information on bog expansion or constriction over time, will aid our understanding of the causes of Alaska-cedar decline.

In conclusion, my epidemiological studies provide insight into possible causes of Alaska-cedar decline. The specificity of mortality to Alaska-cedar and the patterns of spread seem to suggest a pathogen-caused disease; however, no new sites of mortality have developed since the nearly simultaneous onset of Alaska-cedar decline some 80 to 100 years ago at numerous locations throughout southeast Alaska. Snags that represent the original extensive mortality were present at every sampling location and observed on all good-quality 1927 aerial photographs of sites where cedars are currently dying. It is difficult to imagine a pathogen capable of inciting and continuing to cause the level of destruction that occurs on remote and dispersed islands in isolated wilderness, but not capable of re-initiating the problem on other, similar bog sites. These results support the hypothesis that a pathogen is not the primary cause of mortality (Shaw et al. 1985).

LITERATURE CITED

- Dachnowski-Stokes, A.P. 1941. Peat resources in Alaska. USDA Tech. Bull. No. 769. 84p.
- Downing, G.L. 1960. A cedar bark beetle outbreak. USDA For. Serv., Alaska For. Res. Cent., For. Insect Surv. Rep. 6. 2p.
- Frear, S.T. 1982. What's killing the Alaska yellow-cedar? Amer. For. 88(11):41-43, 62-63.
- Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge. 298 p.
- Harris, A.S. 1971. Alaska-cedar. USDA For. Serv. American woods-FS 224. 7p.
- Harris, A.S. and W.A. Farr. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. USDA For. Serv. Gen. Tech. Rep. PNW-25. Pacific Northwest Forest and range experiment station. 109 p.
- Hill, M.O. and H.G. Gauch. 1980. Detrended correspondence analysis; an improved ordination technique. Vegetatio 42:47-58.
- Laurent, T.H. 1982. Cedar dieback--is it the problem. Pp. 104-107. In: Proceedings of the second Alaska integrated pest management conference. Univ. Alaska, Anchorage, AK. Coop. Ext. Serv. 112p.
- Lawrence, D.B. 1958. Glaciers and vegetation in southeastern Alaska. American Scientist 46:89-122.
- McCauley, K.J. and S.A. Cook 1980. Phellinus weirii infestation of two mountain hemlock forests in the Oregon Cascades. For. Sci. 26:23-29.
- Neiland, B.J. 1971. The forest-bog complex of southeast Alaska. Vegetatio 22:1-64.
- Noble M.G. 1984. Sphagnum invasion beneath an evergreen forest canopy in southeastern Alaska. Bryologist 87:119-127.
- Paine, D.P. 1981. Aerial photography and image interpretation for resource management. Wiley & Sons, New York, NY. 571p.
- Rigg, G.B. 1925. Some sphagnum bogs of the North Pacific Coast. Ecology 6:260-279.
- Rigg, G.B. 1940. The development of sphagnum bogs in North America. Botanical Review 6:666-693.

Ruth, R.H. and A.S. Harris. 1979. Management of western hemlock-Sitka spruce forests for timber production. USDA For. Serv. Gen. Tech. Rep. PNW-88. Pacific Northwest Forest & Range Exp. Sta. 197 p.

Sargent, R.H. and F.H. Moffit. 1929. Aerial photographic surveys in southeastern Alaska. USGS Bulletin 797-E. Government Printing Office. Pp.43-160.

Shaw, C.G. III, T.H. Laurent, A. Eglitis, and P.E. Hennon. 1985. Decline and mortality of Chamaecyparis nootkatensis in southeastern Alaska, a problem of long duration but unknown cause. Plant Dis. 69:13-17.

Sprugel, D.S. 1976. Dynamic structure of wave-regenerated Abies balsamea forest in North-eastern United States. J. Ecology 64:889-911.

Wenger, K.F. 1984. Forestry handbook. Wiley & Sons, New York. 1333p.

Wilson M.V. 1981. A statistical test of the accuracy and consistency of ordinations. Ecology 62:8-12.

Zach, L.W. 1950. A northern climax, forest or muskeg? Ecology 31:304-306.

CHAPTER IV

FUNGI ON CHAMAECYPARIS NOOTKATENSIS

ABSTRACT

The lack of information on fungi that occur on Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) has hindered attempts to determine the cause of an extensive decline and mortality of this valuable tree species in southeast Alaska. Fungi were isolated or collected directly from Alaska-cedar trees and identified to determine if any were the primary cause of decline. Twenty-one taxa of fungi were isolated, and 31 were collected from Alaska-cedar. Of these, 37 are new reports on Alaska-cedar and 26 are new reports from Alaska on any host. Including 41 fungi previously reported on Alaska-cedar, a total of 78 fungi have now been reported on this tree species in its native range. Several potential pathogens were found in southeast Alaska: Armillaria sp., Gymnosporangium nootkatense, Seiridium cardinale, and Apostrasseria sp.; however, their low incidence or association with non-symptomatic tissues of Alaska-cedar suggests that none is the primary cause of decline and mortality.

INTRODUCTION

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a slow-growing forest tree species ranging from Prince William Sound in Alaska, south through British Columbia, to the Oregon-California border (Harris 1971). Its tight-grained, decay-resistant heartwood makes Alaska-cedar a valuable and useful tree (Frear 1982). Alaska-cedar is currently suffering from an extensive decline of unknown cause throughout southeast Alaska (Shaw et al. 1985). To date, no comprehensive list of fungi, pathogenic or saprophytic, exists for Alaska-cedar. Insufficient information about pathogens of this tree species limits efforts to determine potential agents responsible for this problem.

The purpose of this paper is two-fold. Since previous reports of fungi on Alaska-cedar are scattered in the literature, I compiled them into one source (Table IV.1). Few of these reports are from southeast Alaska where so many cedars have died. Consequently, I collected, isolated, and identified as many fungi as possible from live, declining, or dead Alaska-cedars in areas expressing mortality to determine which, if any, fungi contribute to the death of these trees. Many fungi are new reports for Alaska-cedar, are newly reported fungi from Alaska, or both.

Table IV.1. Fungi previously reported from Alaska-cedar (Chamaecyparis nootkatensis).

Fungi ^{1/}	REFERENCE SOURCE ^{2/}							
	A	B	C	D	E	F	G	H
ASCOMYCETES								
<u>Asterina cupressina</u>	+	+	+		+			
<u>Eriosphaeria vermicularis</u>							+	
<u>Chloroscypha seaveri</u>								+
<u>Cyanodiscus occidentalis</u>							+	+
<u>Gelatinodiscus flavidus</u>					+		+	
<u>Herpotrichia juniperi</u>			+	+			+	
<u>Pleospora laricina</u>								+
<u>Seynesiella juniperi</u>				+				
<u>Tryblidaria washingtonensis</u>					+		+	
<u>Venturia lanea</u>		+	+		+			
BASIDIOMYCETES								
<u>Aleurodiscus weirii</u>				+				
<u>Armillariella mellea</u>			+		+			
<u>Botryobasidium obtusisporum</u>				+				
<u>Fomitopsis pinicola</u>			+		+			
<u>Gymnosporangium nootkatense</u>	+	+	+	+	+		+	
<u>Hyphodontia pallidula</u>				+				
<u>Hyphodontia subalutacea</u>				+				
<u>Jaapia argillacea</u>				+				
<u>Lenzites saepiaria</u>		+	+		+			
<u>Nidularia sp.</u>				+				
<u>Peniophora crassa</u>	+	+						
<u>Peniophora sanguinea</u>				+				
<u>Phellinus pini</u>		+	+		+		+	
<u>Phellinus weirii</u>		+	+	+	+		+	
<u>Polyporus sericeomollis</u>				+			+	
<u>Poria lenis</u>	+	+	+		+			
<u>Poria xantha</u>		+	+		+			
<u>Serpula himantioides</u>			+	+	+		+	
<u>Tubulicrinus regificus</u>				+				
<u>Xeromphalina campanella</u>			+	+			+	
OOMYCETES								
<u>Phytophthora lateralis</u>				+	+			

(Table IV.1, continued)

IMPERFECTS

<u>Seiridium cardinale</u>			+	
<u>Coryneum berckmanii</u>	+			
<u>Cytospora abietis</u>				+
<u>Engelhardtella alba</u>				+
<u>Gibbera</u> sp.			+	
<u>Kabatina thujae</u>				+
<u>Pestalotiopsis funera</u>				+
<u>Pestalotia thujae</u>				+
<u>Phomopsis juniperovae</u>		+		

1/ Authorities for these taxa are listed in Table IV.4.

2/ References used: A= Cash 1953; B= USDA 1960; C= Connors 1967; D= Lowe 1982; E= Hepting 1971; F= Strouts 1972; G= Shaw 1973a; H= Funk 1973, 1974, 1881, and 1985. See Literature Cited for complete citations.

MATERIALS AND METHODS

Fungi were isolated from tissues collected from 60 healthy, declining, or dead cedars whose roots were excavated (Chapter V). These trees were located in areas expressing cedar mortality on Baranof and Chichagof Islands. Methods of isolation, media used, and tree symptoms are reported elsewhere (Chapter V). Many of the isolated fungi were placed on a temperature gradient plate with near ultra-violet illumination (approx. 360 nm) to induce sporulation (Leach 1963) before identification was attempted.

Fungi sporulating on Alaska-cedar were collected from the Peril Strait and Slocum Arm region of Baranof and Chichagof Islands in southeast Alaska from 1981 to 1985. The location, tissue type, tissue condition (live or dead), crown condition of tree, forest type (e.g., bog, semi-bog, hemlock-cedar forest, etc.), elevation, and date were noted for all collections. Collected fungi were air-dried or fixed in Formol-acetic-acid (FAA) (Commonwealth Mycological Institute 1983) for later microscopic identification. Representative fungal samples were placed in the Oregon State University Herbarium.

RESULTS

Fungi previously reported from Alaska-cedar, in the form of host lists and mycological studies, are listed in Table IV.1. The pathological role of these fungi in other forest systems range from strict saprophytes to specialized obligate parasites. Of the fungi

previously reported on Alaska-cedar, Armillaria sp., Gymnosporangium nootkatense, Phytophthora lateralis, and Seiridium cardinale are all known pathogens.

Fruiting bodies of 31 fungi were collected from Alaska-cedar were identified to genus (Table IV.2); 18 of these fungi were identified to species. Twenty-three fungi were found to be new reports on Alaska-cedar.

Twenty-one fungi were isolated from Alaska-cedar (Table IV.3); 19 of these were identified to genus, and seven were identified to species. Eighteen of these fungi are new reports from Alaska cedar. Of the fungi collected and isolated, 38 are new reports on Alaska-cedar and 25 are new reports from Alaska for any host (Table IV.4).

The fungi isolated or collected from Alaska-cedar in southeast Alaska are listed below with their diagnostic characteristics:

Apostrasseria (Phacidiopeyensis) sp.

Figure IV.5.

Fruiting body -- no sexual fruiting body found, but probably =

Phacidium sp. (A. Funk, pers. comm.)

Conidia -- hyaline, spindle-shaped tapering to points on both ends, many are biguttulate.

In culture -- black, appressed growth with whitish aerial patches, black sporodochia present.

Habit -- present on foliage and twigs of seedlings on Prince of Wales Island where it is associated with a shoot dieback; also on natural regeneration in stands cutover 20 years ago on

Table IV.2. Fungi sporulating on Alaska-cedar (*Chamaecyparis nootkatensis*) in southeast Alaska.

Fungi ^{1/}	O R I G I N							Foli- age	Seed- ling
	Stem Lesion	Bear Scar	Live Bark	New Snag	Old Snag	Down Log	Twig		
ASCOMYCETES									
<u>Asterina cupressina</u>								+	+
2/ <u>Scutellinia scutellata</u>						+			
<u>Hernotrichia</u> sp.		+			+		+	+	
234/ <u>Dermaea</u> sp.	+		+						
23/ <u>Pezicula</u> sp.			+						
23/ <u>Stictis radiata</u> subsp. <u>radiata</u>			+						
2/ <u>Ceratocystis</u> sp.		+							
2/ <u>Nectria</u> sp.				+		+			
2/ <u>Dothidea</u> sp.					+				
23/ <u>Bertia moriformis</u>	+	+	+	+	+	+	+		
<u>Chloroscypha seaveri</u>								+	+
23/ <u>Pithya cupressina</u>								+	+
3/ <u>Gelatinodiscus flavidus</u>									+
BASIDIOMYCETES									
<u>Armillaria</u> sp.	+	+		+		+			
23/ <u>Auricularia auricularis</u>		+		+					
2/ <u>Cyathus olla</u>		+							
2/ <u>Dacromyces deliquescens</u> subsp. <u>deliquescens</u>		+		+	+	+	+		
2/ <u>Galerina</u> sp.		+		+	+	+	+		
<u>Gymnosporangium</u> <u>nootkatense</u>								+	+
235/ <u>Hyphodontia aspera</u>		+							
<u>Lycoperdon</u> sp.		+							
235/ <u>Skeletocutis amorpha</u>		+							
23/ <u>Pistillaria</u> sp.		+							
<u>Fomitopsis pinicola</u>						+			
2/ <u>Heterobasidion annosum</u>						+			
23/ <u>Lactarius deliciosus</u>		+		+	+	+	+		
<u>Lenzites saecloria</u>		+		+	+	+			
23/ <u>Naematoloma dispersum</u>				+	+	+			
2/ <u>Polyporus elegans</u>		+		+		+			
<u>Xeromphalina campanella</u>		+		+		+	+		
IMPERFECTS									
234/ <u>Apostrasseria</u> sp.									+

1/ Authorities for these fungi are listed in Table IV.4.

2/ First report on Alaska-cedar.

3/ First report from Alaska from any host.

4/ Identification by A. Funk gratefully acknowledged.

5/ Identification by R. Gilbertson gratefully acknowledged.

Table IV.3. Fungi isolated from Alaska-cedar (*Chamaecyparis nootkatensis*) in southeast Alaska.

Fungal species ^{1/}	No. of isolates	Fine roots	Coarse roots	Root collar	Stem lesion	Live bark	Bear scar	Sap stain
ASCOMYCETES								
2/ <i>Ceratocystis</i> sp. (anamorph = <i>Chalara</i> sp.)	5						+	
23/ <i>Dermea</i> sp. (anamorph = <i>Gelatinosporium</i> sp.)	79				+	+		
2/ <i>Gnomoniella</i> sp.	2	+						
BASIDIOMYCETES								
2/ <i>Polyporus elegans</i>	8				+			+
Unidentified #1	29	+		+	+			+
Unidentified #2	31	+	+	+	+			+
IMPERFECTS								
24/ <i>Acrostaseria</i> sp.	15							
23/ <i>Cryptosporiopsis</i> sp.	89	+	+		+			
23/ <i>Cylindrocarpum didymum</i>	70	+	+		+			
23/ <i>Dictyosporium elegans</i>	2							+
23/ <i>Ditangium</i> sp.	1							+
2/ <i>Leptographium</i> sp.	40		+	+			+	+
23/ <i>Gliocladium</i> sp.	1	+						
23/ <i>Phialophora melinii</i>	50		+	+	+		+	+
23/ <i>Phoma</i> sp.	3		+					
23/ <i>Septonema secedens</i>	1				+			
3/ <i>Seiridium cardinale</i>	1						+	
23/ <i>Spegazzinia tricholophyllia</i>	11	+	+	+			+	
23/ <i>Sporidesmium</i> sp.	75	+	+	+	+		+	+
2/ <i>Verticillium</i> sp.	1				+			
MYCELIA STERILIA								
23/ <i>Mycelium radialis atrovirens</i>	235	+	+	+	+	+		+

^{1/} Authorities for fungi are listed in Table IV.4.

^{2/} First report from Alaska-cedar.

^{3/} First report from Alaska from any host.

^{4/} Identification or verification by A. Funk gratefully acknowledged.

Table IV.4. Newly compiled list of fungi on Alaska-cedar, including all taxa from Tables IV1-3.

ASCOMYCETES

Asterina cupressina Cke.
Bertia moriformis Tode.
Ceratocystis sp.
Chloroscypha seaveri Seaver
Cyanodiscus occidentalis E. Muller & Farr
Dermea sp. Fr.
Dothidea sp. Fr.
Eriosphaeria vermicularis (Nees ex Fr.) Sacc.
Gelatinodiscus flavidus
Gibbera sp. Fr.
Gnomoniella sp. Sacc.
Herpotrichia juniperi (Duby) Petr.
Nectria sp. Fr.
Opegrapha sp. Ach.
Pezicula sp. Tul.
Pithya cupressina (Fr.) Fckl.
Pleospora laricina Rehm.
Scutellina scutellata (L. ex Fr.) Lambotte
Sevnesiella juniperi (Desm.) Arn.
Stictis radiata (L.) Pers. subsp. radiata
Tryblidaria washingtonensis
Venturia lanea Dearn.

BASIDIOMYCETES

Aleurodiscus weirii Burt
Armillariella sp. (Fr.) Staude
Auricularia auricularis (Hooke.) Underw.
Botryobasidium obtusisporum
Cyathus olla (Batch) ex Pers.
Dacromyces deliquescens (Merz) Duby subsp. deliquescens
Fomitopsis pinicola (Swartz ex Fr.) Karst.
Galerina sp. Earle
Gymnosporangium nootkatense (Trel.) Arth.
Heterobasidion annosum (Fr.) Bref.
Hyphodontia aspera
Hyphodontia pallidula (Bres.) J. Erikss.
Hyphodontia subalutacea (Karst.) J. Erikss.
Jaapia argillacea Bres.
Lactarius deliciosus
Lenzites saepiaria Wulf. ex Fr.
Lycoperdon sp. Tournef. ex Pers.
Naematoloma dispersum
Nidularia sp. Fr.
Peniophora crassa Burt
Peniophora sanguinea (Fr.) Hoehn. et Gilbertson
Phellinus pini (Thore ex Fr.) Pilat
Phellinus weirii (Murr.) Gilbertson
Pistillaria sp.

(Table IV.4, continued)

BASIDIOMYCETES

Polyporus elegans Bull. ex Fr.
Polyporus sericeomollis Rom.
Poria lenis Karst.
Poria xantha (Fr.) Cke.
Serpula himantioides (Fr.) Bond.
Skeletocutis amorphia (Fr.) Kotl. et Pouz.
Tubulicrinus regificus (Jacks & Deard.) Donk
Xeromphalina campanella (Batsch ex Fr.) Kuehner & Maire

OOMYCETES

Phytophthora lateralis Tucker & J.A. Milbrath

IMPERFECTS

Apostasseria sp.
Chalara sp.
Coryneum berckmanii Milb.
Cryptosporiopsis sp. Bubak & Kabat
Cylindrocarpon didymum (Hart.) Wollenw.
Cytospora abietis Sacc.
Dictyosporium elegans Corda
Ditangium sp.
Engelhardtiella alba
Gelatinosporium sp.
Gliocladium sp.
Kabatina thujae Schneid. & Arx
Leptographium sp. Lagerberg & Melin
Pestalotiopsis funera Desm.
Pestalotia thujae Sawada.
Phialophora melinii (Nannf.) Conant
Phoma sp. Sacc.
Phomopsis juniperovae Hahn
Septonema secedens Corda
Seiridium cardinale (Wagener) Sutton & Gibson
Spegazzinia tricholophilia
Sporidesmium sp. Link ex Fr.
Verticillium sp. Nees ex Link

MYCELIA STERILIA

Mycelium radicis atrovirens Melin

Mitkof Island where it causes shoot (including terminal) dieback.

Reference -- (A. Funk, pers. comm.)

Asterina cupressina

Ascocarp -- crustose, shield-shaped perithecium opening by radiating fissures.

Ascospores -- hyaline, approx. 6-7 x 12-15u.

Conidia -- hyaline, three to five-septate, approx. 4-5 x 15-18u.

Habit -- on live foliage, apparently not causing symptoms.

Reference -- (Dennis 1968)

Bertia moriformis

Figure IV.6.

Ascocarp -- black pseudothecium, warty exterior, appearing as a blackberry, one locule.

Asci -- stalked when free.

Ascospores -- hyaline, one septate, approx. 6-9 x 25-50 u.

Habit -- Common on dead wood of bole, branches, or twigs; very common on dead, suppressed branches; sometimes on live bark causing no apparent symptom.

Ceratocystis sp.

Figure IV.2.

Ascocarp -- Dark, long-necked slightly imbedded perithecium, globose to flattened at base, ostiolate; hyphae usually 30-50u but up to 100u, usually with blunt tips.

Ascospores -- in globose asci, spores thin walled, nonseptate, hyaline, 3-4 x 6-9u, flattened on one side, with or without musilaginous sheath.

Conidia -- Chalara sp. anamorph stage, phialospores hyaline, nonseptate, smooth, cylindrical with blunt ends, 2.5-4 x 10-16u, produced on short conidiophore.

In culture -- appressed or submerged tan mat, both Ceratocystis and Chalara stages sporulating.

Habit -- on recently killed wood (less than two years) and bark of basal scars caused primarily by brown bears; collected once on bark of non-scarred, but recently killed tree.

Note: Most similar to C. fimbriata, but apparently an undescribed species.

References -- (Griffin 1968, Hunt 1956)

Chloroscypha seaveri

(Kriegeria seaveri (Rehm) Seaver)

Ascocarp -- small (0.5mm diam) greenish apothecium, short stipitate.

Ascospores -- large 15-20 x 8-10u, hyaline to yellowish, one end tapering to a curved tip.

Habit -- On dead foliage, trees and seedlings.

Reference- (Funk 1985)

Cryptosporiopsis sp.

Figure IV.4.

Fruiting body -- none.

Conidia -- Large, apparently nonseptate, curved, bean-shaped, 8-13 x 25-35u, granular appearing contents apparently non-septate, maturing brown and one-septate upon germination; conidia produced on short, stout, branched conidiophores that may or may not be grouped in sporodochia; small, hyaline 1 x 2-3 microconidia present in some cultures.

In culture -- tan to cream-colored appressed mat, patchy brownish areas, numerous slimy areas (spore masses from sporodochia).

Habit -- On root lesions and fine roots.

References -- (Grove 1935, Sutton 1980)

Cyathus olla

Basidiocarp -- Bird's nest fungus with fine textured, three-part peridium wall which is enlarged for the upper one third.

Habit -- On dead, decaying wood.

Reference -- (Brodie 1975)

Cylindrocarpon didymum

Figure IV.3.

Fruiting body -- no sexual fruiting body, but if it occurs, may be Nectria sp. or closely allied genus (Booth 1966)

Conidia --

Macroconidia -- hyaline, cylindrical, one septate (some zero, two, or three septate), phialospores, approx. 4 x 12-25u.

Microconidia -- hyaline, oblong, non-septate, approx. 4 x 3-7u.

In culture -- tan, semi-aerial mycelium, crystals sometimes form

imbedded below the mat and are visible to the unaided eye, chains of yellow to golden chlamydospores in some cultures.

Habit -- In stem and root lesions, on fine roots of declining cedars, has weak pathogenic abilities.

Reference -- (Booth 1966)

Dacromyces deliquescens var deliquescens

Basidiocarp -- orange, "jelly-fungus," few clamps in internal hyphae.

Basidiospores -- usually three septate, pale, slightly curved, 3 x 10u.

Conidia -- arthrospores present, 3 x 15u.

Habit -- On dead wood of snags or basal scars.

Reference -- (Kennedy 1958)

Dermea sp.

Figure IV.1.

Ascocarp -- small dark apothecium.

Ascospores -- hyaline aging to brown, zero- to one-septate, approx. 4.5 x 13u.

Habit -- On live or recently killed bark, it may be associated with corky bark condition (see Chapter V)

Anamorph -- probably the Gelatinosporium sp. that was commonly isolated. Conidia identical to those found in culture were twice found associated with this Dermea on recently killed bark.

Note: A new species of Dermea and Gelatinosporium (A. Funk, pers. comm.), see Gelatinosporium.

Reference -- (Groves 1946; Kuijt 1969; Funk 1976, 1979, 1981)

Dictyosporium elegans

Fruiting body -- none.

Conidia -- Large, dark, multiseptate, thick-walled dictyospores, solitary, (13-20 x 20-40u), not always present or abundant.

In culture -- dark, somewhat aerial brownish-grey mat.

Habit -- Basal scars

Reference -- (Damon 1952)

Dothidea sp.

Figure IV.6.

Ascocarp -- small black erumpet pseudothecium

Ascospores -- brownish at maturity, one septate with septum towards one end and constricted there, end furthest from septum is somewhat pointed.

Habit -- on wood.

Galerina sp.

Basidiocarp -- small pale brown capped mushroom with broad (2-3 cm) pileus and indistinct annulus.

Basidiospores -- rusty-brown in mass, have phage and apiculus, basidiospores 3 x 6u which are smaller than those of G. autumnalis.

Habit -- on wood

Gnomoniella sp.

Figure IV.6.

Ascocarp -- bright brown perithecium with globose base and long neck.

Ascospores -- dark brown, nonseptate.

Habit -- isolated only twice (from fine root and branch).

Herpotrichia sp.

Figure IV.6.

Ascocarp -- small black perithecium, ostiolate with one or more slits.

Ascospores -- brownish, 3-septate, noticeable constricted at middle septum.

Habit -- on wood.

Hyphodontia aspera

Basidiocarp -- white resupinate, non poroid, smooth hymenium, elongated vertically on scars and snags, ages to yellowish with cracks.

Basidiospores -- thin walled, non-septate (5-6 x 3-5 u).

Habit -- on dead exposed wood of snags or basal scars, probably causing sapwood decay.

Reference (R. Gilbertson, pers. comm.)

Gelatinosporium sp.

Figure IV.1.

Fruiting body -- pycnidium, variously-colored, opening by slits.

Sexual fruiting body is probably a Dermea sp. apothecium.

Macroconidia -- hyaline or yellowish or reddish with age,

uniseptate, lunate, sharper point on one end, some with foot cell, (3-4 x 30-55u) may or may not be formed in pycnidium.

Microconidia -- hyaline, sigmoid or curved (1 x 10-16u)

In culture -- whitish to cream color with aerial tufts of hyphae at center, appressed at edge, pycnidia dark, with or without a stroma.

Habit -- isolated from stem lesions (necrotic) and branches with corky bark condition (live phloem, but bark is rough, with fissures, and thicker than normal (Chapter V)).

References -- (Groves 1946; Kuijt 1969; von Arx 1970; Funk 1976, 1979, 1981).

Gibbera sp.

Ascocarp -- black pseudothecium on stroma

Ascospores -- nonseptate, hyaline

Habit -- on wood

(Dearness 1926, Dennis 1968)

Gymnosporangium nootkatense

Telial stage -- not found.

Uredospores -- in uredia, orange and ornamented spores, same as those described by Ziller (1974).

Habit -- present on live foliage or young twigs of healthy trees or prostrate layering patches.

Reference -- (Ziller 1974)

Leptographium sp.

Figure IV.3.

Fruiting body -- none, not associated with the Ceratocystis reported elsewhere in this paper (it has a Chalara sp. anamorph).

Conidiophores -- dark synema, sometimes branching near base, 60 to 100 u tall, conidiogenous cells hyaline.

Conidia -- small, hyaline, 2-3 x 3-6u, nonseptate.

In culture -- Dark to black mat with submerged dense white portions, tan radiating lines, synema present.

Habit -- associated with blackish stain of sapwood, also associated with galleries of Phloeosinus (bark beetle) in sapwood.

Mycelium radialis atrovirens

Figure IV.7.

No sexual fruiting body.

No conidia.

In culture -- dark appressed mat forming a hard surface crust with age and deep furrows radiating from the center. Submerged spots seen on underside of culture are loose clusters of thin-walled chlamydospore-like hyphal cells.

Habit -- common intracellular parasite of cortical cells of fine roots, also a root and stem saprophyte.

References -- (Gams 1963, Ricard and Fortin 1973, Chapter V).

Nectria sp.

Ascocarp -- small, orange perithecium, no stroma.

Ascospores -- pale, smooth, uniseptate, non-striate.

Habit -- on bark or wood of dead trees.

Reference -- (Booth 1959)

Opegrapha sp.

Ascocarp -- small branching hysterothecium with green hymenium.

Habit -- a crustose lichen on decorticated wood.

Pezicula sp.

Figure IV.5.

Ascocarp -- small reddish brown ~ 1 mm wide.

Ascospores -- subhyaline to light brown, oblong, wider at one end, multiseptate (3-5 x 10-12u), similar to P. livida

Habit -- on bark

Phialophora melinii

Figure IV.4.

No sexual fruiting body.

Conidia -- phialospores hyaline various shapes often, biguttulate, produced on short and branched conidiophores. Conidia often budding.

In culture -- aerial black at center, spreading white slime of budding conidia near margin.

Habit -- dead roots, dead cambium, black-stained sapwood.

Reference -- (Schol-Schwarz 1970)

Pistillaria sp.

Basidiocarp -- small white cylindrical club shaped (approx. 5mm long), basidia cover most of "club" once, collected with a definite basal stroma.

Basidiospores -- small, hyaline, nonseptate (2-3 x 3-5 u).

Habit -- recently killed cambium and sapwood.

Reference -- (Corner 1950)

Pithya cupressina

Ascocarp -- small stout yellowish apothecium.

Ascospores -- large, brownish thin walled non-septate (approx. 11 x 16 u).

Habit -- on dead foliage.

Reference -- (Denison 1972)

Polyporus elegans

Basidiocarp -- stipitate, upper pileus cream white soft, brittle with age, pore surface cream white poroid, stipe distinctly black up most of its length.

Habit -- found on basal scars and newly dead snags on cedar, also observed on dead Sitka alder stems.

Reference -- (Overholts 1953)

Scutellinia scutellata

Ascocarp -- apothecium with red hymenium and black or brown setulose "hairs".

Ascospores -- hyaline or pale, nonseptate with pseudoseptum.

Habit -- on wood of downed logs.

Reference -- (Denison 1961)

Septonema secedens

No sexual fruiting body.

Conidia -- appear as arthrospores but are blastically produced, often septate.

Habit -- Isolated from fine roots

Reference -- (Barron 1968)

Seiridium cardinale

Figure IV.5.

No sexual fruiting body.

Conidia -- 5 septate (6 celled) with the 4 median cells brown, the 2 distal cells hyaline with setulae (2-6 u long). Conidia (measured without setulae) 7-11 x 25-35 u. This species seems intermediate between S. cardinale and Monochaetia unicornis.

Funk (pers. comm.) suggests that our isolates are the former.

In culture -- slow growing white-semiaerial. Purple or rose colored reverse stain, sporulation uncommon, perhaps triggered with light.

Habit -- isolated once from 6 year old bear scar, collected once on dead foliage of dying cedar.

References -- (Groves 1946, Guba 1961, Funk 1985, A. Funk, pers. comm.)

Skeletocutis amorpha

Basidiocarp -- annual resupinate or effused reflexed, upper pileus tomentose, lower surface distinctly pinkish.

Basidiospores -- smooth, hyaline, thin walled, elongated (2 x 5 u).

Habit -- on dead, decorticated wood in basal scars or snags.

Reference -- (R. Gilbertson, pers. comm.)

Sporidesmium sp.

Fruiting body -- none

Conidia -- dark septate conidia, solitary, intercalary or terminal, usually not formed in abundance.

In culture -- grey-brown aerial mycelium, black from underneath, conidia not usually formed in abundance.

Habit -- associated with black stain of wood, also isolated from root and stem lesions.

Stictis radiata subsp. radiata

Ascocarp -- white emersed apothecium, sterile white hirsute margin.

Ascospores -- filiform, (approx 1.5-2.0 x 80-100 u) multiseptate (20+ septa), hyaline.

Habit -- on live bark.

Reference -- (Sherwood 1977)

Xeromphalina campanella

Basidiocarp -- mushroom; upper surface yellow-brown, 0.5-2cm diam, spore print pale buff, gills decurrent.

Basidiospores -- narrowly ellipsoid, 3-4 x 6-8u, hyaline to yellow.

Habit -- On down and decaying logs.

Reference -- (Miller 1968)

Unidentified basidiomycete #1

Basidiocarp -- not found.

In culture -- No sporulation, hyphae thin diameter with clamp connections, crystals present; mat slow growing bright white and appressed without reverse stain.

Habit -- isolated primarily from stem and root lesions and dead wood.

Unidentified basidiomycete #2

Basidiocarp -- not found.

In culture -- No sporulation, hyphae with clamp connections, crystals present; mat fast growing with patches of thick cotton-like aerial growth, white in color.

Habit -- isolated from fine roots, but also from root and stem lesions.

DISCUSSION

A total of 78 taxa of fungi have now been reported from Alaska-cedar -- 41 previously, and 37 reported here for the first time. Twenty-six of the fungi newly reported on Alaska-cedar are also new reports from Alaska on any host. Fungi from Alaska-cedar deposited in herbaria, but unreported, and obscurely reported fungi have probably been overlooked, but all major host lists, especially from Canada and the United States, where Alaska-cedar is native, were reviewed. Other micro-fungi likely exist on Alaska-cedar in many parts of its range but have not been collected and identified.

Basal scars on Alaska-cedar have a higher diversity of fungal species than many other tree parts. Basal scars are wounds on the base of cedars (approximately 2 m high) that are primarily caused by Alaska brown bears (Ursus arctos) stripping bark from cedars in the spring (Chapter VI). In many forest stands, one-half of Alaska-cedar trees have these scars, either fresh, or more often, old and callusing. A succession of fungal species exists as scars age from fresh to old (Chapter VI). Ceratocystis may be confined to the tops or bottoms of very fresh scars (e.g., one or two years old); it was only found sporulating on freshly-stripped bark and sapwood.

Fungal diversity on basal scars reaches a peak during sapwood decay, then drops off sharply after the rotted sapwood falls away, exposing the heartwood. The same trend occurred for dead cedars, with the same fungi, except for Ceratocystis. The exposed heartwood in snags and old basal scars was, except for lichens, nearly devoid of fungal fruiting bodies, especially large Basidiomycetes. Alaska-cedar

heartwood is extremely decay resistant (Harris 1971), and many cedars killed more than 80 years ago remain standing (Chapter II) with the heartwood sound and unstained.

Several dark-colored fungi isolated from black- or dark-stained wood of Alaska-cedar may be the fungi isolated, but not identified, by Smith (1970) in his study of black-stained heartwood of Alaska-cedar. These fungi may degrade compounds which make the wood of Alaska-cedar resistant to decay (Rennerfelt et al. 1955), therefore rendering the black-stained wood more susceptible to decay (Smith and Cserjesi 1970).

