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Patterns of growth, mortality and biomass change in a coastal *Picea sitchensis - Tsuga heterophylla* forest

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Abstract. Ten years (1979-1989) of growth and mortality were determined in a 130-yr old stand on the Oregon coast based on periodic remeasurements in 44 1000 m^2 plots. Western hemlock (*Tsuga heterophylla*) constituted 90 % of the individuals and 57 % of the biomass. Wind is a major form of disturbance in this area, creating both small discrete and large diffuse disturbance patches; wind therefore has a direct effect on the location and extent of regeneration. Rates of tree mortality were high for this coastal stand (2.8 %/yr), especially compared to similar-aged stands in the western and eastern Cascade Ranges. Though low in absolute density, Sitka spruce (*Picea sitchensis*) persisted in competition with the more tolerant western hemlock. Net production of bole biomass (4.9 Mg ha^{-1} yr^{-1}) did not equal mortality (8.7 Mg ha^{-1} yr^{-1}), and total biomass declined over the 10-yr measurement period from 499 to 460 Mg/ha; this trend may have begun as early as the mid-1950's at a peak biomass of about 600 Mg/ha. The decline may have been due to a positive feedback in which new gaps and enlarging gap perimeters exposed more and more trees to potential wind damage.

Keywords: Bole biomass; Disturbance; Gap; Oregon; Wind.

Nomenclature: Hitchcock & Cronquist (1973).

Introduction

In the western United States natural disturbance and succession occur on both large and small scales. Work in the Pacific Northwest demonstrates that infrequent and catastrophic fires have created large landscape patterns (Hemstrom & Franklin 1982). Within these large patches are smaller patches created by smaller and more frequent fires (Stewart 1986; Morrison & Swanson 1990), windstorms (Veblen 1986; Harcombe 1986; Harcombe, Harmon & Greene 1990; Taylor 1990; Deal, Oliver & Bormann 1991), or insect infestations (Veblen et al. 1989). Disturbance patterns can have a strong effect on stand structure and development (Deal, Oliver & Bormann 1991).

Most studies examining the relationships between natural disturbance and forest dynamics have concentrated on species composition changes over time and space, but biomass change and related patterns of mortality are also important (Peet 1981; Sprugel 1985; Harcombe, Harmon & Greene 1990) and suggest many questions. How long does biomass continue to increase after stand initiation? What is the magnitude of temporal and spatial variation in these forests? How is the variation distributed across a land unit? What role does biomass loss from mortality play in determining temporal and spatial patterns?

Long-term studies of forest change in the Sitka spruce-western hemlock (*Picea sitchensis-Tsuga heterophylla*) zone on the Oregon coast offer an opportunity to examine effects of disturbance on late-successional forests. These long-term studies have been conducted at the Cascade Head Experimental Forest on the Oregon coast in plots established during the 1930s, ’40s, ’60s, and ’70s. This forest system is especially interesting because it is characterized by long-lived individuals, is strongly wind-dominated, and is highly productive (Fujimori et al. 1976; Grier 1978; Ruth & Harris 1979; Sollins 1982; Smith et al. 1984; Hoyer & Swanzy 1986; Harcombe 1986; Harcombe, Harmon & Greene 1990).

Most of these studies have been carried out in the portion of Cascade Head Experimental Forest that is 4 - 5 km inland from the Pacific Ocean, and thus is removed from the direct effects of wind and salt spray. Because much of the *Picea - Tsuga* zone is along the coast, studies of the forest’s susceptibility to the environmental extremes of wind and salt spray are needed to document fully the range of dynamic processes and landscape patterns within this zone. The Neskowin Crest Research Natural Area (NCRNA) on the coastal edge of the Cascade Head Experimental Forest provides an opportunity for such a study. This paper reports changes in populations and biomass, temporal and spatial patterns of ingrowth, mortality, and net production of bolewood on permanent sample plots established in

1979 in a 130-yr old stand. Detailed reconstructions of plot disturbance histories such as those described in the *Picea sitchensis - Tsuga heterophylla* zone of southeastern Alaska by Deal, Oliver & Bormann (1991) were beyond the scope of this paper.

