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Did climatic warming trigger the onset and development of yellow-cedar decline in southeast Alaska?*

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Abstract

Yellow cedar (*Chamaecyparis nootkatensis*) is a valuable tree species that is experiencing an extensive forest decline on over 200 000 ha of unmanaged forest in southeast Alaska. Biotic factors appear secondary and some abiotic factor is probably the primary cause of this naturally occurring decline. A warming climate, which coincided with the onset of extensive tree mortality about 100 years ago, may have triggered one of the possible abiotic causes such as freezing damage and/or soil toxicity.

Key words: *Chamaecyparis* – decline – abiotic – stress – climate – freeze – toxicity.

1 Introduction

Yellow cedar, *Chamaecyparis nootkatensis* (D. Don) Spach, is an ecologically important and extremely valuable tree species in coastal Alaska. Its ecology, silvics, and methods of management are, however, poorly understood (HARRIS and FARR 1974; HARRIS 1990). Yellow cedar is suffering from the most severe forest decline in western North America, and the decline now covers more than 200 000 hectares of unmanaged forest in southeast Alaska (USDA FOREST SERVICE 1992).

In 1981, the first detailed studies on reproduction, community relationships, etiology and epidemiology of decline of yellow cedar in southeast Alaska were initiated. Through these studies much was learned about the autecology of yellow cedar. In addition, several suspected biotic factors were eliminated as possible primary causes of decline. Even though many aspects of the decline are still unresolved, results from these studies have indicated the probably involvement of some additional, unexplored factors. This paper summarizes results from earlier studies, presents new information, and discusses several probable abiotic causes of decline and in what way their development may be associated with climatic warming.

1.1 Silvics of yellow cedar

Yellow cedar has a natural distribution from near Port Wells in Prince William Sound in Alaska, south through southeast Alaska and British Columbia, to near the Oregon-California border at Mount Grayback (HARRIS 1971). It occurs from tidewater to timberline (about 1 000 m) in southeast Alaska (HARRIS and FARR 1974) where it can grow in nearly

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pure stands, but, more commonly, exists in scattered groups or as individual trees mixed with other conifers (RUTH and HARRIS 1979). In its natural range south of Vancouver Island, yellow cedar is restricted to higher elevations (e.g. 600–2300 m). It grows within 200 km of the Pacific Coast, except for several isolated, disjunct stands that occur to the east in British Columbia and Oregon. Little is known about the historical distribution of yellow cedar since its pollen is not persistent (HEUSSER 1955).

Throughout its range, yellow cedar is confined to a cool, humid climate where it grows in areas that have relatively short growing seasons, but where winter temperatures are not exceptionally cold. It can grow on extremely poor soils if there is an abundant supply of moisture (ANDERSON 1959), and may be uncommon on more productive sites because of its inability to compete with faster-growing tree species (HARRIS 1971).

Yellow cedar is among the conifers with the greatest longevity: trees more than 1 000-years old are common (FRANKLIN and DYRNESS 1973). It is one of the slowest growing conifers in North America. Radial growth rates of 2 rings/mm have been previously recorded (HARRIS 1971) and this study examined trees with 12 rings/mm. The largest known yellow cedar was found in Mount Rainier National Park, Washington, and had a diameter at breast height of 243 cm and was 40.2 m tall (HARRIS 1970).

1.2 Southeast Alaska

Southeast Alaska, the location of cedar decline, comprises a thin strip of mainland, occupied by mountains and bisected by fjords and glaciers, with a scattering of large and small islands to the west. The maritime, cool, moist climate has a heavy annual precipitation ranging from 150 to 500 cm (HARRIS et al. 1974). Winters have relatively moderate temperatures although brief cold periods occur.

Snowfall is heavy in some areas, especially at higher elevations. Summers are without prolonged dry periods and lightening is rare; thus, fire is not an important factor in forest succession (HARRIS et al. 1974). Poorly drained soils, which are highly organic and shallow or deep, generally occur on sites that are not steep and overlay unfractured bedrock or compact glacial till. Bogs and scrub forests occur on these poorly drained sites, but patterns of plant succession are not understood.

This region is dominated by undisturbed old-growth forests of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.), which account for 89% of the volume of commercial forests. By comparison, yellow cedar, western red cedar (*Thuja plicata* Donn), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), and shore pine (*Pinus contorta* Dougl.) comprise far less volume and are, thus, less, commercially important. Yellow cedar accounts for about 4% of the volume of commercial forests in southeast Alaska (HUTCHISON and LABAU 1975), but, if lower volume forests, which are numerous and expansive in some areas, were included, then the percentage of the total volume would be greater.

2 Symptoms and biotic factors

The cause of decline has been attributed at various times to bark beetles, root disease, and winter injury, but these suggestions were based on brief observations (SHAW et al. 1985). The causes of decline did not receive detailed investigation until 1981 when a study of the symptoms of dying trees, organisms associated with symptomatic tissues, and the ability of these organisms to incite disease, was initiated.

2.1 Symptoms of dying trees

The symptoms of the dying trees suggest a root or below-ground problem (SHAW et al. 1985; HENNON et al. 1990d). Crowns of declining trees die suddenly or slowly as a unit, rather than as individual dying branches. Annual observations of more than 200 dying cedars have been made over a period of 11 years and indicate that symptoms can develop very slowly. A number of trees that had thin, off-colour crowns 11 years ago, are still alive today, but they are in an advanced stage of decline. The root systems of 62 yellow cedars in various stages of decline were excavated and systematic observations of symptoms were made (SHAW et al. 1985; HENNON et al. 1990d). The initial symptom of a tree beginning to decline is death of the fine-root system. As the crown begins to show symptoms of thinning and off-colour foliage, small-diameter roots die and larger roots develop necrotic cambial lesions. In the final stages of decline, necrotic lesions spread vertically from the dead roots up the bole of trees. Slowed radial growth occurs, sometimes for many years, before tree death. Dying fine roots and small-diameter coarse roots often occur in a dark, water-saturated, organic soil. Most of the root system of yellow-cedar trees on poorly drained sites is very shallow and occurs in the top 15 cm of the soil. This may be a response to low oxygen availability.

2.2 Insects and pathogens

Bark beetles (*Phloeosinus* spp.) are the only damaging insects commonly found on dead and dying yellow-cedar trees; however, they only attack in the late stages of tree decline (SHAW et al. 1985). None of the 50 taxa of fungi that have been isolated from symptomatic tissues or collected from yellow cedar (HENNON 1990) is consistently associated with dying or dead trees. Of the 10 most common fungi isolated from symptomatic tissues, none has been shown to be capable of killing unstressed seedlings in inoculation trials (HENNON et al. 1990d). Four genera of nematodes have been found in declining forests, but their low populations and association with healthy forests indicate that they do not cause decline (HENNON et al. 1986). From beneath dying trees, five species of *Pythium* have been recovered, but their recovery rates are not associated with mortality (HAMM et al. 1988). Viruses and mycoplasmas, which are unlikely threats to conifers, are currently under investigation. Preliminary results from a study in which off-colour shoots from declining trees were grafted onto healthy cedar saplings indicate no transmission of symptoms.

A concentrated effort to determine whether any species of *Phytophthora* were present in declining forests was made since necrotic lesions on the roots and root collars of dying yellow cedars suggested a similarity to the serious disease of Port-Orford cedar (*C. lawsoniana* (A. Murr.) Parl.) in southwest Oregon, caused by *P. lateralis* (Tuck. and J. A. Milb.) (ROTH et al. 1972). The occurrence of dying yellow cedar on wet sites and patterns of local spread also suggested *Phytophthora* involvement. *Phytophthora lateralis* was not recovered, but another species of *Phytophthora* was successfully isolated from baits placed below four of 69 yellow cedars (HANSEN et al. 1988; HENNON et al. 1990d). No species of *Phytophthora* was isolated directly from cedar tissues even though selective media were used. The fungus was identified as *P. gonapodyides* (Petersen) Buisman, a species that has been found in healthy, non-declining forests in Oregon (HANSEN and HAMM 1988). The fungus lacked strong pathogenicity on yellow cedar (HANSEN et al. 1988). *Phytophthora gonapodyides* is not the cause of decline and yellow cedar may not even be a host to the fungus.