Many fungi on rotting sapwood of Alaska-cedar are not specific to cedar but appear to be rather cosmopolitan. Species such as Auricularia auricularis, Dacromyces deliquescens, and Lenzites saepiaria occur on dead wood of a wide range of coniferous hosts (Shaw 1973b). Polyporus elegans, the only large polypore (Aphylllophorales) that frequently sporulated on cedar, was confined to bear scars and the boles of recently-killed Alaska-cedars, but was also collected from dead stems of Sitka alder (Alnus sinuata (Regel) Rydb.). Fomitopsis pinicola, an extremely common saprophyte on other coniferous hosts in southeast Alaska (Laurent 1974), was only observed and collected once on Alaska-cedar. Two Basidiomycetes were frequently isolated from dead portions of Alaska-cedar but did not sporulate in culture and were not identified.

Fungi collected from the foliage of Alaska-cedar are probably more host-specific than those from wood. Gymnosporangium nootkatense, Asterina cupressina, Pithya cupressina and Apostrasseria sp. (the latter is possibly a new species, A. Funk, pers. comm.) are all probably restricted to Alaska-cedar, Chamaecyparis, or Cupressaceae.

The aromatic foliage of Alaska-cedar probably contains anti-fungal compounds restricting the growth of unspecialized fungi, although this has apparently not been studied. One unidentified tiny perithecial fungus from Alaska-cedar foliage was never found actively sporulating. It was common on healthy trees with vigorous foliage, as well as on declining cedars, and may be a commensal fungus.

Fungi occurring on the bark of Alaska-cedar show a range of host specialization. Stictis radiata and Bertia moriformis are not host-specific, but the new Dermea sp. and Ceratocysits sp. probably occur only on Alaska-cedar. Both occurred on recently-killed bark.

In conclusion, previously reported fungi from Alaska-cedar are compiled here, and 37 new fungal taxa have been added to this host list, now totalling 78 fungi. Some of these fungi were identified only to genus. Of these fungi, several known pathogens were found associated with Alaska-cedar in southeast Alaska. None, however, was found consistently on dying cedars nor had the pathogenic abilities (Chapter V) to be considered the primary incitant of the widespread and destructive mortality occurring in southeast Alaska.

I hope this compilation of previously reported fungi and new host records will benefit future mycological and pathological studies of this important tree species.

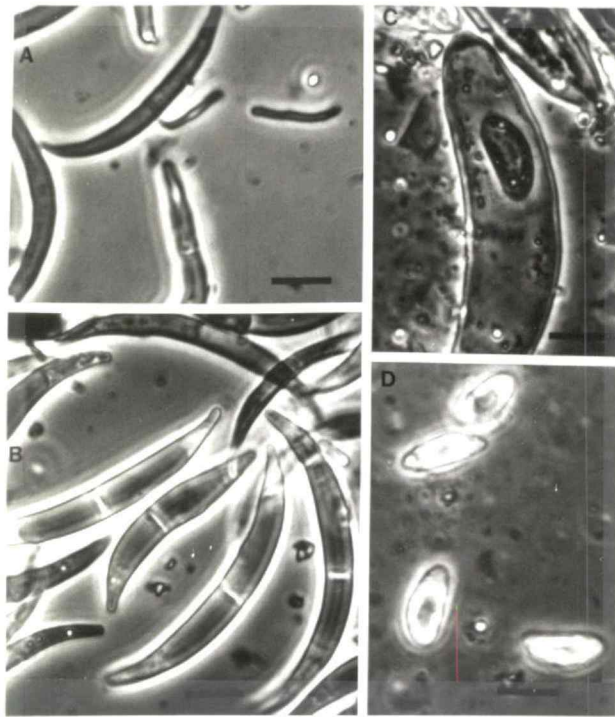


Figure IV.1. Dermea sp. and its Gelatinosporium sp. anamorph. A. Macro and microconidia, B. Macroconidia, C. One remaining ascospore in ascus, and D. Ascospores. Bars = 10u.

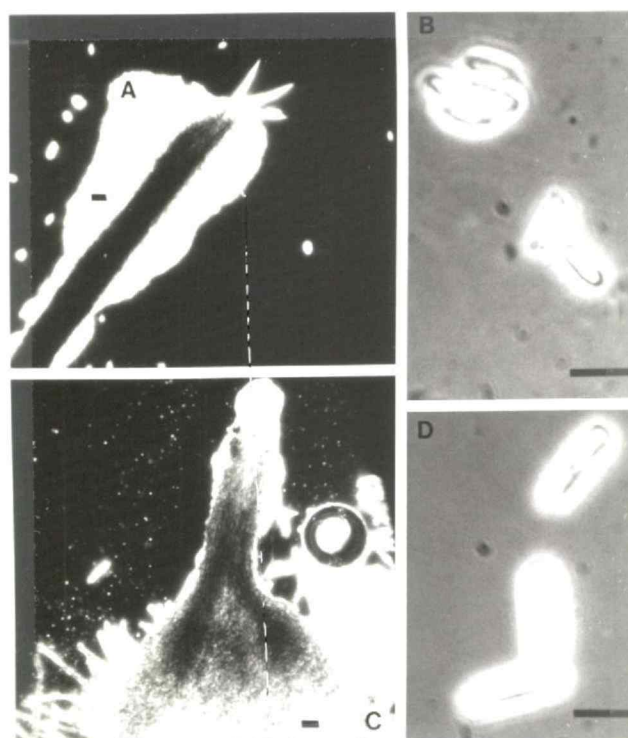


Figure IV.2. Ceratocystis sp. A. Neck and ostiolar appendages of perithecium, B. Ascospores and ascospores in an ascus (upper left), C. Perithecium, and D. Conidia of the anamorph, Chalara sp. Bars = 10u.

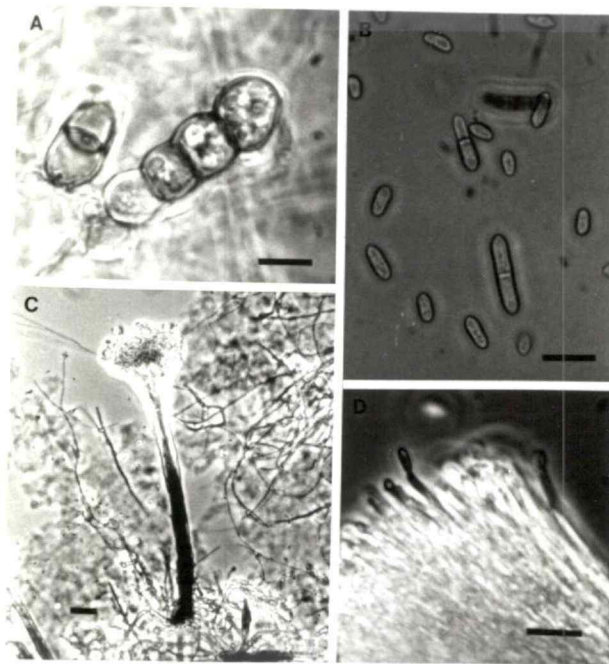


Figure IV.3. A-B. *Cylindrocarpon didymum*. A. Chlamydospore, B. Microconidia and septate macroconidia. C-D. *Leptographium* sp., C. Synemata, and D. Sporogenesis. Bars = 10u.

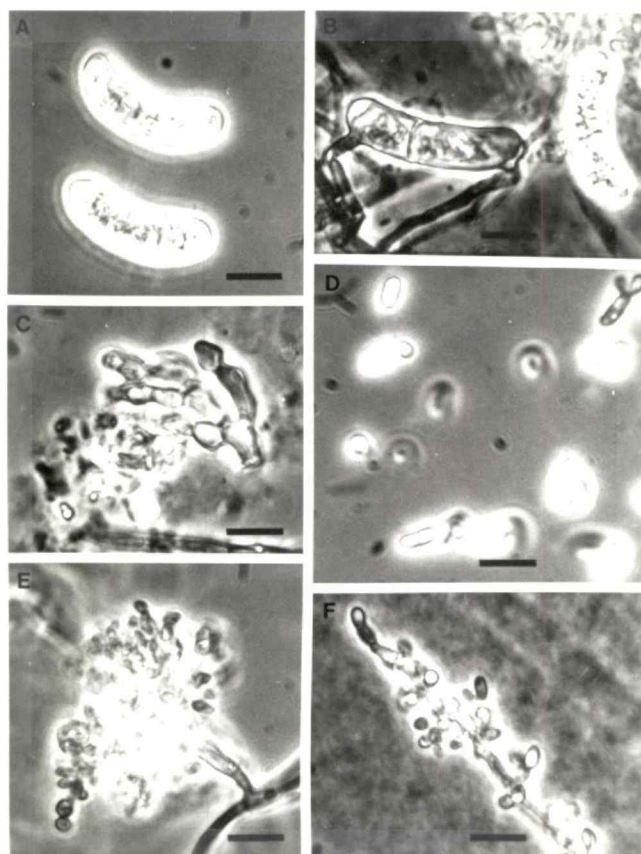


Figure IV.4. A-C. *Cryptosporiopsis* sp. A. Conidia, B. Conidia appear septate only after germination, and C. Short branched conidiophore. D-F. *Phialophora melinii*. D. Conidia that are budding, E and F. Conidiophore. Bars = 10u.

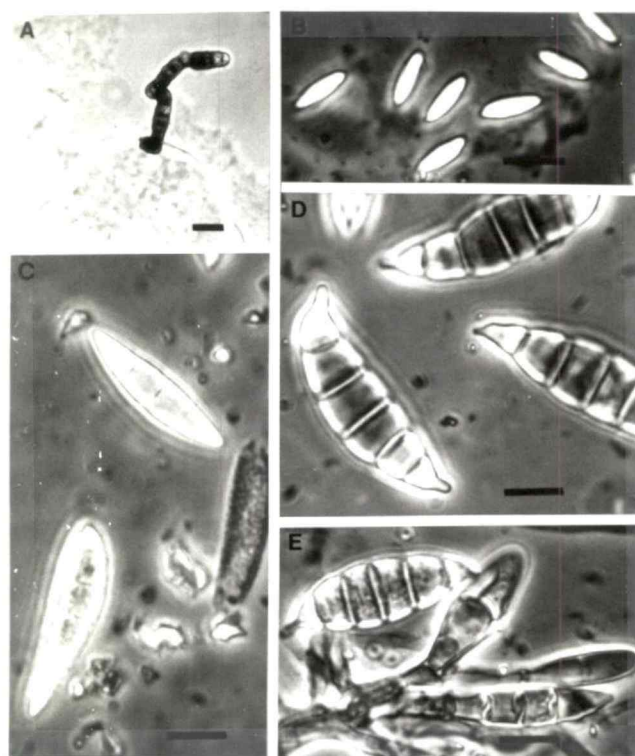


Figure IV.5. A. Solitary conidium of *Sporidesmium* sp., B. Conidia of *Apostrasseria* sp., C. Ascospores of *Pezicula* sp., D. Conidia and E. Sporogenesis of *Seirdium cardinale*.

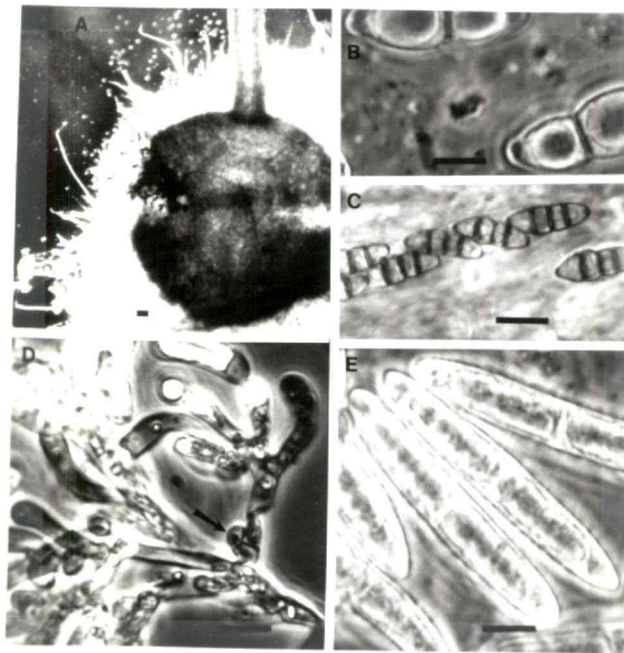


Figure IV.6. A. Peritheciium of Gnomoniella sp., B. Ascospores of Dothidea sp., C. Ascospores of Herpotrichia sp., D. Branched conidiophore and conidia of Ditangium sp. (note the clamp connection (arrow), and E. Septate ascospores of Bertia moriformis. Bars = 10u.

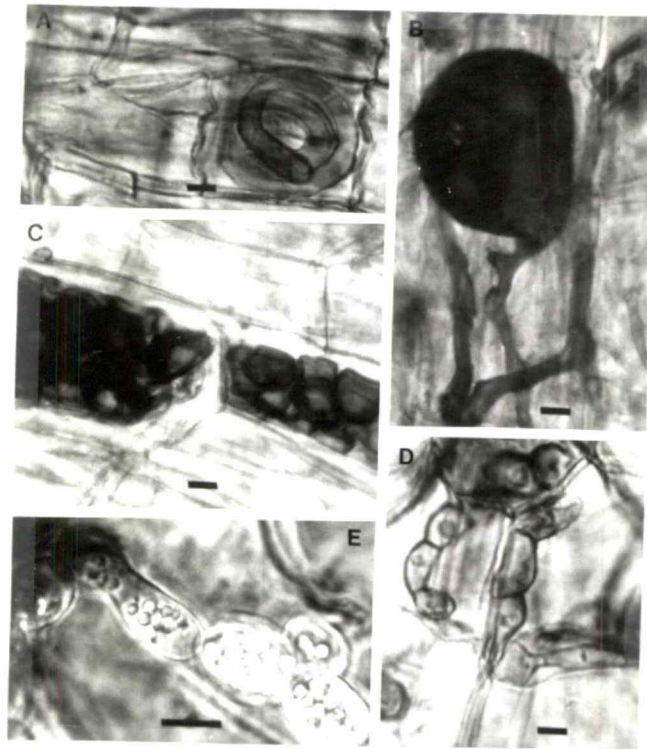


Figure IV.7. Fungi in cortical cells of fine roots on Alaska-cedar. A-B. VA mycorrhizae. A. Hyphal coil, B. vesicle. C-D. Infection by dark fungus, probably Mycelium radialis atrovirens, and E. hyphae of M. radialis atrovirens in culture. Bars = 10u.

LITERATURE CITED

- Barron, G.L. 1968. The genera of hyphomycetes from soil. Williams & K Wilkins Co., Baltimore, MD. 364p.
- Booth, C. 1959. Studies of the Pyrenomyces IV. Nectria (Part I). Mycol. Pap. 73:1-115.
- Booth, C. 1966. The genus Cylindrocarpon. Mycol. Pap. 104:1-56.
- Brodie, H.J. 1975. The bird's nest fungi. Univ. of Toronto Press, Toronto. 199p.
- Cash, E.K. 1953. A check list of Alaskan fungi. Plant Dis. Repr. Supplement 219. 70p.
- Commonwealth Mycological Institute. 1983. Plant pathologist's pocketbook. Cambrian News Ltd., Aberystwyth, Wales. 439p.
- Connors, I.L. 1967. An annotated index of plant diseases in Canada and fungi recorded on plants in Alaska, Canada and Greenland. Canada Dept. of Agric. Research Branch. Publ. 1251. 381p.
- Corner, E.H. 1950. A monograph of Clavaria and allied genera. Oxford Univ. Press, London. 740p.
- Damon, S.C. 1952. Type studies in Dictyosporium, Speira, and Cattanea. Lloydia 15:110-124.
- Damon, S.C. 1953. Notes on the hyphomycetous genera Spegazzinia and Isthmospora. Bull. Torr. Bot. Club 80:155-165.
- Dearnness, J. 1926. New and noteworthy fungi. Mycologia 18:246.
- Denison, W.C. 1972. Central American Pezizales. IV. The genera Sarcoscypha, Pithya, and Nanoscypha. Mycologia 64:609-623.
- Denison, W.C. 1961. Some species of the genus Scutellinia. Mycologia 51:605-635.
- Dennis, R.G. 1968. British Ascomycetes. J. Cramer, Lehre. 455p.
- Ellis, M.B. 1971. Dematiaceous Hyphomycetes. Commonwealth Mycological Institute. Kew, Surrey, England. 608p.
- Frear, S.T. 1982. What's killing the Alaska yellow-cedar? Amer. For. 88(11):41-43, 62-63.
- Funk, A. Personal Communication. Canadian Forestry Service. Pacific Forest Research Centre. 506 West Burnside Road, Victoria, B.C. V8Z 1M5

- Funk, A. 1973. Some mycoparasites of western bark fungi. Can. J. Bot. 51: 1643-1645.
- Funk, A. 1974. Microfungi associated with dieback of native Cupressaceae in British Columbia. Can. Plant Dis. Surv. 54(4):166-168.
- Funk, A. 1976. The genus Dermea and related conidial states on Douglas fir. Can. J. Bot. 54: 2852-2856.
- Funk, A. 1979. New species of Gelatinosporium on western conifers. Can. J. Bot. 57: 765-767.
- Funk, A. 1981. Parasitic microfungi of western trees. Can. For. Serv., Pac. For. Res. Cent. Report BC-X-222. 190p.
- Gams, W. 1963. Mycelium radialis artoovirens in forest soils, isolation from soil microhabitats and identification. Pp. 176-182. In: Soil organisms (symposium). Eds. J. Docksens and J. van der Drift. North-Holland Publishing Co., Amsterdam, Holland.
- Griffin, H.D. 1968. The genus Ceratocystis in Ontario. Can. J. Bot. 46:689-718.
- Grove, W.B. 1935. British leaf and stem fungi. 2. Sphaeropsidales and Melanconiales. Cambridge, MA 406 p.
- Groves, J.W. 1946. North American species of Dermea. Mycologia 38:351-431.
- Guba, E.F. 1961. Monograph of Monochaetia and Pestalotia. Harvard Univ. Press, Cambridge, MA. 342p.
- Harris, A.S. 1971. Alaska-cedar. USDA Forest Service. American Woods--FS 224. 7p.
- Hepting, G.H. 1971. Diseases of Forest and shade trees of the United States. USDA Forest Service. Agric. Handbook No. 386. 658p.
- Hughs, S.J. 1953. Some folicolous Hyphomycetes. Can. J. Bot 31:560-576.
- Hughs, S.J. 1953. Conidiophores, conidia and classification. Can. J. Bot. 31:577-659.
- Hunt, J. 1956. Taxonomy of the genus Ceratocystis. Lloydia 19:1-58.
- Kennedy, L.L. 1958. The genus Dacromyces. Mycologia 50:896-915.
- Kuijt, J. 1969. Cork-bark, a disease of Alpine fir in British Columbia. Northwest Science 43: 74-79.
- Leach, C. 1963. The qualitative and quantitative relationship of monochromatic radiation to sexual and asexual reproduction of Pleospora herbarum. Mycologia 55:151-163.

Lowe, D.P. 1982. Check list and host index of bacteria, fungi, and mistletoes of British Columbia. Pacific Forest Research Centre, Victoria, B.C., Canada. Inf. Rept. BC-X-32. 540p.

Miller, O.K. 1968. A revision of the genus Xeromphalina. Mycologia 60:156-188.

Overholts, L.O. 1953. The Polyporaceae of the United States, Alaska, and Canada. Univ. of Michigan Press, Ann Arbor, MI. 466p.

Rennerfelt, E. and G. Nacht. 1955. The fungicidal activity of some constituents from heartwood of conifers. Svensk Bot. Tidskr. 49(3):419-432.

Ricard, C. and J.A. Fortin. 1973. The identification of Mycelium radicis atrovirens (Phialocephala dimorphospora) Can. J. Bot. 51:2247-2248.

Schol-Schwarz, M.B. 1970. Revision of the genus Phialophora. Persoonia 6:59-94.

Seymour, A.B. 1929. Host index of the fungi of North America. Harvard Univ. Press. Cambridge, MA. 732p.

Shaw, C.G. 1973a. Host index for the Pacific Northwest I. Hosts. Wash. Agr. Exp. Sta. Bull. 765. 121p.

Shaw, C.G. 1973b. Host index for the Pacific Northwest II. Fungi. Wash. Agr. Exp. Sta. Bull. 766. 162p.

Smith, S.C. 1965. The morphology of Verticillium albo-atrum, V. dahliae, and V. tricorpus. New Zealand J. Ag. Res. 8:450-478.

Smith, R.S. 1970. Black stain in yellow cedar heartwood. Can. J. Bot. 48: 1731-1739.

Smith, R.S. 1970. Degradation of nootkatin by fungi causing black heartwood stain in yellow cedar. Can. J. Bot. 48: 1727-1729.

Strouts, R.G. 1972. Canker of cypress caused by Coryneum cardinale Wag. in Britian. Eur. J. For. Path. 3:13-24.

Sutton, B.C. 1970. Coelomycetes. Commonwealth Mycological Institute. Kew, England. 696p.

USDA Forest Service. 1960. Index of plant diseases in the United States. Washington, D.C. Agric. Handb. 165. 531p.

Wang, C.K. 1965. Fungi of pulp and paper in New York. Techs. Pub. Syracuse Univ. Coll. Forestry 87.

Ziller, W.G. 1974. The tree rusts of Western Canada. Can. For. Serv.,
Dept. of Environment. Publ. No. 1329. Victoria, B.C. 272p.

CHAPTER V

ALASKA-CEDAR DECLINE: POTENTIAL PATHOGENIC AGENTS

ABSTRACT

Alaska-cedar (Chamaecyparis nootkatensis) is a valuable tree in southeast Alaska that has been suffering from an extensive decline and mortality of unknown cause since about 1880. The objective of this study was to evaluate the potential pathogens that could be primarily responsible for this decline. Roots of 35 dying or healthy Alaska-cedar trees were excavated to study symptoms and isolate fungi. Dying fine roots and necrotic lesions on roots and boles were common on cedars with declining crowns. Of the 1,864 isolation attempts, 1,047 yielded cultures of fungi; however, when cedar seedlings were inoculated with the twelve most commonly isolated fungi, only Cylindrocarpon didymum caused necrotic lesions, and no fungi killed seedlings. Most fungal species were isolated from healthy, as well as dying, cedars. Both vesicular-arbuscular mycorrhizae and Mycelium radialis atrovirens were common (83 and 79% of the samples, respectively) in cortical cells of 42 fine root samples that were collected from 26 healthy and declining Alaska-cedar trees. Baiting soil from beneath cedar trees for Pythiaceaus fungi yielded no species of Pythium, but an unidentified Phytophthora sp. was obtained. It was recovered too infrequently, however, to be considered the major cause of decline. Likewise, plant parasitic nematodes (e.g., Sphaeronema sp.

and Crossonema sp.) were commonly recovered from dying and healthy cedars, but only in low numbers. Defoliating or root feeding insects were not found. Phloeosinus sp. bark beetles, which were infrequently found, were confined to dying cedars in later stages of decline. Pieces of necrotic phloem removed from dying cedars and implanted into live cedars either failed to induce lesions or induced small lesions that developed callus tissue after two years. Similar small lesions were produced by mechanical wounding alone. These results suggest that neither pathogens nor insects are the primary cause of Alaska-cedar decline and support the hypothesis of an abiotic cause.

INTRODUCTION

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a slow-growing, valuable forest tree that ranges from Prince William Sound in Alaska, south through British Columbia, to south of the Oregon-California border (Harris 1971). In undisturbed areas of southeast Alaska, old-growth Alaska-cedar stands are suffering from a spectacular mortality problem (Frear 1982) that began before the turn of the century (Chapter II). Studies on the dynamics of mortality have shown that Alaska-cedar is the principal victim and that the boundaries of mortality have spread from bogs to sites with better soil drainage (Chapter III), a pattern that suggests possible involvement of a pathogen.

Shaw et al. (1985) made a preliminary evaluation of symptoms and the roles of pathogens in this decline. Crown symptoms suggested root

or root-related problems, since entire crowns of affected trees fade slowly with gradually thinning foliage, or die quickly with all foliage turning shades of brown without thinning (Fig. V.1). In addition, necrotic lesions occurred on the boles and roots of some dying Alaska-cedars (Fig. V.2 and V.5), symptoms indicative of root disease pathogens. By excavating affected cedars, Shaw et al. (1985) observed that many coarse roots were dead, and Armillaria sp. was common on dying trees.

The objective of this study was to determine which microorganisms are associated with dying Alaska-cedar and to evaluate their roles in Alaska-cedar decline. Fungi were isolated from systematically excavated root systems and dissected crowns to distinguish primary from secondary colonization. The pathogenicity of isolated fungi was deduced by their incidence from particular symptomatic tissues and tree conditions and tested by inoculations of seedlings of Alaska-cedar. The identity and diagnostic characteristics of the fungi isolated by Shaw et al. (1985) and the fungi isolated in this study are reported in Chapter IV.

A special effort was made to determine if any species of Phytophthora were present because symptoms, mortality-spread patterns, and a serious disease of another species of Chamaecyparis all suggest these pathogens as candidates for causing Alaska-cedar decline. Phytophthora lateralis (Tuck. & J.A. Milb.) causes a serious disease of Port-Orford-cedar (C. lawsoniana (A. Murr.) Parl.) in southwest Oregon (Roth et al. 1972). Necrotic lesions on roots and root collars of dying cedars are characteristic of this disease (Zobel et al. 1985). The concentration of dead and dying Alaska-cedar trees on wet sites and

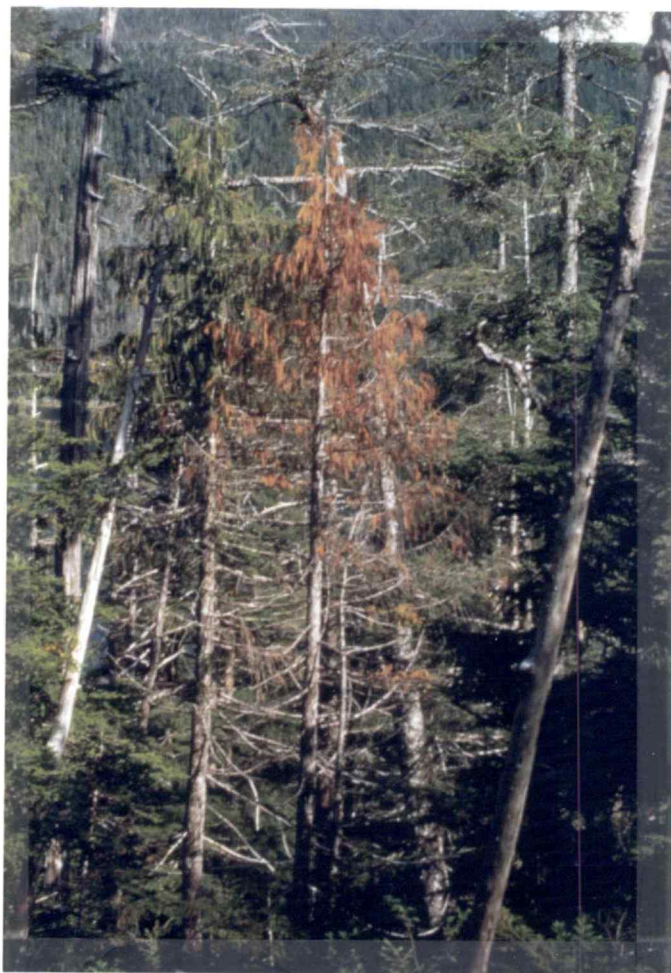


Figure V.1. Crown symptoms of dying Alaska-cedar trees suggest a possible below-ground problem, as the entire crown dies as a unit.



Figure V.2. Necrotic lesion on root and lower bole of an Alaska-cedar tree

local patterns of spread (Chapter III) are also suggestive of Phytophthora diseases.

Similarly, the pathogenicity of Armillaria was investigated since it was commonly present on dead and dying Alaska-cedars (Shaw et al. 1985), and elsewhere it can be a virulent killer of forest trees (Wargo and Shaw 1985).

MATERIALS AND METHODS

Root and Crown Symptoms

Root systems of 35 dying or apparently healthy Alaska-cedars were excavated. Duff and soil were removed from around root collars and all major roots near the root collar. These roots were measured for diameter and the proportion of the circumference with living phloem as determined by color. From these measurements, an overall proportion of live and dead root surface area entering the root collar was calculated. Removing bark, observing phloem, and measuring the proportion of tissues that were live and dead was repeated at the root collar, on the bole just above entering roots, and at breast height (1.37 m) up the bole.

On all excavated trees, three major, live roots were randomly chosen and along with their secondary roots were excavated by hand until dead portions were reached, or until the root diameter was less than 1 cm. Root diameter, proportion of circumference alive, and presence of fine roots were determined at 15 cm intervals along each root. Ten fine roots were collected, if present, from each 15 cm

interval and rated dead or alive by observing cortex color after removing the epidermis (cortex of live roots was white, that of dead fine roots was tan or brown). An overall percentage of live fine roots was calculated for each tree by averaging the proportion alive from each sampling interval. Also, sampling intervals along roots that lacked fine roots were tallied. Differences, between healthy and declining trees, in the percentage of fine roots that were alive and in the percentage of sampling intervals lacking fine roots were tested using Student's t test for three different size classes of coarse roots.

Tree heights, diameters at breast height, signs of Armillaria sp. (i.e., mycelial fans and rhizomorphs), and the presence of basal scars (Chapter VI) were recorded for each tree. Also, crowns were rated visually for percent foliage fullness and proportion of different colors of retained foliage, as described by Shaw et al. (1985). An overall "percent green" was calculated for tree crowns as the product of percent fullness and percent green of retained foliage. Cedars referred to as "healthy" had crowns with percent green exceeding 75%. Crowns were inspected for insects and symptoms of disease on foliage, branch, and bole tissues; symptomatic tissues were collected for isolation.

Fungal Isolations

Isolations were attempted from 31 of the 35 cedars that were excavated. Most (77%) of the 1,864 isolation attempts were from fine roots, or lesions on roots, stems (Fig. V.2), or branches. Fine roots were surface-sterilized for 30 to 60 seconds in 1% sodium hypochlorite,

rinsed twice in sterile water, blotted dry with sterile paper, and placed in petri plates containing one of the several media described below. Other tissues were not surface sterilized prior to isolation. Stem lesions were collected by removing a patch (4 cm. per side) of sapwood and attached bark with a chisel (Fig. V.3). These patches were then split along the cambium to expose clean sapwood and phloem surfaces. Chips were then removed with a sterilized scalpel and placed onto agar media. Root and branch lesions were treated similarly, except for the size and shapes of field-collected pieces of tissues.

Media used in these studies included: Potato Dextrose Agar (PDA), 1.5% Water Agar, 1.5% Malt Extract Agar (with 2 ppm benomyl) and a medium selective for Phytophthora species. The latter medium consisted of 1.5% cornmeal agar, 40 ppm active ingredient pimarinol, 200 ppm vancomycin (Vancocin), 100 ppm Penicillin G. Hymexazol (25 ppm) was sometimes added to this medium to reduce Pythium contamination (Philip B. Hamm, personal communication). Media selective for Phytophthora were always stored in darkness and used within seven days of preparation since their antibiotics break down with time or when exposed to light. The first three media contained 100 ppm streptomycin to reduce bacterial contamination. All fungi isolated were routinely transferred to PDA for identification or storage.

Fine Root Observations

Forty-two samples of fine roots (<2 mm diameter) were collected from 26 Alaska-cedar trees that ranged from healthy trees growing some distance from mortality to trees in final stages of decline. Fine roots were fixed in FAA, cleared (to remove pigments) with warm



Figure V.3. Squares containing bark and sapwood were removed from bole lesions for isolation attempts and also used as patch inoculations.

potassium hydroxide, stained with Trypan blue in lactophenol (Phillips and Hayman 1970), and sectioned by hand lengthwise. Sections were squash mounted in lactophenol and viewed microscopically. The presence or absence of mycorrhizal fungi and infections by other fungi were noted.

Sampling for Phytophthora sp.

Sampling for species of Phytophthora by baiting was conducted around 69 Alaska-cedar trees over a three-year period. Methods for such sampling are reported elsewhere (Linderman and Zeitoun 1977) and are only briefly reviewed here. Soil, fine roots, and organic matter were collected from two or three locations around the base of each cedar and combined for each tree. Each sample was placed in cheesecloth and washed several times with water to remove most mineral soil; two to three grams of this remaining organic soil was placed in the bottom of each of 10 styrofoam cups. A second cup, with its bottom removed and replaced with a single layer of cheesecloth, was placed into each of the whole cups. Each "double-cup" was filled to within 2 cm of the top with water and five baits floated on the surface of the water. Baits were 2-3 cm long pieces of Alaska-cedar foliage with side foliage removed. After seven days of incubation at room temperature, baits were removed, surface-sterilized, and placed into petri plates containing the Phytophthora-selective medium. Besides baiting, isolations were attempted directly from symptomatic tissues (e.g., dying fine roots, root and stem lesions) by placing small pieces (not surface-sterilized) onto the same Phytophthora-selective medium.

Nematode Sampling

Nematode sampling was conducted because several nematodes were incidently isolated along with fungi from fine roots of dying cedar trees. Sampling was conducted at six sites along Peril Strait on Baranof and Chichagof Island. Soil, organic matter, and fine roots were collected from beneath 27 dying and 5 healthy Alaska-cedar trees. Approximately 200 ml of this material from beneath each tree was sent to the Plant Disease Clinic at Oregon State University where nematodes were collected by a modified Baerman funnel technique (Agrios 1978), identified to genus, and counted. Estimates of nematode population per gram of soil material were made for nematode taxa occurring around each tree.

Pathogenicity Testing

The pathogenicity of the 12 fungi most commonly isolated from Alaska-cedar trees was determined by inoculating these fungi onto Alaska-cedar seedlings. These seedlings were approximately 20 cm tall and grown in cold frames at Corvallis, Oregon. Each fungus was grown on PDA medium and induced to sporulate. Agar containing each fungus was cut into 1 cm squares, placed adjacent to 1 mm wide wounds just below the root collar of seedlings, and then both the fungal inoculum and root were wrapped in moistened cheesecloth. An outer wrapping of 1 mil plastic was placed over the cheesecloth and fastened with twist ties. Ten seedlings were inoculated for most fungi. Inoculations were conducted in the fall and spring to determine if host resistance might be seasonal.

