

Dynamics of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska

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Alaska-cedar, *Chamaecyparis nootkatensis* (D. Don) Spach, has been dying in undisturbed forests throughout southeast Alaska for the last 100 years. To determine if decline spreads, boundaries of mortality at seven sites with decline were mapped using aerial photographs taken in 1927, 1948, 1965, and 1976. Mortality was present at all seven sites in 1927. The boundaries of mortality have since expanded, but not by more than 100 m beyond the 1927 limit. In ground surveys, dead Alaska-cedar trees, classified according to their degree of deterioration, were recorded in 427 plots along 39 transects. Fifty-five taxa of understory vegetation were also recorded from 280 plots along these 21 transects; an ordination was produced from their distribution that represented a gradient from bogs to sites with better drainage. Most mortality was associated with bog and semibog sites. Alaska-cedar has a disproportionate level of mortality (65% of basal area dead) relative to other conifers. Local spread of cedar decline occurred along this gradient, as 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). Snags that probably date from the onset of extensive mortality were relatively common (at least 8% of all snags) on all 23 sites where intensive mortality was surveyed on the ground. As all sites with mortality that we investigated throughout southeast Alaska have these snags, decline does not appear to have spread to new sites since its onset. Although decline is relatively species specific and has patterns of local spread, the spread of mortality is along a specific, preexisting ecological gradient. These results, and the apparent lack of any site to site spread in the last 100 years, suggest that Alaska-cedar decline is not caused by some biotic agent.

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Depuis les derniers 100 ans, le Cyprès jaune, *Chamaecyparis nootkatensis* (D. Don) Spach, meurt dans les forêts vierges du sud-est de l'Alaska. En vue de déterminer si son déclin s'étend, on a cartographié, à l'aide de photographies aériennes prises en 1927, 1948, 1965 et 1976, les limites de mortalité dans sept sites. En 1927, la mortalité était présente dans les sept sites. Depuis, ses limites se sont étendues, mais pas plus de 100 m par rapport à la limite de 1927. Lors de la prospection au sol, les cyprès jaunes morts, classés par leur degré de détérioration, ont été relevés dans 427 places-échantillon distribuées le long de 39 transects. On a aussi relevé 55 taxons appartenant à la végétation du sous-bois, dans 280 places-échantillon distribuées le long de 21 des transects. Une ordination, à partir de leur distribution, en a alors été faite; elle représentait un gradient allant des tourbières aux sites mieux drainés. Le maximum de mortalité a été associé avec la tourbière et les sites semi-tourbeux. Le Cyprès jaune présentait un niveau de mortalité disproportionné (65% de la surface terrière des arbres morts) par rapport aux autres conifères. Des zones de déclin du Cyprès jaune sont apparues localement le long de ce gradient, étant donné que les places-échantillon comprenant les arbres morts plus récemment avaient des valeurs moyennes d'ordination élevées (sites mieux drainés), alors que les places-échantillon avec les arbres morts depuis longtemps avaient des valeurs moyennes d'ordination basses (sites tourbeux). Les chicots, datant probablement de l'époque de l'attaque provoquant une forte mortalité, étaient relativement communs (au moins 8% de tous les chicots) sur les 23 sites où on a relevé au sol une forte mortalité. Comme tous les sites prospectés contiennent de ces chicots, le déclin du Cyprès jaune ne semble pas s'être propagé aux nouveaux sites depuis que l'attaque s'est produite. Bien que le déclin soit relativement spécifique et qu'il présente localement des patrons de propagation, la propagation de la mortalité se fait le long d'un gradient écologique spécifique, préexistant. Les présents résultats, et le manque apparent de propagation d'un site à l'autre au cours des derniers 100 ans, suggèrent que le déclin du Cyprès jaune n'est pas causé par un quelconque agent biotique.

[Traduit par la revue]

Introduction

Alaska-cedar, *Chamaecyparis nootkatensis* (D. Don) Spach, also known as yellow cypress, 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. 1) have occurred since about 1880 (Hennon 1986; Hennon *et al.* 1990a) in many stands of Alaska-cedar (Laurent 1982; Frear 1982; Shaw *et al.* 1985) and now cover more than 150 000 ha throughout south-



FIG. 1. Decline and mortality of Alaska-cedar in southeast Alaska. Dead trees appear white or light grey.

east Alaska (USDA Forest Service 1988). Decline is most often associated with bog (muskeg) or semibog sites (Downing 1960; Laurent 1982) in large, expansive areas extending for several kilometres or in smaller, discrete patches of only a few hectares. Dying Alaska-cedar trees sometimes occur on the perimeters of large and small mortality sites, suggesting that the problem may be spreading, although this has not been previously studied. The primary cause of mortality is unknown; no single biotic or abiotic factor has been shown to be primarily responsible for tree death (Hennon *et al.* 1985, 1990b; Shaw *et al.* 1985). Many 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 growing in any one of three forest types (bog, forest, and an intermediate community). Recently, Martin (1989) described plant association classifications for northern southeast Alaska, including two series that involved Alaska-cedar, but occurrence of cedar decline or mortality was not discussed. The ecology of Alaska-cedar and successional patterns of communities of plants on wet sites where cedar often grows are also poorly understood in southeast Alaska.

The lack of critical ecological and epidemiological assessment of the mortality problem has limited our understanding of the probable causes of the decline. Knowledge of which conifer species are affected, 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 and may indicate what type of pathogen could be present.

The objectives of this paper are (i) to clarify if the incidence of mortality on sites expressing decline is the same for other tree species as it is for Alaska-cedar, (ii) to describe the plant community associations of Alaska-cedar in areas where mortality is severe and in surrounding stands, (iii) to document

whether mortality is spreading over short or long distances, or both, and (iv) if mortality is spreading, to describe patterns of spread (i.e., correlations of distance spread with slope, aspect, and forest community type).

Materials and methods

Site description

Most studies were conducted in an area of severe forest decline in the vicinity of Peril Strait on Baranof and Chichagof islands (latitude 57°N), about 50 km northwest of Sitka in southeast Alaska (Figs. 2 and 3). Surveys were also conducted at Kennel Creek and Waterfall Cove on Chichagof Island, and on Prince of Wales and Wrangell islands. This region is dominated by undisturbed old-growth forests of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) on well-drained soils, and by Alaska-cedar, western hemlock, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), and shore pine (*Pinus contorta* Dougl.) on poorly drained, deeply organic soils (Harris *et al.* 1974). On extremely boggy sites, shore pine and prostrate Alaska-cedar are the only conifers.