Study site

The *Picea sitchensis - Tsuga heterophylla* zone occupies a narrow strip extending from Coos Bay, Oregon (43° 20' N), to Prince William Sound, Alaska (61° 00' N). It is one of the most productive conifer forest zones in the world (Fujimori et al. 1976). The Neskowin Crest Research Natural Area (476 ha), set aside in 1941 as an example of the coastal Sitka spruce-western hemlock zone, is comprised of mature stands of dense, tall *Picea sitchensis* and *Tsuga heterophylla*, with an occasional Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*) or red alder (*Alnus rubra*). The herb communities of these stands are primarily dominated by *Polystichum munitum*, *Oxalis oregana*, *Blechnum spicant*, *Maianthemum bifolium*, and *Montia siberica*. The dominant shrubs are *Vaccinium parviflorum*, *Menziesia ferruginea*, and *Rubus spectabilis* (Greene 1982).

The climate at NCRNA is temperate and is strongly influenced by proximity of the site to the Pacific Ocean. The nearest weather station, at Cascade Head Experimental Forest headquarters, is several km inland. Rainfall at the headquarters averages 240 cm/yr, falling primarily during the winter months. Temperatures average 13.3 °C; mean January temperature is 5.3 °C; mean July temperature is 25.3 °C. Summer drought, typical of most of the Pacific Northwest, does not occur because fog drip is common in summer. In the winter strong ocean winds from the southwest prevail, although east winds do occur periodically.

NCRNA occupies a rugged headland dissected by numerous drainages. Slopes are generally steep and the entire area is bisected by a north-south trending ridge (Fig. 1). Elevation ranges from sea level to 415 m. Tops of the ocean cliffs - the lowest elevations with forests - are 45 to 75 m above sea level.

The soils at NCRNA are inceptisols. They developed from tuffaceous siltstones with some local modification from basalt bedrock outcrops. Soils are finely textured, moderately well-drained, strongly acid, and high in nitrogen and organic matter (Greene 1982).

The forest here originated after the Nestucca Fire, which burned sometime between 1845 and 1849 (Morris 1934; Munger 1944). It is not known for sure whether the fire was human-caused or not. The fire apparently started on the west side of the Willamette Valley and was pushed west over the Coast Range by strong east winds, burning 142 000 - 152 000 ha. Munger (1944) reported no evidence of subsequent fires in the Cascade Head area. Scattered individual trees on ridges and along drainages predate the Nestucca Fire. In recent years (at least since the 1940's) wind storms during fall and winter have been the major form of disturbance in NCRNA.

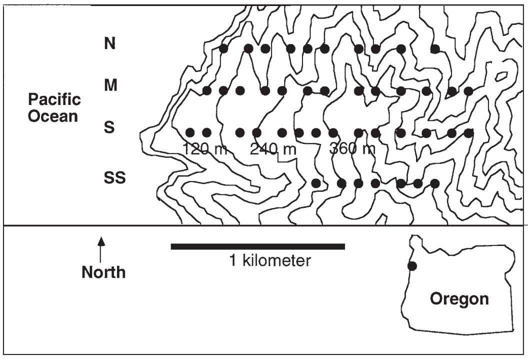

Fig. 1. Topographic map showing plot locations arranged in rows (transects). Transects are labeled N, M, S, SS, from north to south. Contour interval is 60 m.

Methods

In 1978 - 1979, 44 permanent sample plots were established at 200-m intervals along four east-west transects in NCRNA. The transects, 400 m apart, cross the ridge that runs north/south through the center (Fig. 1). All trees ≥ 5 cm diameter at breast height (dbh) were tagged on 1000 m^2 slope-corrected circular plots ranging in elevation from 125 to 390 m. The number of trees on plots ranged from 6 to 197. All plots were remeasured and trees that grew to be over ≥ 5 cm in diameter (in growth) between measurement periods were tagged in 1984 and 1989.

From 1980 through 1989, annual mortality checks were made in spring by locating every tagged tree on each plot and determining whether the tree was alive or dead. For dead trees, position (i.e. standing, broken, uprooted) and physical or biological conditions that might help explain probable cause of death were recorded. Death by suppression was attributed to standing dead trees in subordinate canopy positions with small, flat-topped crowns. Annual rates of individual mortality were calculated by dividing the number of dead trees in a specific year by the total number of live trees in the previous year. Before analysis, error checking routines were run and corrections were made for missing data. Data files are available upon request from the Oregon State University Forest Science Data Bank.