One fungus, Dermea (Gelatinosporium) sp. was also inoculated onto branchlets because it was isolated exclusively on above-ground tissues of symptomatic Alaska-cedar trees.

Seedlings were unpotted after seven months and examined for lesions. All lesions were measured for distance above and below the points of inoculation, and re-isolation attempts were made. Significant differences in linear extent of lesion development above and below points of inoculation between each fungus treatment and controls were tested using Student's t test ($p=0.05$).

Armillaria Inoculations

Roots of 16 mature, healthy Alaska-cedars were inoculated with an isolate of Armillaria sp. obtained from a dead Alaska-cedar to test pathogenicity of Armillaria. Alder (Alnus rubra Bong.) branch segments (approximately 3 cm in diameter by 10 cm long) were colonized with Armillaria, as described by Shaw (1977). Uncolonized alder segments served as controls. A control and an Armillaria-colonized segment were placed in contact with live roots (e.g., 1-4 cm diameter) on each tree. One-half of the inoculated roots (including controls) were wounded by cutting bark and outer sapwood away, and the other half were left unwounded. All inoculations were covered with soil and moss, re-excavated after two years, and examined for symptoms and signs of Armillaria infection.

Root Wounding

Roots on mature cedars were wounded to determine if lesions similar to those on symptomatic trees could be induced by the death or

damage of distal tissues. Four roots on five live cedars at each of three sites (total of 60 roots) received one of the following treatments: 1) one-half of the circumference wounded through the cambium, 2) entire circumference girdled through the cambium, 3) one-half of the circumference wounded through the cambium and sapwood, and 4) no wounding (control). Roots were then covered with soil and duff. After two years, the roots were uncovered and measured for lesion development and extent. Also, 76 isolation attempts were made from lesions to determine if the same fungi were present in these induced lesions as in lesions found on declining trees. Differences in linear extent of lesion development were tested using a one-way analysis of variance (ANOVA).

Stem Lesions and Square Patch Inoculations

Vertical stem lesions that arise from dead roots and that darkened the phloem are common on declining Alaska-cedars (Shaw et al. 1985). When these lesions were encountered, square portions were removed with a 4 cm wide chisel and isolations attempted, as previously described. The upper margin of the lesion, one square (4 cm per side) above the lesion (with healthy phloem and sapwood), and three or four squares from below the top margin were sampled.

The square directly below the upper margin was not typically used for isolations; rather it was used directly as a form of inoculum, and placed into a nearby healthy cedar by removing a similarly-sized section of phloem and bark. Each section of lesion inoculum was then fitted into the bark of the healthy cedar (Fig. V.4), covered with petroleum jelly and left for two years. Seventeen such inoculations



Figure V.4. Patch inoculations. Piece of necrotic phloem is removed from the bole of a dying Alaska-cedar tree and placed into the bole of a healthy Alaska-cedar. Such inoculations were revisited after two years to determine if inoculations induced lesions.

from necrotic lesions and 23 from live cambium (controls) were conducted.

Following this incubation period, inoculations were checked for lesion development, and any lesions that were present were measured and isolations were attempted. Differences in lesion development from control and necrotic lesion patch inoculations were tested using Student's t test ($p=0.05$). Differences in frequencies of fungi isolated from lesions developing from lesion- and control-patch inoculations were compared by a chi-square test ($p=0.05$). The species of fungi isolated from lesions that developed in inoculated trees were contrasted with those isolated directly from lesions on declining trees.

RESULTS

Root and Crown Symptoms

On dying cedar trees, the entire crown appears to decline and die as a unit rather than as individual scattered dying branches (Fig. V.1). Closer inspection indicates that proximal (older) foliage died first, often with a color change from green to yellow to brown. In slowly declining cedars, this dead proximal foliage fell away before the distal foliage died, leaving a crown with a thin appearance. In cedars that died quickly, the entire complement of foliage died, leaving a relatively full, but dead, crown.

Symptoms in the roots of affected Alaska-cedar trees included: a high proportion of dead or missing fine roots, dead small diameter

roots, large diameter coarse roots completely dead or with lesions, and cambial lesions that extended from dead coarse roots vertically up the main bole (Fig. V.2).

A significantly greater proportion of fine roots was dead on declining trees (38%) than on healthy trees (7%) (Table V.1). Differences were pronounced among fine roots on small diameter coarse roots. Fine roots found on medium and large diameter coarse roots were more often alive on healthy trees than on declining trees, but differences were not significant. Fine roots occurred most commonly (either live or dead) on small, coarse roots and were least common on large, coarse roots for both healthy and declining trees. More fine roots were missing (no fine roots found within an interval) on all three root-size classes of declining cedars, but differences with healthy cedars were not significant. Fine roots attached to dead coarse roots were never live and were, therefore, not sampled.

Small, coarse roots from distal parts of the root systems of cedars in the early stages of crown decline were frequently dead; these dead roots were often located in a water-saturated, black, organic muck (Chapter VII). As crowns continued to decline, a greater proportion of small coarse roots died; larger coarse roots were also dead or had necrotic cambial lesions that had apparently spread from smaller, more distal roots. These lesions spread from dead roots vertically up the bole, occasionally reaching to nearly the top of the bole on dying cedars. In the final stages of tree death, patches of phloem on the bole, not connected to the vertical lesions, appeared mottled or necrotic and dark brown. The cambium in the upper portions of the bole appeared to be the last tissue to die.

Table V.1. Condition^{1/} of fine roots (< 2 mm diam) on three size classes of coarse roots from 8 healthy and 23 declining Alaska-cedars

Coarse root size	Fine roots on healthy trees		Fine roots on declining trees	
	Mean (%)	Std dev	Mean (%)	Std dev
Over 3 cm diameter:				
Fine roots alive	92	14	63	38
Intervals with fine roots missing	52	32	56	28
From 1-3 cm diameter:				
Fine roots alive ^{2/}	93	7	63	27
Intervals with fine roots missing	35	23	48	26
Less than 1 cm diameter:				
Fine roots alive ^{2/}	93	12	61	20
Intervals with fine roots missing	20	18	29	20
All Coarse roots:				
Fine roots alive ^{2/}	93	10	62	18

^{1/} Values are percent of live (vs. dead) fine roots on three size classes of coarse roots. Fine root presence and health were determined at 15 cm intervals along living coarse roots. Fine roots were determined to be alive or dead based on the color of cortex tissues under the epidermis; sampling intervals along coarse roots that lacked fine roots were designated "missing" fine roots.

^{2/} Significant difference between healthy and declining Alaska-cedars based on Student's t test ($p = 0.05$).

Root death is probably the initial phase of decline and seems to precede crown symptoms. A higher proportion of the cambium was dead on roots entering the bole than for the cambium at the root collar (just above soil line) for cedars in the earlier stages of crown decline (Table V.2). A high proportion of the cambium on the bole at breast height was dead only on cedars that were in the final stages of dying. Condition of these tissues was more easily quantified than distal roots because they could be completely sampled. The relationship between the condition (proportion live) of the cambium for each of these sampling locations to the crown condition (proportion green) is presented in Figure V.5. A steeper slope in this figure indicates a greater proportion of the cambium being dead in earlier stages of crown decline. Although the slopes were not significantly different from one another, slopes do show a trend of earlier symptoms (steeper slope) for roots entering the bole, and later symptoms in the bole at breast height.

An unusual bark malformation was common on small diameter branches (e.g., 1-3 cm diameter) of both declining and healthy Alaska-cedar trees. Bark on affected branches appeared to be "roughened" with shallow fissures running parallel to the axis of the branch. Bark on such small branches is normally smooth. Branches were slightly swollen (almost imperceptibly) for the 2-5 cm length of affected tissue. The phloem, cambium, and sapwood of these tissues appeared live and undamaged; the bark was somewhat thicker than adjacent, unaffected tissue. No fungal fruiting bodies were associated with these symptoms.

Table V.2. Characteristics^{1/} of Alaska-cedars for which roots were excavated and whose symptomatic tissues were used for fungal isolation. Trees are arranged in order of the crown rating^{2/}, with healthy cedars at the top and dead trees at the bottom of the list.

Tree No.	Diam (cm)	Height (m)	Basal Scar	Armillaria present	Crown rating ^{2/}	Living cambium (% circumference)			Fine Root Observations	
						Root	Collar	Bole	VA Myco- rhizae	M. radicis atrovirens
202	30.2	15.8	-	-	1.00	100	100	100	+	+
222	34.9	17.3	-	-	.95	100	100	100	+	+
301	25.5	13.1	+	-	.95	86	100	100	+	-
212	18.3	10.1	+	-	.90	100	100	100	+	+
316	18.1	10.7	+	-	.90	69	100	100	NA	NA
315	17.8	11.9	+	-	.90	66	100	100	NA	NA
205	50.8	22.8	+	-	.80	78	100	100	+	+
304	15.9	9.1	+	-	.77	100	100	100	+	+
311	5.1	2.8	-	-	.72	72	100	100	+	+
217	16.4	12.1	-	-	.68	98	100	100	NA	NA
302	38.0	18.2	+	+	.60	76	92	100	NA	NA
308	27.6	16.8	+	+	.60	94	100	100	+	+
213	13.5	11.4	-	+	.53	86	100	100	+	+
309	16.8	14.0	+	-	.49	82	100	100	+	+
206	21.1	15.4	+	+	.48	78	100	100	-	+
215	31.4	17.1	+	+	.48	78	100	100	+	+
210	19.4	9.1	+	-	.45	89	100	100	+	+
314	17.9	11.6	-	-	.42	84	84	74	+	+
201	13.7	10.2	-	-	.42	62	42	100	NA	NA
306	27.0	16.7	-	-	.41	100	100	100	NA	NA
312	26.6	12.0	+	-	.36	52	53	58	+	+
207	23.6	16.0	+	-	.36	47	87	100	+	+
313	11.0	8.2	-	-	.30	20	40	80	NA	NA
208	46.9	21.3	+	-	.26	40	46	27	+	+
307	22.6	14.5	-	-	.18	13	13	25	+	-
305	23.0	15.3	-	-	.16	0	0	0	+	+
204	17.8	10.9	+	-	.16	0	85	100	+	+
310	21.4	13.6	-	-	.14	32	40	34	+	+
303	17.0	11.1	+	-	.10	0	0	74	NA	NA
211	20.7	11.8	-	-	.09	70	100	100	-	+
221	33.7	17.1	-	+	.06	33	32	43	NA	NA
218	29.4	14.5	+	-	.00	62	85	100	+	+
219	19.9	7.7	-	+	.00	16	100	100	NA	NA
214	12.0	7.7	-	+	.00	0	4	100	NA	NA
203	10.7	8.7	-	+	.00	0	4	100	NA	NA

^{1/} Non-numerical values are: + = present, - = absent, and NA = not sampled

^{2/} Crown rating is the product of proportion of foliage remaining (relative to a tree with a full crown) and the proportion of that remaining foliage that is green

^{3/} See Chapter VI

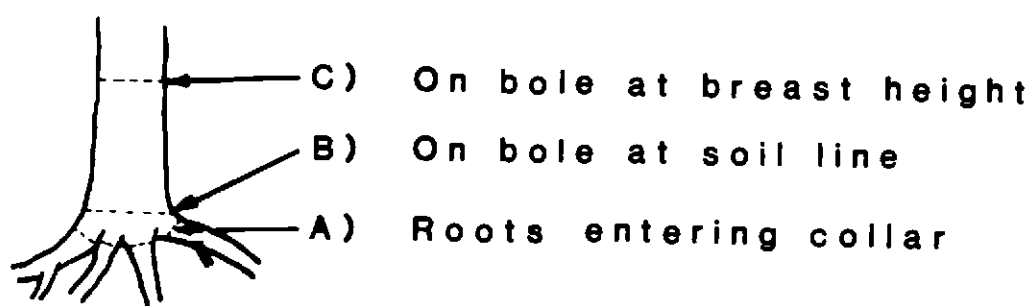
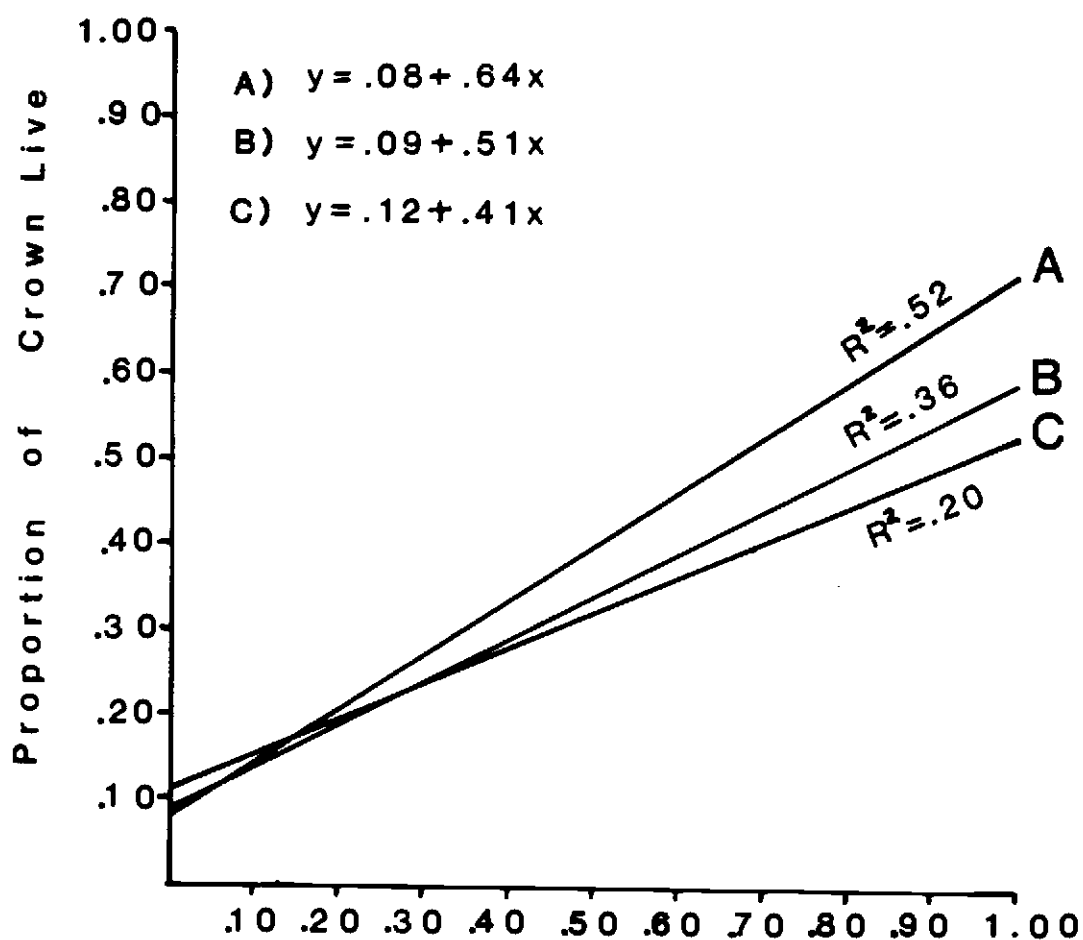


Figure V.5. Relationship of live crown to proportion of cambium live at three sampling locations: A) roots entering bole, B) bole at soil line, and C) bole at 1.37 m height

Fungal Isolations

Of the 1,864 attempted isolations, 1,047 (56%) yielded fungi, 486 (26%) were sterile (no growth after three weeks of incubation), and 331 (18%) were contaminated by bacteria or airborne fungi. Of the fungi isolated, 812 isolates were assigned to a genus, species, or an unidentified group based on microscopic observations of spore or hyphal characteristics (Table V.3). Most fungi isolated from dying trees were also isolated from apparently healthy cedars (as judged by the lack of crown symptoms). Fungal species were not particularly associated with trees at certain stages of crown decline; rather they were more closely associated with symptoms such as lesions, dead fine roots, or stained sapwood (Table V.3). For example, 75% of the 235 isolates of Mycelium radicis atrovirens came from fine roots and 66% of all Phialophora melinii were isolated from bole lesions. Two fungi, Cryptosporiopsis sp. and Cylindrocarpon didymum, were commonly isolated from all of the three important symptomatic tissues: fine roots, root lesions, and stem lesions.

Fungi isolated from vertical bole lesions (Fig. V.3) had a sequential distributional pattern (Fig. V.6). Isolation attempts from 4 cm above the margin of lesions were generally sterile. Cryptosporiopsis sp. had a peak frequency of isolation at the upper lesion margin and dropped off to zero at 12 cm below the lesion top. Cylindrocarpon sp. and Sporidesmium sp. peaked at 4 and 8 cm, respectively, below the lesion top. Isolation frequency for Phialophora melinii peaked at the furthest sampling point below the lesion top. Attempts to isolate fungi several meters below lesion tops usually yielded Phialophora melinii. Polyporus elegans, a

Table V.3. Fungi isolated from various tissues of declining and healthy Alaska-cedar trees

Fungus ^{1/}	Isolations		Tree Condition		Tissue Type						
	Verified (No.)	% of Isolations ^{2/}	Declining n=25 -----No.-----	Healthy n=6	Fine root	Root lesion	Root collar	Stem lesion	Bole scar	Sap stain	Branch
<i>Mycelium radicis atrovirens</i>	235	29	22	6	75	11	1	11	1	1	0
<i>Cryptosporiopsis</i> sp.	89	11	15	5	42	33	0	26	0	0	0
<i>Gelatinosporium</i> sp. ^{3/}	79	10	6	2	0	0	2	70	0	0	28
<i>Armillaria</i> sp.	83	10	11	0	0	16	29	48	7	0	0
<i>Scoridesmium</i> sp.	75	9	13	4	35	3	4	52	3	4	0
<i>Cylindrocarpus didymus</i>	70	9	11	3	50	12	1	34	1	1	0
<i>Phialophora melinii</i>	50	6	8	3	2	2	2	64	18	12	0
Unknown Basidiomycete #1	31	4	7	2	1	3	3	66	3	23	0
Unknown Basidiomycete #2	29	4	4	1	28	0	14	55	3	0	0
<i>Apostrasseria</i> sp.	15	2	0	0	0	0	0	0	100 ^{4/}	0	0
<i>Spiegelia tricholophila</i>	11	1	6	1	18	0	27	27	27	0	0
<i>Polyporus elegans</i>	6	1	2	0	0	0	0	17	83	0	0
<i>Leptographium</i> sp.	5	1	1	1	0	0	0	0	20	80	0
Total = 797											

^{1/} Fungi accounting for less than 1% of those isolated were: *Caratocystis* sp. (scars), *Ditangium* sp. (scars), *Gliocladium* sp., *Septonema secedens*, *Penicillium* sp., *Sporothrix* sp., *Gnomoniella* sp., *Seiridium cardinale*, and *Verticillium* sp.

^{2/} Based on 797 isolations (out of 1864 isolation attempts) that yielded fungi that were identified

^{3/} 75 of these isolations were from mycelial fans or rhizomorphs

^{4/} Isolated from dying shoots on Alaska-cedar regeneration; not found on Alaska-cedars that were root-excavated.

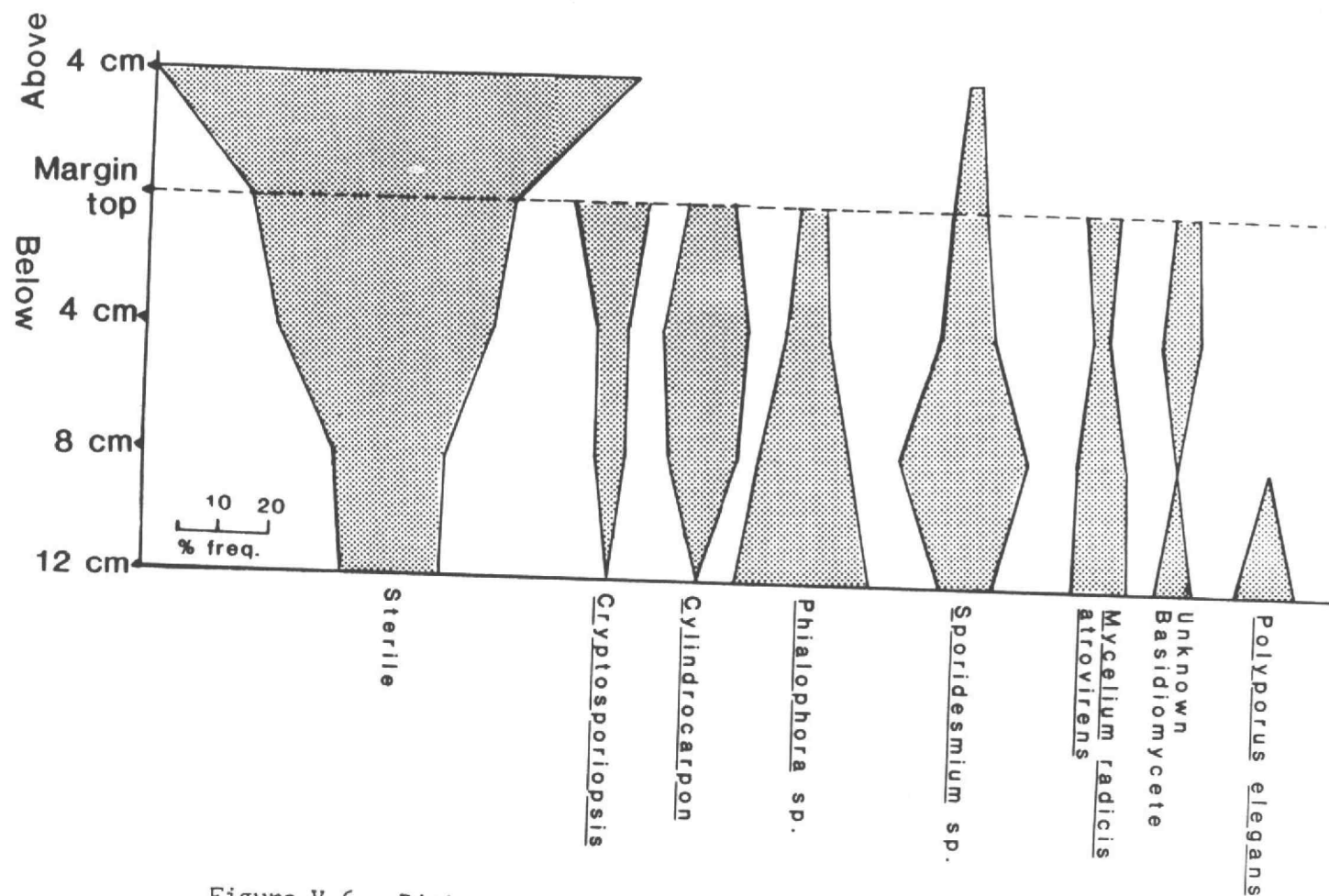


Figure V.6. Distribution of fungi in bole lesions: proportion of isolates yielding different species of fungi (and sterile isolations) from different intervals on necrotic lesions on boles of dying Alaska-cedar trees: 4 cm above the top of lesions, at the top of lesions, and at 4 cm intervals below the top of lesions

sapwood-decay fungus that frequently produces its basidiocarps on the boles of recently-killed Alaska-cedars, followed the same trend as Phialophora in being isolated some distance below the top of lesions.

This sequential distribution of fungi in stem lesions was not consistent from lesion to lesion. Lesions had almost any combination of these fungi and several were sterile. Other lesions had Cryptosporiopsis sp., or Cylindrocarpon sp., or both, at the lesion top. Several lesions had mycelial fans of Armillaria sp. at, or near, the leading margin of bole lesions (Fig. V.7).

Lesions were probably spreading up the boles on declining cedars as live tissues adjacent to lesions did not develop callus tissue. Lesions were consistently connected to one or more dead roots from which they appeared to originate. The same complement of fungi was isolated from root lesions of similar appearance with Cryptosporiopsis sp., Cylindrocarpon sp., and Mycelium radialis atrovirens being the most common (Table V.3). An exception, Gelatinosporium sp., was sometimes isolated from bole lesions, but not from root lesions.

No species of Phytophthora was isolated directly from Alaska-cedars even though many of the isolation attempts were made onto a Phytophthora-selective medium. Many fungi eventually grew from symptomatic tissues placed on this media, but their growth was often delayed for a week or two. Seiridium cardinale, another potential pathogen of Chamaecyparis species (Bannister 1962, Strouts 1973), was isolated once from the top of a callusing basal scar. Apostrasseria sp., a new fungal species (A. Funk, pers. comm.), was common on regeneration of Alaska-cedar at some sites (Fig. V.8), but was not found on the mature trees that were dying.



Figure V.7. Mycelial fan of Armillaria sp. at the leading edge of a necrotic lesion that is apparently girdling the root collar of a dying Alaska-cedar tree



Figure V.8. Shoot dieback in regeneration of Alaska-cedar caused by Apostrasseria sp. Damage by this fungus was not found in mature trees.

Fine Root Observations

Vesicles and arbuscules of VA mycorrhizae were present (Fig. V.9) in cortical cells from 83% of the fine roots that were observed. They were equally common from healthy and dying Alaska-cedar trees (Table V.2), and these structures were even present in fine roots that had recently died but were not deteriorated. Tightly coiled hyphae of arbuscules were the most common structure of these endomycorrhizal fungi.

Infections of cortical cells of fine roots by another fungus were nearly as common (79% of fine root samples). Brownish septate hyphae were frequently observed penetrating individual cortical cells of live fine roots (Fig. V.10). Once cells were fully colonized, they contained a brownish cellular-like material (Fig. V.9). The appearance of such cells was very similar to cortical cells of strawberry colonized by Mycelium radicis atrovirens (Wilhelm et al. 1969). Infected cortical cells of fine roots were equally common on live Alaska-cedar trees that were located some distance from mortality areas and on dying Alaska-cedar trees in areas with many dead cedars (Table V.2). Infected cortical cells were also observed in dead fine roots.

Sampling for Phytophthora sp.

Four isolates of a species of Phytophthora (Fig. V.11) were recovered by baiting soil collected from around four of the 69 cedar trees sampled. All four isolates were recovered from locations along Peril Strait: two were from beneath declining cedars, and two were from beneath apparently healthy cedars with full, green crowns. All

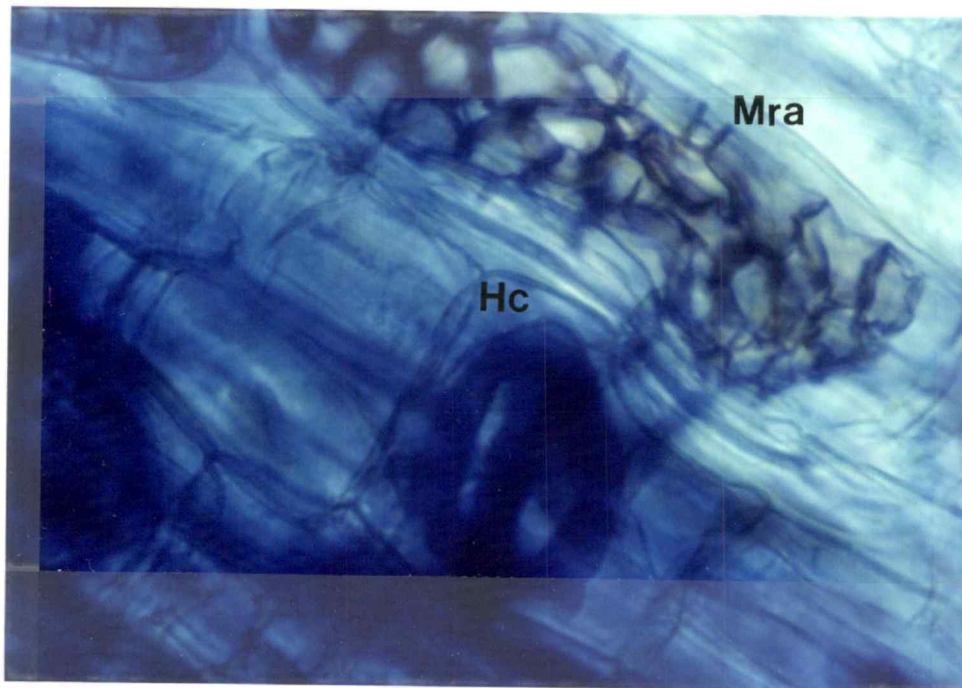


Figure V.9. Infection by Mycelium radicis atrovirens (Mra) and hyphal coil (Hc) of vesicular-arbuscular mycorrhizae in cortical cells of fine roots on Alaska-cedar trees.

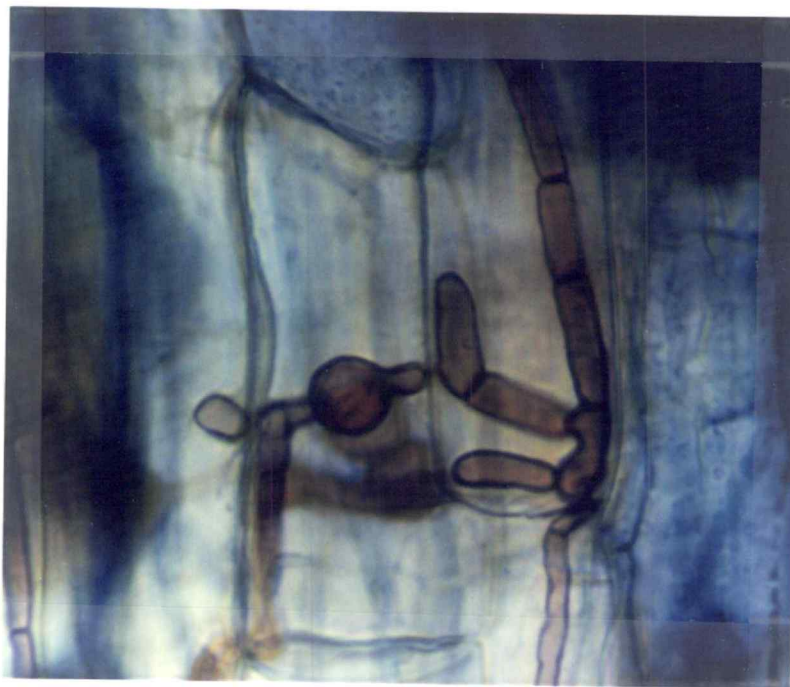


Figure V.10. Hyphae of Mycelium radicis atrovirens infecting cortical cells of fine roots on Alaska-cedar trees.



Figure V.11. Sporangia of Phytophthora sp. recovered from soil that was collected from beneath Alaska-cedar tree.

trees, however, were within the boundaries of areas suffering from decline.

Nematode Sampling

Nematodes from four genera of plant parasites occurred in the organic material beneath Alaska-cedars: 1) Sphaeronema sp. (Tylenchulidae), 2) Crossonema sp. (Criconeitidae), 3) Pratylenchus sp., and 4) Aphelenchoides sp. The first two species were common, occurring in 20 and 26 of the 32 samples, respectively. These two nematode genera never occurred in high populations (only one sample had more than five nematodes per gram dry weight of soil) and were equally common from beneath declining and healthy Alaska-cedar trees. Pratylenchus sp. were recovered from only three Alaska-cedars, all at the same site. Aphelenchoides sp. was recovered in only one sample from a dying tree.

Pathogenicity Testing

In spring inoculations, Cylindrocarpus didymus was the only fungus to cause lesions on seedlings (Table V.4). No seedlings inoculated with C. didymus, or any other fungus, died. C. didymus was re-isolated from two of the eight lesions. The small wounds made during inoculation had all callused over, or nearly so, on seedlings lacking lesions.

Regardless of treatment, lesion development was common on seedlings inoculated in the fall (Table V.4). Lesions developed callus tissue seven months after inoculation, and no seedlings died. Re-isolation of the inoculated fungus was generally unsuccessful. C.

Table V.4. Pathogenicity of fungi isolated from declining Alaska-cedar trees on 2-year old wound inoculated seedlings of Alaska-cedar

Fungus	Spring Inoculations			Fall Inoculations		
	Lesions produced ^{1/}	Mean Lesion Length (cm)		Lesions produced ^{1/}	Mean Lesion Length (cm)	
		Up	Down		Up	Down
<u>Cylindrocarpon</u>	8/10	3.80	1.81	11/15	0.83	1.16
<u>didymium</u>						
<u>Phialochoa</u>	0/10	0	0	8/10	0.65	0.88
<u>melinii</u>						
<u>Armillaria</u> sp.	0/10	0	0	6/10	0.34	0.34
<u>Gelatinosporium</u>	0/10	0	0	6/10	0.30	0.30
sp.						
<u>Gelatinosporium</u> ^{2/}	0/5	0	0	3/11	0.24	0.24
sp.						
Branch control ^{2/}	0/5	0	0	3/7	0.45	0.31
<u>Sporidesmium</u> sp.	0/10	0	0	1/4	0.13	0.50
<u>Leptographium</u>	0/10	0	0	4/5	0.28	0.28
sp.						
<u>Mycelium radialis</u>	0/10	0	0	4/8	0.21	0.21
<u>atrovirens</u>						
<u>Cryptosporiopsis</u>	0/10	0	0	4/10	0.31	0.40
sp.						
<u>Dostrasseria</u> sp.	0/10	0	0	13/20	0.51	1.01
<u>Ceratocystis</u> sp.	0/10	0	0	-	-	-
<u>Seridium cardinale</u>	0/10	0	0	-	-	-
Control	0/10	0	0	4/10	0.30	0.20

^{1/} Number of inoculations yielding lesions after 6 mo / number of inoculations attempted.

^{2/} Gelatinosporium sp. and some control inoculations were made on branches in addition to root collars of seedlings since this fungus was always isolated from above-ground parts of mature cedar trees.

didymum was reisolated from seven lesions on the 11 inoculated seedlings, and, surprisingly, from two seedlings that were not inoculated with C. didymum.

Armillaria inoculations

Armillaria sp. caused no lesions on the 16 inoculated trees; however, in one tree, Armillaria colonized a dead secondary root that was adjacent to the inoculum piece. All wounding treatments had callused shut. Most pieces of Armillaria inoculum appeared viable with white and tan mycelium and some rhizomorphs emerging after the two-year incubation period.

Root Wounding

Lesions developed on 61% of the wounded roots of mature cedars (Table V.5). Lesions, and wounds without lesions, were callusing two years after injury. Roots without wounding had no lesions. Lesions on wounded roots were similar in appearance to those on declining cedars (Fig. V.12); they had dead, brown phloem and tan-to-dark-stained sapwood. The fungus most frequently isolated from this stained sapwood was a Leptographium sp., followed by the other fungi commonly found in necrotic lesions of declining Alaska-cedar trees (Table V.6).