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; thus, fire is not an important factor in forest succession. Windthrow and landslides are common disturbances of forests in this region (Harris and Farr 1974). Patterns of plant succession on poorly drained sites are not understood.

Extensive glaciation has modified the landscape, but few glaciers are now located on islands where our studies were conducted. Most soils are spodosols, but histisols and several others are also common. Poorly drained soils, which are highly organic and shallow or deep, generally occur on sites without steep slope and overlay unfractured bedrock or compact glacial till (Martin 1989).

Aerial photographic analysis of mortality

Seven areas currently expressing mortality of Alaska-cedar, all on Chichagof and Baranof islands near Peril Strait (Fig. 3), were examined on aerial photographs taken 1927, 1948, 1965, and 1976 (Hennon 1986). The 1976 photographs were in color, others were black and

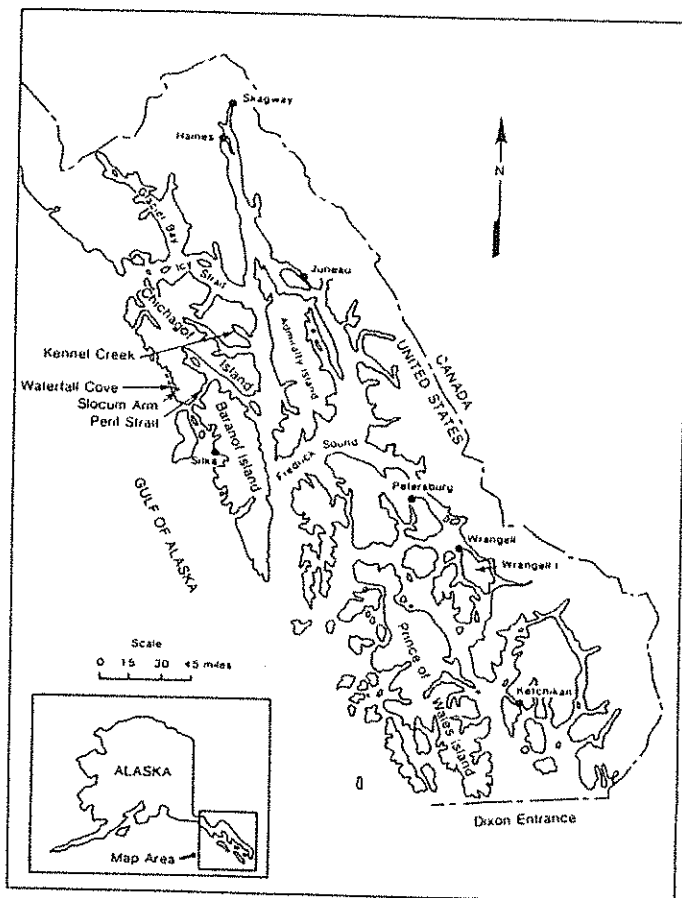


FIG. 2. Location of study sites in southeast Alaska (1 mile = 1.61 km).

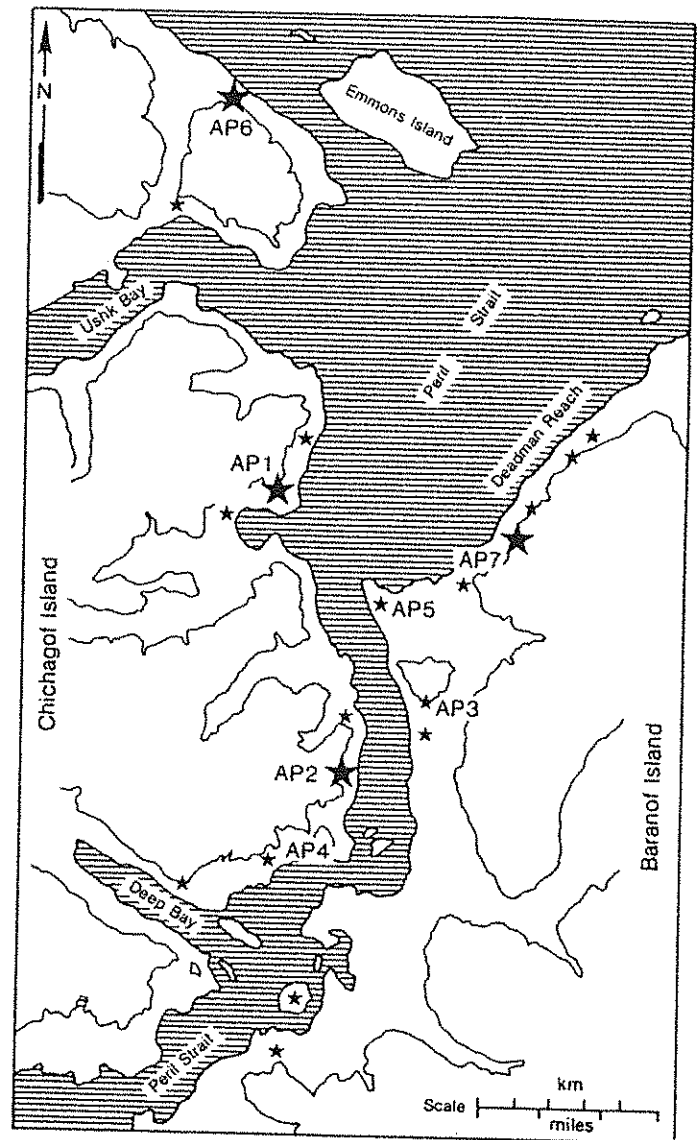


FIG. 3. Map of Peril Strait in southeast Alaska showing extensive (small stars) and intensive (large stars) sampling transects and aerial photographic mapping locations (AP).

white. All seven sites were bounded on at least one side by healthy forest; two sites of mortality were completely surrounded by healthy stands and shoreline.

Stereopairs (two adjacent and overlapping photographs) of each mortality site from each photographic series were viewed with a stereoscope. Perimeters of mortality, 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 (representing the four sets of aerial photographs) were combined into one map by using a mapograph machine that brought individual maps to a common scale.

The Poison Cove site (Fig. 3) was mapped more intensively. In addition to plotting boundaries of mortality, we visually stratified mortality 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 advance of the front of dying trees.

In addition to detailed mapping, the general distribution of mortality and its association with topographic relief and forest types were examined and described from 75 of the aerial photographs taken in 1976 (Hennon 1986), which covered most of the forested land (about 22 km²) along Peril Strait (Fig. 3).