An optical dendrometer (Grosenbaugh 1963) was used to estimate wood and bark volumes on a subsample of the tagged trees. The subsample, 25 Sitka spruce and 43 western hemlock, was chosen to represent a range of diameters between 30 and 200 cm. Regressions were then constructed for each species between volume (V) and dbh (D) of the form:

$$\ln(V) = \ln B_0 + B_1 \ln(D) \qquad (1)$$

where B_0 and B_1 are regression constants. The correction factor proposed by Baskerville (1972) was used to correct for bias introduced by the logarithmic transformation. Estimates of wood and bark biomass were obtained by using these regressions and wood and bark densities for each species (Table 1).

Biomass calculations were limited to bole and bark components because Harcombe, Harmon & Greene (1990) determined that leaf biomass was overestimated by published regression equations by at least a factor of 2, which would result in large (≈ 50 %) overestimates of total above-ground production. Total live biomass estimates would be less affected by this error; a total biomass expansion factor of 1.31 (Grier 1976) to 1.40 (McKee, LaRoi & Franklin 1982) should be used by those wishing to estimate total live biomass from the biomass data reported here. In this paper, biomass will be used to indicate total bolewood biomass (wood + bark).

Comparison of allometric equation parameters calculated for this site with those from a study 2 - 4 km inland at Cascade Head Experimental Forest (CHEF plots, described in Harcombe, Harmon & Greene 1990) showed that the slope of the biomass vs dbh regression is lower at NCRNA than at CHEF. Trees in this study were shorter for a given diameter by up to 10 m, as might be expected on a more exposed site.

Biomass of a tree at death was estimated by using dbh at the previous measurement. Biomass loss from mortality was calculated as the sum of biomass of all trees that died during an interval. Net primary production (*NPPB*) was calculated as follows:

$$NPPB = dB + M \qquad (2)$$

where dB is the difference in standing live biomass between one measurement period and the next, and M is the biomass of the trees that died during the interval. This method is equivalent to calculating the sum of the biomass increments for all stems that survived a remeasurement interval.

A few *Alnus*, *Thuja* and *Pseudotsuga* were present in the plots, but they represented less than 1% of the total tree population, and so were not included in the analyses. Confidence intervals given in the text are ± 1 standard deviation. Frequency distributions of plot variables (stem density, live biomass, biomass loss from mortality, net primary production; Fig. 2) were generated by grouping values into classes one standard deviation in width. Grouping in this manner was done to avoid biasing the form of the distributions through arbitrary delimitation of size classes. Such standardization also can facilitate comparisons with other studies.

Table 1. Regression coefficients for equations to calculate tree volume (V) in cubic meters (stump, wood and bark) from DBH (D). Regressions were of the form $\log V = B_0 + B_1 \log D$. C = correction factor (see text).

	B_0	B_1	c	r^2	N	Density
Picea sitchensis:						
Wood	– 8.963	2.499	1.077	0.93	27	0.360[1]
Bark	– 10.068	2.089	1.076	0.91	27	0.538[2]
Literature[3]	– 8.263	2.401	1.007	0.98	138	0.369
Tsuga heterophylla						
Woo	– 8.526	2.421	1.014	0.98	41	0.421
Bark	– 9.586	2.083	1.034	0.94	41	0.415
Literature[3]	– 8.497	2.467	1.004	0.98	201	0.420

[1] Maeglin & Wahlgren (1972); [2] Smith & Kozak (1971); [3] Harcombe, Harmon & Greene (1990).

In 1986, tree age determinations were made along the south transect in four areas that had been disturbed by wind in the past 50 yr. The areas were chosen based on familiarity with the transects and by use of air photos. Increment cores or disks were collected at ground level. Some larger trees were cored at breast height. Age of the cores and disks or patterns of release on older trees were used to date storm events and to detect spatial patterns.

Results

Population and community structure

Absolute density of the tree population in 1979 was 438 ± 414 trees/ha, with a range of 60 - 1970 stems/ha. The frequency distribution of stem density among plots was a reverse J-shaped curve (Fig. 2a). *Tsuga* stems comprised 90 % of the total population (Table 2), and 44 % of these stems were in the 10-cm diameter class (Fig. 3). *Picea* was evenly distributed across diameter classes (Fig. 3). Although the density of spruce was low (42 stems/ha), large spruce (> 100 cm) were twice as abundant as large hemlock (14 spruce/ha as opposed to 7 hemlock/ha). Most of the hemlock in the 10-cm diameter class occurred in 15 of the 44 plots; all but one of these plots were on the west side of the ridge, and half of them were on the south transect. The spruce in the 10-cm class were distributed over 11 plots.