2.3 Bears

Basal scars are common on many cedar trees in declining stands — nearly one-half (49%) of the yellow cedars sampled in several areas on Chichagof and Baranof Islands have either fresh or old, callusing scars (HENNON et al. 1990a). Fresh scars consistently have teeth or bite marks and are the result of feeding by Alaskan brown bears (*Ursus arctos*) (HENNON et al. 1990a). A smaller number of scars are caused by Alaskan Native people stripping bark from cedar trees (HENNON et al. 1990a). Regardless of the cause, basal scars are not the primary cause of cedar decline. Scar incidence is not greater on dying cedar trees than on healthy trees, nor is it greater on cedars in declining stands than in healthy stands (HENNON et al. 1990b). Numerous yellow-cedar trees die with no basal scars (HENNON et al. 1990d). To summarize, these studies have not supported the hypothesis that any biotic factor is the primary cause of decline.

3 Epidemiology and ecological factors

Many results reported in this paper on site factors associated with decline and population trends for yellow cedar are from data that were collected during ground surveys in yellow-cedar forests on Baranof and Chichagof Islands in southeast Alaska (HENNON et al. 1990b). Surveys were also conducted on the Prince of Wales and Wrangell Islands near the northern limit of the natural distribution of western redcedar to determine whether this species is suffering from decline. Each dead yellow cedar encountered in ground surveys was placed into one of six snag classes (HENNON et al. 1990c) based on degrees of foliage, twig, or branch retention, and deterioration of its bole (Table 1). Along with data on overstory trees (HENNON et al. 1990b), the abundance of 55 understory plant taxa, including regenerating yellow-cedar, was recorded from 280 variable radius plots on 21 transects on Baranof and Chichagof Islands. These data were used in an ordination analysis to indicate relationships of plant communities with forest trees, reproduction, and decline. In addition, aerial photographs, some dating back to 1926, were analysed to document the occurrence of decline in different forest communities and to describe patterns of spread.

3.1 Forest communities affected

Aerial observations and examinations made from recent, colour aerial photographs confirm DOWNING's observation (1960) that cedar decline is strongly associated with forests that occur on poorly drained sites. Mortality occurs on the edges of nearly all open bogs in many areas where the elevation is less than 200–350 m. Some bogs extend, contiguously or in chains, for many km along fairly flat terrain. Mortality is consistently associated with the edges of these bogs. Decline is also severe in scrub forests on large areas without open bogs, but the understory flora and the stature of trees suggest that these sites are influenced by moderately poor drainage. Within the general distribution of severe mortality, low-elevation forested areas without concentrated mortality generally lack bogs and are dominated by high-volume hemlock forests.

Data from ground surveys indicate that the incidence of mortality is significantly more common in bog communities and is progressively less common in communities with better drainage (HENNON et al. 1990b). Ordination of understory plant taxa produced only one important axis that represents a gradient from bog communities to those with better drainage

Table 1. **Average time since death is estimated for five of the snag classes of yellow cedar**

Snag class	Snag description	Average time since death (years)
I	dead, foliage retained	4
II	dead, twigs retained	14
III	dead, secondary branches retained	26
IV	dead, primary branches retained	51
V	dead, no branches retained	81
VI	dead, bole broken and deteriorated	death not dated

(HENNON et al. 1990b). The first axis of ordination also produced scores for each plot that represent the same gradient from bog (low scores) to better drainage (high scores). Based on the average basal areas of live trees from these plots as measured by prism sampling, yellow cedar was the dominant overstory component along most of the vegetation gradient (Fig. 1). Shore pine was common in the open bogs where total conifer basal area was at a minimum. At the other extreme (better drainage), where total conifer basal area was greatest, western hemlock was predominant. Although less dominant, yellow cedar attained its greatest dimensions of height and diameter on those productive sites. Sitka spruce also had its greatest basal area on the better-drained sites, but was less common than western hemlock. The distribution of mountain hemlock roughly paralleled but was less dominant than that of yellow cedar. Thus, the occurrence of yellow cedar appears to be relatively unrestricted by the major factor (soil drainage) that controls the distribution of plants in these forests.

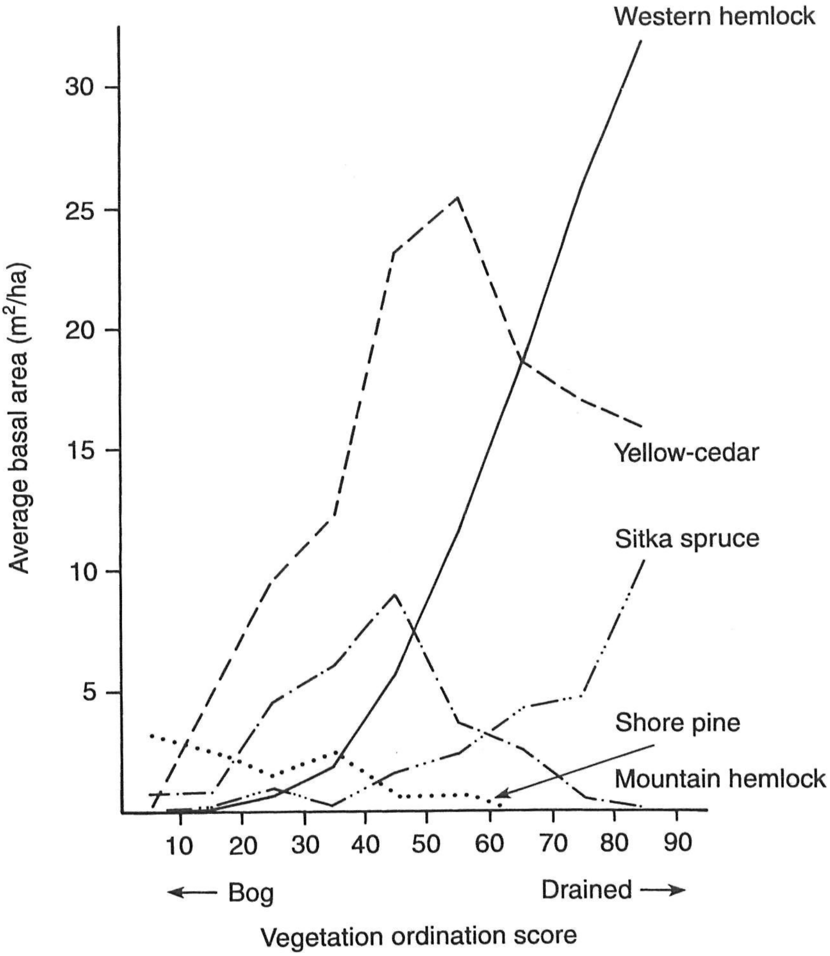

Fig. 1. Basal area of Alaska yellow-cedar and other conifers along the gradient from bog to better drainage. The bog–drainage gradient (x-axis) is from an ordination of 55 understory plants on 280 plots

3.2 Tree species dying

Yellow cedar is the principal species that is dead or dying in stands with a high proportion of mortality, accounting for 74% of the dead basal area (HENNON et al. 1990b). Dead hemlock accounts for 16.8% of the mortality in declining stands, with other species having only negligible dead basal area.

Since yellow cedar predominates in most declining stands, the percentage dead basal area for each species provides a better measure of which species have been affected. In this study, 65% of yellow-cedar basal area is dead, nearly twice the percentage of any other species. Yellow cedar is also dying at disproportionate levels in stands with western redcedar: on Prince of Wales Island, 34% of the basal area of yellow cedar is dead compared to 9% for western redcedar; on Wrangell Island, 54% of yellow cedar is dead but only 3% of western redcedar is dead.

3.3 Age structure of dying trees and stands

MUELLER-DOMBOIS (1986) hypothesizes that many forest declines can be explained by 'synchronous cohort senescence' where dying stands are comprised of cohorts (even-aged) trees that die together because they reach old age (senescence) at about the same time. The age structure of declining cedar stands of southeast Alaska has not been previously described. In addition, whether mortality is limited to the oldest individuals in declining stands and whether these trees are dying near the limits of their life expectancies are not known. Tree age was determined by counting annual rings from increment cores taken from over 150 yellow-cedar trees at four locations of dying cedar forests. Many trees had been dead for up to 7 years, but counting rings in the discoloured sapwood and the visually unaltered heartwood was generally not difficult.