Forest community associations

Understory plants were surveyed to determine community relationships among forest stands. The dominance of 55 understory plant taxa was recorded within a 3-m radius of plot centers on 280 plots. Dominance was rated as follows: nearly pure in its layer (>50%), dominant (25–50%), common (5–25%), rare (0–5%), and absent (0%). Understory plant distribution was analyzed by a computer ordi-

nation 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: eigenvalues and lengths of gradients.

Gauch (1982) recommended graphing environmental parameters (we used coniferous overstory) with axes to detect any related distribution for an aid in interpretation of gradients. Also, known habitat preferences of species used in the ordination were used to assist with interpretation of these gradients (Gauch 1982).

Ordination plot scores along important gradients were grouped into nine intervals, and class means were compared with (i) mean values for live and dead basal area of each coniferous species, (ii) the presence or absence of cedar mortality using χ^2 analysis of ordered proportions ($P = 0.05$) (Fleiss 1981), (iii) deterioration classes of cedar snags (see snag classes below), and (iv) deterioration classes of dead 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 (Hennon *et al.* 1984, 1990a). Snag classes and snag classes of the dead tops of rope trees were related to ordination plot score intervals using a one-way anal-

ysis 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 (i) which tree species were dead or declining, (ii) the severity of mortality, (iii) the patterns of spread of the mortality, (iv) the general growth habits of Alaska-cedar, and (v) understory ordination data. The sites surveyed were selected because they appeared to have the concentration of dead trees that is characteristic of cedar decline, generally had distinguishable boundaries of mortality, and were accessible (primarily by small boat). In all, 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 Kennel Creek, and one at Waterfall Cove in Slocum Arm (Fig. 2). All but two transects were at elevations under 300 m. Plots were established every 50 m along transect lines, beginning 25 m from beaches (sea level), and progressed upslope through areas of mortality. Transects ended when two consecutive plots contained few, if any, dead trees.

The basal area of live trees and snags (dead trees) was measured for each species of conifer by using a 3- or 6-m²/ha basal area factor (BAF) wedge prism (Wenger 1984) (13- and 26-ft²/acre, respectively). A 3-m²/ha BAF prism was only used if fewer than 10 trees were selected by the 6-m²/ha BAF prism. Snags of Alaska-cedar were distinguished from other species by the aromatic heartwood, detectable even in stems that were dead for 80 years or more (Hennon 1986; Hennon *et al.* 1990a). Snags of other conifers were identified to species by bark or wood characteristics. Western and mountain 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, 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. 3), with a total of 147 plots on 18 transects. Plot trees were selected using the BAF prisms. Bole diameter at breast height (dbh) was measured for all Alaska-cedar trees, and six places on the cambium around the root collar (60° apart) were examined by removing bark with a knife. These examinations were made to detect necrotic lesions that may occur on declining cedars (Shaw *et al.* 1985) and to correlate their occurrence with azimuth as tested by χ^2 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 calculated to determine quantitatively levels of mortality by species.

Two additional areas of declining stands of Alaska-cedar farther south, within the range of western redcedar (*Thuja plicata* Donn), were surveyed to determine if this species is suffering from decline. Sixty-four plots from three areas on Prince of Wales Island and 80 plots from one area on Wrangell Island were surveyed.

Snag classes

Each dead Alaska-cedar was placed into one of six snag classes (Fig. 4), based on degree of foliage, twig or branch retention, and deterioration of its bole. Average time since death has been estimated for five of these snag classes (Hennon *et al.* 1984, 1990a): class I, foliage retained, $\bar{x} = 4$ years; class II, twigs retained, $\bar{x} = 14$ years; class III, secondary branches retained, $\bar{x} = 26$ years; class IV, primary branches retained, $\bar{x} = 51$ years; class V, no branches retained, $\bar{x} = 81$ years; class VI, bole broken and deteriorated, death not dated.

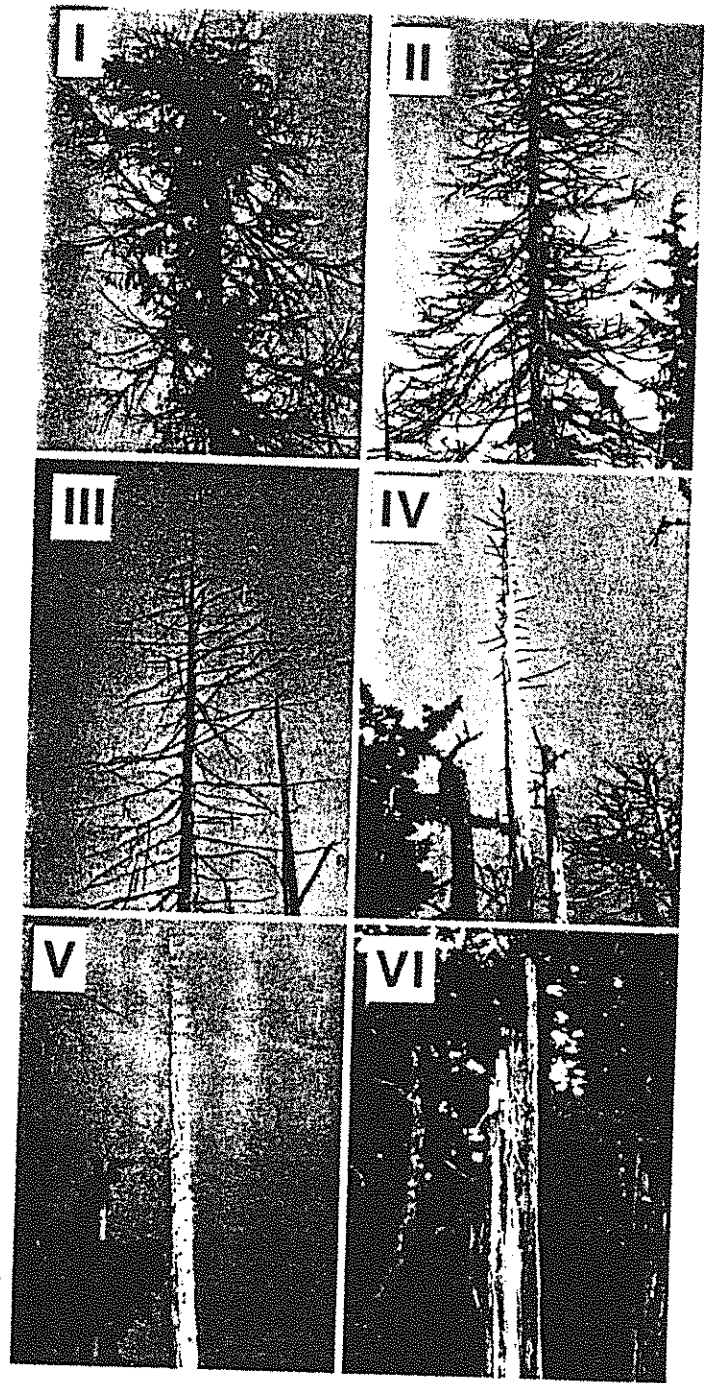


FIG. 4. Six snag classes (I–VI) of dead Alaska-cedar trees based on retention of dead foliage (I), twigs (II), secondary branches (III), or primary branches (IV), and branches not retained but bole intact (V) or deteriorating (VI).