Stem Lesion and Patch Inoculations

Nine of the 23 (39%) cedar trees with patch inoculations (sections of lesions removed from declining cedars and placed into healthy cedars) developed new lesions after two years; however, 7 of 17 (41%) emplacements of control sections (live, white phloem) also developed

Table V.5, Lesion development on roots two years after mechanical wounding^{1/}

Wounding <u>Treatment</u>	Lesions <u>produced (%)</u>	Mean Linear Extent <u>of Lesion (cm)</u> ^{2/}
1) Cut through cambium (1/2 circumference)	50	9.1 ± 5.7
2) Cut through cambium (entire circumference)	67	17.0 ± 15.9
3) Cut through sapwood (1/2 circumference)	73	11.6 ± 15.4
4) No wound (control)	0	-

^{1/} Each of 15 Alaska-cedar had four wounding treatments, one to each of four roots.

^{2/} Wounds without lesions were not included; means followed by standard error

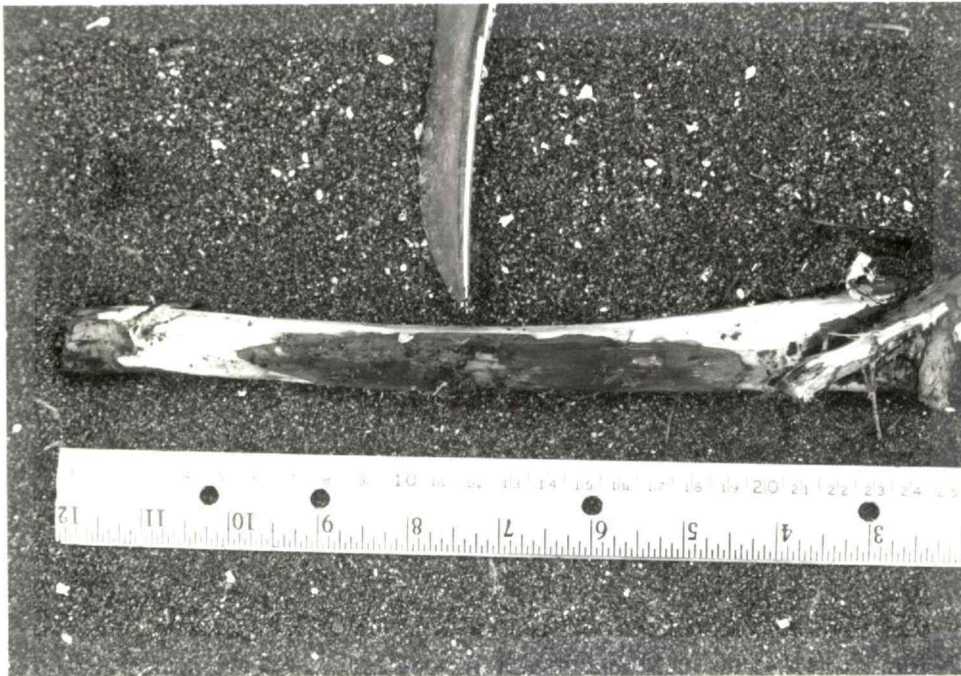


Figure V.12. Lesion on root of Alaska-cedar that developed after mechanical wounding.

Table V.6. Fungi isolated from lesions that developed two years after roots were mechanically wounded without inoculation

Fungus Isolated	I s o l a t i o n s	
	(No.)	(%)
<u>Leptographium</u> sp.	14	18
Unknown Basidiomycete #2	12	16
<u>Cylindrocarpon didymum</u>	3	4
Unknown Basidiomycete #1	1	1
<u>Penicillium</u> sp.	6	8
<u>Polyporus elegans</u>	2	3
<u>Phialophora mellini</u>	2	3
<u>Speggazinia tricholophilia</u>	2	3
<u>Mycelium radicis atrovirens</u>	4	5
<u>Cryptosporiopsis</u> sp.	1	1
Unknown mycelia sterilia	7	9
Unknown fungi	2	3
Sterile, no growth	20	26
	<hr/>	<hr/>
Totals	76	100

lesions in inoculated trees, and the mean linear extent of induced lesions did not differ between treatments (Table V.7). Induced lesions were similar in appearance to stem lesions on declining cedars, except that induced lesions developed callus tissue after two years.

The species of fungi isolated from these induced lesions (Table V.8) were similar to those isolated from lesions on declining cedars (Table V.3), except for a greater incidence of Leptographium sp. in induced lesions.

DISCUSSION

The crowns of declining Alaska-cedars died as a unit, slowly or relatively quickly, rather than as isolated dying branches or portions of the crown. This symptomology suggests a below-ground, root-related, problem. Root excavations support this hypothesis. Trees in early stages of crown decline have dead and missing fine roots, as well as root lesions which spread from small distal roots into and along larger proximal roots to the root collar. In the final stages of tree decline, vertical lesions spread from dead roots up the tree's bole. If a pathogen is primarily responsible for killing Alaska-cedar trees, it should be located in one or more of these necrotic tissues.

The vertical bole lesions apparently do not develop as a result of pathogenic activity. Lesion tops were either sterile or contained a variety of non-pathogenic fungi. Only one fungus, Cylindrocarpus didymum, caused stem lesions in inoculation trials. Patch inoculations using pieces of healthy bark caused as many lesions as those using

Table V.7. Lesion development on boles of Alaska-cedar trees 2 years after patch inoculations^{1/}

	<u>Inoculation Type</u>	
	<u>Necrotic patches</u>	<u>Live patches</u>
Inoculation attempts (No.)	17	23
Induced lesions (%)	39	41
Lesion extent--up (cm) ^{2/}	7.4 ± 6.1	4.1 ± 2.5
Lesion extent--down (cm) ^{2/}	5.1 ± 3.4	4.5 ± 2.4

^{1/} Patch inoculations were accomplished by removing bark and phloem from near the top of necrotic lesions on declining cedar trees and transferring them into the stems of healthy cedar trees. Controls were inoculated patches of live phloem and bark.

^{2/} Mean ± standard deviation; means were not significantly different (p=0.05)

Table V.8. Fungi isolated from lesions that developed after 2 years from patch inoculations

<u>Fungus Isolated</u>	<u>Inoculation Type ^{1/}</u>	
	<u>Necrotic Patch (%)</u>	<u>Control Lesion (%)</u>
<u>Leptographium</u> sp.	37	25
Unknown Basidiomycete #2	14	16
<u>Cylindrocarpon didymum</u>	2	13
Unknown Basidiomycete #1	6	0
<u>Penicillium</u> sp.	5	9
<u>Phialophora mellinii</u>	2	3
<u>Phoma</u> sp.	1	0
<u>Speggazinia tricholophilia</u>	1	0
<u>Mycelium radialis atrovirens</u>	1	0
Unknown fungi	13	3
Sterile, no growth	19	31
Total (%)	<u>100</u>	<u>100</u>

^{1/} Percentages based on 108 isolations from 15 lesions that developed from necrotic patch inoculations and 32 isolations from lesions developing from 9 control (live) patch inoculations. Percent fungi isolated from lesions developing from necrotic and control patch inoculations did not differ significantly ($p=0.05$).

necrotic bark taken from lesions on symptomatic trees. Indeed, lesions were caused by mechanically wounding in several experiments: small wounds on the root collars of seedlings in fungal and control inoculations; wounds associated with the transfer of lesion and control patches to healthy, mature cedar; and a variety of root wounding treatments on mature cedars. These various wounds eventually callused closed, perhaps due to the relatively high vigor of these cedars, but an area of necrotic cambium often formed above the wound. Such wound-induced lesions appeared similar to natural lesions, and were colonized by a similar array of fungi.

Lesions on the larger roots and boles of declining cedars were oriented along the root axis or vertically on boles and did not spread circumferentially. Two mature cedars in late stages of crown and root decline that had lesions on their root collar were exceptions. On these trees, mycelial fans of Armillaria sp. were present at the upper margin of lesions that were advancing tangentially across the phloem at the root collar (Fig. V.7). In general, however, lesions did not develop a girdling pattern typical of those induced by a pathogen. For example, bole lesions on Chamaecyparis lawsoniana which are caused by the aggressive pathogen, Phytophthora lateralis, spread circumferentially and typically reach only about two bole diameters in height above the ground (Zobel et al. 1985).

Rudinski and Vite (1959) induced narrow and vertical stain columns in Chamaecyparis lawsoniana (A. Murr.) Parl. by introducing dye into one root. They suggest that the narrow, vertical stain, which was similar to the configuration of necrotic lesions on dying Alaska-cedar trees, is a result of sapwood anatomy. In their study, similar

treatments to other conifers caused wider or more spiralling lesions than for Chamaecyparis.

These results suggest that necrotic lesions on the large roots or boles, which are common on declining cedars, are not the result of activity by pathogens and are secondary symptoms, perhaps resulting from the death of smaller roots, and are not caused by a continuously advancing pathogen. Dead fine roots and small diameter roots may be more closely associated with the primary cause of mortality, however. These symptoms occurred earlier in tree decline than did stem lesions or severe crown decline.

None of the more than 50 species of fungi isolated or collected from Alaska-cedar in these studies can be considered to be primarily responsible for the extensive mortality. The twelve fungi most commonly isolated from fine roots, root lesions or stem lesions were only weakly pathogenic or non-pathogenic when inoculated on cedar seedlings. Cylindrocarpon didymum was the only fungus to show any pathogenicity; it caused necrotic lesions, but failed to kill any inoculated cedar seedlings. Also, it was isolated from three apparently healthy Alaska-cedars. Most of the fungi that were consistently collected from dying cedars were also found on healthy Alaska-cedars.

Several fungi were commonly isolated from symptomatic tissues such as dying or dead fine roots, and lesions on roots or boles. The most common of these fungi were: Mycelium radicis atrovirens, Cryptosporiopsis sp., Gelatinosporium sp., Cylindrocarpon didymum and Sporidesmium sp.

Mycelium radicis atrovirens was a common component of Alaska-cedar forests, as it was isolated 235 times, mainly from fine roots, and was most likely the fungus that was observed in the cortical cells on nearly all fine roots. The appearance of these infected cells was very similar to cortical cells infected with M. radicis atrovirens in the roots of strawberry (Wilhelm et al. 1969). Little is known about this organism's importance as a root parasite of conifers or its importance as a mycorrhizal fungus, but it has been repeatedly isolated from roots of various forest trees (Gams 1963). Richard et al. (1971) considered it ubiquitous in boreal forest soils. It was previously isolated from another Cupressaceae host, Juniperus communis (Linhell 1939), but this is the first report on Alaska-cedar or any other host in Alaska.

Even the taxonomic status of M. radicis atrovirens is uncertain. It has twice been called Phialocephala dimorphospora Kendrick because of rare conidial sporulations (Gams 1963, Richard and Fortin 1973). None of the 235 isolates in this study sporulated, even though they were grown on many different media, exposed to near UV light at different temperatures, and nearly all isolates examined microscopically. They were identified by cultural characteristics (Gams 1963) and by the microsclerotial-like structures in root-cortex cells.

The role of M. radicis atrovirens in Alaska-cedar decline is unclear. It exhibited no pathogenic ability on inoculated seedlings of Alaska-cedar and could conceivably benefit trees whose rootlets are infected. It is exceedingly common in the fine roots of dying Alaska-cedars but equally common in fine roots of apparently healthy Alaska-cedars, both adjacent to and several hundred meters away from

dead or dying trees. Wilhelm et al. (1969) showed its pathogenicity on strawberry and believed that it weakened plants for secondary infection by other organisms. M. radicis atrovirens could contribute to Alaska-cedar decline, but my evidence suggests that it is not a primary pathogen in this area.

Armillaria sp. is a common forest fungus occurring on a large number of hosts throughout the world (Raabe 1962). Its ecological role ranges from a wood-decaying saprophyte to an aggressive primary pathogen (Wargo and Shaw 1985). Considerable confusion exists concerning the taxonomy of Armillaria mellea (Vahl: Fr.) Kummer, because it is now being segregated into several species (Watling et al. 1982, Wargo and Shaw 1985)); this situation may clarify the varying pathogenicity and host ranges of Armillaria (Morrison 1985). Isolates of Armillaria sp. from Alaska-cedar have a partial affinity with A. cepaestipes Vel. subsp. pseudobulbosa Romagn. et Marxmuller (North American biological species V and IX) based on partial compatibility with those species in mating trials (Shaw 1983; C.G. Shaw III, unpublished data). Morrison (1985) and Wargo and Shaw (1985) suggest that the Roman numeral system (Anderson and Ullrich 1979) be used whenever possible to refer to unnamed North American species until they are properly described taxonomically. Studies are currently underway to confirm the identity of Armillaria isolates from Alaska-cedar and other hosts in Alaska (C.G. Shaw III, pers. comm.)

Armillaria sp. occurred on 11 of the 36 excavated Alaska-cedar trees. It was common on dead parts of declining cedars, but was twice found advancing across the cambium of the root collar in a clearly pathogenic manner (Fig. V.7). Because rhizomorphs and mycelial fans of

Armillaria are macroscopically visible, its presence and distribution in dying trees are easily determined. Armillaria was never isolated from cedar tissues without observable mycelial fans or rhizomorphs near the points of isolation. In inoculation tests, Armillaria did not initiate lesions and did not kill roots. In another study, isolates of Armillaria sp. from dying Alaska-cedars failed to infect Alaska-cedar seedlings that were inoculated and grown in pots at the nursery in Petersburg, Alaska, even though the inoculum readily produced rhizomorphs (C.G. Shaw III, unpublished data). Armillaria appears to be a common secondary pathogen on declining cedars, colonizing roots that are already dead or dying, and occasionally hastening the death of declining trees by killing the cambium at the root collar.

Cylindrocarpon didymum was commonly isolated from symptomatic tissues and caused lesions on inoculated seedlings. The teliomorph (sexual stage) of this species is not known, but many other species of Cylindrocarpon belong to the genus Nectria (Boothe 1966).

Cylindrocarpon didymum is pathogenic on Pinus sylvestris L. seedlings (Houlten 1939). Jehne (1976) isolated a species of Cylindrocarpon from the fine roots of Eucalyptus obliqua suffering from a dieback problem. A toxin "similar to Nectrolide" was apparently produced by that fungus. In my study, Cylindrocarpon sp. showed some pathogenic ability by causing lesions on seedlings, but it was unable to sustain the lesion and seedlings were not killed. This fungus is probably able to kill tissues on already declining cedars.

Gelatinosporium sp. was the most commonly isolated fungus from branches of Alaska-cedar, particularly on the rough-appearing bark with shallow fissures that occurred on branches of seemingly healthy trees;

Gelatinosporium sp. was the only fungus isolated from such symptoms. No fruiting bodies of Gelatinosporium nor its presumed sexual stage (Dermea sp., Chapter IV) were found with this symptom. Interestingly, another Dermea, D. balsamea (Peck) Seaver, causes a bark disease of subalpine fir (Abies lasiocarpa (Hooke.) Nutt.) in British Columbia (Kuijt 1969). Although symptoms are similar, the disease of subalpine fir occurs on boles of trees of all sizes with deep fissures occurring in the bark, and infection often leads to mortality. In comparison, the effects on Alaska-cedar are less severe: shallow fissures in bark, occurrence on small diameter branches, no death to underlying phloem or cambium, and no apparent effect on tree vigor.

Gelatinosporium sp. was also isolated from necrotic lesions on boles, where the anamorph, Gelatinosporium sp., and teliomorph, Dermea sp., were twice found sporulating together. Both are new species (A. Funk, pers. comm.) and will be properly described at some future date. Gelatinosporium sp. is not considered to be strongly pathogenic on Alaska-cedar since it failed to cause symptoms on inoculations of seedlings and, even if it causes bark symptoms on branches of Alaska-cedar trees, the incidence of these bark symptoms do not correlate with foliage, cambial, or root symptoms of decline.

Ironically, members of both Phytophthora and Seiridium, genera known to cause serious diseases to Chamaecyparis elsewhere, were found associated with Alaska-cedar in southeast Alaska; however, both fungi were rare. Seiridium cardinale was isolated only once, from a bear-caused scar, and was not pathogenic in inoculation studies. This species varies in its pathogenicity from an aggressive pathogen to a

saprophyte (Wagener 1939); the isolate from Alaska-cedar lacked pathogenicity.

The role of Phytophthora sp. in decline cannot be adequately determined at this time. Root and crown symptoms of dying Alaska-cedar trees are generally similar to symptoms of Port-Orford-cedar that is attacked by Phytophthora lateralis. On the latter, trees die quickly without thinning of crowns, necrotic lesions girdle circumferentially on boles, and lesions do not typically spread higher than two stem diameters above the roots on the bole. Since it was isolated by baiting from soil around cedar trees only four times out of several hundred attempts, the Phytophthora sp. could be viewed as an uncommon component of the mycoflora in stands of Alaska-cedar. The efficiency of this baiting technique is not known for this Phytophthora sp., but this procedure has worked successfully for isolating P. lateralis from soil around dying Port-Orford-cedar (Hansen et al. 1977). The Phytophthora sp. isolated in the present study has not been isolated directly from Alaska-cedar tissues even though several hundred attempts were made using media selective for Phytophthora; thus, Alaska-cedar may not even be a host for this fungus. Future studies will involve the taxonomy of these Phytophthora isolates, their pathogenicity on Alaska-cedar, and the efficiency of various sampling techniques to determine the frequency of occurrence of this fungus in different forest stands.

Root-feeding nematodes were neither prevalent enough nor sufficiently associated with dying cedars to be primary inciters of Alaska-cedar decline. Initially, Aphelenchoides sp. was of interest since it was isolated from the fine roots of dying cedars during

attempts to isolate fungi, and because it is closely related to Bursaphelenchus xylophilus (Nickle 1970), which is the cause of pine wilt disease of conifers (Mamiya 1983). The latter species has not been reported from Alaska, however. Aphelenchoides sp. was recovered from beneath only one Alaska-cedar tree. Little is known of the role that nematodes have in forest declines, however. A species of Sphaeronema was recently recovered from declining spruces in the eastern United States (Eisenback and Hartman 1985) which suggests that these nematodes should receive future study (Hennon et al. 1986).

The lack or dysfunction of beneficial mycorrhizae could potentially contribute to Alaska-cedar decline. In this study, however, vesicular-arbuscular mycorrhizae were common in the cortical cells of live fine roots on both declining and healthy Alaska-cedars, as long as their fine roots were living.

In conclusion, Alaska-cedar decline is probably not incited by a pathogenic agent. Our studies, by necessity, have not included all types of plant pathogenic agents. Bacteria, mycoplasmas, and viruses were not studied since none has been shown to cause significant mortality to conifers in natural stands. Known pathogenic fungi were found (e.g., Cylindrocarpon didymum, Armillaria sp., and Dermea sp.), but none proved capable of killing unstressed cedar seedlings. Necrotic lesions on large roots and boles of declining cedars are probably not the result of pathogens killing tissue at their leading margins; similar-appearing lesions were produced by mechanical wounding.

This conclusion is, and must, be based upon cumulative negative results. My approach to test the hypothesis of whether or not a

biological agent is the primary cause of Alaska-cedar mortality has been to exhaustively search for such a pathogen. In the absence of finding such an organism, some other cause is assumed to be more likely. These results suggest abiotic factor(s) as the primary stress affecting Alaska-cedars. Pathogenic fungi, along with the Phloeosinus bark beetle, can only be concluded to have secondary or contributing roles in Alaska-cedar decline. The distribution, magnitude, and timing of mortality in southeast Alaska is not typical of familiar disease epidemics. It now seems most likely that the primary cause of Alaska-cedar decline is some abiotic factor.

ACKNOWLEDGEMENTS

Gene B. Newcomb is gratefully acknowledged for extracting, identifying and quantifying nematodes. Michael McWilliams, Marybetts Sinclair, and Susan Hennon will forever be remembered for their cheerful assistance in excavating muddy roots and isolating fungi. Lewis Roth is acknowledged for the idea of patch inoculations.

LITERATURE CITED

- Agrios, G.N. 1978. Plant pathology. Academic press, New York. 703 p.
- Anderson, J.B. and R.C. Ullrich. 1979. Biological species of Armillaria mellea in North America. Mycologia 71:402-414.
- Bannister, M.H. 1962. Prospects for selection in the cypresses. New Zealand J. For. 8:545-559.
- Boothe, C. 1966. The genus Cylindrocarpon. Mycol. Papers, No. 104:1-56.
- Eisenback, J.D. and K.M. Hartman. 1985. Sphaeronema sasserii n. sp. (Tylenchulidae), a nematode parasitic on Fraser fir and red spruce. J. Nematol. 17:346-354.
- Frear, S.M. 1982. What's killing the Alaska yellow-cedar? Amer. For. 88(11):41-43, 62-63.
- Furk, A. Personal communication. Canadian Forestry Service, Forestry Research Centre, 506 West Burnside Road, Victoria B.C., V8Z 1M5
- Gams, W. 1963. Mycelium radialis atrovirens in forest soils, isolation from soil microhabitats and identification. Pp. 176-182. In: Soil Organisms, Eds., J. Doekoen and J. vander Drift, North-Holland Publishing Co., Amsterdam, Holland.
- Hamm, Philip, personal communication, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR, 97331.
- Hansen, E.M., P.B. Hamm, A.J. Julis, and L.F. Roth. 1977. Isolation, incidence and management of Phytophthora in forest tree nurseries in the Pacific Northwest. Plant Dis. Repr. 63:607-611.
- Harris, A.S. 1971. Alaska-cedar. USDA For. Serv., Am. Woods-FS 224. 7p.
- Hennon, P.E., G.B. Newcomb, C.G. Shaw III, and E.M. Hansen. 1986. Nematodes associated with dying Chamaecyparis nootkatensis in Southeastern Alaska. Plant Dis. 70:352.
- Jehne, W. 1976. Phytotoxins in Cylindrocarpon root-rot of Eucalyptus obliqua regrowth trees. Aust. Plant Pathol. Soc. Newsl. (supplement). 5(1):65 (abstract).
- Kuijt, J. 1969. Cork-bark, a disease of Alpine fir in British Columbia. Northwest Sci. 43:74-79.
- Linhell, D. 1939. Untersuchungen über die Mykorrhizen und die Wurzelpilze von Juniperus communis. Symb. Bot. Upps. 2(3):293.
- Mamiya, Y. 1983. Pathology of the pine wilt disease caused by Bursaphelenchus xylophilus. Ann. Rev. Phytopathol. 21:201-220.

- Morrison, D.J. 1985. Species differentiation in Armillaria. Pp. 44-47. In: Proceedings of the thirty-third annual Western International Forest Disease Work Conference. Olympia, WA. Sept 24-27, 1985.
- Nickle, W.R. 1970. A taxonomic review of the genera of the Aphelenchoidea. J. Nematol. 2:375-392.
- Phillips, J.M. and D.S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizae fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55:158-161.
- Faabe, R.D. 1962. Host list of the root rot fungus, Armillaria mellea. Hilgardia 33:25-88.
- Richard, C., J.A. Fortin, and A. Fortin. 1971. Protective effect of an ectomycorrhizal fungus against the root pathogen Mycelium radicis atrovirens. Can. J. For. Res. 1:246-251.
- Richard, C. and J.A. Fortin. 1973. The identification of Mycelium radicis atrovirens (Phialocephala dimorphospora). Can. J. Bot. 51:2247-2248.
- Roth, L.F., H.H. Pynum, and E.E. Nelson. 1972. Phytophthora root rot of Port-Orford-cedar. USDA For. Serv. Pest Leaflet. 131. 7p.
- Rudinski, J.A. and J. P. Vite. 1959. Certain ecological and phylogenetic aspects of the pattern of water conduction in conifers. For. Sci. 5:259-266.
- Shaw, C.G. III, personal communication, USDA Forest Service, Forestry Sciences Laboratory, P.O. Box 909, Juneau, Alaska, 99801.
- Shaw C.G. III. 1977. Armillaria isolates from pine and hardwood differ in pathogenicity to pine seedlings. Plant Dis. Reptr. 61:416-418.
- Shaw, C.G. III. 1984. In vitro responses to gallic acid fail to distinguish between pathogenic and "non-pathogenic" species of Armillaria. Proceedings of the sixth international conference on root and butt rots of forest trees. Melbourne, Victoria and Gympie, Queensland, Australia. Aug. 25-31. Pp.161-183.
- Shaw, C.G. III, A. Eglitis, T.H. Laurent, and P.E. Hennon. 1985. Decline and mortality of Chamaecyparis nootkatensis in Southeastern Alaska, a problem of long duration but unknown cause. Plant dis. 69:13-17.
- Strouts, R.G. 1973. Canker of cypresses caused by Corvoneum cardinale Wag. in Britian. Eur. J. For Pathol. 3:13-24.
- Wagener, W.W. 1939. The canker of Cupressus induced by Corvoneum cardinale n. sp. J. Agric. Res. 58:1-46

Wargo, P.M. and C.G. Shaw III. 1985. Armillaria root rot: the puzzle is being solved. Plant Dis. 69:286-832.

Watling, R., G.A. Kile, and N.M. Gregory. 1982. The genus Armillaria--nomenclature, the identity of Armillaria mellea and species differentiation. Trans. Br. Mycol. Soc. 78:271-285.

Wilhelm, S., P.E. Nelson, and D.H. Ford. 1969. A gray sterile fungus pathogenic on strawberry roots. Phytopathology 59:1525-1529.

Zobel, D.B., L.F. Roth, and G.M. Hawk. 1985. Ecology, pathology, and management of Port-Orford-cedar (Chamaecyparis lawsoniana). USDA For. Serv., Pacific Northwest For. & Range Exp. Sta., Portland, OR. Gen. Tech. Rep. PMW-184. 161p.

CHAPTER VI

CAUSES OF BASAL SCARS ON ALASKA-CEDAR

ABSTRACT

Scars on the lower boles of Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) trees in southeast Alaska are common in some stands, but their cause has not been determined. The association of these basal scars with an extensive decline and mortality of unknown cause that affects Alaska-cedar also has been unclear. Data from ground transects indicate that over one-half of the Alaska-cedar trees in some stands are scarred, even though other tree species are unaffected. Scars generally face upslope, are limited to portions of the bole circumference, average 1.5 m in height, and are most common on the best drained, most productive sites. Recent scars consistently have teeth marks in the exposed wood--evidence that bears cause this damage. Such basal scars are common on islands in southeast Alaska inhabited by brown bears (Ursus arctos), but not on islands inhabited by black bears (Ursus americanus). Callus tissue slowly forms over these basal scars, but decay columns develop in the wood, which results in losses of wood volume from the valuable butt log. The fungi that occur on scars of varying ages are described. Decline occurs on several islands not inhabited by brown bears and where cedars are not scarred, and decline usually is associated with poorly drained sites; thus, basal scars are not associated with Alaska-cedar decline.

INTRODUCTION

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a long-lived, slow growing tree that ranges from Prince Williams Sound in Alaska, south through British Columbia, to near the Oregon-California border (Harris 1971). This conifer grows from sea level to timberline in southeast Alaska (Harris and Farr 1974) where it can occur in nearly pure stands, but more commonly exists in scattered groups or as individual trees mixed with other conifers (Harris and Farr 1974). Its narrow annual rings, extreme decay resistance, and bright yellow, aromatic heartwood make Alaska-cedar wood valuable and useful (Frear 1982).

Scars, or cat faces, are common on the lower bole of Alaska-cedar trees in southeast Alaska (Anderson 1959) (Fig. VI.1) where stands of Alaska-cedar have been dying since before the turn of the century (Chapter II, Shaw et al. 1985). Ruth and Harris (1979) note that bears may cause this damage, but this has not been substantiated. Presently, there is no information on tree species affected, the geographical extent of the problem, or, except for the idea proposed by Ruth and Harris, what may be causing these tree scars. Also, the question arose as to whether death and decline of cedar was associated with basal scarring since scars were commonly observed on dead and dying trees (Chapter III, Shaw et al. 1985).

The objectives of this study were to: 1) determine the cause(s) of scarring, 2) determine if there was an association between the occurrence of scarring and Alaska-cedar mortality, and 3) describe scar characteristics and tree responses to scarring.



Figure VI.1. An old basal scar on Alaska-cedar

MATERIALS AND METHODS

Study areas were located on Chichagof and Baranof Islands, about 50 km NE of Sitka, Alaska. The occurrence and size of basal scars were noted for 779 Alaska-cedars and all other conifers present on 280 plots along 21 survey lines (Chapter III). Individual trees were selected on each plot with a 3 or 6 m²/ha basal area factor prism. Most sampling sites were along Peril Strait (Fig. VI.2), but survey lines were also located in Slocum Arm near Waterfall Cove and Kennel Creek, both on Chichagof Island. Scar heights and orientation with slope were measured from an additional 490 Alaska-cedars at three sites in Peril Strait. In total, 1269 Alaska-cedar trees were examined. A Chi-square analysis ($p=0.05$) was used to test if the incidence of scarring differed with location (Peril Strait, Slocum Arm, and Kennel Creek). Frequency distributions were drawn for scar height and orientation and the latter was tested using a chi-square analysis ($p=0.05$) to determine if scars faced any particular direction.

An understory plant gradient technique (Chapter III) was used to determine if the occurrence of basal scarring was correlated with forest type. Fifty-five plant taxa were recorded on each of the 280 plots and a gradient of plot scores calculated from a computer ordination technique--Detrended Correspondence Analysis (DECORANA) (Gauch 1982, Hill and Gauch 1980). These plot scores represent the gradient from bogs to plant communities with better drainage (Chapter III). DECORANA plot scores were visually compared to the proportion of Alaska-cedars with basal scars and the proportion of plots having scarred trees.

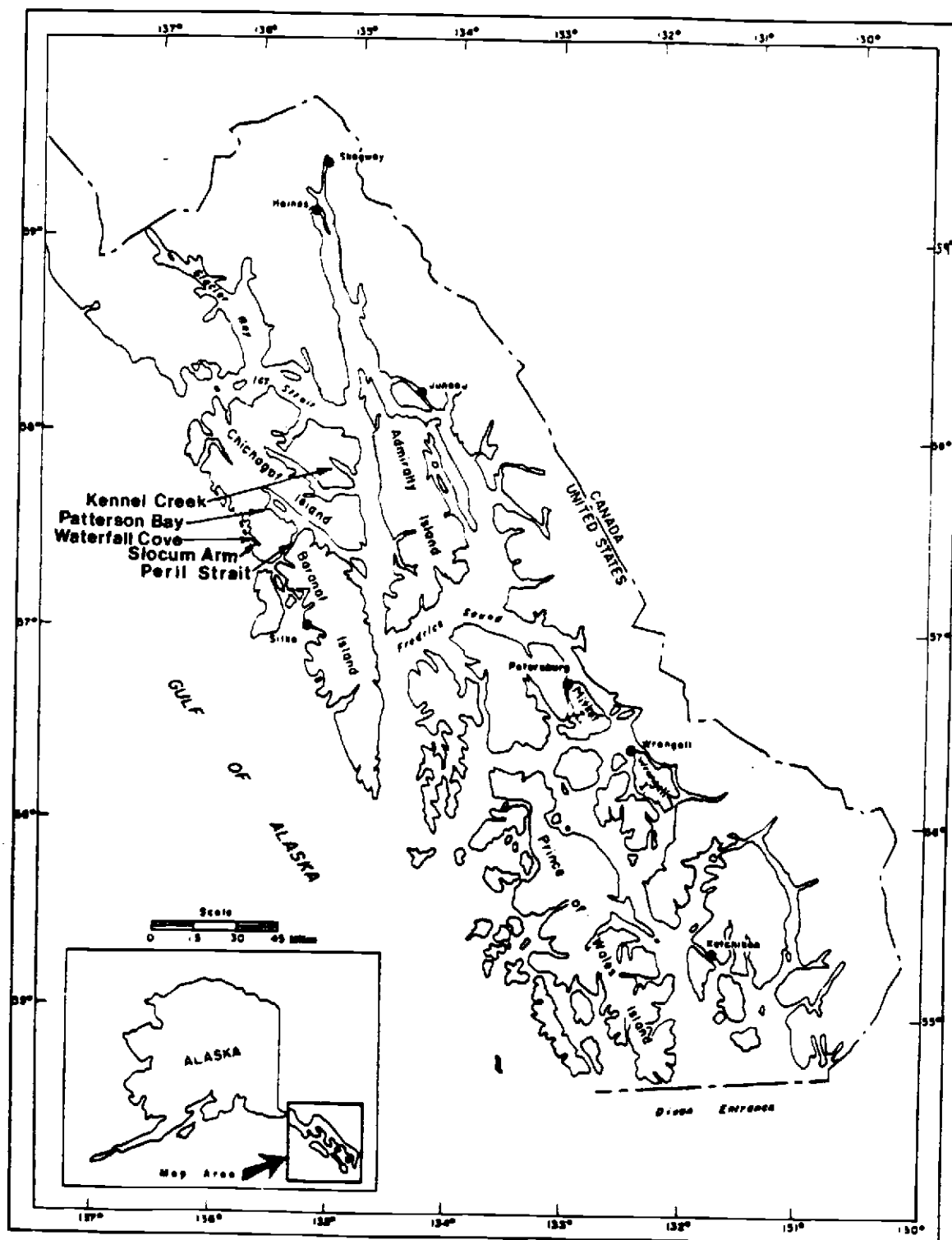


Figure VI.2. Map of study sites.

Three Alaska-cedars with scars were dissected transversely with a chain saw to allow for examinations of decay characteristics and tree responses to wounding. Single discs were cut from the boles of 15 other Alaska-cedars with basal scars and similarly examined.

Fruiting bodies of fungi were collected from fresh and old basal scars to determine the species present on scars of different ages. The general appearance of these scars (e.g., depth of wound in relation to amounts of callus tissue, condition of exposed wood, presence of fungal fruiting bodies, and presence of moss or higher plants growing on scars) were also recorded. In addition, fungi were isolated from basal scars (Chapter V). Most of the scars from which fungi were isolated were less than five years old.