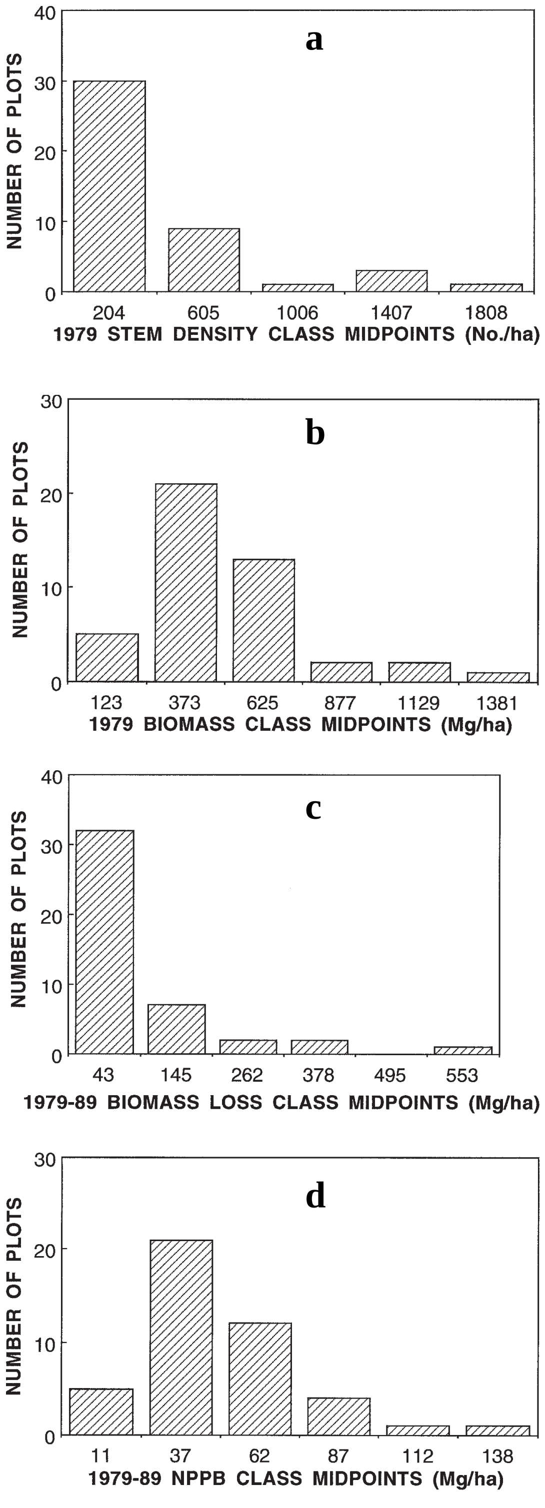

Fig. 2. Frequency distributions of vegetation properties for plots. Abscissa values are class midpoints. Class widths were standardized to 1 SD unit to facilitate comparison and to avoid biasing distribution shapes. a. Stem density; b. Biomass in 1979 (Mg/ha); c. Biomass loss 1979 - 1989 (Mg/ha); d. Net primary production 1979 - 1989 (Mg/ha).

Table 2. Population statistics for *Tsuga heterophylla* and *Picea sitchensis* (slope-corrected).

	Trees stems/ha			Ingrowth trees/ha		Total trees dead/ha	
	1979	1984	1989	1984	1989	1979 - '84	1985 - '89
Tsuga heterophylla	396	420	422	90	48	64	46
Picea sitchensis	42	41	41	2	3	3	3
Total	438	461	463	92	51	67	49

By 1989, density had increased by 25 trees/ha (Table 2). The largest increase was in the 10-cm diameter class for hemlock, primarily on the west side of the ridge. Hemlock stem numbers decreased in the 30-cm to 50-cm diameter classes; the spruce diameter distribution remained essentially constant with a slight increase in the 10-cm diameter class from 1979 to 1989.