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 of the cedar alive and symptomless were rated as healthy. Plots with more than one-third dead and 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 case of ties, plots were assigned a snag rating equal to

TABLE 1. Increase in area affected by Alaska-cedar decline from 1927 through 1976 on seven sites in southeast Alaska as measured on aerial photographs

Site	1927	1948		1965		1976		Total increase in area 1927-1976 (%)	
	Total area (ha)	Total area (ha)	Increase 1927-1948 (ha/year)	Total area (ha)	Increase 1948-1965 (ha/year)	Total area (ha)	Increase 1965-1976 (ha/year)		
AP1	22.0	28.0	0.29	34.3	0.37	38.7	0.40	76	
AP2	1.1	1.4	0.02	2.5	0.06	3.5	0.09		
AP3	22.4	24.9	0.12	27.2	0.13	28.4	0.11		27
AP4	18.3	20.6	0.11	21.2	0.04	21.6	0.04		18
AP5	19.8	21.5	0.08	24.3	0.16	25.4	0.10		28
AP6	33.7	41.8	0.39	45.8	0.24	48.1	0.21		43
AP7	60.3	64.6	0.20	70.0	0.32	72.6	0.24		20

the longer dead (higher number) class, which best reflects when mortality began for that local area.

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. In 1927, the mortality apparent on each site covered a large portion of the area where trees are now dead and dying. Subsequent mortality has rarely extended more than 100 m beyond the 1927 boundary. This subsequent mortality occurred in all directions (upslope, along the contour, and downslope); however, mortality encroached upslope most commonly. Although spread occurred, the area occupied by mortality in 1927 accounted for most of the area occupied by 1976, except at one site (Table 1). This was the smallest site of decline, and it had active perimeters in all directions. While mortality increased at some sites more than other sites since 1927, the rate of spread for each site did not seem to vary among the intervals of 1927-1948, 1948-1965, and 1965-1976 (Table 1).

On the site mapped intensively at Poison Cove (Fig. 5), 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 mortality in 1976. This central area appeared on recent photographs as a green region contrasting with the grey of peripheral regions with heavy mortality; ground checks showed the presence of surviving hemlocks and vigorous, smaller cedars among the old cedar snags. Mortality fronts apparently stopped at obvious and abrupt changes in forest type.

Along Peril Strait, mortality appeared to be associated with the edges of nearly all open bogs. Some bogs extend, contiguously or in chains, along fairly flat terrain at lower elevations. Mortality was consistently associated with the edges of these bogs, some of which extend over 10 km. Large forested areas without mortality generally lacked bogs and were dominated by high-volume hemlock forests.

Only four bogs found on the aerial photographs in the Peril Strait area lacked adjacent mortality; all four sites were above 150 m elevation and were 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 the 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 to have mortality extending from sea level to above 300 m elevation in a contiguous area of concentrated dead and dying trees.

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. Ordination analysis (DECORANA) of the 55 understory plant taxa from 280 plots produced only one important axis. Only axis I is considered to be important because values for both measures of axis importance, eigenvalues and gradient lengths, fell off sharply and stabilized for the second and subsequent axes. Thus, the eigenvalue and gradient length for axis I were 0.412 and 2.70, respectively, and 0.123 and 1.74, 0.101 and 1.33, and 0.082 and 1.09 for axes II, III, and IV, respectively.

Understory plant taxa are ranked (Table 2) according to their ordination scores from the first axis (axis I). 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 only grew in open bogs (Fig. 6). For example, two species with low ordination scores, *Vaccinium uliginosum* and *Drosera rotundifolia*, occurred predominantly on the edges of pools of water in open bogs. 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* and *Cladanthamnus 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*).

Distribution of conifers along the gradient from bog to better drainage

DECORANA also produced ordination scores for each plot that represent the same gradient from bog (low scores) to better drainage (high scores). Plot ordination scores were compared with tree 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. 7). Shore pine (*Pinus contorta* var. *contorta*) was com-