Declining cedar forests are not comprised of cohort trees (Fig. 2), rather, trees range in age from less than 100 years old to some individuals that are 400–600 years old. Smaller, younger cedars are not common in these declining stands. The oldest trees cannot be accurately aged due to the presence of heartrot. At one of the sites (Waterfall Cove), all yellow-cedar trees were relatively small and 100–300 years old. No clear patterns occurred at any of the sites of a relationship between tree age and mortality (Fig. 2).

3.4 Mortality spread

Maps delineating the extent of mortality at seven sites made from aerial photographs taken in 1927, 1948, 1965, and 1976 clearly show that peripheral boundaries of mortality have expanded over short distances at all sites where this has been studied (HENNON et al. 1990b). In 1927, the mortality apparent on each site covered a large portion of the area where trees are now dead and dying, thus, local spread since 1927 accounts for only a small proportion of the total area of decline. Subsequent mortality has rarely extended more than 100 m beyond the 1927 boundary.

Results from ground surveys also indicate local spread at most sites that were surveyed. In such stands, dying and recently killed cedars often surround areas containing the old snags. This mortality spread, which commonly occurs upslope and in all cardinal directions, has been along the gradient from bog to better drainage, as evidenced by the ordination of understory plants. Snags with no limbs (class V) predominate in bog and semibog plant communities while plots with more recently killed snags (classes IV, III, II, and I) support progressively better-drained plant communities. See Table 1 for a description of snag classes. Snags in the longest-dead class VI (deteriorating boles) are uncommon, are not associated with severe mortality, and are not confined to bogs, as are class V snags. Thus, spread of mortality within any one site has occurred as a slow advance along an established ecological

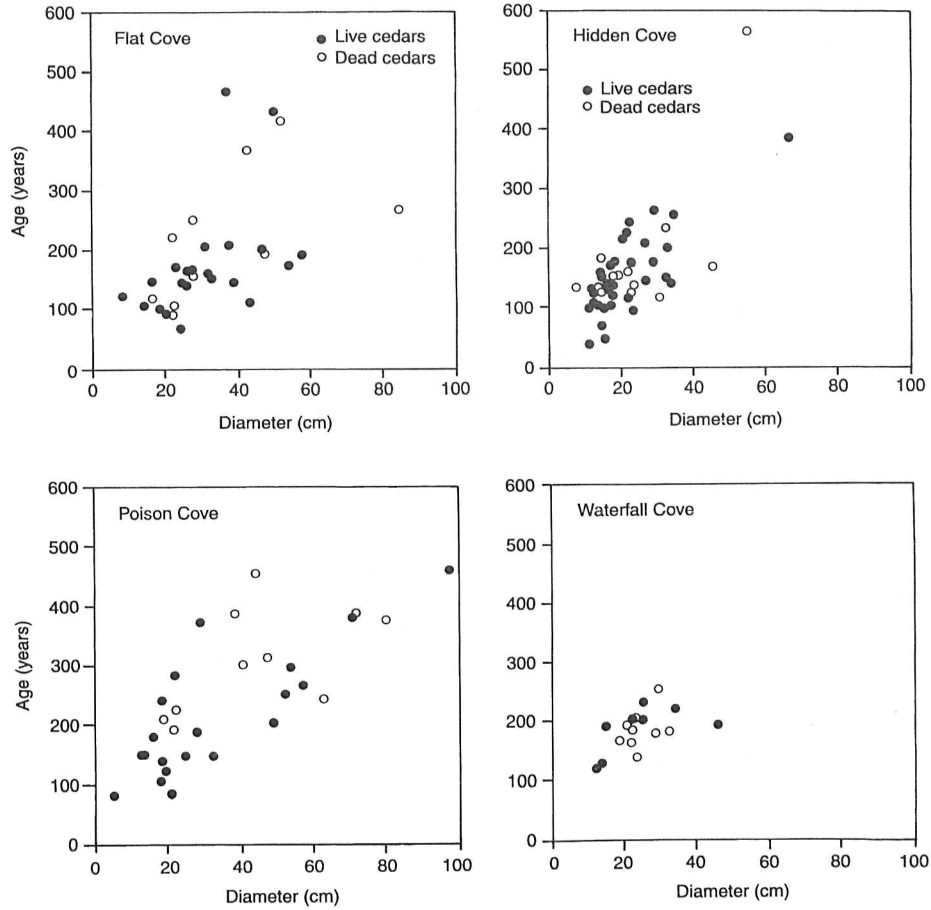

Fig. 2. Relationship of age and diameter of both living and recently-dead yellow-cedar trees at four declining sites. Note the lack of relationship between mortality and tree age and also that stands are not even-aged

gradient which is often related to slope. Mortality does not show spread where abrupt forest-type changes occur or where the plant community remains fairly constant but the perimeter occurs above 200 m. In the latter cases, intensive mortality ceases at about 200–300 m and a healthy cedar scrub forest with little evidence of current or past mortality exists above these elevations. This is consistent with the general observations of healthy yellow-cedar forests on bog and semi-bog communities above 300 m, as observed on colour aerial photographs.

Snags of yellow cedar that lack limbs (class V) were present on all declining sites and constituted at least 8% (range: 8–60%) of all snags on 23 sites surveyed with heavy mortality. More recently killed trees (i.e. snag classes I–IV) were also present at all transects, indicating that the mortality has continued at all locations since initiation. General reconnaissance revealed only one site that has only long-dead class IV and V snags and lacks recent mortality. No sites, however, have recently killed trees in the absence of long-dead class V snags. Thus, no evidence of long-range site-to-site spread of decline exists.

3.5 Reproduction of yellow-cedar

Results from these surveys indicate that seedlings of yellow cedar were never frequent, and that their density closely parallels the amount of live yellow-cedar basal area. Seedlings were uncommon in bogs, reached peak densities of only 0.1 seedlings/m^2 in communities with moderate drainage, and became less common on sites with better drainage dominated by western hemlock. Seed dispersal distances for yellow cedar are normally short (less than 120 m; FOWELLS 1965), perhaps because of its small seed wings (OWENS and MOLDER 1984), and may account for the close association of cedar seedlings and live-cedar basal area. Most seedlings were in the germling stage (i.e. up to 3-years old with recognizable cotyledons). Larger, established seedlings of yellow cedar, but still with juvenile foliage, were less common than germlings; still larger seedlings with mature foliage were rare, except where occasionally found establishing on bogs. Sapling-stage yellow cedars were rare or absent in forests with moderate-to-high basal area. Poor reproduction from seed of yellow cedar is independent of decline. In fact, the several sites where reproduction from seed is successful (e.g. Beacon Point on Kupreanof Island) are severely affected by decline. Factors limiting successful establishment of seedlings of yellow cedar on most non-bog sites are not understood, but deer browsing and inadequate light and soil disturbance have been suggested.

Yellow cedar frequently occurs as a low-growing, prostrate, asexually-reproduced growth form in southeast Alaska. These patches typically contain several-to-many small upright stems which sweep downslope, or in many directions on flat terrain, and have their short crowns (e.g. 1 m tall) intermingled. The incidence of prostrate patches of cedar is strongly associated with bog understory plants, where they are abundant, and becomes less common, and eventually absent, along the gradient to plant communities on sites with better drainage. This is not surprising: rooting of lower limbs (layering) occurs in bogs where trees are short and lower branches are in contact with the ground. Layering would presumably be infrequent in the closed-canopy forests on well-drained sites where lower limbs are usually far above the ground. Perhaps due to improving soil characteristics or escaping heavy snows, some upright stems on wet sites slowly acquire conical form and grow into small trees. It is speculated that many mature yellow-cedar trees that are growing on wet sites originated from this form of vegetative reproduction and, thus, their genetic diversity is limited.

3.6 Ecological effects of decline

Succession is leading to a change in forest composition on sites with intense cedar decline. Different forest conditions have developed in some areas of early mortality where the long-dead (class V) snags are present. A new stand of vigorous-looking trees has grown up beneath the bark-free, white snags at some sites. Western hemlock, mountain hemlock, and, to a lesser extent, yellow cedar, are the dominant tree species in these areas and appear as a green zone from a distance or on colour aerial photographs. Most or all of these trees are older than 100 years and were probably present as understory conifers during the initial mortality or, in the case of hemlock, are surviving overstory trees.