RESULTS

Occurrence of Scars

Basal scars occurred on 49% of the Alaska-cedar trees sampled. Scars were common at Waterfall Cove (62%) and along Peril Strait (51%) but were significantly less frequent at Kennel Creek (16%). Basal scars were common throughout the study area at Peril Strait with over 30% of the Alaska-cedar trees from each of the 16 transects having scars. Except for trees less than 10 cm dbh, all size classes were scarred. Scars on Alaska-cedar had a significant upslope orientation at each of the three sites where orientation was measured (Fig. VI.3). Most scars were about 150 cm tall, but scar heights of 450 and 800 cm were also common (Fig. VI.4).

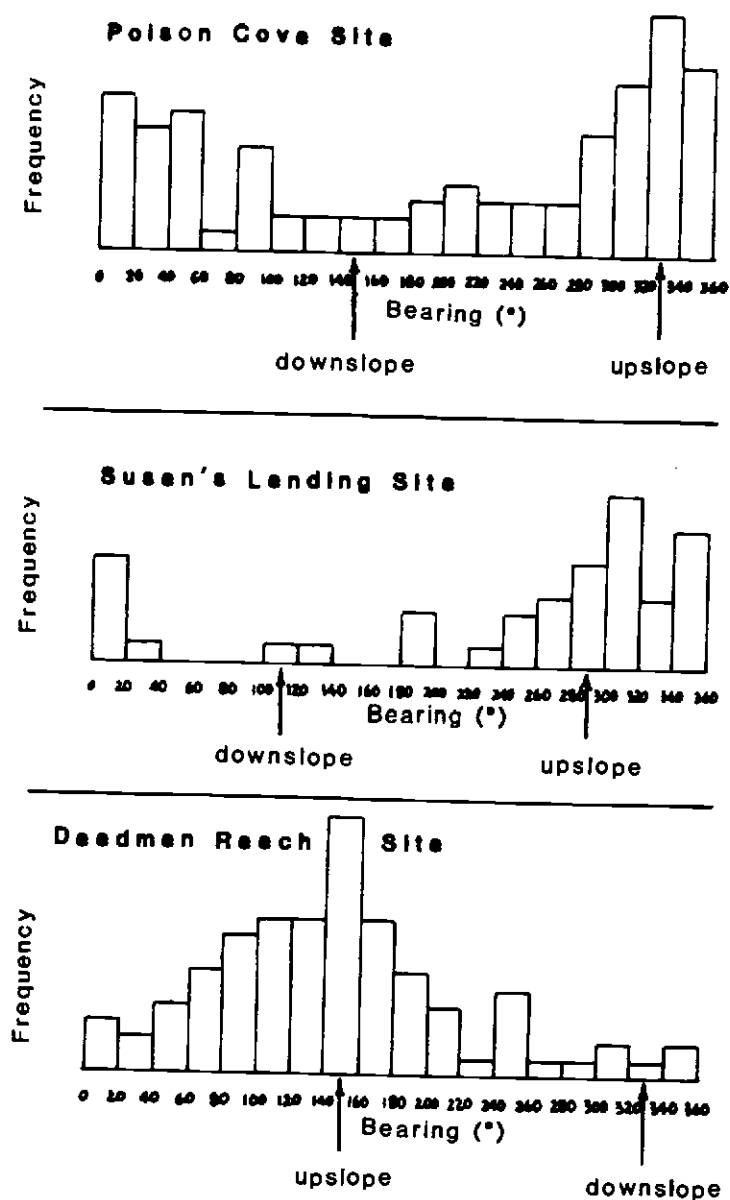


Figure VI.3. Frequency distribution of the orientation of basal scars on Alaska-cedars at three sites at Peril Strait, Alaska. Note the upslope orientation of most scars at the three sites.

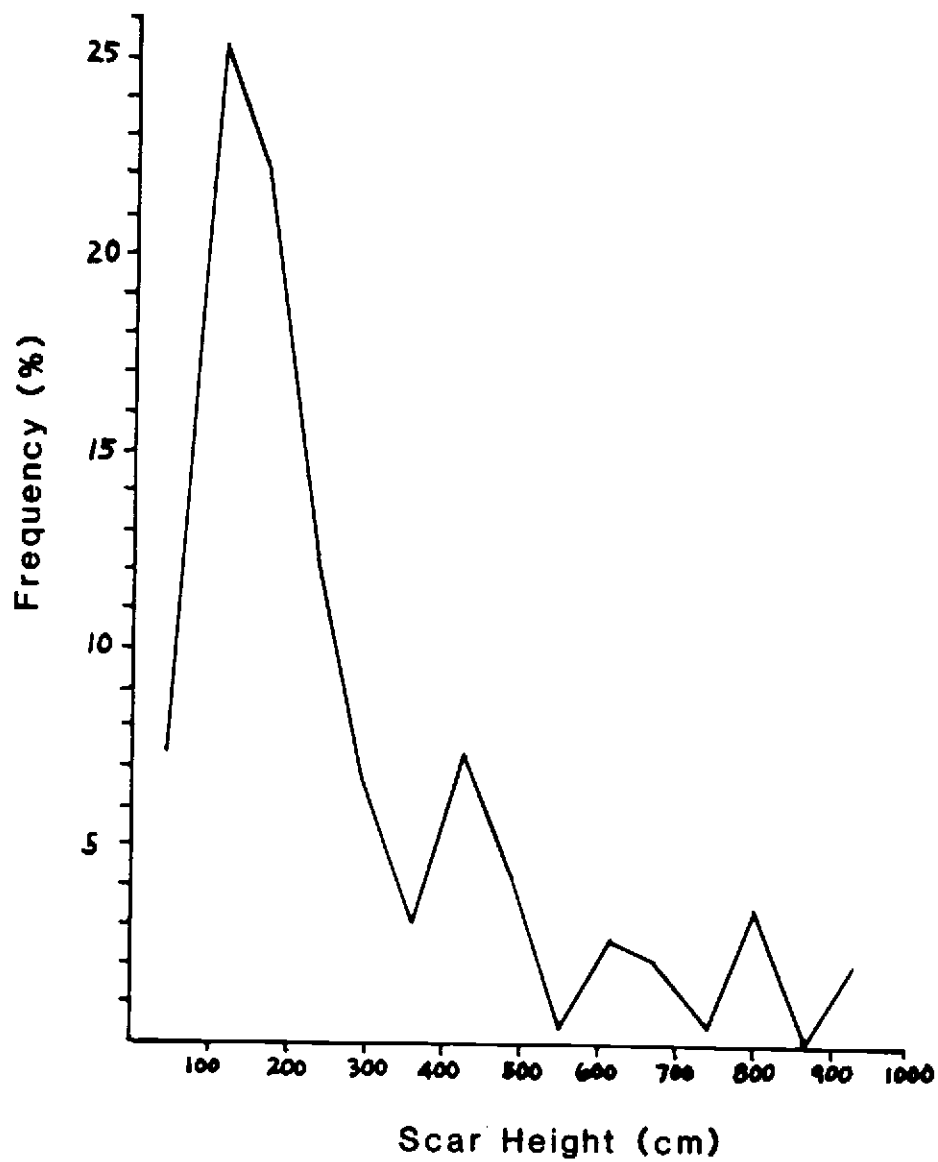


Figure VI.4. Frequency distribution of scar heights on 229 Alaska-cedar trees

Marks, apparrenly made by animals, were present on nearly all fresh scars (Fig. VI.5). Some Alaska-cedar trees had several adjacent basal scars usually with different depths of callus folds as if they occurred at different times (Fig. VI.6). Scars were more common in better drained forest types than on bog or semi-bog forest types (Fig. VI.7). Very few basal scars were found on conifers other than Alaska-cedar, and the few observed did not resemble the scars on Alaska-cedars in size or shape.

A different type of basal scarring was found on 11 Alaska-cedars along Peril Strait. These scars were distinguishable from others by the presence of a distinct horizontal cut across the top, and often the bottom, of the scars; they were also taller than the scars described above (Fig. VI.8). These scars were on some of the largest Alaska-cedars in the stand, almost all were found close to the beach, and scars did not show any trend for occurring on the upslope side of trees.

Responses to Wounding

The first noticeable tree response was evident the first spring after wounding when callus tissue began to develop along the sides, bottom, and top of the wound. Cross sections cut through tree wounds showed that changes in the sapwood on the edges of the wound occurred within several years. Sapwood directly behind the wound was dead (Fig. VI.9), but live sapwood adjacent to both sides of the wound turned bright-yellow. This color was more intense than normal Alaska-cedar heartwood. As callusing sapwood slowly engulfed the sides of the wound, it also developed this bright yellow color. Cross sections cut

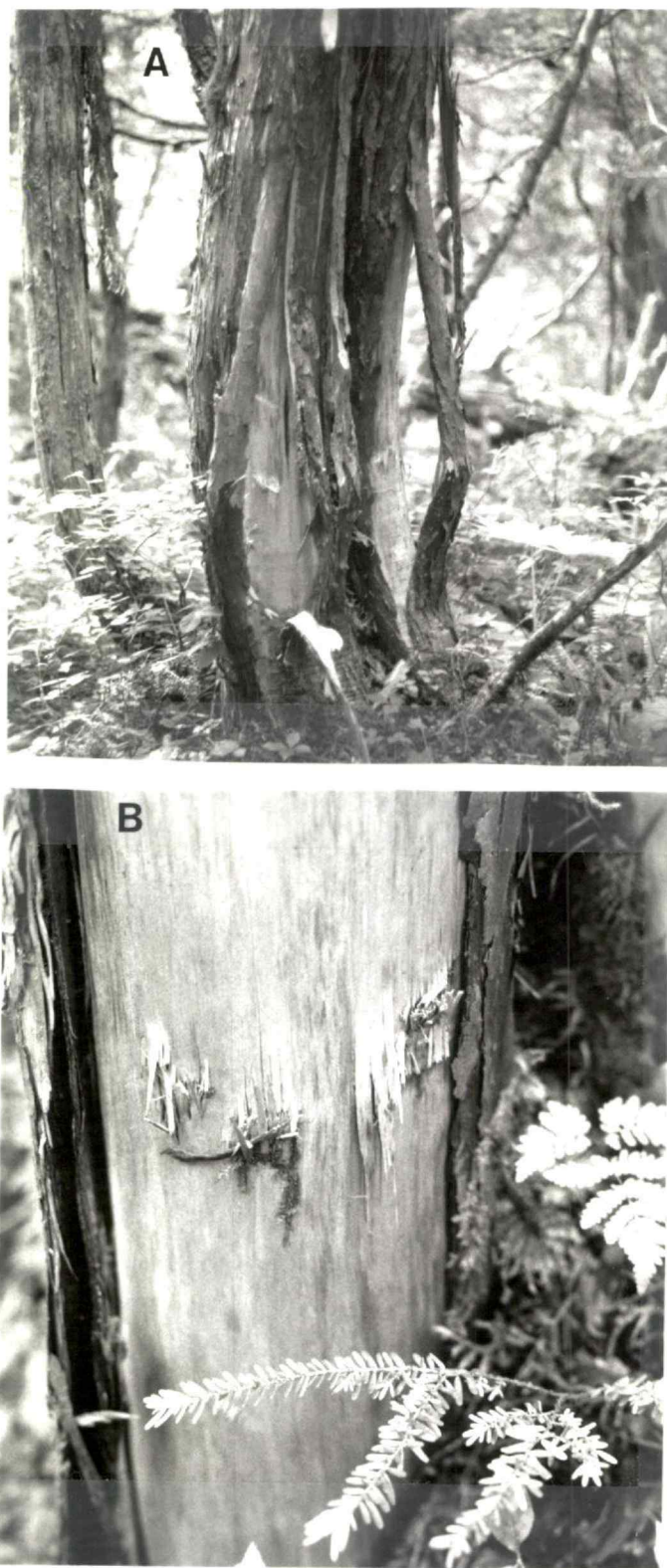


Figure VI.5. A) Fresh basal scar on Alaska-cedar caused by brown bears. B) Note the teeth marks in exposed wood caused by bears tearing bark from these trees.



Figure VI.6. An Alaska-cedar tree that has endured numerous bear scars.

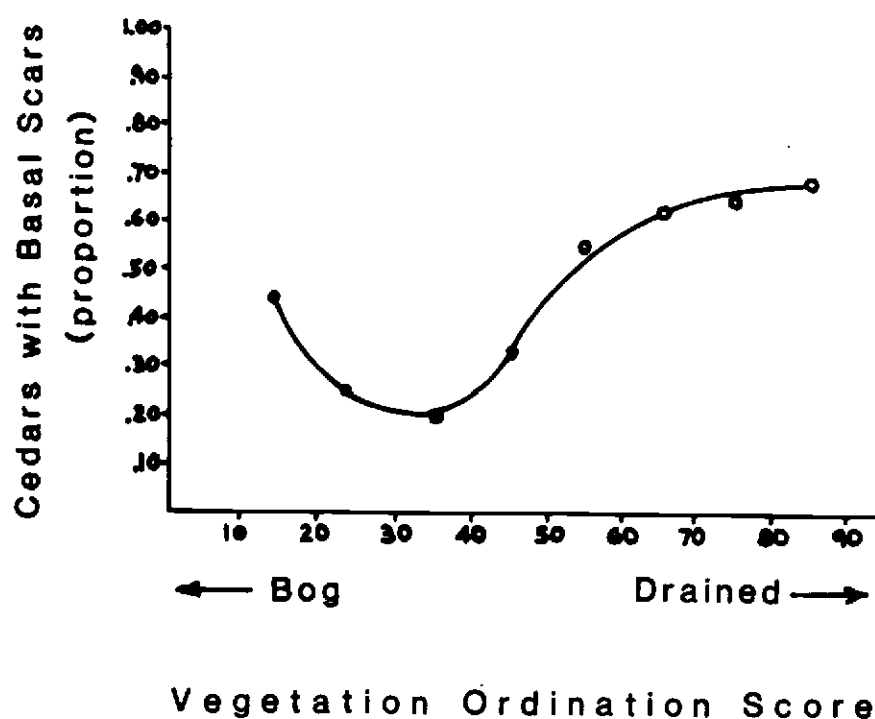


Figure VI.7. Proportion of Alaska-cedars with basal scars from 8 intervals of understory vegetation gradient from bog (low scores) to better drainage (high scores). Vegetation ordination scores based on DECORANA (Chapter III) from 232 plots along 16 survey lines with 682 Alaska-cedars from Peril Strait (Baranof and Chichagof Islands, Alaska).



Figure VI.8. Large basal scar caused by humans collecting bark from Alaska-cedars. Note the horizontal hatchet cuts along the top and bottom of the scar.



Figure VI.9. Cross sections through an Alaska-cedar tree with multiple basal scars. Below: note the callus tissue that grows over the wound and the relative restriction of decay to only the sapwood killed during the scarring event. Above: note the incipient decay in this section which was removed from the bole above the scar.

through older wounds suggested that these reactions confined decay to a narrow crescent-shaped band of the sapwood exposed during the scarring event. Heartwood behind the killed sapwood has a great degree of decay resistance due to anti-fungal compounds (Rennerfelt et al. 1955) and inhibited decay fungi from advancing into the bole. Decay around the stem was confined by adjacent, live sapwood and callus tissue, both of which have the bright-yellow color of heartwood.

Fungi on Scars

Stain and decay were not confined in the wood above scars. One decay column extended 3.2 m above the top of the scar, with advanced decay occurring in all but the top 0.2 m of this column. Leptographium sp., probably saprophytic on Alaska-cedar (Chapter V), was the fungus most frequently isolated from the tops of these stain columns.

Dead sapwood within the wound changed from its original near-white color to a tan, and then to a greenish-black or black within several years after scarring. Leptographium sp. was the most common fungus isolated from the tan-colored stain (Chapter V). Fungi isolated from the black-colored stain included: Sporedesmium sp., Phialophora sp., Mycelium radicis atrovirens, and Leptographium sp. (Chapter V)

Phloem (inner bark), freshly exposed through wounding, was bright and creamy white in color. This phloem, which was stripped away from the sapwood, but still attached at the top and bottom of the wound, changed color to a cinnamon brown within a few hours after wounding.

Several Alaska-cedars with very fresh scars, still with white phloem, were revisited one and two years after being scarred; Ceratocystis sp. and Pistillaria sp. were the only two fungi found

sporulating on these one- and two-year old scars. Ceratocystis sp. was found only on one-year old scars and only sporulated on the bark and sapwood located where these two tissues were killed, but not permanently separated (Fig. VI.10). After a year or two, the stripped bark fell off, leaving the sapwood fully exposed.

The diversity of fungal species increased as the scars aged, reached a peak as the sapwood began to decay, but decreased once most of the sapwood was decayed and eventually missing (Table VI.1). Fungi found on older scars were also found growing as saprophytes on other dead tissues of Alaska-cedars (e.g., dead twigs, limbs, and snags) (Chapter IV). None of the fungi collected or isolated from basal scars is capable of causing these scars or killing trees (Chapter V).

DISCUSSION

Scars with teeth marks were almost certainly made by brown bears (Ursus arctos). These marks in sapwood are made by canine teeth as the bears attempt to pull bark from trees with their mouths (J. Shoen, pers. comm.). A hair of a brown bear was found in the bark of a one-year old scar (J. Shoen, pers. comm.). Fresh scars were most often found in clusters of five or more closely grouped trees, all or most with their scars facing upslope--perhaps for easier pulling of bark from trees by the bears. I found such groups of cedars with fresh scars every spring for four consecutive years, suggesting that basal scarring is an event repeated every year. Some Alaska-cedars had been repeatedly scarred, a dozen or more times around the base of tree



Figure VI.10. Fruiting bodies of Ceratocystis sp. (arrow) on a recent basal scar.

TABLE VI.1. Fungi collected (C) or isolated (I) from basal scars on Alaska-cedar. Six classes are based on wood deterioration and plant colonization to show relative age of scars.

Fungal species	Scar Condition ^{1/}					
	1 fresh to 1- yr old	2 sapwood sound, un- stained	3 sapwood stained but firm	4 sapwood soft but intact	5 sapwood decayed partially missing	6 heart- wood ex- posed
<i>Ceratocystis</i> sp.	C,I	C				
<i>Pistillaria</i> sp.	C	C				
<i>Stictis radiata</i>	C					
<i>Dothidia</i> sp.		C,I				
<i>Herpotrichia</i> sp.		C	C			
<i>Bertia moriformis</i>		C	C	C	C	
<i>Auricularia auriculis</i>				C		
<i>Skeletocutis amorphae</i>			C	C		
<i>Hyphodontia aspera</i>				C		
<i>Dacromyces deliquescens</i>		C		C	C	
<i>Polyporus elegans</i>		C,I	C			
<i>Armillaria</i> sp.			C,I	C	C	
<i>Galerina</i> sp.				C	C	
<i>Xeromphalina campanella</i>					C	
<i>Lycomperdon</i> sp.					C	
<i>Lactarius deliciosus</i>					C	
<i>Cyathus olla</i>					C	
<i>Leptographium</i> sp.	I	C,I				
<i>Sporeodesmium</i> sp.	I	I				
<i>Phialophora</i> sp.		I				
<i>Mycelium radicis</i>						
<i>atrovirens</i>		I				
<i>Seiridium cardinale</i>		I				

^{1/} Presence of lichens, moss, or higher plants on the surface of basal scars are indicators of six classes of recent and old scars: 1--no plants, 2--no plants, 3--moss on bottoms and sides, 4--moss covering, 5--moss covering and higher plants (e.g. *Rubus pedatus* or *Cornus canadensis*), 6--no higher plants, moss uncommon, some crustose and fruticose lichens.

boles, showing a range of scar ages. These multi-scarred trees were most often adjacent to well-established bear trails. Brown bears are the only animals on these islands capable of such tree damage (J. Shoen, pers. comm.). Their hair, scat, trails, and our sightings are evidence of their common occurrence in areas where Alaska-cedars are scarred.

The heights of 24 fresh scars with noticeable bite marks were measured to determine how they compared to the heights of the primarily older callusing scars measured on the 229 Alaska-cedars. Heights of scars with bite marks averaged 164 cm ($s=72$ cm, range=26-270 cm) which corresponded closely with the peak frequency of scar heights from all measured scars (fresh and old) in Figure VI.4. Actual teeth marks in the wood on these scars averaged 44 cm in height ($s=20$ cm, range=12-88 cm).

The distribution of bears on the islands and mainland of southeast Alaska may allow testing the hypothesis that brown bears cause most of the scars. Significant brown bear populations are restricted to Admiralty, Baranof, and Chichagof Islands and the mainland with the greatest densities on the three islands (Meehan 1974, Alaska Department of Fish and Game 1977). Most other islands are inhabited by black bears (*Ursus americanus*) but not brown bears. Both bear species occur on the mainland. We also sampled Alaska-cedars for mortality and scars on Prince of Wales Island, which has black but not brown bears. There were very few scarred Alaska-cedar trees, and even those with scars did not resemble the shape of the scars described above. Thus, scars on Alaska-cedar were infrequent in the absence of brown bears; however,

scars were not necessarily frequent wherever Alaska-cedar and brown bears coexist.

Scars were infrequent at Kennel Creek, on Chichagof Island, where brown bears are common. Large areas of nearly pure stands of Alaska-cedar, however, do not occur in the Kennel Creek area, as they do at Peril Strait and Slocum Arm. Perhaps brown bears scar Alaska-cedar trees only where they are more common. Although the proportion of old, callusing scars that were caused by brown bears is unknown, fresh scars with teeth marks were encountered frequently enough along Peril Strait and Slocum Arm to account for most old scars.

Why brown bears scar Alaska-cedars is not clear. Freshly scarred trees (i.e., within hours to a few days) were found only in May or June. These dates coincide with the time when brown bears emerge from their winter dens located at high elevations (Shoen et al., Unpublished manuscript). By autumn, even the most recently caused scars had aged, suggesting that scarring was only a springtime activity for bears.

The bark of Alaska-cedar is thin, offering relatively little protection from mechanical injury (Anderson 1959). Bark is more easily pulled from trees in the spring, just prior to the initiation of cambial growth when the barks "slips" over wood (Kozlowski 1971). Also, after twig elongation begins in the spring, translocation of carbohydrates (primarily sucrose) greatly increases in the stem phloem of temperate gymnosperms (Nelson 1964). Perhaps bears lick the phloem or cambium for sugars or other nutrients. The bite marks produced when bears pull bark away were the only obvious marks on the scar; once bark was pulled away, bears did not use their teeth or tear at exposed wood

with their claws. The upslope orientation of most scars may be due to easier removing of the bark by approaching trees from the upslope.

Bear damage to conifers has been frequently reported, but only once noted on Alaska-cedar (Ruth and Harris 1979). Girdling of young Douglas-fir (Pseudotsuga menziesii (Mib.) Franco) by black bears is a serious problem in portions of western Washington and Oregon (Lawrence et al. 1961). In one tree farm in Washington, 51% of the Douglas-firs were injured by black bears (Lenvin 1954). On the Kenai Peninsula in Alaska, scars interpreted to have been caused by black bears were common on white spruce (Picea glauca (Moench) Voss) and quaking aspen (Populus tremuloides Michx.) (Lutz 1951). The exposed sapwood usually had shallow grooves made with either teeth or claws. These spruces and aspens were damaged by black bears in the spring and early summer. Scars caused by black bears usually occur at the base of trees, but can also be found up to 40 or 50 feet up the bole (Childs and Worthington 1955). Numerous vertical grooves, caused by black bears scraping the sapwood with their lower jaws, were characteristic of black bear-caused injuries (Lawrence et al. 1961). These vertical feeding marks are in sharp contrast to the horizontal bite marks I found on Alaska-cedars.

The 11 scars with horizontal cuts on Alaska-cedar trees were likely caused by humans. Such human-caused scars have been reported previously on Alaska-cedar and western redcedar (Thuja plicata Donn ex D. Don) (USDA Forest Service 1982, Hicks 1984, Stewart 1984). They were probably the result of Alaska Natives collecting bark for making hats, baskets, and clothing (Frear 1982). All but one of these scars was less than 100 m above the beach, where these large pieces of bark

could have been easily gathered and transported. Today, some Alaska Native people still collect and use cedar bark (I. Jimmy, pers. comm.)

Human-caused scars were not common, and this impact will probably be less consequential in the future. No recently caused human scars were found in the study areas. One of the 11 scars was made 102 years ago. Similar scars were found in Prince William Sound, Alaska and were dated to 180 years ago (C.G. Shaw III, unpublished data). The major impact of human-caused scars is that they occur on the largest Alaska-cedar trees and, because of the scar size and age, they are probably associated with extensive decay columns found in these trees.

Basal scars are not the primary cause of Alaska-cedar mortality in southeast Alaska. Numerous Alaska-cedar trees die with no basal scars (Shaw et al. 1985). Basal scars were more common in the well-drained, high volume forest type where mortality was least common (Chapter III). Extensive mortality of Alaska-cedar occurs on Prince of Wales Island where brown bears are absent and basal scarring was rare. A fresh basal scar on a declining, weakened Alaska-cedar could, however, contribute to its death. In only a few cases did I observe where repeated basal scarring had girdled and killed Alaska-cedar trees.

Tree responses to scarring seem to slow the advance of fungi and, thereby, retard decay. The bright yellow color present in surviving sapwood probably is a reaction to wounding and likely retarded fungal advancement. A significant decay column may develop vertically above the scar, however. The concept of tree responses to wounding is not new and has been discussed previously for many other tree species (Hepting and Blaisdell 1936, Shigo and Marx 1977).

Basal scars cause significant defect and may reduce the value of the butt log of scarred Alaska-cedars to cull. Bole sections adjacent to scars may be salvageable unless the scar is very old, in which case decay fungi have decomposed most of the bole's wood. Additional work is needed to quantify volume losses on trees with basal scars and determine which are the most important fungi responsible for causing the vertical decay column. Several of the dark colored fungi we isolated from basal scars (e.g., Phialophora, Sporidesmium, and Mycelium radialis atrovirens) may be the same fungi causing a black stain in the heartwood of Alaska-cedar described by Smith (1970).

The common scarring of Alaska-cedar trees on the better drained, productive sites may affect revenues from future timber sales in these areas. These sites have the tallest trees, the most volume, and the highest proportion of spruce and western hemlock (Chapter III). As such, these stands are among the most likely to be harvested. A high degree of defect or cull of Alaska-cedar, the most valuable wood in these stands, should be expected in stands where basal scarring is common.

Many of the observations from this study may also apply to logging scars on Alaska-cedar. The bark of Alaska-cedar is very thin, even on large, old trees. Because of its thin bark, trees left after logging (e.g., from partial cuts or commercial thinning) will easily scar during the logging operations. Logging scars will probably closely resemble the basal scars caused by brown bears; they may be about the same size, have the same complement of stain and decay fungi, and tree responses to scarring may be similar. Logging during the summer, fall,

or winter may reduce the incidence of scars on Alaska-cedar since its bark is most easily damaged in the spring.

In conclusion, we believe brown bears and, to a much lesser extent, humans are primarily responsible for the basal scarring on Alaska-cedar on Chichagof and Baranof Islands. These basal scars were not consistently associated with dying Alaska-cedars and are not the primary cause of mortality. Other coniferous species growing near scarred Alaska-cedars were rarely affected. The volume and value loss through basal scars is considerable and needs to be quantified.

Acknowledgements: Dr. John Schoen and Vernon Meyer, both of the Alaska Department of Fish and Game, are greatly appreciated for their enthusiastic assistance and descriptions of the habits of brown bears. I also greatly appreciate the use of the Poison Cove cabin, made available by Irene Jimmy, during the course of these studies.

LITERATURE CITED

Alaska Department of Fish and Game. 1977. A fish and wildlife resource inventory of southeastern Alaska. Alaska Department of Fish and Game, Anchorage, AK. 239p.

Anderson, H.E. 1959. Silvical Characteristics of Alaska-cedar. USDA For. Serv. Alaska Forest Research Center, Sta. Pap. 11. 10p.

Childs, T.W. and N.P. Worthington. 1955. Bear damage to young Douglas-fir. USDA For. Serv. Res. Note No. 113. Pacific Northwest For. & Range Exp. Sta. 4p.

Frear, S.T. 1982. What's killing the Alaska-yellow cedar? Amer. For. 88(11):41-43,62-63.

Harris, A.S. and W.A. Farr. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. USDA For. Serv. Gen. Tech. Rep. PMW-25. Pacific Northwest For. & Range Exp. Sta. 109p.

Hepting, G.H. and D.J. Blaisdell. 1936. A protective zone in red gum fire scars. Phytopathology 26:62-67.

Hicks, R. 1984. Precontact dates revealed by ring counts. The midden. 16(5)11-14.

Hill, M.O. 1980. Detrended correspondence analysis; an improved ordination technique. Vegetatio 42:47-58.

Kozlowski, T.T. 1971. Growth and development of trees. Vol II. Cambial growth, root growth, and reproductive growth. Academic press, New York, NY. 514 p.

Lawrence, W.H., N.B. Kverno and H.D. Hartwell. 1961. Guide to wildlife feeding injuries on conifers in the Pacific Northwest. Western Forestry and Conservation Association. 44p.

Levin, O.R. 1954. The south Olympic tree farm. J. For. 52:243-249.

Lutz, H.J. 1951. Damage to trees by black bears in Alaska. J. For. 49:522-523.

Meehan, W.R. 1974. The forest ecosystem of southeast Alaska. 4. Wildlife habitats. USDA For. Serv. Gen. Tech. Rep. PMW-16. Pacific Northwest For. & Range Exp. Sta. 32p.

Nelson, C. D. 1964. The production and translocation of photosynthate - C_{14} in conifers. pp. 243-257. In: The Formation of wood in forest trees. Ed., M. H. Zimmermann, Academic Press, New York, NY.

Rennerfelt, E. and G. Nacht. 1955. The fungicidal activity of some constituents from heartwood of conifers. Svensk Bot. Tidskr. 49(3): 419-432.

- Ruth, R.H. and A.S. Harris. 1979. Management of western hemlock - Sitka spruce forests for timber production. General Technical Report PNW-88. USDA Forest Service. 179 p.
- Shaw, C.G. III, A. Eglitis, T.H. Laurent, and P.E. Hennon. 1985. Decline and mortality of Chamaecyparis nootkatensis in southeastern Alaska, a problem of long duration but unknown cause. Plant Dis. 69:13-17.
- Shigo, A.L. and H.G. Marx. 1977. Compartmentalization of decay in trees. USDA For. Serv. Agr. Inf. Bull. 405. 73p.
- Shoen, J. 1982. Brown bear habitat preferences and brown bear logging and mining relationships in southeast Alaska. Vol. I. Project progress report, Federal aid in wildlife restoration, Project W-22-1, Job no. 4.17r. 44p.
- Smith, R.S. 1970 Black stain in yellow cedar heartwood. Can. J. Bot. 48:1731-1739.
- Stewart, H. 1984. Culturally modified trees. The Midden 16:(5)7-10.
- USDA Forest Service, 1982. Peeled cedar trees give clues to past. USDA Forest Service, R-6 (Pacific Northwest Region), Greensheet, Sept. 3, 1982. No. 1842. 1 p.
- Zeedyk, W.D. 1957. Why bears girdle balsam fir in Maine. J. For. 55:731-732.

CHAPTER VII

FOLIAGE AND SOIL NUTRIENT CONCENTRATIONS
ASSOCIATED WITH ALASKA-CEDAR DECLINE

ABSTRACT

Alaska cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a valuable, slow-growing tree that has been dying since before the turn of the century on boggy sites throughout southeast Alaska. The primary cause of decline and mortality is unknown. Foliar and soil nutrient concentrations were analyzed to determine whether nutrient deficiency or mineral toxicity could be important causal factors. Foliage nutrient concentrations of 23 elements did not differ significantly between foliage collected from live cedar saplings growing on sites with and without severe mortality. Cedars growing near roads had higher levels of several nutrients, however. Soil adjacent to both healthy and dead roots on dying Alaska-cedars was collected and analyzed for pH and six elements: soil adjacent to dead roots had higher pH, higher total N, and less P. Differences in soil characteristics could be due to death of cedar roots. These data suggest that nutrient deficiency and mineral toxicity are probably not primary causes of Alaska-cedar decline.

INTRODUCTION

Extensive mortality of Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) has been occurring in southeast Alaska since before the turn of this century (Shaw et al. 1985, Chapter III). This forest decline has not yet received adequate study and the cause of tree death is unknown. This report is part of a larger effort to evaluate the potential causes of Alaska-cedar decline. Alaska-cedar trees have very slow radial growth 5 to 20 or more years prior to death (Shaw et al. 1985, Chapter V) that could be interpreted as symptomatic of these trees depleting a limited soil nutrient. Foliar and soil nutrient concentrations were analyzed to determine if nutrient deficiencies or toxicities are associated with, or perhaps cause, this decline problem.

Deficient levels of sulfur and boron are factors in another decline of Pinus radiata Don. in New Zealand (Lambert and Turner 1977). Nutrient deficiency or toxicity are potential causes of Alaska-cedar decline, particularly because most mortality has occurred on boggy sites (Downing 1960, Chapter III) where nutrients may be limiting or toxic compounds accumulating due to anaerobic soil conditions. The nutrient or toxicity status of bog soils has not been determined for bogs in southeast Alaska, but elsewhere they been demonstrated to be acidic and nutrient impoverished.

Foliage or soil nutrient analysis has not been previously conducted for Alaska-cedar in southeast Alaska, or, to the best of our knowledge, anywhere else for Alaska-cedar. Therefore, foliar nutrient levels were compared for Alaska-cedars growing in bogs having high

levels of mortality with Alaska-cedars growing in bogs with little to no mortality. Also, soil adjacent to both living and recently dead roots of declining Alaska-cedars was collected and analyzed for nutrient concentrations to determine if soil near dead roots was particularly nutrient deficient.

The objective of this paper is to determine if deficient soil nutrients or toxic levels of soil nutrients are responsible for the widespread decline problem.

MATERIALS AND METHODS

Foliage Nutrients

Foliage samples were collected at 12 sites along Peril Strait on Baranof and Chichagof Islands and from single sites near Kennel Creek on Chichagof Island and Thorne Bay on Prince of Wales Island (Figs. VII.1, VII.2, and Table VII.1). Since Alaska-cedar mortality is most severe near bogs, all foliage sampling was conducted on bog-fringes or cedar-scrub stands (semi-bog forest types with stunted trees). Fourteen sites ranged in degree and timing of mortality, and elevation (Table VII.1) and were designated as either mortality (11) or non-mortality (3), based on the presence of surrounding dead cedar trees. Bog and semi-bog stands lacking appreciable mortality could only be located above 150 m elevation.