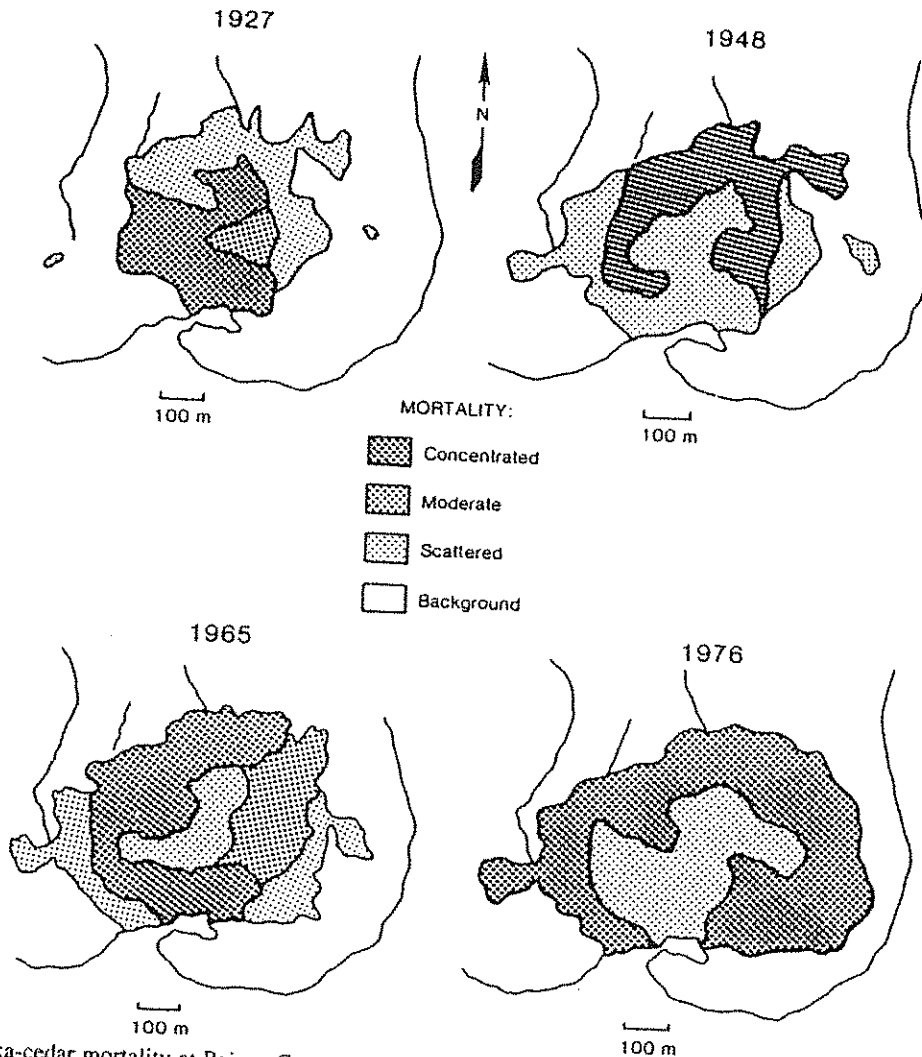


FIG. 5. Maps of Alaska-cedar mortality at Poison Cove based on 1927, 1948, 1965, and 1976 aerial photographs. Severity of mortality was placed into four categories based on densities of dead trees.

mon in the open bogs where total conifer basal area was at a minimum. At the other extreme (better drainage), western hemlock (*Tsuga heterophylla*) was predominant, Alaska-cedar decreased, and shore pine was absent. Sitka spruce (*Picea sitchensis*) also had its greatest basal area on the better-drained sites, but was less common than western hemlock. Mountain hemlock (*T. mertensiana*) had much the same trend as Alaska cedar, but was not a dominant component at lower elevations where most of our sampling was conducted.

Alaska-cedar was rarely missing from plots along the middle portion of the gradient, but cedar trees were often absent in bogs or on well-drained sites. Prostrate Alaska-cedar (e.g., 0.5–1 m tall), not recorded by prisms in the basal area data, were common in bogs and semibogs in the Peril Strait area, even though upright Alaska-cedar trees were not common on these boggy sites. The prostrate form was absent on well-drained sites.

Conifers commonly found dead

Mortality was significantly more common ($P = 0.05$) in bog communities and was progressively less common in communities with better drainage (Fig. 8). Alaska-cedar was the principal species that was dead in stands with a high proportion of mortality, accounting for 74% of the dead basal area

(Table 3). Dead hemlock accounted for 16.8% of the mortality in declining stands, with other species only having negligible dead basal area. The percentage of basal area covered by dead Alaska-cedar in stands not affected by decline (about 23% of its total basal area in these stands) was similar to that recorded for other conifers.

Since Alaska-cedar predominated in most declining stands, the percentage of basal area covered by dead trees 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 (Table 3). Mountain hemlocks were rarely found dying, as determined from thinning or off-green crowns. 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 3).

TABLE 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 taxa	Species ordination score
<i>Vaccinium uliginosum</i> L.	0
<i>Tofieldia glutinosa</i> (Michx.) Pers. ssp. <i>brevistyla</i> Hitchc.	2
<i>Drosera rotundifolia</i> L.	3
<i>Pinus contorta</i> Dougl. ex Loud. var. <i>contorta</i> (seedling)	4
<i>Ledum palustre</i> L. ssp. <i>groenlandicum</i> (Oeder) Hult.	7
<i>Kalmia polifolia</i> Wang	8
<i>Sanquisorba 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 ssp. <i>Langinosum</i> (Bong.) Hult	17
<i>Geum calthifolium</i> Menzies	17
<i>Dodecantheon 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 ssp. <i>glanduliflora</i> (Hook.) Hult.	25
<i>Equisetum</i> spp.	27
<i>Fauria crista-galli</i> (Menzies) Makino	28
<i>Cladothamnus pyrolaeflorus</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. ssp. <i>longiflora</i> (Torr.) Hult.	38
<i>Lysichiton americanum</i> Hult. & St. John	41
<i>Veratum viride</i> (Ait.) Pursh ssp. <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 alaskaense</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> L.	65
<i>Athyrium felix-femina</i> (L.) Roth ssp. <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 ssp. <i>americana</i> (Fisch.) Hult.	83
<i>Echinopanax horridum</i> (Sm.) Decne. & Planch	89
<i>Streptopus roseus</i> Michx. ssp. <i>curvipes</i> (Vail) Hult.	89
<i>Pyrola secunda</i> L. ssp. <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>Corallorrhiza maculata</i> Raf. ssp. <i>Mertensiana</i> (Bong.) Calder & Taylor	100

Neiland (1971) suggested that Alaska-cedar trees decay and deteriorate more slowly than other associated conifers; consequently, more dead Alaska-cedar might accumulate as other tree species deteriorate beyond recognition. If classes IV, V, and VI, in which cedar trees have been dead for 40 years or more (Hennon 1986; Hennon *et al.* 1990a), are excluded from the basal area of dead Alaska-cedar to make data more comparable to the less decay-resistant species, the proportion of Alaska-cedar that was dead (55%) was still substantially higher than other species.

Alaska-cedar was also dying in disproportionate levels in stands with western redcedar: on Prince of Wales Island, 34% of basal area of Alaska-cedar was dead, compared with 9% for western redcedar; on Wrangell Island, 54% of Alaska-cedar was dead, but only 3% for western redcedar. Western redcedar was not a major component of these stands (7% of basal area for Prince of Wales Island and 4% for Wrangell Island), but its decay resistance may be similar to Alaska-cedar, and snags may persist for a similar amount of time (P.E. Hennon, unpublished data).

The frequency of root collar lesions on Alaska-cedar trees was not correlated with azimuth or aspect, but lesions were significantly ($P = 0.05$) more common on cedars with dying crowns (46%) than on 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 constituted 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 mortality has continued at all locations since initiation. Our general reconnaissance revealed only one site 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. 9). Snags with no limbs (class V) predominated in bog plant 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 ($P = 0.05$) in their plot ordination scores. Plots with the longest dead trees (class VI, with deteriorating boles) were uncommon, were not associated with severe mortality, and were not confined to bogs, as were class V snags.

Rope trees (Hennon *et al.* 1984, 1990a) followed the same trend as snags (Fig. 10). Rope trees that had dead tops without limbs (class V) occurred with bog understory plants, whereas those with more recently killed tops occurred on sites with better drained plant communities.