In other stands with long-dead snags, continued mortality of smaller yellow-cedar trees, as well as little response by other conifers, have apparently prevented development of this green zone. Reasons for the recurrence of mortality in some stands, but not in others, are unclear. On extremely boggy sites, a growth response may not have occurred in the remaining live trees, perhaps because factors limiting tree growth (e.g. anaerobic soils) are not improved by the death of yellow cedar. Once the dominant overstory of yellow-cedar dies, soils may become even wetter, as the reduced transpiration causes a degeneration in the site that may affect the survival or growth of other conifer species. Southeast Alaskan tree species suspected of being relatively intolerant to excessive moisture (RUTH and HARRIS

1979) suffer higher rates of death (35% of its basal area for Sitka spruce and 29% for hemlock) than the tolerant shore pine (6%) on sites of mortality. Yellow cedar is the exception: the species is reportedly well adapted to wet sites, but it suffers the greatest mortality (65%) in declining stands.

3.7 Dating the onset

To determine how long decline of yellow cedar has been occurring in southeast Alaska, old aerial photographs were examined, two methods to date the death of standing dead trees were used, and historical accounts of botanical expeditions were inspected (HENNON et al. 1990c). The earliest available aerial photographs of southeast Alaska, taken in 1926 and 1927 by the US Navy, represent one of the first efforts anywhere to photograph large areas of forest (SARGENT and MOFFIT 1929). These 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. Mortality of yellow cedar was obviously already widespread by 1927.

Estimates of the time since death for yellow-cedar trees in snag classes (Table 1) were determined by counting annual rings of hemlock trees growing under large cedar snags and by counting annual rings in callus growth on partially killed stems of yellow cedars (called 'rope trees') that were interspersed among cedar snags (HENNON et al. 1990c). Although not all hemlocks showed a release pattern, those that did have increased growth differed significantly according to the snag classes (I–IV) under which they grew. Rope trees have a dead top (snag classes I–V) and one narrow strip of live tissue, consisting of callusing bark and sapwood, that connects roots to one live and bushy branch cluster. The cause of this condition is not known; however, it is hypothesized that these trees were severely injured, but not completely killed, by whatever caused nearby cedars to die. Most rope trees have dead tops in snag class IV or V; few rope trees have class-I tops. Rope trees in classes II, III, and V differ significantly from one another in the number of callus growth rings and, presumably, in time since death of the top and death of most of the bole (HENNON et al. 1990c). Rope trees were not injured during one sudden incident such as an extreme climatic event; the cambiums among the trees sampled did not die during the same year. Also, their slow decline in growth many years prior to bole death, initiated at different times, does not support a sudden event as the cause of tree injury.

Class-V snags (boles intact, but no primary limbs retained) appear to represent the original extensive mortality. These trees died, on average, 81 years ago (HENNON et al. 1990c), as estimated by the rope-tree method, and are present and common at all mortality sites examined. Because numerous class V snags died before 81 years ago, some yellow cedars probably began to die before the turn of the century, the estimate being about 1880. The early aerial photographs confirm the widespread occurrence of dead trees in 1927. The more-deteriorated snags in class VI, with broken off and decayed boles, were only infrequently encountered in surveys and were not associated with distinct mortality sites (HENNON et al. 1990b). These latter trees probably died prior to the onset of extensive mortality and may represent the non-epidemic or background level of mortality.

The appearance of abundant, dead yellow cedars around 1900 is also supported by historical observations. SHELDON (1912) was the first observer to report extensive mortality and noted dead yellow cedar near Pybus Bay on Admiralty Island in 1909, stating that, 'vast areas are rolling swamp, with yellow cedars, mostly dead.' Numerous botanical expeditions to Sitka and other areas in southeast where cedar decline is now extensive were conducted prior to 1880; some report the occurrence of yellow cedar, but none mentions dead or dying trees (HENNON et al. 1990c).

3.8 Estimating mortality rates since onset

The manner in which dead yellow-cedar trees persist standing for a century or more has allowed the reconstruction of patterns of mortality over time. An attempted has been made to merge results on time-since-death, ascertained using the dating methods (HENNON et al. 1990b), with data on the frequency of different classes encountered during ground surveys (HENNON et al. 1990b). Thus, the mortality rate during spans of time, represented by the death of trees in the snag classes, is estimated and results are presented as annual mortality rate.

Annual mortality rates since 1880 have averaged 0.5–0.7% in areas of cedar decline compared to 0.08% in surrounding 'healthy' forests. Mortality rates have apparently increased, particularly since about 1950, on declining sites (Fig. 3). Results from more intensive surveys at 3 individual sites are similar in that they show increases after 1950, but each has had a different peak period of annual mortality rate since then.

Several assumptions must be considered when interpreting these results. The surveys in this study used a variable-radius sampling method, which has bias for larger diameter trees. Furthermore, downed snags are excluded from analysis, which could result in an underestimate of mortality rate early in the century. Since large trees are the principle victims in cedar decline and snags are generally wind-firm and still standing, these factors may be minimal. Large permanent plots are currently being established to monitor mortality

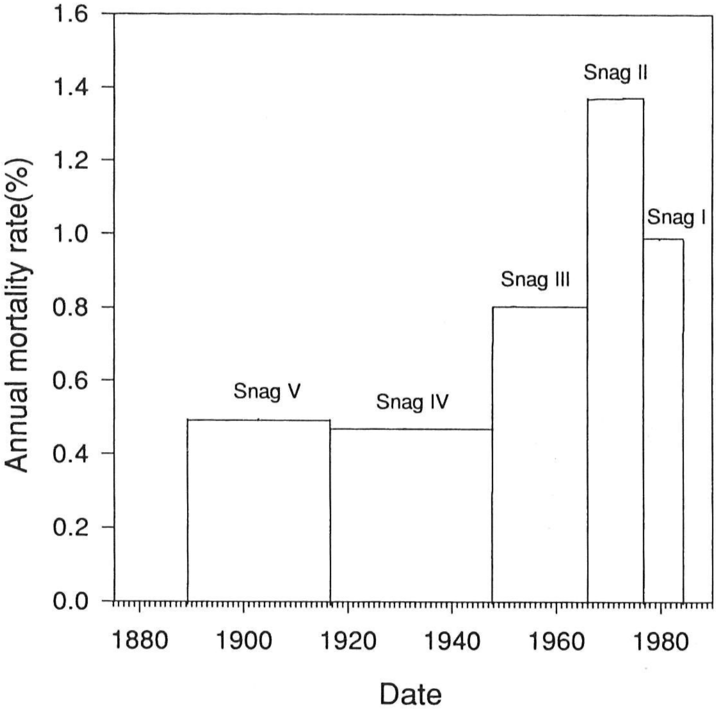

Fig. 3. Estimated mortality rates of yellow cedar since onset of decline. Endpoints of each snag class along the x-axis were determined by overlapping normal distributions of data from the snag-dating study. Annual mortality rates are based on the frequency of snags in each class encountered in ground surveys using variable radius sampling on 280 plots at 22 sites

rates in a more traditional manner. The excessive level of cedar mortality on sites of decline (65% of cedar basal area has died in the last 100 years), time required to establish mature yellow-cedar trees (nearly all trees are well over 100 years old), and inadequate replacement by natural regeneration suggest that the population and genetic diversity of yellow cedar in these forests is diminishing and that intensive mortality could not have been an on-going phenomenon for centuries.

4 Distribution of decline

The distribution of concentrated cedar decline is displayed in Figure 4. It is based on detailed sketchings made on 1:250 000 scale maps during aerial surveys that were conducted annually in the 1980's and early 1990's. More than 200 000 hectares of decline have been mapped in southeast Alaska from the British Columbia-Alaska border near Portland Canal to the northwest side of Chichagof Island (USDA FOREST SERVICE 1992). The area of severe decline occurs in a broad band from northwest to southeast. Decline is either absent or not severe in other portions of the natural range of yellow cedar further south in British Columbia and around the Gulf of Alaska near the northwest limits of its range.

Within the band of severe decline, nearly all stands have numerous dead and dying yellow-cedar trees if: 1. They occur at low elevation; 2. They occur on poorly drained soils; and 3. They have a substantial component of yellow cedar. Forests that lack decline but meet all three conditions occur in areas outside of the decline distribution. Adequate information on the variation of elevational limits of cedar decline within its distribution is not available, however, decline appears to reach higher elevations (e.g. up to 400 m) on the extreme outer coast of Chichagof Island in the Slocum Arm area compared to about 200–300 m further inland.