Foliage samples were taken at each site from two sides of five healthy Alaska-cedars, 5 to 8 m tall. Sapling-sized trees were sampled because trees of this size are more sensitive indicators of some

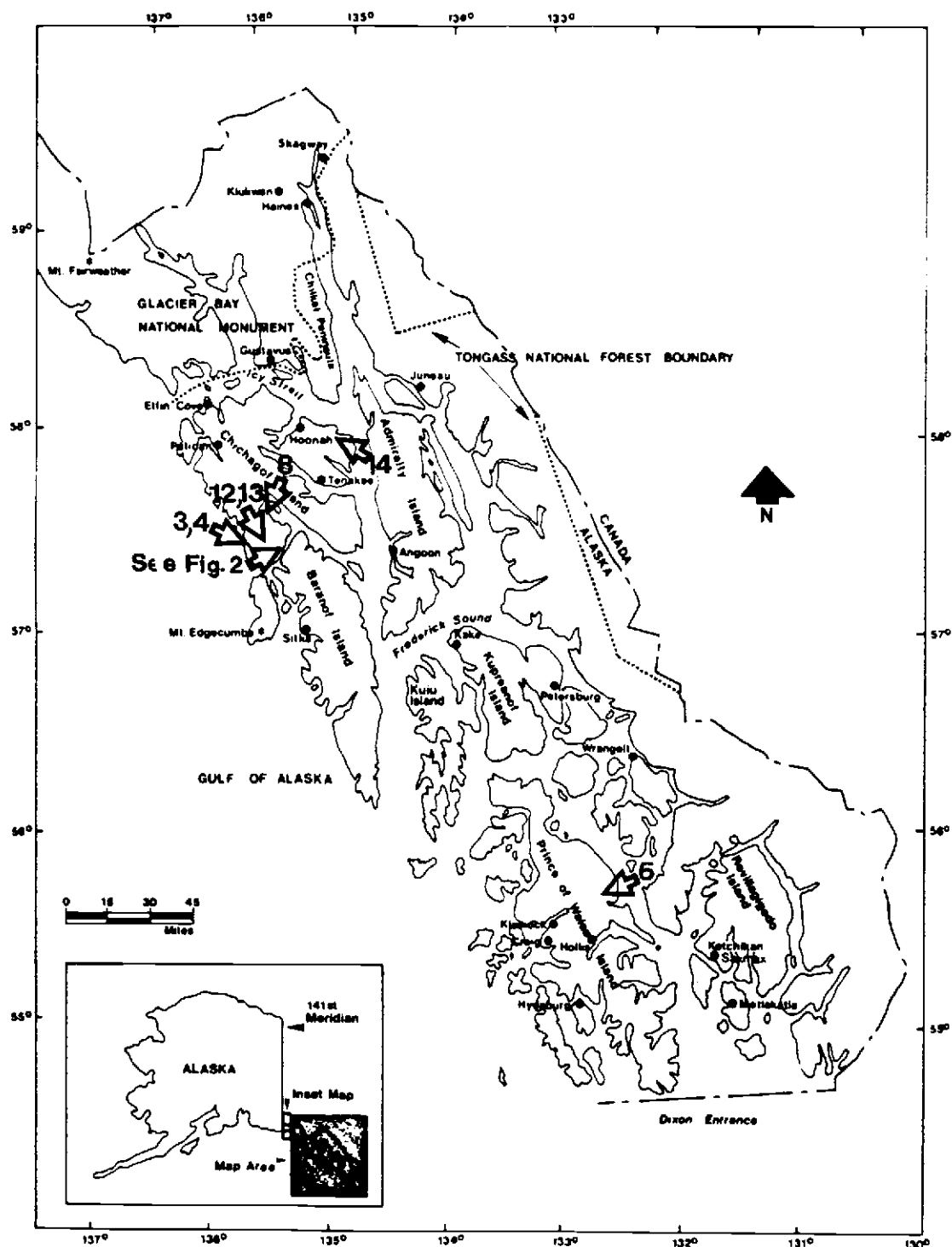


Figure VII.1. Map of sampling locations in southeast Alaska for collecting foliage of Alaska-cedar used in nutrient analysis

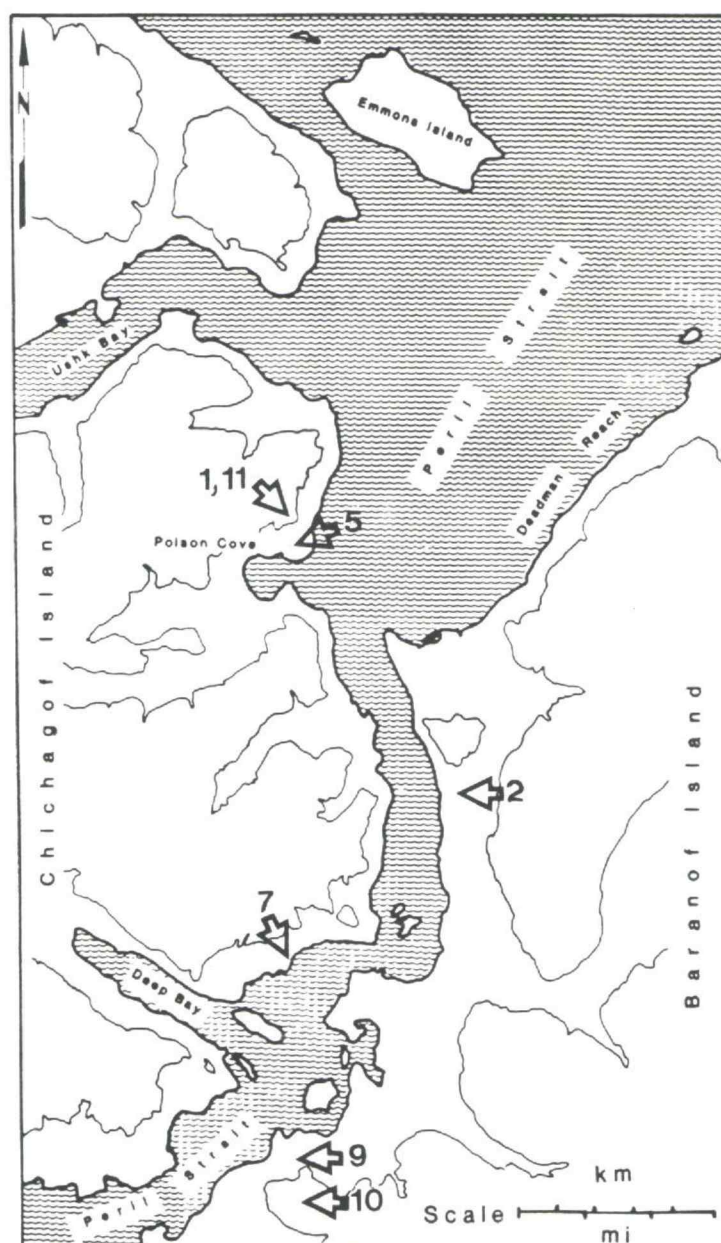


Figure VII.2. Map of sampling locations in the Peril Strait area for collecting foliage of Alaska-cedar used in nutrient analysis

Table VII.1. Characteristics of Alaska-cedar foliage sampling sites.

<u>Plot No.</u>	<u>Date (1983)</u>	<u>Location</u>	<u>Elevation (m)</u>	<u>Forest Type</u>	<u>Mortality Rating^{1/}</u>
1	6/20	Poison Cove, Chichagof I.	262 (860')	bog fringe	healthy
2	6/22	Nixon Shoal, Baranof I.	<50 (165')	bog fringe	mortality (old only)
3	6/23	Waterfall Cove, Chichagof I.	<50 (165')	cedar scrub	mortality (intermediate level)
4	6/23	Waterfall Cove, Chichagof I.	<50 (165')	cedar scrub	mortality (current only)
5	6/24	Poison Cove, Chichagof I.	<50' (165')	cedar scrub	mortality (old and moderately old)
6	6/25	Thorne Bay, Prince of Wales I.	<50 (165')	bog fringe	mortality (old and current)
7	7/19	Arthur Site Chichagof I.	<50 (165')	cedar scrub	mortality (old only)
8	8/23	Patterson Bay, Chichagof I.	<50 (165')	pole size cedar	mortality (very old only)
9	8/13	Bear Bay Chichagof I.	75 (250')	bog fringe	mortality (old and current)
10	8/13	Bear Bay Chichagof I.	275 (905')	bog fringe	healthy
11	8/19	Poison Cove Chichagof I.	320 (1040')	bog fringe	healthy
12	8/28	4 mi. inland (E.) from Poison Cove Chichagof I.	260 (860')	cedar scrub	mortality (current only)
13	8/28	4 mi. inland (E.) from Poison Cove	215 (710')	cedar scrub	mortality (old and current)
14	9/07	Kennel Creek, Chichagof I.	<50 (165')	bog fringe	mortality (old and intermediate)

^{1/} Timing of mortality based on snag foliage, twig, and branch retention (Chapter II)

environmental stresses than are larger trees (Waring and Cleary 1967). Foliage was collected from approximately the 20 cm terminal portion of branches by hand-stripping only green foliage (Zobel and Liu 1979). Foliage samples were bulked for each tree, oven-dried, bulked for each site, and ground before analysis. Nutrient concentrations were determined using spectrometer analysis and total Kjeldahl nitrogen analysis by the Plant Analysis Laboratory, Oregon State University. Student's t ($p=0.05$) was used to test differences in foliage nutrient concentrations between mortality and non-mortality stands.

Soil Nutrients

In a preliminary attempt to evaluate soil nutrients, eight soil samples were collected from Alaska-cedars. Small roots (approx. 1 cm diam) of declining trees were frequently found dying or dead in a water-saturated black organic muck; live roots from the same trees were most often in a drier, lighter-brown organic duff (Chapter V). The root system of Alaska-cedars, even of large trees, is primarily confined to the upper 15 cm of the soil profile (Chapter V). The soil in this rooting zone appeared to be nearly all organic, lying above the mineral layer. Paired soil samples were made from each of three declining cedars growing in the Peril Strait area; one light-brown sample taken adjacent to small live roots, the other black sample adjacent to small dead roots. An additional sampling pair was taken from two separate dying trees. All soil samples were oven dried and analyzed for pH and six soil nutrients by the Soil Testing Laboratory, Oregon State University. Differences in pH and nutrient concentrations

between the two soil types were tested by a Student's t test ($p=0.05$) for paired samples.

RESULTS

Foliage Nutrients

No significant differences were found in concentrations of 23 different elements from foliage collected at sites with and without mortality (Table VII.2). Nutrient concentrations were relatively constant from site to site regardless of mortality rating. The values of some elements (Mn, Al, Na, As, Cd, Ni, Si, Ba, and Sr) were substantially higher for either or both of the Kennel Creek and Thorne Bay sites, however. These relatively high values may reveal road dust influences since these were the only sites near roads.

Soil Nutrients

The drier, brown organic soil near live roots had significantly lower pH, higher concentrations of P, and lower concentrations of N (all $p=0.05$) than the wetter black organic soil (Table VII.3). The concentrations of K, Ca, Mg, and Na did not differ significantly between the two soil types.

Table VII.2. Nutrient concentrations^{1/} of Alaska-cedar foliage gathered from sites with and without appreciable mortality. Port-Orford-cedar foliage nutrient concentrations are included for comparison.

Nutrient 4/	A L A S K A - C E D A R			P O R T - O R F O R D - C E D A R		CEDARS IN T A I W A N 5/
	Mortality Sites 2, 3/	Non-mortality Sites 2, 3/	All Sites (pooled) 3/	(Imper and Zobel 1983)	(Zobel and Hawk 1980)	(Zobel and Liu 1979)
N %	0.72 (0.11)	0.69 (0.08)	0.68 (0.09)	0.9 - 1.9	0.88	0.73-1.45
P %	0.089 (0.010)	0.083 (0.010)	0.09 (0.01)	0.11 - 0.23	0.11	0.07-0.15
K %	0.52 (0.02)	0.51 (0.05)	0.52 (0.04)	0.67 - 1.20	0.52	0.47-0.60
Ca %	1.58 (0.24)	1.49 (0.33)	1.54 (0.30)	0.8 - 1.9	1.11	1.12-1.52
Mg %	0.088 (0.026)	0.108 (0.020)	0.10 (0.02)	0.11 - 0.26	0.25	0.17-0.24
S %	0.098 (0.014)	0.096 (0.013)	0.10 (0.01)			
Mn ppm	14.9 (9.1)	13.4 (8.0)	12.9 (6.0)		406.	913 1269
Fe ppm	52.6 (8.4)	57.2 (25.7)	50.6 (10.1)		20.	211 - 440
Cu ppm	1.76 (0.39)	1.89 (0.33)	1.81 (0.35)		8.7	7 - 15
B ppm	16.0 (2.2)	15.0 (1.4)	15.2 (1.76)		23.	11 - 16
Zn ppm	8.25 (1.56)	8.02 (1.26)	8.03 (1.28)		49.	40 - 56
Al ppm	26.8 (11.1)	27.0 (9.9)	25.7 (7.2)		179.	198 - 409
Mo ppm	0.071 (0.011)	0.076 (0.006)	0.07 (0.01)			
Na ppm	96.5 (41.1)	80.0 (29.1)	88.0 (31.6)			
Se ppm	0.046 (0.002)	0.04 (0.01)	0.04 (0.01)			
As ppm	1.16 (0.30)	1.22 (0.22)	1.16 (0.22)			
Ba ppm	2.5 (0.9)	4.1 (4.6)	2.5 (0.99)			
Cd ppm	0.016 (0.010)	0.024 (0.006)	0.02 (0.01)			
Co ppm	0.062 (0.008)	0.13 (0.19)	0.11 (0.16)			
Li ppm	32.5 (12.4)	46.9 (31.0)	43.1 (25.6)			
Ni ppm	0.41 (0.05)	0.38 (0.03)	0.39 (0.04)			
Si ppm	41.0 (15.1)	41.8 (12.9)	40.3 (10.6)			
Sr ppm	23.5 (5.8)	26.8 (13.2)	24.1 (6.8)			

1/ Mean values followed by standard error in parentheses

2/ Sites 1, 8, 10, and 11 (Table VII.1) were classified as non-mortality; sites 2, 4-7, 9, 12, and 13 were classified as mortality; sites 3 and 14 were excluded from comparison due to intermediate levels of mortality (see Table VII.1).

3/ Sites 6 (Thorne Bay) and 14 (Kennel Creek) excluded due to possible effects of road dust.

4/ Nutrient concentrations reported in % of dry weight or parts per million (ppm)

5/ *Chamaecyparis taiwanensis* Masamune et Suzuki and *C. formosensis* Mats.

Table VII.3. Comparison of nutrient concentrations and pH from soil samples collected adjacent to live or dead roots (approx. 1 cm diam.) on dying Alaska-cedars.

<u>Nutrient</u>	<u>Soil Near Live Roots</u>	<u>Soil Near Dead Roots</u>
pH ^{2/}	3.93 (0.17)	4.78 (0.25)
Total N (%) ^{2/}	0.88 (0.16)	1.48 (0.33)
P (ppm) ^{2/}	11.0 (3.4)	4.8 (1.5)
K (ppm)	376 (131)	161 (47)
Ca (meq./100g)	11.6 (4.3)	7.8 (7.1)
Mg (meq./100g)	6.2 (3.0)	2.8 (2.5)
Na (meq./100g)	0.59 (0.23)	0.36 (0.10)

^{1/} Values are means followed by standard error (in parentheses).

^{2/} Significant ($p = 0.05$) differences between soil collected adjacent to live versus dead roots.

DISCUSSION

The similar concentrations of foliar nutrients between Alaska-cedar trees growing on sites with and without mortality suggests that nutrient deficiency or toxicity are probably not the primary cause of Alaska-cedar decline. The use of foliar nutrient values may be a more sensitive indicator than soil nutrients when testing for deficiency, since the former gives a direct measure of the nutrients the plant has derived from the soil (Mead 1984). The average foliar nutrient concentrations from all plots, excluding the two plots near roads, were below values found in Port-Orford-cedar (Chamaecyparis lawsoniana (A. Murr.) Parl.) by Imper and Zobel (1983) in southwestern Oregon for N, P, K, and Mg but not Ca. Also, the nutrient values were generally lower for Alaska-cedar than for nutrients from the foliage of C. taiwanensis Masamune et Suzuki and C. formosensis Mats. growing in Taiwan. The relatively low nutrient concentrations of Alaska-cedar as compared to those of Port-Orford-cedar are not unexpected on these bog and semi-bog sites, however. The soils of these sites are considered to be anaerobic, acidic, and nutrient poor. Alaska-cedar has long been suspected of being a slow-growing conifer that tolerates poor sites (Harris 1971), but can grow at faster rates on better soils

Results from soil sampling are preliminary due to the small sample size, but suggest that the two soil types were very different nutritionally. Many, but not all, dying roots of excavated declining Alaska-cedars were found in the black mucky soil. The effects of dead and dying roots on the nutrient status of the black organic soil must be considered when comparing it to the brown organic soil supporting

live roots. The increased level of nitrogen in the black soil where dead roots were found could result from nitrogen released from decaying fine roots, mycorrhizae, and larger roots.

The nutrient data suggest that P and K may be deficient in the black soils where roots were dying. Interestingly, bog soils elsewhere have been demonstrated to be poor storers of P and K, while nitrogen concentrations vary widely (Holmen 1968). Despite possible deficiencies of P and K, entire patches of prostrate Alaska-cedars were growing in this soil type in bogs (Chapter VIII), yet had green, full crowns. Foliage nutrient levels did not suggest that a deficiency of P or K was responsible for cedar mortality since their concentrations were very similar in mortality and non-mortality sites.

The selective mortality to Alaska-cedar, compared with other tree species, should be accounted for when evaluating a potential nutrient deficiency or toxicity as the primary cause of Alaska-cedar decline. Western and mountain hemlocks (Tsuga heterophylla (Raf.) Sarg. and T. mertensiana (Bong.) Carr.), Sitka spruce (Picea sitchensis (Bong.) Carr.), and shore pine (Pinus contorta Dougl.) also grow on sites where Alaska-cedars are dead or dying, but are not affected to the same degree by this problem (Chapter III).

Little is known of the particular nutrient deficiency or toxicity levels that may affect the growth of Alaska-cedar. Alaska-cedar must be shown to be more sensitive to a hypothetical nutrient deficiency or toxicity before either could be demonstrated to be an important factor in causing Alaska-cedar decline. This study has not ruled out complex organic toxins as a cause of mortality. Our data, by comparing the nutrient status of Alaska-cedars growing in bogs with and without

mortality, does suggest that nutrient deficiency and strictly inorganic toxicity are probably not primarily responsible for Alaska-cedar decline.

LITERATURE CITED

- Beaton, J.D., A. Moss, I. MacRae, J.W. Konkin, W.T. McGhee, and R. Kosik. 1965. Observations on foliage nutrient content of several coniferous trees in British Columbia. *For. Chron.* 41:222-236.
- Holmen, H. 1968. Afforestation of peatlands in Sweden, classification and site research. pp.371-377. In: Proceedings of the third international peat congress. Quebec, Canada, August 18-23, 1968. 405p.
- Imper, D.K. and D.B. Zobel. 1983. Soils and foliar nutrient analysis of Chamaecyparis lawsoniana and Thuja plicata in southwestern Oregon. *Can. J. For. Res.* 13:1219-1227.
- Lambert, M.J. and J. Turner. 1977. Die back in high site quality Pinus radiata stands--the role of sulfur and boron deficiencies. *New Zealand J. For.* 7:333-348.
- Mead, D.J. 1984. Diagnosis of nutrient deficiencies in plantations. Pp. 259-291. In: Nutrition of plantation forests. Eds. Bowen, G.D. and E.K. Nambiar. Academic press, London, England.
- Waring, R.H. and B.D. Cleary, 1967. Plant Moisture Stress: evaluation by pressure bomb. *Science.* 155:1248-1254.
- Zobel, D.B. and G.M. Hawk. 1980. The environment of Chamaecyparis lawsoniana. *The American Midland Naturalist* 103:280-297.
- Zobel, D.B. and V.T. Liu. 1979. Foliar nutrient concentrations of small Chamaecyparis in Taiwan. *Plant and Soil* 53:373-384.

CHAPTER VIII

REPRODUCTION OF CHAMAECYPARIS NOOTKATENSIS
IN SOUTHEAST ALASKA

ABSTRACT

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a valuable tree species that has been suffering from a decline and mortality of unknown cause throughout southeast Alaska for the last 100 years. Studies were initiated on its natural reproduction to provide information on how to reforest affected areas. The occurrence of seedlings and of a low-growing, shrubby form of Alaska-cedar were recorded from 280 plots along 21 transects across areas of mortality. Fifty-five taxa of understory plants were also recorded; community data were analyzed by Detrended Correspondence Analysis to provide forest type information on each plot. Reproduction from seed is failing on most sites, although small germlings of Alaska-cedar are common on well-drained sites where cedar reaches its best development. Shade intolerance is suspected as the primary reason for germling death. The low-growing form of Alaska-cedar spreads by the rooting of lower limbs (vegetative reproduction) and is confined to bog and semi-bog sites. Germlings and small seedlings are less common on bogs than on better drained sites, but occasionally do establish on bogs where they develop into the low-growing form. Stems of these low-growing Alaska-cedars often turn upright and slowly grow into trees. Mature trees share several characteristics with the low-growing form, including boles that

have a downslope sweep and root systems that extend upslope and terminate in a very shallow, long-dead end. These similarities suggest that most Alaska-cedar trees may originate through vegetative reproduction. These studies will aid with the development of strategies for reforesting different sites with Alaska-cedar (Hennon and Shaw 1985).

INTRODUCTION

Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) is a slow-growing, long-lived, and potentially important commercial tree species in the forests of southeast Alaska. Its reproductive ecology is poorly understood here, but Antos and Zobel (1986) recently discussed natural reproduction of Alaska-cedar in Washington, Oregon, and California.

Alaska-cedar is currently suffering from an extensive decline and mortality throughout southeast Alaska (Frear 1982, Shaw et al. 1985) that began around 1880 (Chapter II). Alaska-cedar trees of all size classes can be found dead or dying (Shaw et al. 1985), particularly on bog and semi-bog forested sites (Downing 1961, Chapter III). The cause of this cedar decline is not clearly understood, nor are the implications for management. Recent research suggests, however, that no biotic agent (e.g., insect or pathogen) is the primary cause of decline and that there has been no contagious spread from site to site (Chapter III).

The large volume of dead and dying Alaska-cedar throughout southeast Alaska has prompted interest in logging operations designed to salvage dead cedars. Such interest raises the question of how Alaska-cedar could be re-established on these sites and whether or not natural reproduction (unplanted) would be a sufficient source of this replacement. On many decline sites, a low-growing, shrubby growth form of Alaska-cedar (Fig. VIII.1) occurs, which contributes to replacing the dead overstory. Reproduction of Alaska-cedar in areas of mortality may be feasible, particularly if the nature of this prostrate form and cedar reproduction, in general, is better understood. Furthermore, information on reproductive ecology would be useful for the artificial establishment of Alaska-cedar in managed, young-growth stands on cut-over areas.

Alaska-cedar does regenerate vegetatively, but the relative importance of vegetative and sexual reproduction is not known. Surprisingly, it is not even known whether old-growth stands of Alaska-cedar originated primarily from seedlings (sexual reproduction) or vegetative reproduction. Establishment of natural seedlings is unsuccessful in some Alaska-cedar stands in southeast Alaska (Shaw et al. 1985, Harris 1971). Several reports note that vegetative reproduction does occur in Alaska-cedar. Harris (1971) noted that root sprouting and rooting of buried branches were common for Alaska-cedar; however, Anderson (1959) considered vegetative reproduction uncommon, but mentioned that details were lacking. Adventitious rooting was noted on Vancouver Island (Schmidt 1955) and, new stems were observed arising from the base of damaged Alaska-cedars (Perry 1954). Arno (1966) observed the low-growing, prostrate form of Alaska-cedar at



Figure VIII.1. Low-growing, prostrate patch of Alaska-cedar in a bog.

timberline in the Olympic Mountains of Washington and interpreted their development to be the result of root sprouting or layering. Antos and Zobel (1986) describe layering of Alaska-cedar in the southern portion of its range. Although this literature on the natural occurrence of vegetative reproduction in Alaska-cedar is sketchy and lacks details, techniques for using vegetative reproduction of nursery stock for reforestation with Alaska-cedar are being used in British Columbia (Karlsson 1974).

The purpose of this paper is to: 1) describe the origins, development, and forest type associations of shrubby, prostrate-growing Alaska-cedar; 2) determine forest type associations for Alaska-cedar seedlings; 3) discuss the possible origins of Alaska-cedar stands; and 4) identify necessary future research needs.

MATERIALS AND METHODS

All studies were located in or near stands exhibiting decline and mortality on Baranof and Chichagof Islands of southeast Alaska. A forest survey was conducted to determine the abundance of Alaska-cedar regeneration in different forest community types. Alaska-cedar germlings (seedlings less than three years old with immature foliage and cotyledons still attached), established seedlings, and patches of prostrate cedar were counted in 280 3 m radius (28 m^2) plots along 21 transect lines. Understory plants were used to classify plant communities; the presence and abundance of 55 understory plant species were recorded from these plots. Understory plant data were analyzed by

Detrended Correspondence Analysis (DECORANA) (Gauch 1982). Plot ordination scores represent the gradient from boggy sites to those with better drainage (Chapter III). Here, we relate these plot ordination scores to the average number of cedar seedlings or germlings per plot and to the incidence of prostrate cedar. Also, the basal area for live Alaska-cedars, the basal area for all tree species, and the ordination plot scores were compared for plots having cedar seedlings (or germlings) vs. plots without seedlings (or germlings) and for plots with prostrate cedar vs. plots without prostrate cedar. These comparisons were evaluated with Student's *t* test ($p = 0.05$).

The roots of two separate patches of prostrate cedar were excavated to determine their origin and growth habit.

RESULTS AND DISCUSSION

Prostrate Cedar Patches

Both patches of prostrate cedar that were excavated consisted of several small upright stems, all of which were sweeping downslope, with their short crowns (e.g., 1 m tall) fully intermingled. The main, shallow root was progressively smaller in diameter upslope from each upright stem and was usually dead where it tapered to about 1 cm diameter. These main roots were never deeper than 10-15 cm and often occurred in a black, organic muck (Chapter VII). Tissues beyond the live/dead margin were sometimes long-dead and nearly rotted away. Other times a living prostrate stem branched off beyond a section of dead root, leading to another system of interconnected stems.

In one case, the main stem of a prostrate cedar was found attached to a dead, fallen cedar (Fig. VIII.2) where an old branch cluster had apparently rooted adventitiously. The main stem of the fallen cedar was partially decayed, indicating that it had been dead for decades (Chapter II). Callus tissue was evident at the live-dead interface where the branch cluster had rooted. This layered stem with its short canopy had, in turn, layered with another upright stem connected by a thin, but long (1 m), shallow root (Fig. VIII.3).

Some small, isolated, and upright stems of cedar were emergent in bogs. These small cedars clearly developed from seedlings (Fig. VIII.4) as their root systems could be followed distally to ends of fine roots and did not attach to other root-stems, as was the case with layering. Several of these seedlings, however, had adventitious roots along more than one upright stem, as if they were beginning to develop into patches of vegetatively-reproduced cedar.

Thus, these prostrate patches of cedar may originate from the stem of a fallen or broken cedar, a lower limb of an existing tree, or a seedling established in the bog. As the prostrate cedars develop and sweep downslope (even on a gradual slope), lower branches root adventitiously and elongate to enlarge and perpetuate the layering patch. Eventually, connections between stems die and decay, while the process of lower limb layering continues.

Comparison of the presence of prostrate cedar patches with the understory plant ordination scores for each plot demonstrates that layering prostrate cedar patches are common in bogs, but less common to absent in better drained forest types (Fig. VIII.5). The better drained sites without cedar layering have higher total basal areas,



Figure VIII.2. Prostrate patch of Alaska-cedar that originated from a fallen tree (arrow).



Figure VIII.3. Prostrate patches of Alaska-cedar spread by rooting of lower limbs (vegetative layering). Note the green crowns (arrows) separated by lower branches that have roots.

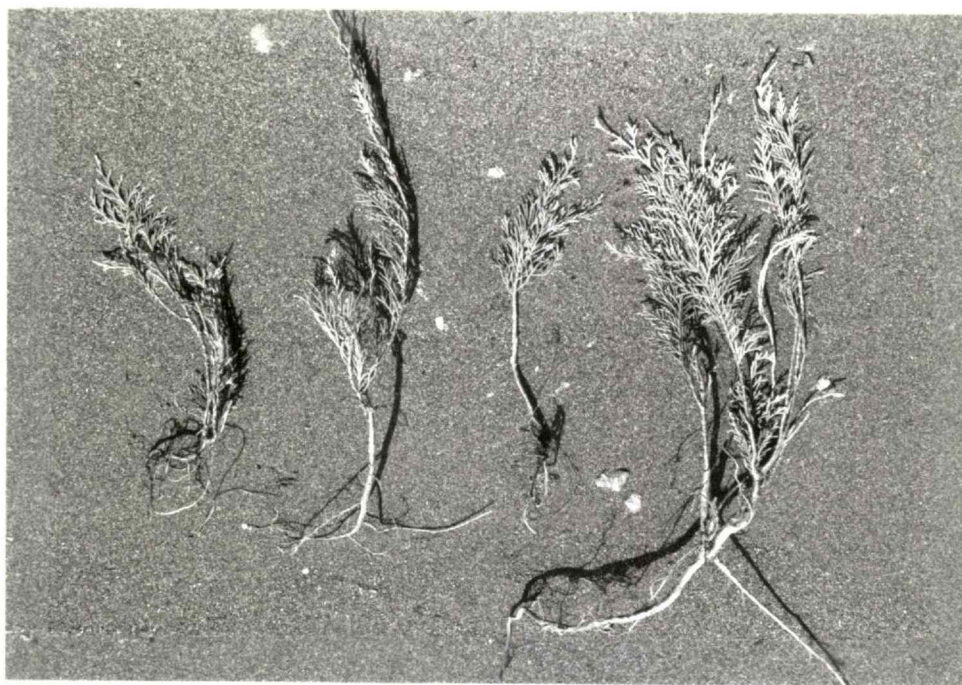


Figure VIII.4. Seedlings of Alaska-cedar found in an open bog

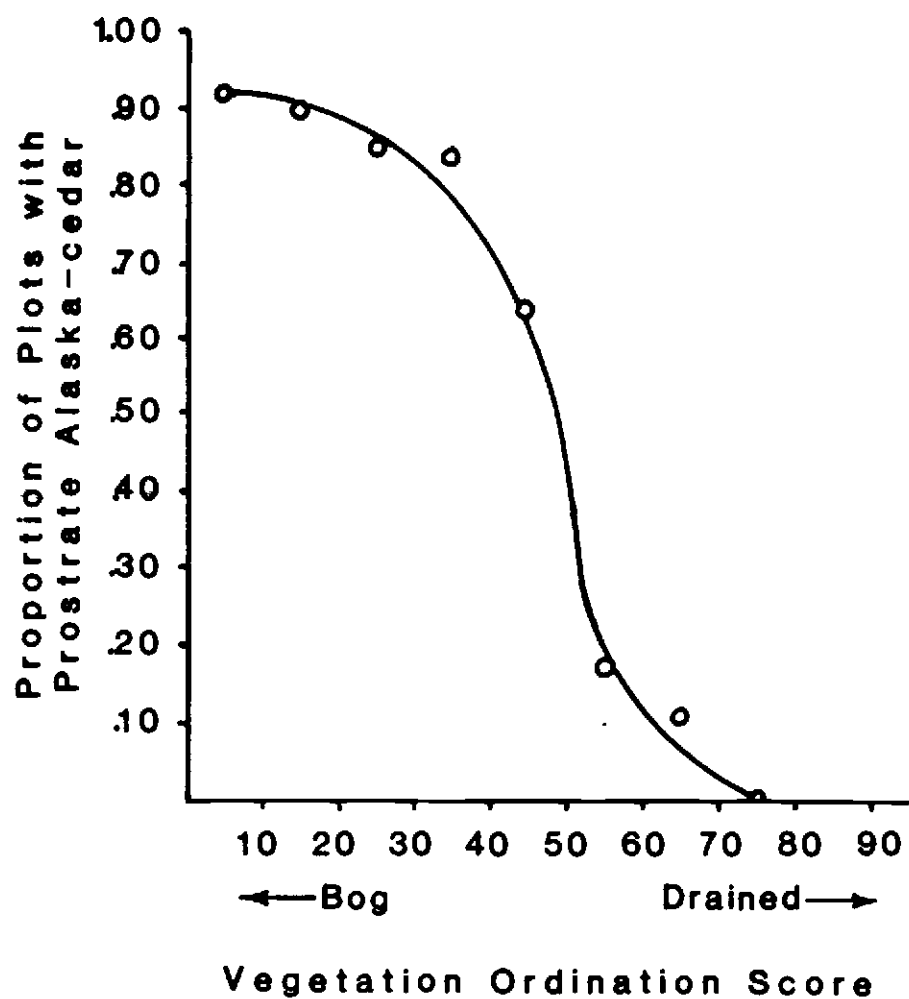


Figure VIII.5. Proportion of plots with prostrately growing Alaska-cedar along the bog to better drainage forest gradient as rated by DECORANA plot ordination scores from 280 plots (Chapter III).

with species other than Alaska-cedar (primarily western hemlock) contributing most of the basal area (Table VIII.1). Plots with prostrate layering had significantly lower (boggier) scores than did plots lacking the prostrate form. The low-growing cedar form was observed to be abundant in the subalpine where the only species growing in a tree-like form is mountain hemlock (Tsuga mertensiana (Bong.) Carr.).

The rarity or absence of cedar layering on better drained sites may be explained by environmental factors or cedar growth habits. Light, which is readily available in bogs, is greatly reduced in high volume forests. Inadequate light could restrict layering on the floor of high volume forests on better drained sites. Also, cedars become taller on better drained sites (Chapter III), and lower limbs, which are important for perpetuating layering, are self-pruned. On bog sites, cedar remains stunted and bushy with many lower limbs available for layering. By contrast, Antos and Zobel (1986) found abundant layering in forests.