Biomass

In 1979, biomass was 499 ± 255 Mg/ha (Table 3), with a range of 108 - 1277 Mg/ha. The frequency distribution of biomass among plots was approximately lognormal (Fig 2b). Although three of the four high-biomass plots were on the west side of the ridge (Fig. 4), a *t*-test showed no significant difference in biomass between the two sides of the ridge. Also, scatterplots showed no relation between biomass and slope steepness or plot aspect. Biomass in 1989 was 460 ± 278 Mg/ha, down from 472 Mg/ha in 1984 and 499 Mg/ha in 1979 (Table 3; $p = 0.05$, repeated measures ANOVA with Greenhouse-Geissen adjustment for non-independence [Anon. 1988]). 24 plots decreased in biomass; the remaining 20 increased. All of the decline between 1979 and 1989 was in hemlock.

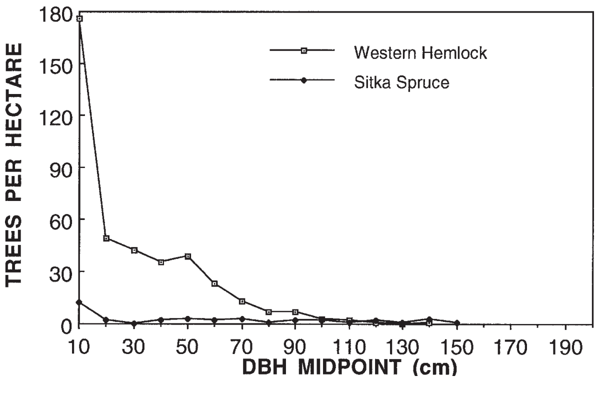

Fig. 3. Diameter distribution in trees/ha for *Picea sitchensis* and *Tsuga heterophylla* in 1979. Abscissa values are diameter class midpoints.

Table 3. Total bolewood biomass, biomass loss to mortality, ingrowth biomass and net primary production of bolewood in each measurement interval.

	Biomass Mg/ha			Mortality Mgha^{-1}yr^{-1}		Ingrowth Mgha^{-1} yr^{-1}		*NPPB* Mgha^{-1}yr^{-1}	
Species	1979	'84	'89	'80 -84	'85 -'89	'80 '84	'85 -'89	'80 -'84	'85 -'89
Tsuga heterophylla	285	256	245	– 8.9	– 5.4	0.2	0.1	3.2	3.2
Picea sitchensis	214	215	215	– 2.0	– 1.2			2.2	1.2
Total	499	471	460	– 10.9	– 6.6	0.2	0.1	5.4	4.4

Mortality

During the 10-yr period of observation, 487 trees died, which was 26 % of the individuals present at the beginning of the study (Table 2). Annual individual mortality rates varied from 1.1 to 6.6 % (average = 2.8 %). Annual mortality rate of individual hemlock was much higher than for spruce (3.2 % vs 1.6 %).

Wind damage, including broken or uprooted boles, snapped off tops, and boles crushed by falling trees or branches, accounted for 63 % of the mortality. Suppression was the second-most important cause of death accounting for 25 % of all dead trees. A large proportion (70 %) of the suppression mortality occurred in two high-density plots due to intense thinning during crown closure (plot 34) or to overstory shading of a regeneration cohort (plot 5). Mortality was not strongly related to dbh class (Fig. 5); this may reflect the fact that both wind (which affects large stems) and suppression (which affects small stems) are important agents of mortality.

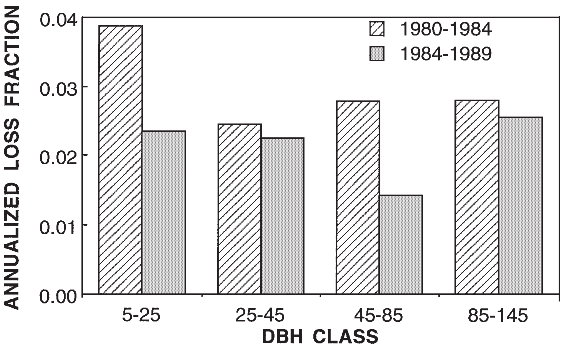

Fig. 5. Site-specific mortality of *Picea sitchensis* and *Tsuga heterophylla*. Class widths were increased from small to large because of low numbers of individuals in large classes.

The increment core data, obtained in a large area of blowdown on the south transect, indicated several episodes of wind-related mortality before plot establishment. Cores from plots 31 and 34 showed release, establishment or both after the storms of the 1960s (Fig. 6). East of plots 33 and 34, establishment and release occurred more gradually as a result of earlier storms (Fig. 6). The south and west edges of plot 33 were exposed to a blowdown patch that started before 1979 but continued to expand thereafter. Ingrowth along the edges of plot 33 also resulted from tree release after these storms. Plot 35 suffered heavy mortality from wind several times after plots were established in 1979. Appearance of ingrowth stems within 10 years suggested that advance regeneration was released in the plot.