Average heights of dominant and codominant Alaska-cedar trees (dead or live) tended to be greater on plots with primarily healthy trees (21.8 ± 5.5 m) and there was a trend toward shorter trees on plots where cedars had been dead longer (class I, 21.2 ± 4.5 m; class II, 18.9 ± 4.1 m; class III, 17.1 ± 2.9 m; class IV, 17.9 ± 3.8 m; and class V, 13.8 ± 4.7 m (means \pm standard error)).

Discussion

Mortality of Alaska-cedar began on bog and semibog sites in southeast Alaska around 1880 (Hennon *et al.* 1984, 1990a).



Fig. 6. Open bog (muskeg) in southeast Alaska with mortality in adjacent forest.

Subsequent spread of mortality onto better drained sites is confirmed by our survey results and analysis of aerial photographs. The former 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 shorter Alaska-cedar trees, all of which are characteristics of wet, poorly drained sites. These snags represent Alaska-cedar trees that were killed at the beginning of this extensive mortality. The deaths of more deteriorated snags (class VI) likely predate the onset of extensive mortality (Hennon *et al.* 1984), and their occurrence was not associated with sites having large concentrations of dead and dying trees. The excessive level of cedar mortality on sites of decline (65% of cedar has died in the last 100 years), the time required to establish mature cedar trees (nearly all trees are well over 100 years old), and inadequate replacement of cedar by regeneration (Hennon 1986) suggest that intensive mortality could not have been an ongoing phenomenon for centuries.

More recently killed trees (classes I–IV) often surrounded areas of old (class V) mortality. They were associated with understory communities having better drainage, more western hemlock, more total conifer basal area, and taller Alaska-cedar trees, indicating spread into forest types with better drainage.

Sites with a gradient from bog to better drainage had a corresponding gradient of snag classes from V to I, respectively. Spread of mortality within any one site occurred as a slow advance along an established ecological gradient, which was often related to slope. The common upslope spread of mortality resulted from mortality originating in bogs and spreading upslope along the gradient to better drained communities. The

downslope transition to better drained hemlock communities was often abrupt, in contrast with the gradual upslope change. According to the classification scheme developed by Martin (1989), decline generally began in the mixed conifer series and spread to the western hemlock – Alaska-cedar series.

However, spreading patterns were not apparent on all sites expressing mortality. Some stands had an abrupt transition from open bog to better drainage and lacked evidence of spread. Many sites lacked overall spreading patterns because initial mortality was extensive and occurred within a mosaic of overlapping bog and semibog types. Such mortality occurs over large areas. Elongated series of bogs often have an extended band of dead and dying trees, parallel to and upslope from the bogs. Thus, mortality consistently started in bogs and semibogs, regardless of bog shape or size, and subsequently spread locally as far as about 100 m to affect cedars in forest communities with better drainage.

We suggest that this spread of mortality is along a pre-existing environmental and vegetational gradient. Conceivably, the forest community gradient (bog to better drainage) could be a consequence of extensive mortality of Alaska-cedar, the principal overstory tree along the gradient. Understory plant communities may have been changed dramatically during the ensuing 80–100 years because of the death of the cedars. Such an event might explain the association of bog plants with the long-dead class V snags. Our data, however, suggest that bogs, and therefore bog plant communities, were in place well before the onset of Alaska-cedar decline. Most trees of all species, and all Alaska-cedars larger than seedlings, were older than 100 years. The distribution of these trees (i.e., pines associated

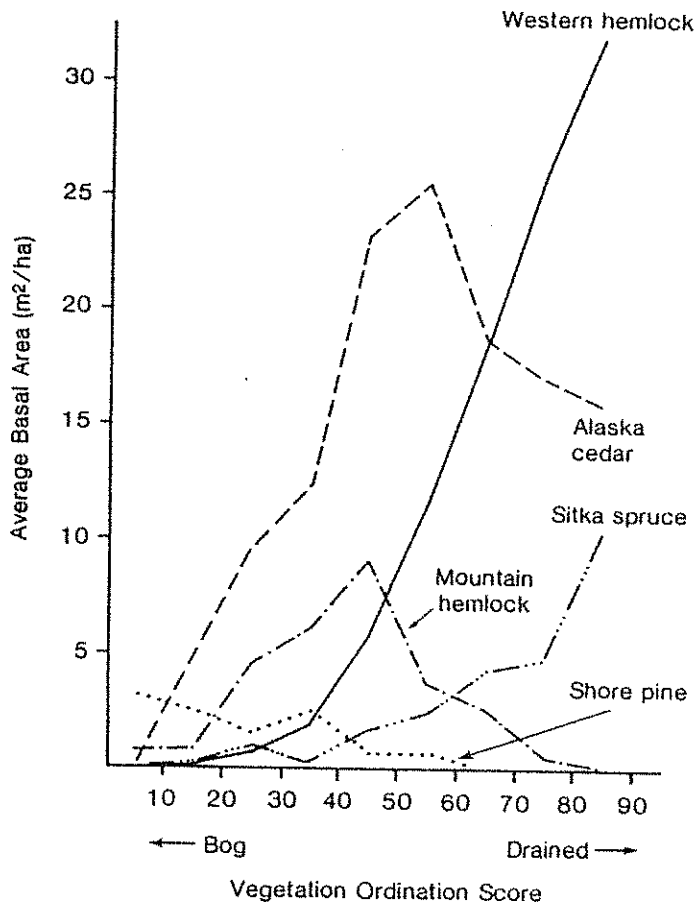


FIG. 7. Average basal area of live conifers along the vegetation gradient (from bogs to sites with better drainage). Ordination scores resulted from a DECORANA analysis of occurrence and distribution of understory species on 280 plots. Mean basal area is plotted for nine equal intervals along the gradient.

with bogs and western hemlock with better drainage) and the heights of Alaska-cedars (shorter in bog stands) are evidence that sites were already bogs or semibogs before extensive mortality began to occur some 80–100 years ago. Furthermore, the few bogs with Alaska-cedar, but lacking cedar mortality, had the same species of bog plants and characteristics of bogs.

Several other forest declines have discernible patterns of local spread. Well-defined waves of mortality spread through stands of *Abies balsamea* (L.) Mill. in mountains of the eastern United States (Sprugel 1976) and through stands of two *Abies* spp. in mountains of Japan (Kohyama 1984). In both cases, mortality waves caused considerable disturbance, which resulted in the same species of conifer regenerating. Subsequent mortality waves occurred when the resulting stands neared their respective life expectancies, about 60 years for *A. balsamea* and 100 years for the two *Abies* spp. in Japan. The causes of these declines have not been conclusively determined, but pathogens have not been implicated.