5 Possible abiotic factors and climate

Epidemiological evidence and the lack of aggressive biotic factors suggest that some abiotic factor is the primary cause of decline. The 'clues' from previous studies (Table 2) should provide some insight into which of the many abiotic factors may be the primary stress that leads to the death of yellow-cedar trees.

5.1 Bog expansion

One hypothesis for an abiotic cause of yellow-cedar decline is that bogs, for climatic and other reasons, are advancing onto the adjacent semi-bog sites where so many trees are dying

Table 2. **Summary of 'clues' from previous studies**

- Yellow-cedar forests began a high rate of mortality around 1880
- Yellow cedar is the principle victim
- Yellow-cedar trees die at various ages
- No pathogen, insect, or any biotic agent appears to be the primary cause
- Fine-root mortality is the initial symptom
- Yellow-cedar root systems are very shallow
- Mortality is concentrated on wet, poorly drained soils; conversely, yellow cedar is not experiencing a high mortality rate on well-drained soils
- Mortality is concentrated in open-canopy stands where trees and soils are exposed
- Mortality occurs at low elevations
- Spread is local and limited to short distances, and occurs along a drainage gradient

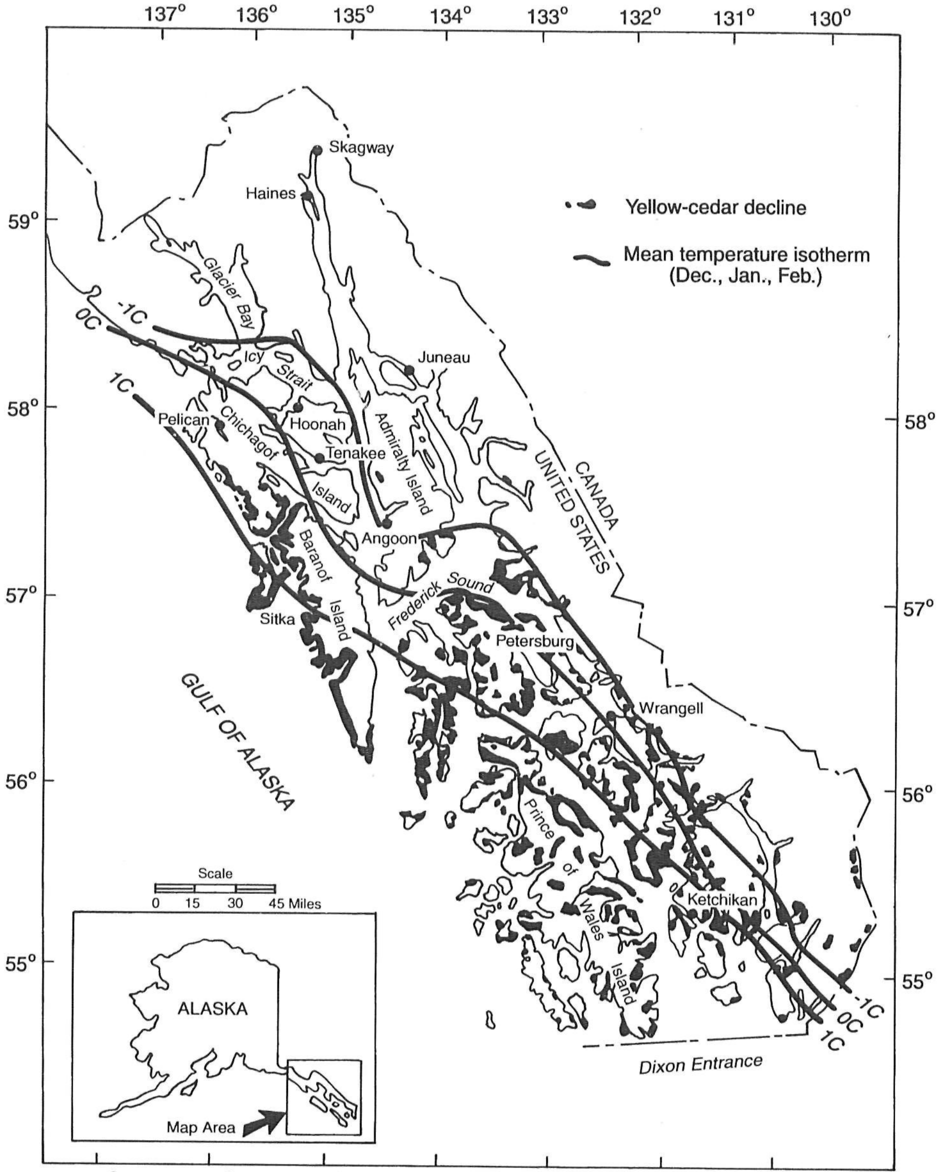

Fig. 4. Distribution of severe decline and mortality of yellow cedar in southeast Alaska. Isotherms for the mean temperature of December, January, and February are redrawn from ANDERSON (ANDERSON 1955)

(KLINGER 1988). The development from forest to bog requires the waterlogging of the forest floor, which may result from the proliferation of *Sphagnum* moss or the development of poor drainage as a result of hardpan formation. This process, paludification, 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, from forest to bog or bog to forest, is presently unresolved.

The observations in this study, however, suggest that, if bogs are advancing on forests, then the rate of advancement is imperceptible. Bogs observable on the 1927 aerial photography have not noticeably expanded, yet cedar mortality has been substantial during this period. One might expect to see some evidence of rapidly expanding *Sphagnum* mats or invasion of other bog plants into forests if bogs have enlarged during the last 100 years. In recent observations of understory flora growing beneath several hundred dying cedars at four sites in southeast Alaska, more than 75% of trees had no *Sphagnum* spp. within a 1-m radius of tree boles (P. E. HENNON unpubl. data). Even if bogs are expanding, the rate of expansion is probably too slow to provide a simple explanation for the widespread decline of yellow cedar. Additionally, the relatively high rate of mortality for yellow cedar, perhaps one of the conifers best adapted to growing in bogs (aside from shore pine), compared to a lower incidence of mortality for other conifers, contradicts the simple hypothesis of expanding bogs killing cedars.

5.2 Soil toxicity

Soil toxins could be considered possible incitants of yellow-cedar mortality. Toxic substances in soils could kill fine roots which would trigger the subsequent sequence of tree symptoms observed. Tree death may be rapid or slow depending upon the concentration of such toxins. Preliminary results from foliar and soil nutrient analyses suggest that an inorganic toxin is probably not to blame because elements have been found at similar levels between healthy and dying trees and sites with and without intense mortality (P. E. HENNON unpubl. data). Organic toxins would be more likely tree stressors in yellow-cedar decline. The chemistry of the saturated, organic soils associated with dying yellow cedars is not well-understood. The decomposition process in these soils is, at least in part, anaerobic, and by-products that develop could be toxic to vegetation. Perhaps yellow cedar is more sensitive to such hypothetical organic compounds than other tree species.

Allelopathic compounds should be considered to be possible toxic substances to yellow cedar. The heartwood and foliage of yellow cedar have high concentrations of defensive compounds, which reduce attack from insects and pathogens (BARTON 1976). One or more of these compounds could damage fine roots of yellow cedar directly before decomposition or indirectly after being altered during a stage of decomposition.

5.3 Freezing

Another hypothetical explanation for yellow cedars dying around bogs and on wet sites is the limited protection from atmospheric events that these sites offer. Yellow-cedar trees on such sites are open-grown and probably more vulnerable to extreme weather events (e.g. freezing, desiccation) than trees growing within protective canopies. Perhaps the death of some trees along bog edges following such a hypothetical weather event would cause adjacent trees to lose their protection and thus become vulnerable to damage. Such action might lead to the documented (HENNON et al. 1990b) slow, local spreading of mortality from the open stands in bogs and semi-bogs to the more productive adjacent forests.

The actual freezing damage may be to fine roots, as fine root necrosis is apparently the initial symptom on declining trees. Death of yellow cedars might be expected on wet sites that encourage shallow rooting. The root systems of yellow cedars growing in soils with better drainage are probably deeper. Wet soils would be expected to be less insulating and conduct heat more quickly than drier soils on better drainage.

AUCLAIR et al. (1992) recently proposed the hypothesis of 'xylem injury by cavitation' to explain the etiology of several forest declines. Chronic injury to xylem results from sudden shifts from mild to frigid weather conditions. Such events can lead to cavitation where the translocation stream in trees is disrupted by the formation of gas bubbles when fluids and tissues freeze. This process can be reversible if gases are dissolved, but may be irreversible if trees endure extreme or repeated weather events. A. N. AUCLAIR (pers. comm.) indicates that this form of injury could damage the shallow fine roots of yellow-cedar.