Annual biomass loss from mortality ranged from 1.4 Mg/ha in 1981 to 21.9 Mg/ha in 1982 (Fig. 7). Nearly half of the biomass loss occurred as a consequence of storms in the winters of 1981-82 and 1983-84.

Although 86% of the plots experienced mortality, the distribution of biomass loss among plots was highly

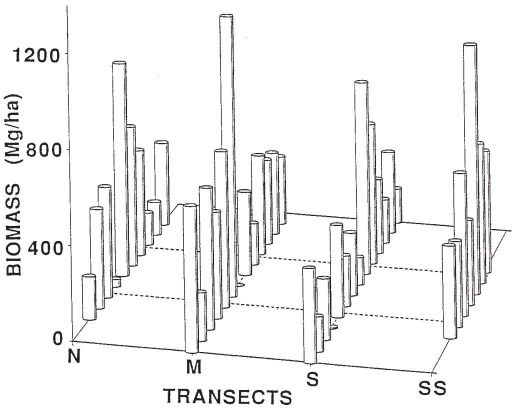

Fig. 4. Spatial distribution of plot biomass in 1979 across the ridge. Transect lines run east-west as in Fig. 1.

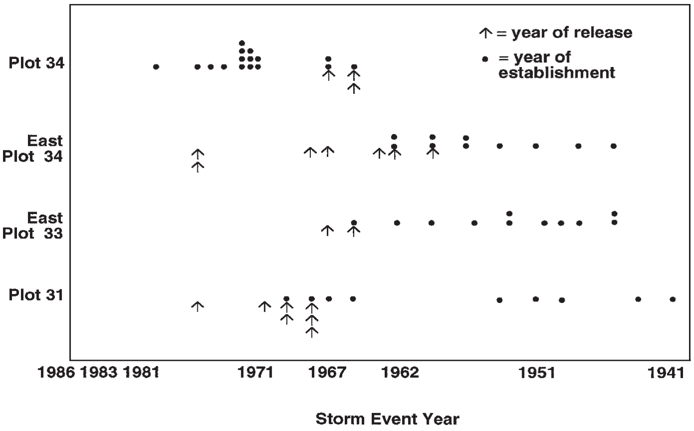

Fig. 6. Year of establishment or (approximate) growth release for selected trees. Dates on abscissa mark known storm events. Plots 31, 33 and 34 were all located on the western end of the south transect. 'East Plot 33' and 'East Plot 34' were sampling areas in blowdown patches ca. 50 m east of plots 33 and 34.

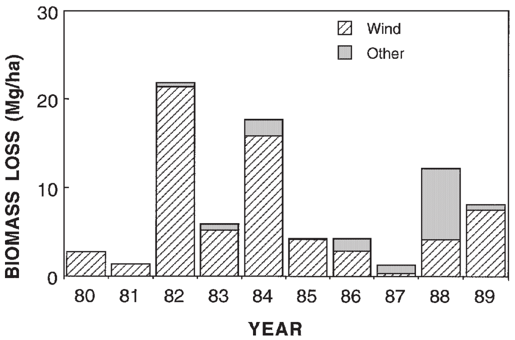

Fig. 7. Annual bolewood mortality by cause (Mg/ha).

skewed (Fig. 2c), with most plots losing relatively little, and 7 plots losing from 50 to 85 % of their initial biomass. This high loss did not occur in single wind storms, but was spread over several years. For the 7 plots with high mortality (> 15 Mg ha^{-1} yr^{-1}), every plot experienced mortality at least twice, and some experienced mortality in as many as 8 of the 10 yrs of observations. The largest single mortality event was the loss of 334 Mg/ha (50 % of 1979 biomass) from plot 13 during the 1983 wind storm. Over the 10-year period, this plot sustained the greatest biomass loss from mortality (581.5 Mg/ha; 85 % of initial biomass).

Biomass loss was not significantly correlated with slope, aspect, or initial plot biomass, though the plots on the west side of the ridge did sustain somewhat greater mortality (10.5 ± 14.3 Mg ha^{-1} yr^{-1} vs 6.3 ± 8.7 Mg ha^{-1} yr^{-1}; Fig. 8). The lack of a significant effect of plot biomass, aspect, or slope position on mortality suggested that either historical differences among plots obscured such effects or the topographic position effects cited by others (e.g. Ruth & Harris 1979; Foster 1988) only appear at larger landscape scales.