Spreading mortality can also result from spread of pathogenic organisms. Circular, slowly expanding patterns of mortality and subsequent conifer regeneration are the result of the root rot fungus, *Phellinus weirii* (Murr.) Gilb., in stands of mountain hemlock in Oregon (McCauley and Cook 1980; Waring *et al.* 1987), and of *Armillaria* spp. in several species of conifers in the western United States (Williams *et al.* 1982).

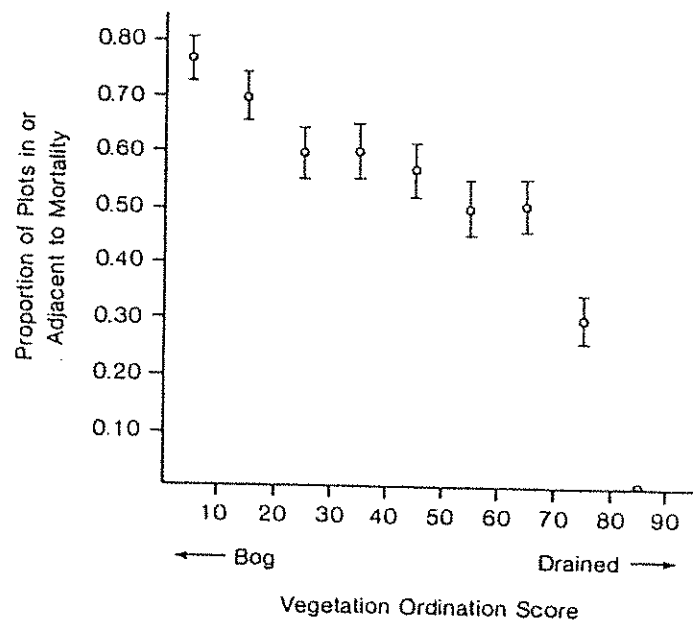


FIG. 8. Frequency of mortality in Alaska-cedar along 9 intervals of the vegetation gradient (from bog to better drainage). Each of 280 plots was designated as within or outside of mortality perimeters based on field observations; χ^2 analysis of ordered proportions = 31.9, $df = 8$.

TABLE 3. Percentage that each conifer species contributed to total basal area of dead conifers and percent of basal area dead for each conifer species

Tree species	Individual species contribution to total basal area of dead conifers (%)	Basal area dead within each conifer species (%) ^a
Sitka spruce	2.7	34.8
Hemlock ^b	16.8	22.3 ^c , 29.7 ^d
Shore pine	0.2	5.9
Alaska-cedar	74.4	65.3
Unknown	5.9	—
Total	100	

NOTE: Data from 92 plots expressing mortality at three sites.

^aPercent dead basal area (BA) = (dead BA ÷ total BA) × 100.

^bSnags of western and mountain hemlock could not be distinguished and are grouped as dead hemlock.

^cPercent dead hemlock = (dead hemlock BA ÷ total hemlock BA) × 100.

^dPercent dead western hemlock = (dead hemlock BA) ÷ (dead hemlock BA + live western hemlock BA) × 100 (assumes that all dead hemlock is western hemlock).

ance and in a new age structure in these stands, but its spread does not follow physical or plant community gradients that existed prior to the mortality, as it does for Alaska-cedar.

Different forest conditions developed where the long-dead (class V) snags had been dead for 80 or more years. A new stand of vigorous-looking 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 (P. E. Hennon, unpublished data) and were probably present as understory conifers during the initial mortality or, in the case of hemlock, are surviving

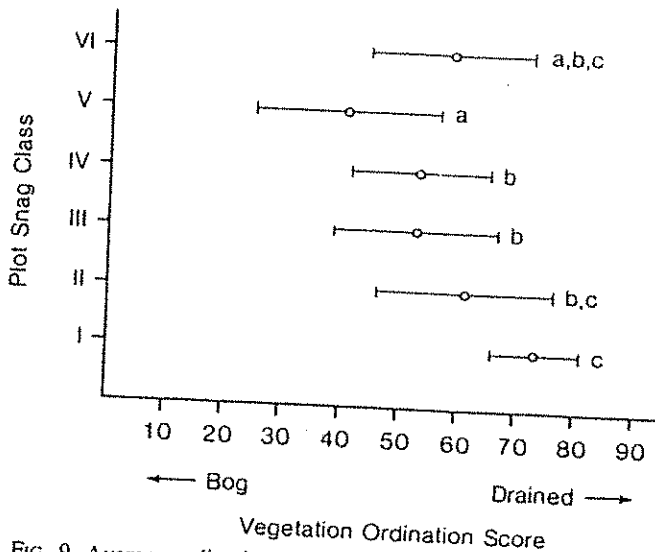


FIG. 9. Average ordination scores (\pm SD) of plots assigned modal snag classes along the vegetation gradient (from bog to better drainage). Modal snag classes were the most commonly occurring snag class on each plot. Snag classes were based on degree of foliage and twig or branch retention. Ordination by DECORANA based on understory from 280 plots. Means followed by different letters differed significantly ($P = 0.05$).

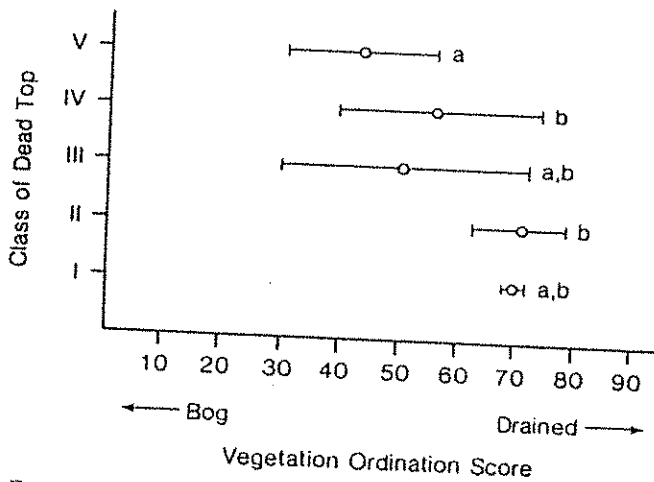


FIG. 10. Average ordination scores (\pm SD) for plots with rope trees that have different classes of dead tops. Understory ordination by DECORANA based on 280 plots. Means followed by different letters differed significantly ($P = 0.05$). Rope trees are Alaska-cedars with dead tops and dead boles, except for a narrow, vertical strip of callus tissue connecting roots to a single live branch cluster (Hennon *et al.* 1990a).