D. ZOBEL (pers. comm.) has suggested that cedar phenology could play a role in decline. Yellow-cedar trees may suffer freezing damage because they enter winter dormancy too late in the fall or lose dormancy too early in spring. Thus, freezing could occur as early autumn or late spring events. Yellow-cedar trees at higher elevations or located in forests to the north or east might be unaffected because of a longer dormancy period.

5.4 Interaction of climate

The relatively sudden emergence of cedar decline late in the 1880s on sites with intact yellow-cedar forests suggests that, if an organic toxin is the primary cause of dying yellow cedars, then something triggered its presence, or much higher concentrations of it, at the time of decline onset. Likewise, a change in weather patterns would apparently be necessary to make the bog expansion-and-freezing hypotheses plausible. Furthermore, the lack of decline in cedar forests at higher elevation or outside the distribution of cedar decline must be reconciled with all three hypotheses.

A climatic shift in southeast Alaska would result in an altered evapotranspiration balance of yellow-cedar forests. Since these forests are on the ecocline of moisture drainage, they may be particularly sensitive to any increase in soil moisture. A decrease in temperature (i.e. less evaporation, less transpiration) or increase in precipitation could cause sites to become wetter. As some trees died, transpiration would be further reduced and site productivity might deteriorate as sites became wetter and wetter. Thus, a warmer or wetter climate could lead to bog expansion. Sites can also become wetter through decreased drainage that is the result of soil-development processes (e.g. paludification, discussed above), and does not absolutely require climatic warming. Increased soil moisture could also result in more anaerobic decomposition and be a triggering factor in the soil-toxicity hypothesis.

Mild climatic warming during winter months would dramatically effect patterns of snow deposition and duration in southeast Alaska. Due to the maritime influences of the Pacific Ocean, winter temperatures currently average around freezing and precipitation is heavy throughout much of the region. Thus, the state of precipitation, whether rain or snow, is controlled by minor fluctuations in temperature. A slight increase in average winter temperatures would change much precipitation from snow to rain, reducing or eliminating the snowpack or its duration at low elevations.

Freezing damage to fine roots could occur in winter when soils are unprotected because of inadequate snowpack during periods when cold continental air moves over the region. Southeast Alaska weather sometimes produces frigid winter temperatures when the cold Arctic Front from interior northwest Canada pushes the low-pressure warmer system offshore (Fig. 5). This results in clear, sometimes windy, weather with dramatic drops in temperature. These events occur sporadically every winter and have variable duration before returning to the more typical maritime conditions (MILLER 1985). Trees growing in wet soils at low elevations where decline has been severe would be susceptible due to their shallow root system. Less decline on wet sites at higher elevations could then be explained by the persistent winter snowpack at those elevations, even in today's warmer climate.

The distribution of yellow-cedar decline appears to be associated with known climatic

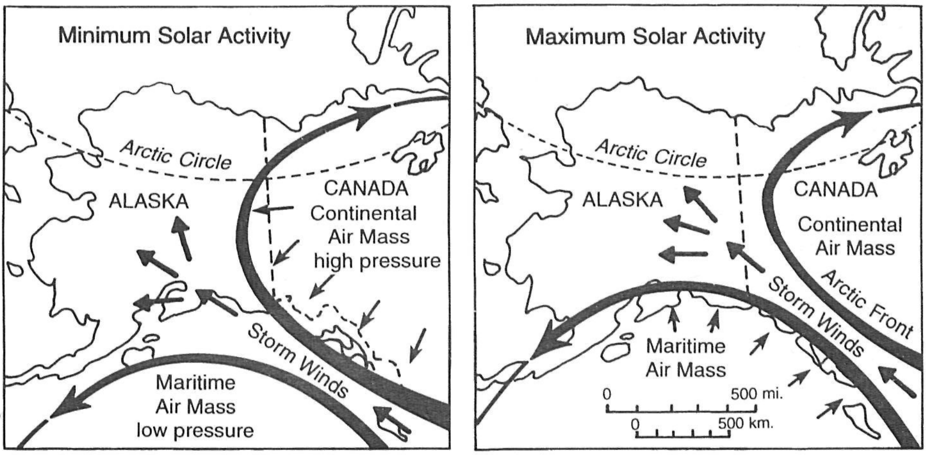

Fig. 5. Typical influences of maritime air mass (right) in southeast Alaska and its displacement offshore by the continental air mass (left) (MILLER 1985). These models may be used to understand general climatic patterns that are influenced by cycles of solar radiation or sudden shifts to frigid temperatures during winter in southeast Alaska

patterns in southeast Alaska. The eastern perimeter of decline is somewhat restricted to the warm side of isotherms (ANDERSON 1955) derived from the 3 winter months (Fig. 4). The perimeter is apparently associated with slightly warmer isotherms (– 1– + 1 °C) as latitude increases. Mean January isotherms (NOAA, unpubl. report ('Climate of Alaska,') on file at Forestry Sciences Laboratory, Juneau AK) are somewhat similar to ANDERSON'S (1955) 3 winter-month isotherms, except that NOAA's + 1 °C completely encompasses the eastern perimeter of the yellow-cedar decline's distribution, even in extreme southeast portions. These latter isotherms are drawn on a cruder, state-wide scale. Methods used to derive the isotherms are not discussed, so it is unclear why slightly warmer isotherms are indicated. In a detailed statistical analysis of climate in the region, distinct climatic zones could not be delineated as too few weather stations were present (FARR and HARD 1987). They did find, however, that distinct groups of stations, sometimes geographically separated, produced significantly different results based on seasonal temperatures, precipitation, frost-free days, and total number of growing-degree days.

A relationship between winter climate and the distribution of decline suggests that snowpack could be a factor in the etiology of decline. Heavy snowfall occurs at all elevations within the range of yellow cedar north of the distribution of cedar decline; to the south, perhaps the Arctic continental air masses do not cause such an extreme or rapid drop in temperature. The restriction of concentrated mortality to low elevations also suggests climate or, specifically, snowpack, as a factor in yellow-cedar decline. Unfortunately, trends on snowpack throughout southeast Alaska have not been adequately described. The few stations at middle and higher elevations make estimating the effects of elevation difficult. BOWLING and SLAUGHTER (1983) examined weather data to report the percentage of days (September–May) with bare ground or several different depths of snow, but they noted that data were too limited to construct isohyets. They did note that their results supported the trends of greater winter snowpack with increasing latitude, proximity to the mainland, and elevation.

5.5 Evidence for climatic warming in southeast Alaska

Good documentation of recent weather data in southeast Alaska exists but there are few instrument records of temperature before 1900 (JUDAY 1984). Those weather records that predate 1900 are from stations that have since changed location. Evidence of climate before 1900 generally comes from extrapolating data from several weather stations (with changed locations) or from interpreting patterns of glacial advancement/retreat and vegetation abundance based on pollen profiles.

HAMILTON (1965) concluded that a warming trend has occurred in most of Alaska since the late 1800's. This conclusion was based on comparing Alaska's 20th Century weather with locations that have longer weather records, and then reconstructing Alaska's climate (Fig. 6). MILLER (1985) suggested that the Little Ice Age ended during the 1880's but states that there has been much variation within this time of warming. By studying pollen profiles in peat bogs of southeast Alaska and determining vegetation patterns, HEUSSER (1952) concluded that the last 200 years have been warm and dry compared to the previous 1700 years which where colder and wetter.