Ingrowth

Average annual ingrowth was 14 trees ha^{-1} yr^{-1}, adding about 0.2 Mg ha^{-1} yr^{-1} of biomass (Tables 2 and 3). Mean ingrowth over 10 yr was 142 ± 469 stems/ha with a range among plots of 0 - 2740 stems/ha. Ingrowth biomass was concentrated on three plots: 33 % on 34, 22 % on 31, and 12 % on 33. The coring study, concentrated on or near the same three plots, showed that trees were established, released or both over a long period (Fig. 6). Hemlock comprised 96 % of the ingrowth, which is consistent with the fact that 90 % of stems present in 1979 were hemlock (Table 2). Spruce ingrowth occurred in 16 % of the plots in sufficient numbers to replace dying trees almost exactly (24 ingrowth vs 25 dead over 10 yr).

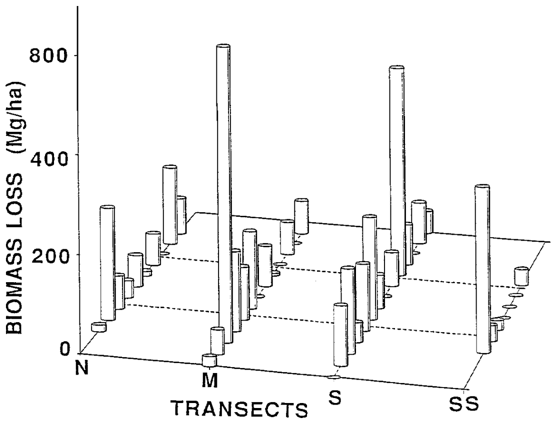

Fig. 8. Spatial distribution of total mortality loss by plot for the period 1979-1989. Transect lines run east-west as in Fig 1.

Net primary production

Total net primary production (*NPPB*) over the 10-year period was 4.9 ± 2.7 Mg ha^{-1} yr^{-1}. *NPPB* ranged from 1.4 to 15.2 Mg ha^{-1} yr^{-1} and exhibited an approximately lognormal distribution (Fig. 3d). Variation in NPPB was not significantly correlated with slope, aspect, or plot biomass. However, four of the five plots with highest production were among the highest in biomass and the lowest in mortality. The 5th, plot 34, was low in initial biomass, but highest in production, because it contained a young, vigorous stand of hemlock approaching crown closure.

Variability was high in almost all community- and ecosystem-scale characteristics. Frequency distributions (Fig. 2) fell into two general classes, approximately negative exponential distributions and approximately log-normal distributions. The characteristics displaying negative exponential distributions are the ones most sensitive to disturbance (biomass loss via mortality, ingrowth and stem density), which is more or less random. The ones with a stronger central tendency (biomass and net primary production) are a product of the aggregate behavior of individuals, and thus are not so sensitive to random events.

Discussion

NCRNA is at the extreme end of a wind disturbance gradient that starts at the Oregon coast and declines steeply in severity inland to the east side of the Oregon Cascade Range (Harmon et al. 1986). Over half the plots lie on the west side of a ridge facing the Pacific Ocean where they are annually exposed to winter wind storms (Fig. 1). This gradient is important to keep in mind, especially in comparing the NCRNA plots to the CHEF spruce-hemlock plots (Harcombe, Harmon & Greene 1990), 2 - 4 km to the east. Although the two sets of plots are very close to each other and the stands originated after the same fire, they are different in many respects.

Mortality

Individual mortality rates were high at NCRNA (2.8 % per year) compared to other stands in the Pacific Northwest. Harcombe (1986) calculated an individual mortality rate of 0.99 %/yr for spruce and 1.03 %/yr for western hemlock for the nine 0.4-ha CHEF plots. For 30-yr to 50-yr old plots in southeast Alaska (Deal, Oliver & Bormann 1991) annualized mortality was 1.19 %/yr for spruce and 1.68 %/yr for hemlock. The mortality rate of old-growth spruce-hemlock stands on the Olympic Peninsula of Washington was 1.1 % over 7 yr (M. E. Harmon pers. comm.). The average rate for old-growth Douglas-fir stands in the western Cascade Range was 0.5 % (Franklin & DeBell 1988). Annual mortality was 1.23 - 1.26 % in old-growth eastern deciduous forests (Abrell & Jackson 1977; Parker, Leopold & Eichenberger 1985) and 1.02 - 2.03 % in tropical forests (Lieberman et al. 1985).