Cedar Germlings and Seedlings

The density of Alaska-cedar germlings closely paralleled the amount of live cedar basal area (compare Fig VIII.6 with Fig. III.10). The distance of seed dispersal for Alaska-cedar was normally short (less than 120 m) (Fowells 1965), perhaps because of its small seed wings (Owens and Molder 1984). The relatively short seed dispersal could account for the close association of cedar germlings and live cedar basal area. Plots having at least one germling or seedling tended to have higher cedar basal area, higher total tree

Table VIII.1. Basal area (m^2/ha) and understory vegetation ordination scores ^{1/} for plots with and without Alaska-cedar vegetative reproduction (layering).

	Layering ^{2/}	No Layering ^{2/}
Number of Plots	101	173
Live Basal Area for all tree species	25.1 \pm 19.2	45.9 \pm 22.1
Live Basal Area for Alaska-cedar	14.0 \pm 14.5	19.2 \pm 16.1
Dead Basal Area for Alaska-cedar	7.3 \pm 11.6	8.3 \pm 10.7
Ordination score ^{1/}	33.4 \pm 15.7	64.6 \pm 14.6

^{1/} Ordination scores are based on Detrended Correspondence Analysis of 55 understory plant taxa. Scores represent the gradient from open bog (scores approach zero) to communities with better drainage (scores approach 100). Means differed significantly ($p=0.05$)

^{2/} Basal areas and forest type scores are means followed by standard deviations.

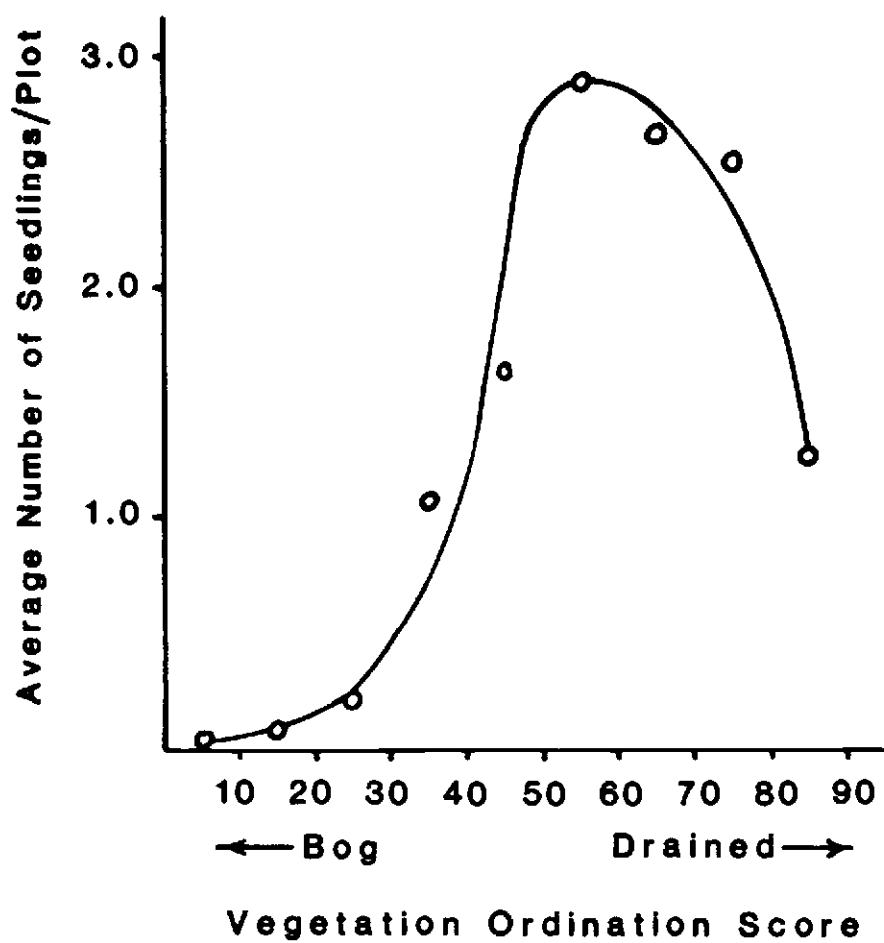


Figure VIII.6. Average number of seedlings per plot from plots occurring along the bog to better drainage forest gradient as rated by DECORANA plot ordination scores from 280 plots (Chapter III).

species basal area, and were less boggy (lower ordination score) (Table VIII.2).

Most seedlings we found were in the germling stage (Fig. VIII.7), distinguished from all other conifers in this region by having only two cotyledons (Franklin 1961). Larger, established seedlings (Fig. VIII.8), but still with juvenile foliage, were less common than germlings; still larger seedlings with mature foliage were rare, except where found occasionally establishing on bogs. Sapling stage cedars were rare or absent in forests with high basal area. The few found and aged were always over 100 years in age. Established seedlings have been found on:

- 1) bogs
- 2) creek outwashes
- 3) road cuts
- 4) exposed soil near windthrown trees
- 5) earth slides
- 6) cutover areas (clearcuts)

Seedling development on creek outwashes and road cuts are inconsequential to stand development. Alaska-cedar appears to be out-competed by faster growing Sitka spruce (Picea sitchensis (Bong.) Carr.) or Sitka alder (Alnus sinuata (Regel) Rydb.) on revegetating earth slides. Seedling establishment near windthrown trees could be important in stand development, but no sizeable cedar seedling were observed on these sites.

Therefore, seedlings are not establishing where germlings are the most abundant--in mature, high volume stands of Alaska-cedar. The

Table VIII.2. Basal area (m^2/ha) and ordination scores^{1/} for plots with and without Alaska-cedar seedlings or germlings.

	Germlings ^{2/}	No Germlings ^{2/}
Number of plots	125	155
Live Basal Area for all tree species	49.9 \pm 21.7	28.7 \pm 20.2
Live Basal Area for Alaska-cedar	24.2 \pm 16.2	11.9 \pm 13.1
Forest type score ^{1/}	60.9 \pm 16.7	46.8 \pm 22.2

^{1/} Ordination scores are based on Detrended Correspondence Analysis of 55 understory plant taxa. Scores represent the gradient from open bog (scores approach zero) to communities with better drainage (scores approach 100).

^{2/} Basal areas and ordination scores are means followed by standard deviations.



Figure VIII.7. Germling of Alaska-cedar. Note its two cotyledons which distinguishes germlings of Alaska-cedar from those of other many coniferous species. The germling on the left emerged from its cone.



Figure VIII.8. Seedling of Alaska-cedar

factors limiting successful establishment of cedar seedlings on most non-bog sites are not currently understood, but a requirement for light and perhaps site disturbance is suggested. Studies are currently being conducted to follow the development of germlings to determine why so few germlings become established seedlings.

The occurrence of established seedlings on open bogs was somewhat surprising. My data suggest that bogs are the sites that have the fewest number of germlings (Fig. VIII.6); however, a higher proportion of these must successfully establish, even in what appears to be the worst of edaphic conditions.

Successful establishment of seedlings has been observed on the edges of some cutover sites where seeds were probably dispersed from large, adjacent Alaska-cedar trees. These seedlings have, in some cases, grown into saplings that are now growing as rapidly in height and diameter as adjacent western hemlocks and Sitka spruces.

Seedling establishment, both on open bogs (poor soils) and on cutover areas (good soils), suggest that adequate light may be necessary for successful establishment and that edaphic requirements are less important. Seedlings may be failing in mature forest simply because light intensity is too low.

Possible Origins of Existing Stands of Alaska-cedar

The origin of mature Alaska-cedar trees in the high volume stands of southeast Alaska is not clear because seedling regeneration is currently failing. Possibly, these trees began as seedlings during a time when the climatic or soil factors (e.g., major soil disturbance) were more conducive for their establishment.

It is also conceivable, however, that these cedars are primarily the product of vegetative reproduction. Pole-size, and even larger cedars, commonly share two important characteristics with the bog-prostrate layering: a downslope sweep to the bole and an upslope, very shallow root with a long-dead, decaying end. The root systems of 34 cedars ranging from small to large trees were excavated and examined for root symptoms in order to determine the cause of Alaska-cedar mortality. Of these trees, 82% (28 of 34) had a downslope sweep to the main bole (Fig. VIII.9) and 85% (29 of 34) had an old, long-dead upslope root with a rotted end (Fig. VIII.10). Larger diameter and taller trees had the downslope bole sweep less frequently, suggesting that this characteristic may be lost over time through continual radial growth of the bole.

The patches of prostrate layering in semi-bog stands commonly had several erect tops of varying heights. These stems were apparently growing into a tree-like form (Fig. VIII.11), often in the presence of numerous dead Alaska-cedar snags. Alaska-cedar may be uniquely adapted to regenerating on bog and semi-bog sites where it reproduces primarily by vegetative layering. The abundant patches of prostrate cedar on sites with numerous dead cedar trees may serve as a source for a new cedar stand.

Most Alaska-cedars affected by decline die standing and remain standing for 100 years or more. Although certain microenvironmental changes may develop after cedars die (e.g., increased availability of light and nutrients), soil mixing or churning does not occur because trees die and remain standing. Soil mixing is probably beneficial in the establishment of seedlings of all conifers in this region (B.

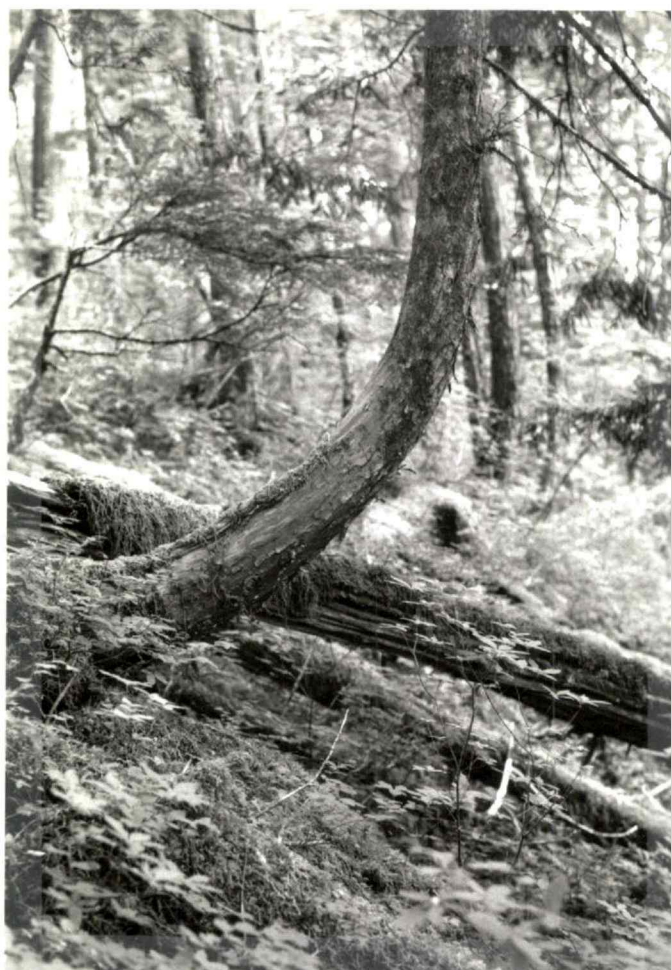


Figure VIII.9. Mature Alaska-cedar tree with sweep in lower bole



Figure VIII.10. Root systems of Alaska-cedar trees suggest that these trees developed through layering. Note the aerial, long-dead primary root (arrow).



Figure VIII.11. Prostrate Alaska-cedar in a bog with some stems turning up into tree form.

Bormann, pers. comm.), particularly on bog and semi-bog sites where the extensive Alaska-cedar mortality problem occurs. Thus, Alaska-cedar may have a distinct advantage, by its successful and extensive vegetative reproduction, over other conifers for colonizing sites afflicted with extensive mortality.

The lack of sexual reproduction would tend to limit genetic diversity in stands of Alaska-cedar that primarily reproduce vegetatively. Limited genetic diversity and restricted recombination suggests a species that is slow to develop genetic resistance to changing environmental threats, whether they be biotic or abiotic. Alaska-cedar is one of the longest-lived of conifers, and it may be slow to respond with changing frequencies of genes resistant to changing environmental factors.

Vegetative reproduction is suggested as a potential origin for extensive and sometimes nearly pure stands of old-growth cedar in southeast Alaska. Future work on the genetic relationships of adjacent trees and stands (i.e., isozyme studies) may address this hypothesis and even determine clone sizes, if they exist. Information is also needed for determining the best manner of regenerating both cutover areas and sites where salvage logging has been conducted. Autecological studies on Alaska-cedar, particularly on shade tolerance, along with other results on the effects of animal browsing (e.g., deer, voles, etc.), may suggest reasons for failing Alaska-cedar seedling regeneration in old-growth forests. This information could best be utilized to improve techniques of using Alaska-cedar to reforest cutover areas or sites with intensive decline.

LITERATURE CITED

- Anderson, H.E. 1959. Silvical characteristics of Alaska-cedar (Chamaecyparis nootkatensis). U.S. Forest Serv. Alaska Forest Res. Cen. Sta. Pap. 11. 10p.,
- Antos, J.A. and D.B. Zobel. 1986. Habitat relationships of Chamaecyparis nootkatensis in southern Washington, Oregon, and California. Can. J. Bot. (In press).
- Arno, S.F. 1966. Interpreting the timberline. M.F. Thesis, Univ. Montana. Printed by West. Res. Off., U.S. Nat. Park Serv., San Francisco, CA. 206p.
- Downing, G.L. 1961. Conditions of forest insects in forest regions, Alaska. In: Forest insect conditions in the United States, 1960. USDA For. Serv. 3p.
- Fowells, H.A. 1965. Silvics of forest trees of the United States. USDA, Washington, D.C., Agric. Handb. No. 271:546-556.
- Franklin, J.F. 1961. A guide to seedling identification for 25 conifers of the Pacific Northwest. USDA Forest Serv. Pacific Northwest For. & Range Exp. Sta. 56p.
- Frear, S.T. 1982. What's killing the Alaska yellow-cedar? Amer. For. 88(11):41-43,62-63
- Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, MA. 298p.
- Harris, A.S. 1971. Alaska-cedar. USDA For. Serv., American Woods-FS 224 7p.
- Hennon, P.E. and C.G. Shaw III. 1985. A management strategy for stands suffering from Alaska-cedar decline. Proceedings of the 1985 Arctic Science Conference. Sept. 1985, Univ. of Alaska, Fairbanks. p.161.
- Karlsson, I. 1974. Rooted cuttings of yellow cedar. Research Notes No. 66. British Columbia Forest Service, Victoria, B.C. 4p.
- Owens, J.N. and M. Molder, 1984. The reproductive cycles of western redcedar and yellow-cedar. Victoria, B.C. Ministry of Forests, Forestry Division Research Branch. 28p.
- Perry, R.S. 1954. Yellow cedar: Its characteristics, properties, and uses. Can. Dep. North. Aff. & Nat. Resources Forest. Br. Bull. 114. 19p.
- Schmidt, R.L. 1955. Some aspects of western redcedar regeneration in the coastal forests of British Columbia. Brit. Columbia Forest Serv. Res. Note 29. 10p.

Shaw, C.G. III, A. Eglitis, T.H. Laurent, and P.E. Hennon. 1985.
Decline and mortality of Chamaecyparis nootkatensis in southeastern
Alaska, a problem of long duration but unknown cause. Plant Dis.
69:13-17.

CHAPTER IX

SUMMARY

This chapter summarizes the results of this thesis on Alaska-cedar decline. It also compares this forest malady with other diseases and declines, suggests several opportunities for forest management to reduce losses, and clarifies future research needs.

Chapter I discusses the characteristics that make Alaska-cedar a valuable tree species and outlines what is known about the species' ecology. The scant literature on Alaska-cedar mortality is discussed, including our preliminary examination of the problem in 1981 (Shaw et al. 1985). In that study, we characterized the symptoms of dying cedars, described the extent of the problem in southeast Alaska, and discussed several potential causes; however, we did not determine the primary cause.

Also in Chapter I, the known pests of Alaska-cedar are summarized to allow me to predict which, if any, may cause Alaska-cedar decline. The setting for field studies, primarily in the Peril Strait area of southeast Alaska, is described. Then, the primary objective of the study is stated: to determine if the primary cause of Alaska-cedar decline is some biotic agent.

Chapter II indicates that extensive mortality began around 1880, or about 100 years ago. I established this date by determining the time of death for numerous individual, dead Alaska-cedar trees. This date was supported by examining aerial photographs of mortality areas

taken in 1927 and by reviewing comments made during earlier botanical explorations (i.e., in the late 1700s, 1800s, and early 1900s). These data and observations also suggest that decline was initiated about 100 years ago.

Many Alaska-cedar trees that died in the 1880s remain standing today, slowly decomposing. Time since death for more recently killed cedar trees was also determined; in Chapter III, this information is used to help interpret the temporal, spatial, and forest type relationships of this decline.

Chapter III, an investigation of epidemiological aspects of decline, adds data in support of mortality being initiated 100 years ago. Transects were established on 32 sites with mortality. Each dead Alaska-cedar on the 427 plots was placed into one of six classes of snags, based on degrees of retention of dead foliage, twigs, branches, and deterioration of the bole. Five classes of dead trees were relatively common on each mortality site, but snags in the sixth class, with no branches retained and boles deteriorating, were uncommon and not associated with any particular forest type; their death probably predates the onset of extensive mortality. By contrast, dead Alaska-cedar trees in the fifth snag class, with branches absent but boles intact, were present on all sites with mortality and, I believe, represent the onset of mortality. These trees, on average, died 81 years ago, but variation on either side of this mean suggests that extensive mortality began about 100 years ago.

Chapter III also provides information on spreading patterns of mortality. Spread was documented on seven sites by mapping from aerial photographs the boundaries of dying trees in 1927, 1948, 1965, and

1976. These maps clearly show that mortality has spread, but this local spread has been confined to within 100 m of where trees died about 100 years ago. Ground transects confirm the spread of mortality as more recently killed snags were most frequently encountered near the current edge of mortality. The spread of mortality may suggest a contagious organism; however, I analyzed the distribution of understory plants that occurred along the same transects and showed that mortality has spread along an ecological gradient from bog types to more productive forest types with better drainage. This strict ecological pattern of spread is not consistent with the epidemiology of many forest pathogens.

Although mortality has spread limited distances along known ecological gradients, it has not spread to new sites. All declining stands that were ground surveyed or observed from the air also have dead cedars in the fifth snag class, the original mortality. The lack of any spread of mortality to new sites in the last 100 years suggests that the problem is not contagious, and is strong evidence in support of an abiotic cause of decline.

Fungi associated with Alaska-cedar are reported in Chapter IV. A literature review of pathogens on Alaska-cedar and other species of Chamaecyparis suggests that few recorded organisms could be capable of causing this extensive mortality. Two fungi, neither known to occur in southeast Alaska, are destructive pathogens to other species of Chamaecyparis in locations outside of southeast Alaska--Phytophthora lateralis on Port-Orford-cedar and Seiridium cardinale on several species of Chamaecyparis and Cupressus. In general, relatively few fungi, pathogenic or saprophytic, were reported on Alaska-cedar prior

to my study, particularly in southeast Alaska where the extensive mortality is occurring.

Over 50 taxa of fungi were isolated or collected from Alaska-cedar during the course of these studies; 37 are new reports on Alaska-cedar and 26 are new fungi from Alaska (on any host).

Chapter V is an investigation of the symptoms of dying trees and the isolation and pathogenicity testing of fungi from Alaska-cedar. Crowns of dying Alaska-cedars are characteristic of trees suffering from root disease, as the entire crown dies as a unit. Necrotic symptoms on the roots, including dead fine roots, dead small diameter roots, and necrotic lesions on larger diameter roots, also suggest a possible root disease. Dead fine roots are probably the initial symptom of declining cedars. These dead rootlets decompose quickly and are frequently not replaced, which results in many coarse roots lacking fine roots. Small diameter coarse roots are frequently dead. Necrotic lesions on larger coarse roots appear to spread proximally towards the root collar. As crowns are in the final stages of decline, narrow, vertical lesions spread far up the bole on many affected trees.

Although dead fine roots and lesions on roots are suggestive of root disease, the fungi most commonly isolated from these symptomatic tissues lacked the ability to kill inoculated seedlings of Alaska-cedar. Only one fungus, Cylindrocarpus didymus, caused necrotic lesions in the cambium on inoculated seedlings, but the fungus was unable to sustain these lesions and seedlings eventually developed callus and survived. Necrotic lesions of the cambium on large roots and boles are probably not caused by an organism. Such lesions did not harbor an aggressive pathogen, did not advance in a girdling manner

(lesions were long and narrow), and tended to be associated with cedars in advanced stages of decline. Similar lesions developed from the mechanical wounding of coarse roots.

The most likely location for the primary cause that initiates tree decline is where fine roots and small diameter coarse roots die. Although many fungi were isolated from dead and dying fine roots, none was strongly pathogenic. Vesicular-arbuscular mycorrhizae were common in cortical cells of fine roots on both healthy and declining trees. Therefore, Alaska-cedars are probably not dying because of the degeneration of mycorrhizae, a hypothesis for the cause of decline in other species suggested by Manion (1981). Cortical cells were also infected by a dark-colored fungus, probably Mycelium radialis atrovirens. It is not likely responsible for the death of fine roots since it was common in these fine roots on healthy, as well as declining, trees (see below).

Small, nearly imperceptible, crown galls are common but are not associated with decline since they were found on healthy, as well as dying, Alaska-cedars and occurred in trees some distance from mortality areas. Since phloem, cambium, and sapwood tissues remain alive, these galls are probably not very harmful to infected trees. Dermea sp. was consistently isolated from these galls and is the most likely cause of this bark malformation.

The involvement of Armillaria sp., Phytophthora sp., Mycelium radialis atrovirens, other potential pathogens, mycorrhizae, and nematodes are discussed in Chapter V. These organisms are present in stands of Alaska-cedar, but none appears to be the primary inciter of mortality. One test of an organism's role as the primary cause of

decline is its incidence on dying versus healthy Alaska-cedar trees. An aggressive pathogen should be consistently associated with dying trees, and present within that tree in a population or distribution capable of greatly reducing tree vigor. On the other hand, the organism should occur less frequently or be absent in healthy stands of Alaska-cedar. A potential pathogen should have a high degree of association with trees in early stages of decline and might be expected to occur on some trees not yet expressing crown symptoms.

None of the fungi isolated in this study met these criteria and, thus, none appear to initiate mortality. Mycelium radicis atrovirens and several other fungi were common on dying cedars, but they were as common on healthy trees. Armillaria sp. was absent on most dead and dying trees and, when present, was primarily saprophytic. When Armillaria sp. was present on healthy trees, it was usually restricted to dead wood (e.g., basal scars and long-dead roots). Inoculations of Armillaria onto the roots of mature trees failed to cause lesions. Nematode species were either equally common on healthy Alaska-cedar trees or occurred in populations too low to cause significant damage.

The Phytophthora sp. is unlikely to be the major inciter of decline. Necrotic lesions on roots and boles of Alaska-cedar trees, somewhat similar to symptoms caused by P. lateralis on Port-Orford-cedar, do not girdle large roots or boles and are most likely not the direct result of pathogen activity. Phytophthora sp. was never isolated directly from tissues of Alaska-cedar even though over 500 attempts were made using media selective for them. Four isolates of Phytophthora sp. were recovered from organic material collected beneath Alaska-cedar trees using cedar foliage as baits. Future work on

Phytophthora should clarify the taxonomic classification of these four isolates, test their pathogenicity on Alaska-cedar and determine their frequency and distribution in stands of Alaska-cedar.

Large scars are very common at the base of Alaska-cedar trees and could be interpreted as symptoms of decline. Chapter VI treats the causes of these scars, their association with decline, and the future effects of scars on timber quality. Most basal scars are old; they have exposed and decaying wood, and callus along their sides, top, and bottom. Some scars, however, have been produced more recently; they have bark torn away from the bole and teeth marks in the exposed sapwood. These fresh scars most likely result from the activity of brown bears (Ursus arctos). Such scars on Alaska-cedar trees occur on islands with large populations of brown bears but not on islands uninhabited by these bears. The reason that bears scar Alaska-cedar trees is unknown. Fresh scars are produced only in the spring; perhaps, bears lick the cambium for sugars at that time. Taller scars, with a straight cut line across their top, are far less abundant and were produced by humans who collected large pieces of cedar bark, a practice common among people native to southeast Alaska.

Basal scars are not associated with decline; in fact, they are most abundant on well-drained, productive sites with the least mortality. These are the sites most likely to be harvested for timber, however. Since trees with old scars have associated columns of wood decay, a significant number of decayed butt logs should be expected if stands with a high incidence of scars on Alaska-cedar trees are harvested.

Bear-caused basal scars provide a good model for the effects that basal scars caused by logging activities have on log quality. The bark of Alaska-cedar is among the thinnest of conifers, even in old age (Anderson 1959, Bones 1962). If stands of Alaska-cedar ever receive commercial thinning or partial cuts (both require the removal of some, but not all, large trees), then a high incidence of wounding to the cedars left may be expected. Logging scars may closely resemble the appearance and dimensions of bear-caused scars. If so, tree response to wounding, fungi on scars, and the columns of wood decay may be similar to bear-caused scars reported in Chapter VI. Future work on scars caused by bears could estimate losses if volume and value with scars of different ages; this information could aid in our understanding of how best to manage commercial stands of Alaska-cedar.

Chapter VII provides a preliminary examination of the nutrient status of Alaska-cedar trees. There were no significant differences in the concentration of 26 elements between cedars growing on sites with extensive mortality and sites lacking mortality. Although these results should be viewed as preliminary due to the limited number of samples, the lack of any significant differences, or even trends, in the nutrient data of cedars growing on sites with and without decline suggests that nutrient deficiency is probably not the primary cause of mortality.

Chapter VIII discusses natural reproduction of Alaska-cedar on different forest types. Although this information does not directly aid in determining the cause of decline, but it will be useful to managers interested in using Alaska-cedar to reforest cutover areas and sites of mortality that have been salvage-logged. Alaska-cedar is

presently failing to reproduce from seeds in the well-drained, most productive forests in southeast Alaska. Seeds germinate and begin to establish in stands with a cedar overstory, but seedlings usually die before they are 10-15 cm tall. Shade intolerance is suspected as the primary reason for this failure.

Alaska-cedar is regenerating successfully on bog and semi-bog sites by the rooting of lower limbs, however. Alaska-cedar may be well adapted to reproducing on these poorly drained sites. Such sites are where concentrated mortality occurs; thus, vegetative reproduction may be important to the reforestation of sites that are salvage-logged.

The extent of asexual reproduction in the origin of mature Alaska-cedar forest is not known, but mature trees have evidence of originating from vegetative reproduction since they share characteristics with prostrate cedar forms that are layering: a downslope sweep to their bole and their primary root ending in a long-dead, shallow end. The lack of sexual reproduction would tend to limit the genetic diversity of this species and could make cedar populations more susceptible to forest pests and changing environmental conditions. Such genetic rigidity may be particularly detrimental for Alaska-cedar, one of the longest-lived conifers (Harris 1970). The other conifers that are neither as long-lived as Alaska-cedar, nor suffering mortality in the same proportions in declining stands, are reproducing primarily from seedlings and, therefore, may be more adaptable to the changes in pests or environments.

The objective of my study was to determine the primary cause of Alaska-cedar decline. My approach was to test the hypothesis that some biotic agent (organism) is the primary cause of decline. All

pathological, ecological, and epidemiological evidence gathered in these studies suggests that no organism is the primary inciter; an abiotic cause is more likely.

Alaska-cedar decline is similar to other declines that occur in forests throughout the world. Pathogens have been found to be the primary cause of such declines in only a few cases. Most declines are presumed to have an abiotic cause, but, typically, the etiologies of these declines are poorly understood (Shigo 1985) because very few declines have received adequate pathological and epidemiological study.

Decline syndromes affect many hardwood tree species. For example, birch dieback, ash dieback, maple decline, oak decline and sweetgum blight all occur in the eastern United States or Canada (Manion 1981). A variety of diebacks or declines affect a single genus of trees, Eucalyptus, in Australia (Palzar 1981). Frequently, the term "dieback" is applied interchangeably with decline. I prefer to reserve "dieback" for the symptom of the death of tissue back from a growing point (e.g., shoot dieback). There are also declines of conifers: pole blight of western white pine, little leaf disease of pines (Manion 1981), and wave mortality of true firs in the eastern U.S. (Sprugel 1976) and Japan (Iwaki and Totsuka 1959), to name several. Waldsterben, or the general forest decline of central Europe, has similar symptoms to the declines mentioned above, but differs in that many tree species, and even herbaceous plants, die (Schutt and Cowling 1985).

These declines have several characteristics in common. They have weak pathogens or secondary insects as contributing factors, climatic or site factors that may lead to predisposition, feeder roots or mycorrhizae that degenerate prior to the development of above-ground

symptoms, depletion of reserve carbohydrates, and the presence of Armillaria sp. (Manion 1981).

Pole blight of western white pine (Pinus monticola Dougl.) had several symptoms similar to Alaska-cedar decline. Long, narrow lesions on the boles of white pines were probably a secondary symptom since lesions developed only after trees experienced a reduction in height and radial growth rates. Crown decline was probably a secondary reaction following decline of the root system (Leaphart 1958, Leaphart and Stage 1971). McMin (1956) discussed the difficulty in determining if dying fine roots were the cause of declining tree crowns or if dying fine roots were also a secondary symptom and merely the result of the general physiological decline that these trees were experiencing. The species of Leptographium that frequently were isolated from lesions on pines, when inoculated into healthy pines, caused lesions that eventually callused. Fungi were not primarily associated with fresh lesions and were more common in older lesions. Leaphart and Stage (1971) concluded that a 25-year drought probably triggered pole blight.

Because the mortality of Alaska-cedar that I have described in this thesis shares many characteristics with other declines, it seems appropriate to refer to this forest problem as a decline. The term "decline" is broad and has several implications. First, the cause is unknown or incompletely understood. In fact, some suggest that those maladies for which a biotic cause is found should no longer be referred to as declines or diebacks. For example, littleleaf disease of shortleaf pine, is associated with the presence of Phytophthora cinnamomi, which may be the primary cause. Perhaps this may be referred to as a root disease, but one in which trees die slowly.

A similar array of symptoms and the poorly understood etiology of declines may suggest that many of the declines throughout the world have a similar cause. I suggest, however, that the characteristics common to most declines, such as the presence of Armillaria, imply that the common denominator for declines is that declining trees lose vigor and die slowly. All of the previously mentioned characteristics should be expected in such slowly dying trees. Podger (1981) states that the type of causal agent (i.e., insect, pathogen, or environmental factor) should not classify a forest problem as a decline. Far more important, he concludes, is the set of symptoms and protracted death. The primary cause of slowly dying trees can be difficult to determine, as has been the case for declines. Pathogens that may be involved would be expected to be less virulent or abundant (since they are unable to kill trees quickly), and thus, pathogenicity may be more difficult to establish. Careful pathological and ecological study of declines may determine that each has a distinct etiology.

One unique aspect of Alaska-cedar decline is that humans have probably not been a significant factor in its development. Decline and mortality of Alaska-cedar occurs extensively throughout southeast Alaska, an area with numerous islands and many remote, sparsely inhabited locations. It is difficult to imagine that the direct activities of humans (e.g., logging or mining) have influenced the development of decline. The location of the decline in remote Alaska and its onset before 1900 also provide evidence that factors such as industrial pollution are not directly responsible for tree death. The effects of a general climatic change on a global scale since the Industrial Revolution is a factor that cannot be ruled out, however.

It may seem feasible that some pathogen was introduced onto Alaska-cedar which could cause decline, but the lack of such a virulent, widespread pathogen in my studies as well as the nearly simultaneous appearance of mortality about 100 years ago extensively scattered throughout southeast Alaska refutes a potential introduction.

The lack of human involvement distinguishes the etiology of Alaska-cedar decline from factors associated with most other declines. Forests currently in trouble elsewhere are mainly those on tops of mountains and ridges, near mining and smelting areas, or areas that have been repeatedly cut-over (Shigo 1985). Many of these trees are growing with minimal energy reserves (Shigo 1985). They are stressed, and any new destructive agent--insects, fungi, or pollution--can easily accelerate stress to strain and then finally, to death (Shigo 1985). Alaska-cedar decline can serve as a model, or even as a control, for studies on declines suspected to be caused by such human activities. It demonstrates that declines can occur as a natural part of a forest ecosystem.

Subtle variations in climate may be responsible for initiating some declines, such as those of maple, birch and ash (Weaver 1965). Since climate is not static, and presumably is continually changing, vegetation may be constantly adjusting to reflect its new environment (Smith 1970). Interestingly, by examining weather records from five locations, Hamilton (1965) concluded that most of Alaska has experienced a warming trend of 0.6 to 0.8 C from the late 1800s (which roughly corresponds with when Alaska-cedar decline began) to 1950. By examining radial growth of white spruce (Picea glauca (Moench) Voss) growing at treeline in the Brooks Range, Garfinkel and Prubaker (1980)

indicated a warming trend from 1829. They calculated that the twentieth century has been approximately 2.1 C warmer during the May-July months than those months for the nineteenth century. Juday (1982) speculates that this warming trend may have begun about 200 years ago and may have been initiated at the end of the Little Ice Age and the beginning of the Industrial Revolution with high CO₂ production. The effects of a gradual warming of 1 or 2 C may have on stands of Alaska-cedar is not clear. It seems unlikely that a slightly warmer temperature over a period of one or two centuries would be damaging directly to Alaska-cedar. However, the indirect effect of increased precipitation, or the physical, chemical, or microbial changes in bog soils could alter the growth of Alaska-cedar trees on sites with poor drainage.

My study documents the association of Alaska-cedar decline with low-quality, boggy sites. Local spread of mortality is also initiated from bog and semi-bog sites. Because symptoms suggest a root problem, and fungal or nematode pathogens or root-feeding insects are not the primary cause of decline, the effects of soils in bogs and semi-bogs on Alaska-cedar trees should be evaluated in the search for the primary cause.

The expansion of bogs is another hypothesis for the occurrence of forest decline in southeast Alaska. This phenomenon could result from the proliferation of sphagnum moss or the development of poorly drained soils, or both. This process is referred to as paludification (Noble 1984) and results in the death of surrounding forest trees as a consequence of inadequate aeration to the roots and insufficient nutrient supply (Lawrence 1958; Heilman 1966, 1968). Whether muskegs

in southeast Alaska are actually expanding, contracting, have done both, or are static is not currently known. Thorough ecological studies on the dynamics of these bogs would enhance our understanding of Alaska-cedar decline.