The climate of Alaska appears to be greatly affected by variation in solar radiation associated with sunspots that occur in approximately an 11-year period (MILLER 1985). Studies on glacial advancement and retreat suggest that these short cycles are superimposed on larger ones that occur on about 90-year cycles and perhaps even larger cycles (e.g. 180, 940, and 2400–2600 years). The chief factor that affects glacier movement is thought to be snowfall on the icefields that feed glaciers (MILLER 1985). Conditions that influence amount of snowfall at these higher elevations in the maritime–continental transition may not correlate with weather patterns at low elevations on the outer coasts where yellow-cedar decline occurs. Thus, interpretations of climatic change taken from changes in glacier positions

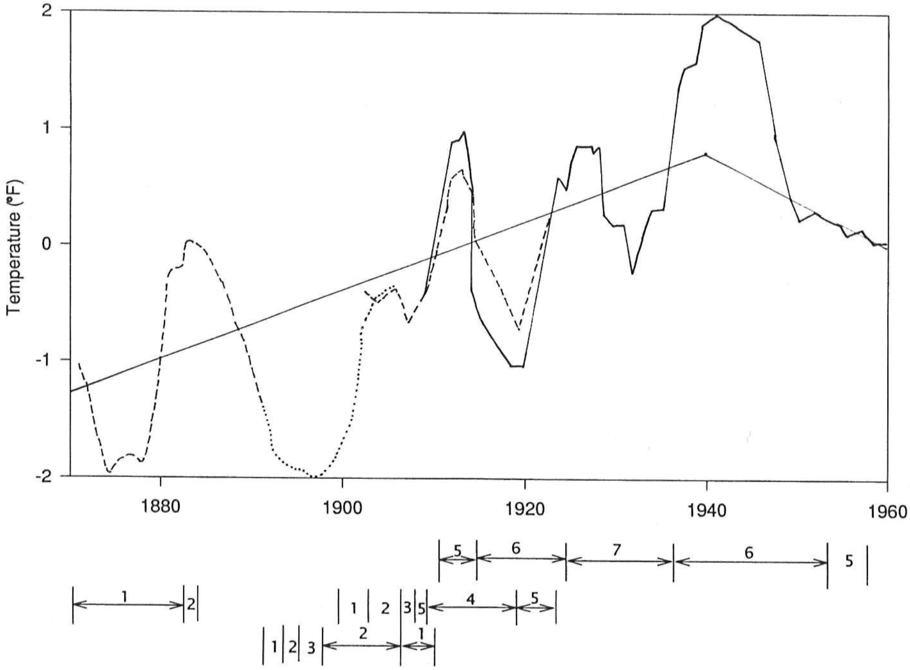

Fig. 6. Composite reconstruction of mean annual temperature (8-year running means) accounting for weather stations throughout Alaska (HAMILTON 1965). The small numbers represent the minimum number of stations represented in each segement; the top line refers to the solid curve, middle line to the dashed curve, and bottom line to the closely dotted curve. Alaska's 20th Century weather was compared with locations in North America with longer weather records to reconstruct Alaska's early weather where data were limited

should be made carefully when applied to yellow-cedar decline in low-lying coastal areas. HEUSSER (1952) stated that recent maximum glacial advance occurred in the 1600's through the early 1800's, but that, since about 1850, recession has been continuous in most areas of southeast Alaska. Recession was very rapid about the turn of the century and during the 1930's. Meteorological records indicate that the late 1880s were colder than today in many locations in western North America (HEUSSER 1952).

Climatic variation since 1900, after the onset of decline, is more easily documented. JUDAY (1984) described noteworthy warm periods in Southeast Alaska (1905, 1914, 1926, early 1940's, late 1950's, and late 1970's–1981). These are in general agreement with HAMILTON'S (1965) mean annual-temperature composite for the entire state during the 1900's (Fig. 6). MILLER (1985) noted generally cooling temperatures between 1940's and 1970 when global mean temperature dropped, which is in agreement with HAMILTON'S (1965) interpretation (Fig. 6). JUDAY (1984) described weather data for Sitka and Juneau with a simple linear regression fitted to the 5-year running means of MAT (mean annual temperature: mean of the monthly means over 1 calendar year). By this calculation, the Sitka station has warmed at the rate of 0.60 °C per century. For the first half of the century, however, Sitka warmed at the rate of 2.08 °C per century. Within this warming trend, the variation in MAT appears to be cyclical with the warm and cold cycles repeated about every 11 years. There is a positive relationship, although not a perfect fit, between sun-spot activity and the peak temperatures in these cycles. Note that all of these temperature trends are after the beginning of the probable, marked warming that began in the late 1800's. Thus, the best evidence for climatic variation in the areas of cedar decline are for times after its onset.

Interestingly, global-change-modeling scenarios indicate that climatic warming will (has?) occurred almost entirely in the night-time temperature record with no appreciable warming in daily maximums (ESCADY and MURPHY 1992). In addition, global-change-model predictions for the 'higher latitudes', within which lies southeast Alaska, indicate that warming will be initially greatest in late fall/winter; eventually warming will be greatest in mid winter (KRÄUCHI 1993). And finally, most snow in any area falls at night (R. SOMMERFELD pers. comm.). Thus, if the warming is greatest at night in mid-winter, it ought to change precipitation from snow to rain, particularly at lower elevations where cedar decline is most evident.

6 Conclusions

Yellow-cedar decline appears to be a unique and outstanding example of a naturally induced forest decline. The extreme decay resistance of this species has allowed a rare opportunity to reconstruct the onset and development of decline. The occurrence of extensive mortality before 1900 in countless remote, undisturbed sites without nearby sources of pollutants argues against atmospheric pollution as the cause of decline. Additionally, no introduced exotic pathogen or insect (another potential form of anthropogenic activity) was found to be associated with decline. Climatic warming, which apparently began at about the same time as extensive yellow-cedar mortality, is probably responsible for triggering some stress factor that has lead to the demise of yellow-cedar forests over more than 200 000 hectares. Warmer temperatures could influence key environmental factors such as changing winter precipitation from snow to rain. Changes in temperature or precipitation may affect decomposition processes, perhaps resulting in the formation of compounds toxic to yellow cedar. Research on the possible abiotic factors, such as freezing of fine roots and soil toxicity, and their link to climatic change, could resolve the etiology of this mysterious forest decline. If, as the authors suspect, climate has played a major triggering role, then cedar decline may provide an excellent example of the devastating effects of a moderate climate shift on a forest ecosystem.

Summary

Decline and mortality of yellow cedar (*Chamaecyparis nootkatensis*) is occurring on over 200-000 hectares of remote, unmanaged forest in southeast Alaska. All evidence suggests that biotic agents are not responsible for tree death and the primary cause is probably abiotic. Extensive mortality began about 1880, a date that apparently coincides with initiation of a warming climate in coastal Alaska. Decline occurs on sites with poor drainage, generally below 250-m elevation in forests dominated by yellow cedar. An estimated 65% of yellow cedar's volume in these dying forests has been killed during the last century. One perimeter of the distribution of decline is closely associated with winter isotherms. Several hypotheses are presented to suggest how a warming climate may have triggered decline by altering key environmental processes such as reducing winter snowpack or modifying decomposition.

Résumé

Le réchauffement climatique: déclenche-t-il le dépérissement du Chamaecyparis nootkatensis dans le Sud-Est de l'Alaska?

Le dépérissement et la mortalité du *C. nootkatensis* a lieu sur 200 000 ha de forêts non aménagées de l'Alaska. Tous les faits suggèrent que les agents biotiques ne sont pas responsables de la mort des arbres et que la cause primaire est abiotique. L'importante mortalité a commencé vers 1880, date qui coïncide apparémment avec le début du réchauffement sur les côtes de l'Alaska. Le dépérissement se développe dans des sites mal drainés, généralement au-dessous de 250 m d'altitude dans des forêts où domine *C. nootkatensis*. On estime que la mortalité correspond à 65% du volume de cette espèce dans ces forêts au cours du siècle écoulé. Une limite de répartition du dépérissement coïncide étroitement avec les isothermes hivernaux. Plusieurs hypothèses sont émises pour indiquer comment le réchauffement climatique peut avoir déclenché le dépérissement en altérant des processus environnementaux clés, tels que la réduction de la couverture neigeuse ou la modification de la décomposition.

Zusammenfassung

Wurde das Chamaecyparis nootkatensis-Sterben in Südost-Alaska durch eine Klimaerwärmung ausgelöst?