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 recurrence 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. Once the dominant overstory of Alaska-cedars dies, soils may become wetter as reduced transpiration causes a degeneration of the site that may affect the survival or growth of other conifer species (L. Roth, personal communication). Interestingly, tree species suspected of

being relatively intolerant to excessive moisture (Minore 1979; Ruth and Harris 1979) suffered higher rates of death (35% of its basal area for Sitka spruce and 29% for hemlock) than did the tolerant shore pine (6%) on sites of mortality. Alaska-cedar is the exception; the species is reportedly well adapted to wet sites, but it suffered the greatest mortality (65%) in declining stands.

The development from forest to bog requires the waterlogging of the forest floor, which may result from the proliferation of *Sphagnum* moss, the development of poor drainage, or both. This process, paludification (Noble 1984; Klinger 1988), 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. Dachnowski-Stokes (1941) showed evidence that forests encroach on bogs. Zach (1950) and Lawrence (1958) interpreted buried logs as evidence of change from forest to bog. Soil profiles were used to interpret that forests have become bogs (Ugolini and Mann 1979) and that bogs have become forests (Stephens *et al.* 1970) in southeast Alaska. Neiland (1971) reported floristic evidence that forest-bog transitions are proceeding in both directions.

Understanding the process of paludification may help resolve the cause of Alaska-cedar decline. In this paper, we determined that cedars are dying primarily in bog and semibog plant communities; elsewhere (Hennon *et al.* 1990b), we determined that biotic factors are probably not primarily responsible for the widespread mortality. One hypothesis for an abiotic cause of tree death is that bogs, for climatic or other reasons, are advancing onto the adjacent semibog sites where so many trees are dying (Klinger 1988). Our observations, 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. Even if bogs are expanding, the rate of bog expansion is probably too slow to provide a simple explanation for the widespread decline of Alaska-cedar. Also, the relatively high rate of mortality for Alaska-cedar, perhaps one of the conifers best adapted to growing in bogs (aside from shore pine), compared with a lower incidence of mortality for other conifers, contradicts the simple hypothesis of expanding bogs killing cedars.

Another hypothetical explanation for cedars dying around bogs and on wet sites is the poor protection from atmospheric events that these sites offer. Cedar trees on such sites grown in the open and are probably more vulnerable to extreme weather events (e.g., freeze, desiccation) compared with cedars growing within protective canopies. It is conceivable that once some trees die on the edge of a bog site from such a hypothetical weather event, then trees in adjacent forest stands lose protection and become vulnerable to damage, and thus account for slow local spread of mortality from bogs.

Subtle variations in climate may be responsible for triggering some forest declines, such as those of maple, birch, and ash (Weaver 1965). Since climate is not static, vegetation may be constantly adjusting to reflect its new environment (Smith 1970). Interestingly, a warming trend has occurred in most of Alaska since the late 1800s (Hamilton 1965), which coincides with the onset of Alaska-cedar decline. A slight increase in

average temperatures in winter could result in much precipitation occurring as rain rather than snow in southeast Alaska; thus, snowpack would be diminished at low elevations. Perhaps the primary cause of cedar decline is freezing damage to root systems (fine root necrosis is apparently the initial symptom of dying cedars (Hennon *et al.* 1984, 1990b)) during periods when cold continental air moves over the region and roots are inadequately protected by snow. Trees growing in wet soils at low elevations would be susceptible due to their shallow root system (Hennon 1986) and the poor insulation offered by saturated soils. Less decline on wet sites at higher elevations could be explained by the persistent winter snowpack at those elevations, even in today's warmer climate.

The accumulative results from this paper and other research where we studied symptoms of dying trees and tested the pathogenicity of organisms that we isolated from dead and dying trees (Hennon 1986; Hennon *et al.* 1990b) support the hypothesis that an organism is not the primary cause of mortality. The specificity of mortality to Alaska-cedar and evidence of local spread seem to suggest a pathogen-caused disease; however, no new sites of mortality have apparently developed since the nearly simultaneous onset of Alaska-cedar decline some 80–100 years ago (Hennon *et al.* 1984, 1990a) 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 reinitiating the problem on other, similar bog sites. The pattern of local spread, along a preexisting physical gradient, also suggests that a pathogen is not involved.

In his "cohort senescence" concept of forest decline, Mueller-Dombois (1986, 1987) emphasized senescence as an important predisposing factor in the etiology of several declines, including Ohia (*Metrosideros* sp.) in Hawaii, wave mortality of *Abies* spp. in Japan and eastern United States, and several others. He stated that when stands originate from a large disturbance and are comprised of physiologically and genetically similar individuals, they are predisposed for a large dieback (decline) later when the cohort stands eventually become senescent. Others (Hodges *et al.* 1986) stated that even if trees are in a stage of senescence before the onset of decline, external stress is still necessary to initiate decline. Cohort senescence is particularly relevant in forest ecosystems such as southeast Alaska, where fire and other major disturbing factors are uncommon or infrequent and trees are allowed to reach very old ages. The age at which Alaska-cedar might reach senescence is unknown, but it is among trees in North America with the greatest longevity (Harris 1970). Currently, we do not have data on the range of stand or individual tree ages of Alaska-cedar and do not know whether or not they exist as cohort stands; however, small Alaska-cedars (dbh, 6–40 cm) that we sampled for root-excavation or suppression-release studies ranged from 95 to 538 years old. Mature, 700- to 1200-year-old trees are fairly common (Harris 1971). Dendrochronological studies are needed to determine the age structure and possible past episodes of poor growth or decline of stands of Alaska-cedar in southeast Alaska.

Although the primary stress(es) in Alaska-cedar decline is unknown, future research on etiology should focus on abiotic factors, such as properties of wet, organic soils (e.g., soil tox-

ins from anaerobic decomposition) or atmospheric conditions that would affect cedars in bog and semibog communities where trees are poorly protected.

Alaska-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 us the 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 pollution argues against atmospheric deposition as the cause of decline. Additionally, no introduced exotic pathogen or insect (another potential form of human involvement) was found to be associated with decline. Whether or not a general warming trend, perhaps caused by humans, has affected the onset and development of decline, is an open question. Except for the probable abiotic cause, the specific primary stresses in the etiology of Alaska-cedar decline remain a mystery.

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