Future studies, perhaps involving soil scientists and plant physiologists, should critically examine the soil development process on bog and semibog sites. I hypothesize that some factor, to which Alaska-cedar is particularly intolerant, developed (or reached a level to which Alaska-cedar is critically sensitive) on bog sites about 100 years ago. Its influence has slowly encroached onto more productive, better-drained forest types. Poor soil aeration, caused by water-saturated soils, is a potential causal factor of decline. Autecological characteristics of conifers in affected stands, such as the relative tolerance of Alaska-cedar to poorly drained sites, suggest that poor soil aeration, alone, does not adequately explain the disproportionate level of mortality to Alaska-cedar. The association of edaphic and microclimatic changes along this gradient are probably exceedingly complex (i.e., changes in light, rain, and snow that reaches the ground; and differences in humidity, soil temperature, pH, nutrients, microbial populations, toxins, etc.). Determining which, if any, of these variables may incite decline may prove to be a difficult task. Since Alaska-cedar, and particularly its roots, have selective sensitivity to the factor(s) causing decline, Alaska-cedar could be used as a bio-assay to screen these abiotic variables.

Because Alaska-cedar decline is probably not caused by a contagious, biological agent, stands with numerous snags could be salvage-logged without threat of spreading the problem to new sites.

The value and decay resistance Alaska-cedar wood suggest that there is commercial merit in salvage operations (Hennon and Shaw 1985). The dates of death for five snag classes, discussed in Chapters II and III, have been determined. A mill recovery study could quantify the commercial utility of salvaging snags in each of these classes and thus, clarify the feasibility of salvage operations.

In summary, decline and mortality of Alaska-cedar is most likely caused by an abiotic factor. Data collected during the course of these pathological and epidemiological studies do not support the biotic hypothesis that an organism is the primary cause. Future workers attempting to determine the cause of Alaska-cedar decline should focus their studies on abiotic factors, particularly those associated with poorly drained, boggy soils.

LITERATURE CITED

- Anderson, H.E. 1959. Silvicultural characteristics of Alaska-cedar. USDA For. Ser. Alaska Forest Research Center, Sta. Pap. 11. 10p.
- Bones, J.P. 1962. Relating outside- to inside-bark diameter at the top of 16-foot logs for Southeast Alaska. USDA For. Serv. Tech. Note No. 52. Northern For. Exp. Sta., Juneau, AK. 2p.
- Garfinkel, H.L., and L.B. Brubaker. 1980. Modern climate tree-growth relationships and climatic reconstruction in sub-arctic Alaska. *Nature* 286:872-874.
- Hamilton, T.D. 1965. Alaskan temperature fluctuations and trends: an analysis of recorded data. *Arctic* 18(2):105-117.
- Harris, A.S. 1970. The loners of Alaska. *Amer. For.* 76(5):20-23,55-56.
- Heilman, P.E. 1966. Change in distribution and availability on nitrogen with forest succession on north slopes in interior Alaska. *Ecology* 47:825-831.
- Heilman, P.E. 1968. Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. *Ecology* 49:331-336.
- Hennon, P.E. and C.G. Shaw III. 1985. A management strategy for stands suffering from Alaska-cedar decline. P.161. In: Technology and the scientist. Proceedings of the 1985 Arctic Science Conference. Sept. 27-29, 1985. Univ. of Alaska, Fairbanks, AK. 244p.
- Iwaki, H. and T. Totsuka. 1959. Ecological and physiological studies on the vegetation of Mt. Shimagare. II. On the crescent-shaped "dead trees strips" in the Yatsugatake and Chichibu Mountains. *Botanical Magazine, Tokyo* 72:255-260.
- Juday, G. 1982. Climatic trends in the interior of Alaska, moving toward a high CO₂ world. *Agroborealis* 14:10-15.
- Lawrence, D.B. 1958. Glaciers and vegetation in southeastern Alaska. *American scientist* 46:89-122.
- Leaphart, C.D. 1958. Pole blight--How it may influence western white pine management in light of current knowledge. *J. For.* 56:746-751.
- Leaphart, C.D. and A.R. Stage. 1971. Climate: A factor in the origin of the pole blight disease of Pinus monticola Dougl. *Ecology* 52:229-239.
- Manion, P.D. 1981. Tree disease concepts. Prentice-Hall. Englewood Cliffs, NJ. 399p.

- McMinn, R.G. 1956. Ecology of tree roots and root disease problems. Proceedings of the Fourth International Western Forest Disease Work Conference. Pp. 31-35.
- Noble, M.G. 1984. Sphagnum invasion beneath an evergreen forest canopy in southeastern Alaska. Bryologist 87:119-127.
- Palzar, C. 1981. Eucalypt diebacks in forests. Pp. 9-12. In: Eucalypt dieback in forests and woodlands. Eds. Old, K.M., G.A. Kile, and C.P. Ohmart. Proceedings of the CSIRO Division of Forest Research, Canaberra, Australia. Aug. 1980. 285p.
- Podger, F.D. 1981. Definition and diagnosis of diebacks. Pp. 1-8. In: Eucalypt dieback in forests and woodlands. Eds. Old, K.M., G.A. Kile, and C.P. Ohmart. Proceedings of the CSIRO Division of Forest Research, Canaberra, Australia. Aug. 1980. 285p.
- Shaw, C.G. III, A. Eglitis, T.H. Laurent, and P.E. Hennon. 1985. Decline and mortality of Chamaecyparis nootkatensis in Southeastern Alaska, a problem of long duration but unknown cause. Plant Dis. 69:13-17.
- Shigo, A.L. 1985. Wounded forests, starving trees. J. For. 83:668-673.
- Schutt, P. and E.B. Cowling. 1985. Waldsterben, a general decline of forest in central Europe: symptoms, development, and possible causes. Plant Dis. 69:548-558.
- Smith, W.H. 1970. Tree pathology: a short introduction. Academic Press, New York, NY. 309p.
- Sprugel, D.S. 1976. Dynamic structure of wave-regenerated Abies balsamea forest in North-eastern United States. J. Ecology 64:889-911.
- Weaver, L.O. 1965. Diebacks and declines of hardwoods attributed to climatic changes--a review. Arborist's News 30:33-36.

BIBLIOGRAPHY

- Agrios, G.N. 1978. Plant pathology. Academic press, New York. 703 p.
- Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63:1932-1948.
- Alaska Department of Fish and Game. 1977. A fish and wildlife resource inventory of southeastern Alaska. Alaska Department of Fish and Game, Anchorage, AK. 239p.
- American Forestry Association. 1955. These are the champs. Amer. For. 61(9):31-40.
- Anderson, H.E. 1959. Silvicultural characteristics of Alaska-cedar. USDA For. Ser. Alaska Forest Research Center, Sta. Pap. 11. 10p.
- Anderson, J.B. and R.C. Ullrich. 1979. Biological species of Armillaria mellea in North America. Mycologia 71:401-414.
- Anderson, J.P. 1916. Notes on the flora of Sitka, Alaska. Proc. Iowa Acad. Sci. 23:427-482.
- Antos, J.A. and D.B. Zobel. 1986. Habitat relationships of Chamaecyparis nootkatensis in southern Washington, Oregon, and California. Can. J. Bot. (In press).
- Arno, S.F. 1966. Interpreting the timberline. M.F. Thesis, Univ. Montana. Printed by West. Res. Off., U.S. Nat. Park Serv., San Francisco, CA. 206p.
- Bannister, M.H. 1962. Prospects for selection in the cypresses. New Zealand J. For. 8:545-559.
- Barron, G.L. 1968. The genera of hyphomycetes from soil. Williams & K Wilkins Co., Baltimore, MD. 364p.
- Beaton, J.D., A. Moss, I. MacRae, J.W. Konkin, W.T. McGhee, and R. Kosik. 1965. Observations on foliage nutrient content of several coniferous trees in British Columbia. For. Chron. 41:222-236.
- Bones, J.P. 1962. Relating outside- to inside-bark diameter at the top of first 16-foot logs for southeast Alaska. USDA For. Serv. Tech. Note No. 52. Northern For. Exp. Stn., Juneau, AK. 2p.
- Booth, C. 1959. Studies of the Pyrenomycetes IV. Nectria (Part I). Mycol. Pap. 73:1-115.
- Booth, C. 1966. The genus Cylindrocarpus. Mycol. Pap. 104:1-56.

Brodie, H.J. 1975. The bird's nest fungi. Univ. of Toronto Press, Toronto. 199p.

Brown, J.G. and M.M. Evans. 1933. Crown gall of a conifer. *Phytopathology* 23:97-101.

Carpender, S.E. 1976. Taxonomy, morphology, and ontogeny of Gelatinodiscus flavidus. *Mycotaxon* 3:209-232.

Cash, E.K. 1953. A check list of Alaskan fungi. *Plant Dis. Reprtr. Supplement* 219. 70p.

Childs, T.W. and N.P. Worthington. 1955. Bear damage to young Douglas-fir. USDA For. Serv. Res. Note No. 113. Pacific Northwest For. & Range Exp. Sta. 4p.

Collins, T.M. 1974. Soils and soil development. pp. 20-23. In: The forest ecosystem of southeast Alaska. I. The setting. Forest Service Gen. Tech. Rep. PMW-12. Pacific Northwest Forest and Range Exp. Sta., Portland, OR.

Commonwealth Mycological Institute. 1983. Plant pathologist's pocketbook. Cambrian News Ltd., Aberystwyth, Wales. 439p.

Conners, I.L. 1967. An annotated index of plant diseases in Canada and fungi recorded on plants in Alaska, Canada and Greenland. Canada Dept. of Agric. Research Branch. Publ. 1251. 381p.

Corner, E.H. 1950. A monograph of Clavaria and allied genera. Oxford Univ. Press, London. 740p.

Crosby, D. 1962. Forest insect and disease conditions in Alaska. p. 4. In: Forest insect conditions in the United States, 1961. USDA For. Serv.

Dachnowski-Stokes, A.P. 1941. Peat resources in Alaska. USDA Tech. Bull. No. 769. 84p.

Dall, W.H. 1870. Alaska and its resources. Lee and Shepard, Boston, MA 627p.

Damon, S.C. 1952. Type studies in Dictyosporium, Speira, and Cattanea. *Lloydia* 15:110-124.

Damon, S.C. 1953. Notes on the hyphomycetous genera Spegazzinia and Isthmospora. *Bull. Torr. Bot. Club* 80:155-165.

Dearnness, J. 1926. New and noteworthy fungi. *Mycologia* 18:246.

Denison, W.C. 1961. Some species of the genus Scutellinia. *Mycologia* 51:605-635.

- Denison, W.C. 1972. Central American Pezizales. IV. The genera Sarcoscypha, Pithya, and Nanoscypha. *Mycologia* 64:609-623.
- Dennis, R.G. 1968. British Ascomycetes. J. Cramer, Lehre. 455p.
- Downing, G.L. 1960. A cedar bark beetle outbreak. USDA For. Serv., Alaska For. Res. Cent., For. Insect Surv. Rep. 6. 2p.
- Downing, G.L. 1961. Conditions of forest insects in forest regions, Alaska. p.3. In: Forest insect conditions in the United States, 1960. USDA For. Serv.
- Duncan, John. Personal communication. Divisional Forester. MacMillan Bloedell. P.O. Box 10. Juskatla, B.C., Canada V0T 1J0.
- Duff, S.R., H. Erdtman, and W.E. Harvey. 1954. The chemistry of the natural order Cupressales. XII. Heartwood constituents of Chamaecyparis nootkatensis (Lamb.) Spach. *Nootkatin. Acta Chem. Scand.* 8(6):1073-1082.
- Eisenback, J.D. and K.M. Hartman. 1985. Sphaeronema sasser n. sp. (Tylenchulidae), a nematode parasitic on Fraser fir and red spruce. *J. Nematol.* 17:346-354.
- Ellis, M.B. 1971. Dematiaceous Hyphomycetes. Commonwealth Mycological Institute. Kew, Surrey, England. 608p.
- Embry, R.S. 1963. Estimating how long western hemlock and western redcedar trees have been dead. USDA For. Ser. Research note NOR-2. 2p.
- Emerson, B.K., C. Palache, W.D. Dall, E.O. Ulrich, and F.H. Knowlton. 1904. Harriman Alaska Expedition. Geology and Paleontology. Vol. IV. Harriman Alaska Series of the Smithsonian Institute. Publication 1993. New York Doubleday Page & Co., New York, NY. 173p.
- Farr, W.A. and A.S. Harris. 1979. Site index of Sitka spruce along the Pacific coast related to latitude and temperatures. *For. Sci.* 25:145-153.
- Fowells, H.A. 1965. Silvics of forest trees of the United States. USDA, Washington, D.C., Agric. Handb. No. 271:546-556.
- Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. Pacific Northwest For. and Range Exp. Sta., Portland, OR. 417p.
- Franklin, J.F. 1961. A guide to seedling identification for 25 conifers of the Pacific Northwest. USDA For. Ser., Pacific Northwest For. & Range Exp. Sta. 56p.
- Frear, S.T. 1982. What's killing the Alaska yellow-cedar? *Amer. For.* 88(11):41-43, 62-63.

- Funk, A. Personal Communication. Canadian Forestry Service. Pacific Forest Research Centre. 506 West Burnside Road, Victoria, B.C. V8Z 1M5
- Funk, A. 1973. Some mycoparasites of western bark fungi. Can. J. Bot. 51:1643-1645.
- Funk, A. 1974. Microfungi associated with dieback of native Cupressaceae in British Columbia. Can. Plant Dis. Surv. 54(4):166-168.
- Funk, A. 1976. The genus *Dermea* and related conidial states on Douglas fir. Can. J. Bot. 54:2852-2856.
- Funk, A. 1979. New species of *Gelatinosporium* on western conifers. Can. J. Bot. 57:765-767.
- Funk, A. 1981. Parasitic microfungi of western trees. Can. For. Serv., Pac. For. Res. Cent. Report BC-X-222. 190p.
- Gams, W. 1963. *Mycelium radialis artoovirens* in forest soils, isolation from soil microhabitats and identification. pp. 176-182. In: Soil organisms (symposium). Eds. J. Docksens and J. van der Drift. North-Holland Publishing Co., Amsterdam, Holland.
- Garfinkel, H.L., and L.B. Brubaker. 1980. Modern climate tree-growth relationships and climatic reconstruction in sub-arctic Alaska. Nature 286:872-874.
- Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge. 298p.
- Griffin, H.D. 1968. The genus *Ceratocystis* in Ontario. Can. J. Bot. 46:689-718.
- Grove, W.B. 1935. British leaf and stem fungi. 2. Sphaeropsidales and Melanconiales. Cambridge, MA. 406p.
- Groves, J.W. 1946. North American species of *Dermea*. Mycologia 38:351-431.
- Guba, E.F. 1961. Monograph of *Monochaetia* and *Pestalotia*. Harvard Univ. Press, Cambridge, MA. 342p.
- Hadfield, J.S. 1985. Laminated root rot. A guide for reducing and preventing losses in Oregon and Washington. USDA For. Serv. Pacific Northwest Region, Portland, OR. 13p.
- Hamilton, T.D. 1965. Alaskan temperature fluctuations and trends: an analysis of recorded data. Arctic 18(2):105-117.
- Hamm, Phillip B. Personal communication. Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR. 97331.

- Hansen, E.M., P.B. Hamm, A.J. Julis, and L.F. Roth. 1977. Isolation, incidence and management of Phytophthora in forest tree nurseries in the Pacific Northwest. Plant Dis. Repr. 63:607-611.
- Harris, A.S. 1969. Alaska-cedar. A bibliography with abstracts. USDA For. Serv., Pacific Northwest For. & Range Exp. Sta., Juneau, AK. Res. Pap. PNW-73. 47p.
- Harris, A.S. 1970. The loners of Alaska. American forests 76(5): 20-23, 55-56.
- Harris, A.S. 1971. Alaska-cedar. USDA For. Serv., American woods-FS 224. 7p.
- Harris, A.S. and W.A. Farr. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. Pacific Northwest Forest and Range Exp. Sta. Portland, OR. Gen Tech. Rep. PNW-25. 109p.
- Harris, A.S., O.K. Hutchison, W.R. Meehan, D.N. Swanston, A.E. Helmers, J.C. Hendee, and T.M. Collins. 1974. The forest ecosystem of southeast Alaska. 1. The setting. USDA For. Serv. Pacific Northwest Forest and Range Exp. Sta., Portland, OR. Gen. Tech. Rep. PNW-12. 40p.
- Heilman, P.E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. Ecology 47:825-831.
- Heilman, P.E. 1968. Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. Ecology 49:331-336.
- Hennon, P.E. and C.G. Shaw III. 1985. A management strategy for stands suffering from Alaska-cedar decline. P.161. In: Proceedings of the 1985 Arctic Science Conference. Sept. 1985, Univ. of Alaska, Fairbanks, AK.
- Hennon, P.E., G.B. Newcomb, C.G. Shaw III, and E.M. Hansen. 1986. Nematodes associated with dying Chamaecyparis nootkatensis in Southeastern Alaska. Plant Dis. 70:352.
- Hepting, G.H. 1971. Diseases of forest and shade trees of the United States. USDA For. Serv. Agric. Handb. No. 386. 658p.
- Hepting, G.H. and D.J. Blaisdell. 1936. A protective zone in red gum fire scars. Phytopathology 26:62-67.
- Hicks, R. 1984. Precontact dates revealed by ring counts. The midden. 16(5)11-14.
- Hill, M.O. and H.G. Gauch. 1980. Detrended correspondence analysis; an improved ordination technique. Vegetatio 42:47-58.

- Holmen, H. 1968. Afforestation of peatlands in Sweden, classification and site research. pp.371-377. In: Proceedings of the third international peat congress. Quebec, Canada, August 18-23, 1968. 405p.
- Hughs, S.J. 1953. Conidiophores, conidia and classification. Can. J. Bot. 31:577-659.
- Hughs, S.J. 1953. Some foliclous Hyphomycetes. Can. J. Bot 31:560-576.
- Hulten, E. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press, Stanford, CA. 1008p.
- Hunt, J. 1956. Taxonomy of the genus Ceratocystis. Lloydia 19:1-58.
- Imper, D.K. and D.B. Zobel. 1983. Soils and foliar nutrient analysis of Chamaecyparis lawsoniana and Thuja plicata in southwestern Oregon. Can. J. For. Res. 13:1219-1227.
- Iwaki, H. and T. Totsuka. 1959. Ecological and physiological studies on the vegetation of Mt. Shimagare. II. On the crescent-shaped "dead trees strips" in the Yatsugatake and Chichibu Mountains. Botanical Magazine, Tokyo 72:255-260.
- Jehne, W. 1976. Phytotoxins in Cylindrocarpus root-rot of Eucalyptus obliqua regrowth trees. Aust. Plant Pathol. Newsl. (supplement) 5(1):65.
- Juday, G. 1982. Climatic trends in the interior of Alaska, moving toward a high CO₂ world. Agroborealis 14:10-15.
- Karlsson, I. 1974. Rooted cuttings of yellow cedar. Research Notes No. 66. B. C. For. Serv., Victoria, B.C. 4p.
- Kennedy, L.L. 1958. The genus Dacromyces. Mycologia 50:896-915.
- Kozlowski, T.T. 1971. Growth and development of trees. Vol II. Cambial growth, root growth, and reproductive growth. Academic press, New York, NY. 514p.
- Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of woody plants. Academic Press, Orlando, FL. 881p.
- Kuijt, J. 1969. Cork-bark, a disease of alpine fir in British Columbia. Northwest Sci. 43:74-79.
- Lambert, M.J. and J. Turner. 1977. Die back in high site quality Pinus radiata stands--the role of sulfur and boron deficiencies. New Zealand J. For. 7:333-348.
- Laurent, T.H. 1982. Cedar dieback--is it the problem. Pp. 104-107. In: Proceedings of the Second Alaska Integrated Pest Management Conference. Univ. Alaska (Anchorage), Coop. Ext. Serv. 112p.

Lawrence, D.B. 1958. Glaciers and vegetation in southeastern Alaska. *American scientist* 46:89-122.

Lawrence, W.H., N.B. Kverno and H.D. Hartwell. 1961. Guide to wildlife feeding injuries on conifers in the Pacific Northwest. Western Forestry and Conservation Association. 44p.

Leach, C.M. 1962. The sporulation of diverse species of fungi under near ultraviolet radiation. *Can. J. Bot.* 40:151-161.

Leach, C.M. 1963. The qualitative and quantitative relationship of monochromatic radiation to sexual and asexual reproduction of Pleospora herbarum. *Mycologia* 55:151-163.

Leaphart, C.D. 1958. Pole blight--How it may influence western white pine management in light of current knowledge. *J. For.* 56:746-751.

Leaphart, C.D. and A.R. Stage. 1971. Climate: A factor in the origin of the pole blight disease of Pinus monticola Dougl. *Ecology* 52:229-239.

Levin, O.R. 1954. The south Olympic tree farm. *J. For.* 52:243-249.

Linhell, D. 1939. Untersuchungen über die Mykorrhizen und die Wurzelpilze von Juniperus communis. *Symb. Bot. Upps.* 2(3):293.

Little, E.L. 1953. Check list of native and naturalized trees of the United States (including Alaska). USDA For. Serv. Ag. Handb. No. 41. Washington D.C. 472p.

Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Can. J. For. Res.* 15:200-213.

Lowe, D.P. 1982. Check list and host index of bacteria, fungi, and mistletoes of British Columbia. Forest Research Laboratory. Victoria, B.C. Information report BC-X-32. 540.

Lowery, D.P. 1982. The dead softwood timber resource and its utilization in the West. USDA For. Serv., Intermountain For. & Range Exp. Sta., Ogden UT. Gen. Tech. Rep. INT-125. 18p.

Lutz, H.J. 1951. Damage to trees by black bears in Alaska. *J. For.* 49:522-523.

Mamiya, Y. 1983. Pathology of the pine wilt disease caused by Bursaphelenchus xylophilus. *Ann. Rev. Phytopathol.* 21:201-220.

Manion, P.D. 1981. Tree disease concepts. Prentice-Hall, Englewood Cliffs, NJ. 399p.

Markwardt, L.J. 1931. The distribution and the mechanical properties of Alaska woods. USDA For. Serv., Washington D.C., Tech. Bull. No. 226. 80p.

- Mason, H.L. 1941. The Alaska cedar in California. *Madrono* 6:90.
- McCambridge, W.F. 1954. A summary of forest insect conditions in Alaska, season of 1954. U.S. For. Serv., Alaska For. Res. Cent. 1p.
- McCaughey, W.W. and W.C. Schmidt. 1982. Understory tree release following harvest cutting in spruce-fir forests of the Intermountain West. USDA For. Serv. Res. Pap. INT-285.
- McCauley, K.J. and S.A. Cook 1980. Phellinus weirii infestation of two mountain hemlock forests in the Oregon Cascades. *For. Sci.* 26:23-29.
- McGee, C.E. 1981. Response of overtopped white oak to release. USDA For. Serv. Res. Note SO-273.
- McMinn, R.G. 1956. Ecology of tree roots and root disease problems. Proceedings of the Fourth International Western Forest Disease Work Conference. Pp. 31-35.
- Mead, D.J. 1984. Diagnosis of nutrient deficiencies in plantations. Pp. 259-291. In: Nutrition of plantation forests. Eds. Bowen, G.D. and E.K. Nambiar. Academic press, London, England.
- Meehan, W.R. 1974. The forest ecosystem of southeast Alaska. 4. Wildlife habitats. USDA For. Serv. Gen. Tech. Rep. PMW-16. Pacific Northwest For. & Range Exp. Sta. 32p.
- Mertens, H. 1827. Two scientific notices by the late Dr. Henry Mertens. *Botanical Miscellany* 3:1-35.
- Miller, O.K. 1968. A revision of the genus Xeromphalina. *Mycologia* 60:156-188.
- Morrison, D. J. 1985. Species differentiation in Armillaria. Pp.44-47. In: Proceedings of thirty-third annual western international forest disease work conference. Olympia, WA. Sept 24-27, 1985.
- Munday, D. 1931. Ancients of the sky lines. *Illus. Canadian forests and outdoors*. November: 25-27.
- Neiland, B.J. 1971. The forest-bog complex of southeast Alaska. *Vegetatio* 22:1-64.
- Nelson, C. D. 1964. The production and translocation of photosynthate - C₁₄ in conifers. Pp. 243-257. In: The Formation of wood in forest trees. Ed., M.H. Zimmermann, Academic Press, New York.
- Nelson, E.W. 1887. Part 1. Birds of Alaska. pp. 19-226. In: Report upon natural history collections made in Alaska between the years 1887 and 1881, by Edward W. Nelson. Arctic series of publications issued in connection with the Signal Service, U. S. Army. No. 3.

Newcomb, G.B. Personal communication. Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR. 97331.

Nickle, W.R. 1970. A taxonomic review of the genera of the Aphelenchoidea. *J. Nematol.* 2:375-392.

Noble, M.G. 1984. Sphagnum invasion beneath an evergreen forest canopy in southeastern Alaska. *Eryologist* 87:119-127.

Overholts, L.O. 1953. The Polyporaceae of the United States, Alaska, and Canada. Univ. of Mich. Press, Ann Arbor, Mich. 466p.

Owens, J.N. and M. Molder. 1984. The reproductive cycles of western redcedar and yellow-cedar. Victoria, B.C. Canada Ministry of Forests, For. Div. Res. Br. 28p.

Paine, D.P. 1981. Aerial photography and image interpretation for resource management. Wiley & Sons, New York, NY. 571p.

Palzar, C. 1981. Eucalypt diebacks in forests. Pp. 9-12. In: Eucalypt dieback in forests and woodlands. Eds. Old, K.M., G.A. Kile, and C.P. Ohmart. Proceedings of the CSIRO Division of Forest Research, Canaberra, Australia. Aug. 1980. 285p.

Perry, R.S. 1954. Yellow cedar; its characteristics, properties, and uses. Canada Dept. North Aff. and Nat. Resources. Forestry Branch Bull. 114. 19p.

Petrof, I. 1880. The population and resources of Alaska. Pp. 145-147. In: Committee of military affairs, compilations of narratives, explorations in Alaska. Government Printing Office, Washington D.C.

Phillips, J.M. and D.S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Brit. Mycol. Soc.* 55:158-161.

Podger, F.D. 1981. Definition and diagnosis of diebacks. Pp. 1-8. In: Eucalypt dieback in forests and woodlands. Eds. Old, K.M., G.A. Kile, and C.P. Ohmart. Proceedings of the CSIRO Division of Forest Research, Canaberra, Australia. Aug. 1980. 285p.

Raabe, R.D. 1962. Host list of the root rot fungus, Armillaria mellea. *Hilgardia* 33:25-88.

Rennerfelt, E. and G. Nacht. 1955. The fungicidal activity of some constituents from heartwood of conifers. *Svensk Bct. Tidskr.* 49(3):419-432.

Richard, C. and J.A. Fortin. 1973. The identification of Mycelium radicis atrovirens (Phialocephala dimorphospora). *Can. J. Bot.* 51:2247-2248.

Richard, C., J.A. Fortin, and A. Fortin. 1971. Protective effect of an ectomycorrhizal fungus against the root pathogen Mycelium radicis atrovirens. Can. J. For. Res. 1:246-251.

Rigg, G.B. 1925. Some sphagnum bogs of the North Pacific Coast. Ecology 6:260-279.

Rigg, G.B. 1940. The development of sphagnum bogs in North America. Bot. Rev. 6:666-693.

Roth, L.F., H.H. Bynum, and E.E. Nelson. 1972. Phytophthora root rot of Port-Orford-cedar. USDA For. Serv. For. Pest Leaflet. 131. 7p.

Rothrock, J.T. 1867. Sketch of the flora of Alaska. Smithsonian Institute Annual Report. 1887:433-463.

Rudinski, J.A. and J.P. Vite. 1959. Certain ecological and phylogenetic aspects of the pattern of water conduction in conifers. For. sci. 5:259-266.

Ruth, R.H. and A.S. Harris. 1979. Management of western hemlock-Sitka spruce forests for timber production. USDA For. Serv. Gen. Tech. Rep. PNW-88. Pacific Northwest For. & Range Exp. Sta. 197p.

Sargent, R.H. and F.H. Moffit. 1929. Aerial photographic surveys in southeastern Alaska. USGS Bulletin 797-E. Government Printing Office. Pp. 143-160.

Schmidt, R.L. 1955. Some aspects of western redcedar regeneration in the coastal forests of British Columbia. Brit. Columbia Forest Serv. Res. Note 29. 10p.

Schol-Schwarz, M.B. 1970. Revision of the genus Phialophora. Persoonia 6:59-94.

Seymour, A.B. 1929. Host index of the fungi of North America. Harvard Univ. Press. Cambridge, MA. 732p.

Shaw, C.G. 1973a. Host index for the Pacific Northwest I. Hosts. Wash. Agr. Exp. Sta. Bull. 765. 121p.

Shaw, C.G. 1973b. Host index for the Pacific Northwest II. Fungi. Wash. Agr. Exp. Sta. Bull. 766. 162p.

Shaw, C.G. III. 1977. Armillaria isolates from pine and hardwoods differ in pathogenicity to pine seedlings. Plant Dis. Reprtr. 61:416-418.

Shaw, C.G. III. 1984. In vitro responses to gallic acid fail to distinguish between pathogenic and "non-pathogenic" species of Armillaria. Pp.161-183. In: Proceedings of the sixth international conference on root and butt rots of forest trees. Melbourne, Victoria and Gympie, Queensland, Australia. Aug. 25-31, 1983.

- Shaw, C.G. III, A. Eglitis, T.H. Laurent, and P.E. Hennon. 1985. Decline and mortality of Chamaecyparis nootkatensis in Southeastern Alaska, a problem of long duration but unknown cause. Plant Dis. 69:13-17.
- Sheldon, C. 1912. The wilderness of the north Pacific coast islands. Charles Scribner's Sons, New York, NY. 246p.
- Shigo, A.L. 1985. Wounded forests, starving trees. J. For. 83:668-673.
- Shigo, A.L. and H.G. Marx. 1977. Compartmentalization of decay in trees. USDA For. Serv. Agr. Inf. Bull. 405. 73p.
- Shoen, J. 1982. Brown bear habitat preferences and brown bear logging and mining relationships in southeast Alaska. Vol. I. Project progress report, Federal aid in wildlife restoration, Project W-22-1, Job no. 4.17r. 44p.
- Shutt, P. and E.B. Cowling. 1985. Waldsterben, a general decline of forest in central Europe: symptoms, development, and possible causes. Plant Dis. 69:548-558.
- Smith, R.S. 1970. Black stain in yellow cedar heartwood. Can. J. Bot. 48:1731-1739.
- Smith, R.S. 1970. Degradation of nootkatin by fungi causing black heartwood stain in yellow cedar. Can. J. Bot. 48: 1727-1729.
- Smith, S.C. 1965. The morphology of Verticillium albo-atrum, V. dahliae, and V. tricorpus. New Zealand J. Ag. Res. 8:450-478.
- Smith, W.H. 1970. Tree pathology: a short introduction. Academic Press, New York, NY. 309p.
- Sprugel, D.S. 1976. Dynamic structure of wave-regenerated Abies balsamea forest in North-eastern United States. J. Ecology 64:889-911.
- Stewart, H. 1984. Culturally modified trees. The Midden 16(5)7-10.
- Strouts, R.G. 1973. Canker of cypress caused by Coryneum cardinale Wag. in Britian. Eur. J. For. Path. 3:13-24.
- Sutton, B.C. 1980. The Coelomycetes. Commonwealth Mycological Institute. Kew, England. 696p.
- USDA Forest Service. 1960. Index of plant diseases in the United States. Washington D.C. Agric. Handb. 165. 531p.
- USDA Forest Service. 1978. Tongass land management plan. United States Forest Service, Alaska Region, Juneau, Alaska.

USDA Forest Service, 1982. Peeled cedar trees give clues to past. USDA Forest Service, R-6 (Pacific Northwest Region), Greensheet, Sept. 3, 1982. No. 1842. 1p.

Viereck, L.A. and E.L. Little Jr. 1972. Alaska trees and shrubs. USDA For. Serv. Ag. Handb. No. 410. Washington D.C. 265p.

Wagener, W.W. 1939. The canker of Cupressus induced by Coryneum cardinale n.sp. J. Agric. Res. 58:1-46.

Wang, C.K. 1965. Fungi of pulp and paper in New York. Techs. Pub. Syracuse Univ. Coll. Forestry 87.

Wargo, P.M. and C.G. Shaw III. 1985. Armillaria root rot: the puzzle is being solved. Plant Dis. 69:286-832.

Waring, R.H. and E.D. Cleary. 1967. Plant Moisture Stress: evaluation by pressure bomb. Science. 155:1248-1254.

Watling, R., G.A. Kile, and N.M. Gregory. 1982. The genus Armillaria--nomenclature, the identity of Armillaria mellea and species differentiation. Trans. Br. Mycol. Soc. 78:271-285.

Weaver, L.O. 1965. Diebacks and declines of hardwoods attributed to climatic changes--a review. Arborist's News 30:33-36.

Wenger, K.F. 1984. Forestry handbook. Wiley & Sons, New York. 1333p.

Wilhelm, S., P.E. Nelson, and D.H. Ford. 1969. A gray sterile fungus pathogenic on strawberry roots. Phytopathol. 59:1525-1529.

Wilson M.V. 1981. A statistical test of the accuracy and consistency of ordinations. Ecology 62:8-12.

Zach, L.W. 1950. A northern climax, forest or muskeg? Ecology 31:304-306.

Zeedyk, W.D. 1957. Why bears girdle Balsam fir in Maine. J. For. 55:731-732.

Ziller, W.G. 1974. The tree rusts of Western Canada. Pacific For. Res. Cen. Can. For. Serv. Dept. of Environ. Publ. No. 1329. 272p.

Zobel, D.B. and V.T. Liu. 1979. Foliar nutrient concentrations of small Chamaecyparis in Taiwan. Plant and Soil. 53:373-384.

Zobel, D.B. and G.M. Hawk. 1980. The environment of Chamaecyparis lawsoniana. American midland naturalist 103:280-297.

Zobel, D.B., L.F. Roth, and G.M. Hawk. 1985. Ecology, pathology, and management of Port-Orford-cedar (Chamaecyparis lawsoniana). USDA For. Serv., Pacific Northwest For. & Range Exp. Sta., Portland, OR. Gen. Tech. Rep. PNW-184. 161p.