Chamaecyparis nootkatensis zeigt auf über 200 000 ha in abgelegenen Naturwaldgebieten Südostalaskas einen schlechten Zustand und stirbt ab. Alle verfügbaren Daten deuten darauf hin, dass biotische Faktoren nicht für das Absterben der Bäume verantwortlich sind, und die Ursache wahrscheinlich abiotischer Art ist. Das ausgedehnte Baumsterben begann etwa 1880, einem Zeitpunkt, wo offensichtlich eine Klimaerwärmung in den küstennahen Gebieten Alaskas begann. Die Krankheit kommt an schlecht entwässerten Standorten vor und ist in der Regel auf Lagen unterhalb 250 m ü.M. und auf von *C. nootkatensis* dominierte Wälder beschränkt. Während des letzten Jahrhunderts sind ca. 65% des Volumens an *C. nootkatensis* abgestorben. Eine Randzone dieses Baumsterbens hängt eng mit den Winter-Isothermen zusammen. Es werden verschiedene Hypothesen präsentiert, die erklären könnten, wie eine Klimaerwärmung durch die Veränderung zentraler Umweltprozesse dieses Baumsterben ausgelöst hat, z.B durch eine Reduktion der Schneedecke oder eine Veränderung der Mineralisierungsprozesse.

References

ANDERSON, H. E., 1955: Climate in Southeast Alaska in Relation to Tree Growth. Juneau, AK: USDA For. Ser., Alaska For. Res. Cent. Sta. Pap. 3.

–, 1959: Sivicultural Characteristics of Alaska Cedar. Juneau, AK: USDA For. Ser., Alaska For. Res. Cent. Sta. Pap. 11.

AUCLAIR, A. N.; WORREST, R. C.; LACHANCE, D.; MARTIN, H. C., 1992: Climatic perturbation as a general mechanism of forest dieback. In: Forest Decline Concepts. Ed. by P. D. MANION and D. LACHANCE. St. Paul, MN: American Phytopathological Society pp. 35–58.

BARTON, G. M.; 1976: A review of yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) extractives and their importance to utilization. Wood and Fiber **8**, 172–176.

BOWLING, S. A.; SLAUGHTER, C. W., 1983: Seasonal Snowpack and Air Temperature Data Summary Southeast Alaska, Office Report. Juneau, AK: Forestry Sciences Laboratory.

DOWNING, G. L., 1960: A Cedar Bark Beetle Outbreak. Juneau, AK: USDA Forest Service, Alaska For. Res. Cent., For. Insect Survey Rep. 6.

ESCADY, C. J.; MURPHY, C. G.; 1992: Global climate warming. Water Environment Research **64**, 647–653.

FARR, W. A.; HARD, J. S., 1987: Multivariate Analysis of Climate along the Southern Coast of Alaska — Some Forestry Implications. Portland, OR: USDA For. Ser., Pac., Northwest Res. Sta., Res. Pap. PNW-RP-372.

FOWELLS, H. A., 1965: Silvics of forest trees of the United States. USDA, Washington, D.C. Agric. Handb. **271**, 546–556.

FRANKLIN, G. F.; DYRNESS, C. T., 1973: Natural Vegetation of Oregon and Washington. Portland, OR: USDA For. Serv. Gen. Tech. Rep. PNW-8., Pac. Northwest For. and Range Exp. Sta.

HAMILTON, T. D., 1965: Alaskan temperature fluctuations and trends: an analysis of recorded data. Arctic **18**, 105–117.

HAMM, P. B.; HANSEN, E. M.; HENNON, P. E.; SHAW, C. G. III., 1988: *Pythium* species from forest and muskeg areas of southeast Alaska. Trans. Br. Mycol. Soc. **91**, 385–388.

HANSEN, E. M.; HAMM, P. B., 1988: *Phytophthora* species from remote forests of western North America. Phytopathology **78** (**Abstr.**), 1519.

–; –; SHAW, C. G. III; HENNON, P.E., 1988: *Phytophthora drechsleri* in remote areas of southeast Alaska. Trans. Br. Mycol. Soc. **91**, 379–388.

HARRIS, A. S., 1970: The loners of Alaska. Amer. For. **76**, 5, 20–23, 55–56.

–, 1971: Alaska-cedar. Juneau, A.K.: USDA For. Serv., Am. Woods-FS 224.

–, 1990: *Chamaecyparis nootkatensis* (D. Don) Spach: Alaska-cedar. In: Silvics of North America; Vol. 1: Conifers. Ed. by R. M. BURNS and B. H. HONKALA. Washington D.C.: USDA For. Ser., Agric. Handb. 654.

–; FARR, W. A., 1974: The Forest Ecosystem of Southeast Alaska. 7. Forest Ecology and Timber Management. Portland, OR: USDA For. Ser., Pacific Northwest Forest and Range, Exp. Sta. Portland, OR, Gen. Tech. Rep. PNW-25.

–; HUTCHISON, O. K.; MEEHAN, W. R.; SWANSTON, D. N.; HELMERS, A. E.; HENDEE, J. C.; COLLINS, T. M., 1974: The Forest Ecosystem of Southeast Alaska. 1. The Setting. Portland, OR: USDA For. Ser., Pacific Northwest Forest and Range, Exp. Sta. Portland, OR. Gen. Tech. Rep. PNW-12.

HENNON, P. E., 1990: Fungi on *Chamaecyparis nootkatensis*. Mycologia **82**, 59–66.

–; HANSEN, E. M.; SHAW, C. G. III., 1990a: Causes of basal scars on *Chamaecyparis nootkatensis* in southeast Alaska. Northwest science **64**, 45–54.

–; –; –, 1990b: Dynamics of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. Can. J. Bot. **68**, 651–662.

–; NEWCOMB, G. B.; SHAW, C. G. III., HANSEN, E. M., 1986: Nematodes associated with dying *Chamaecyparis nootkatensis* in Southeastern Alaska. Plant Dis. **70**, 352.

–; SHAW, C. G. III; HANSEN, E. M., 1990c: Dating decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. For Sci. **36**, 502–515.

–; –; –, 1990d: Symptoms and fungal associations of declining *Chamaecyparis nootkatensis* in southeast Alaska. Plant Dis. **74**, 267–273.

HEUSSER, C. J., 1952: Pollen profiles from Southeastern Alaska. Ecological Monographs **22**, 331–352.

–, 1955: Pollen profiles from Prince William sound and Southeastern Kenai Peninsula. Ecology **36**, 185–202.

HUTCHISON, O. K.; LA BAU, V. J., 1975: The Forest Ecosystem of Southeast Alaska. 9. Timber Inventory, Harvesting, Marketing, and Trends. Portland, OR: USDA For. Ser. Pacific Northwest Forest and Range, Exp. Sta. Portland, OR, Gen. Tech. Rep. PNW-**34**.

JUDAY, G. P., 1984: Temperature trends in the Alaska climate record: problems, update, and prospects. The Potential Effects of Carbon Dioxide-induced Climatic Changes in Alaska. Ed. by J. H. MCBEAH, Fairbanks, AK: University of Alaska, Misc. Pub **83–1**. pp. 76–91.

KLINGER, L. F., 1988: Successional change in vegetation and soils of southeast Alaska. PhD Thesis. University of Colorado, Boulder, CO., USA.

KRÄUCHI, N., 1993: Potential impacts of a climate change on forest ecosystems. Eur. J. For. Path. **23**, 28–50.

MILLER, M. M., 1985: Recent climatic variations, their causes and neogenic perspecitves. In: Late Cenozoic History of the Pacific Northwest. San Francisco, CA: Academy of Science. pp. 357–414.

MUELLER-DOMBOIS, D., 1986: Perspectives for an etiology of stand level dieback. Ann. Rev. Ecol. Sys. **17**, 221–243.

OWENS, J. N.; MOLDER, M., 1984: The Reproductive Cycles of Western Red cedar and Yellow-cedar. Victoria, B.C.: Min. of For., Forestry Div. Res. Branch.

ROTH, L. F.; BYNUM, H. H.; NELSON, E. E., 1972: Phytophthora Root Rot of Port-Orford-cedar. U.S. Dep. Agric. For. Serv. Pest Leafl. **131**.

RUTH, R. H.; HARRIS, A. S., 1979: Management of Western Hemlock-Sitka Spruce Forests for Timber production. Portland, OR: USDA For. Serv. Gen. Tech. Rep. PNW-**88**. Pacific Northwest Forest and Range Exp. Sta.

SARGENT, R. H.; MOFFIT, F. H., 1929: Aerial photographic surveys in southeastern Alaska. U.S. Geological Survey Bulletin **797-E. GPO**. 143–160.

SHAW, C. G. III; EGLITIS, A.; LAURENT, T. H.; HENNON, P. E., 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. New York: Scribner's Sons.

USDA FOREST SERVICE, 1992: Forest Insect and Disease Conditions in the United States. Washington, D.C.: Forest Pest Managment.

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