Biomass loss from mortality was also relatively high at NCRNA. The biomass loss was half again that of the nearby CHEF plots [8.7 Mg ha^{-1} yr^{-1} vs 5.8 Mg ha^{-1} yr^{-1} (Harcombe, Harmon & Greene 1990)] and nearly triple that of mature productive conifer forests [3.2 Mg ha^{-1} yr^{-1} (Harmon et al. 1986)]. The wind gradient between NCRNA and CHEF was steep; wind accounted for 63 % of individual mortality at NCRNA compared to 46 % at CHEF. Wind only accounted for 17 - 47% of individual mortality for *Pseudotsuga menziesii-Tsuga heterophylla* forests in the Oregon Cascade Range, and 10 - 18 % for ponderosa pine (*Pinus ponderosa*) forests (Avery, Larson & Schubert 1976; Franklin, Shugart & Harmon 1987).

The high percentage (25 %) of suppression mortality might lead to the conclusion that NCRNA is in an early stage of succession. In fact, the size distributions, net rates of population change and biomass increment indicated that this forest was comprised of many developmental stages. Recurring wind disturbance provides a constant source for new ingrowth, which in turn becomes susceptible to suppression mortality through competition (e.g. plot 34) or overstory shading (e.g. plot 5).

Spatial patterns of mortality

Mortality has created a complex spatial pattern in the canopy at NCRNA. Canopy openings in forests occur in myriad forms in natural systems (Pickett & White 1985; Deal, Oliver & Bormann 1991), but classifying them according to scale, intensity and frequency into three classes – ‘catastrophe’, intermediate disturbance, and single-tree gap formation – is often convenient. Blowdown areas in NCRNA on the mid-to-upper slopes, particularly on the east side, tend to be small, often 1 - 2 trees in size. These areas fit a gap-phase model; stable populations and near-maximum biomass are consistent with this model. Concentration of blowdown in some plots within large blowdown patches on the west side is more consistent with an intermediate or large-scale (catastrophic) disturbance model, however. These blowdown areas originated at least 45 yr ago (Fig. 6; see also Taylor 1990), but they were not instantaneous; some patches and individuals remained. Wind has continued to kill trees within the blowdown areas (e.g. plots 13, 32, 35), and the perimeters of the areas continue to expand making the blowdown areas larger and more distinct.

The wide variation among plots and among years in mortality loss at NCRNA supports Lieberman, Lieberman & Peralta (1989) in their rejection of the assumption that disturbance is discrete and instantaneous, creating patches of uniform age. The NCRNA data showed that disturbances were mostly small to intermediate, but were spatially clumped so that some coalesced into larger blowdown patches with repeated disturbance. This pattern also occurs elsewhere (Harcombe 1986; Glitzenstein & Harcombe 1987; Veblen et al. 1989; Harcombe, Harmon & Greene 1990; Deal, Oliver & Bormann 1991; Ogden et al. 1991; Liu & Hytteborn 1991). The forested areas tend to become as heterogeneous as the large blowdown patches, and this pattern is the background against which new disturbances occur.

Ingrowth

Ingrowth was concentrated spatially in areas with severe wind damage in the past. Plots 34, 31, and 33 contained 78 % of all ingrowth stems in the 10-yr period (44, 26, and 8 % respectively), while most plots had little or no ingrowth. Results of the coring study and lack of a significant correlation between 1985 - 1989 ingrowth and 1979 - 1984 mortality indicated that ingrowth lagged behind mortality by more than 5 yr, and was usually a combined response of recruitment of new stems and release of advance regeneration.

Persistence of Picea sitchensis

Because of its greater shade tolerance, *Tsuga* is often considered to eventually replace *Picea* (Fonda 1974; Ruth & Harris 1979; Franklin & Dyrness 1988). Diameter distributions (Fig. 3) for the two species at NCRNA showed much higher density of small hemlock, and hemlock comprised a much greater percentage of the ingrowth than did spruce. This difference might be taken to indicate that hemlock is replacing spruce, but ingrowth of spruce actually balanced mortality over the last decade. Furthermore, Sitka spruce absolute biomass was constant over the 10 yr, and relative biomass even increased from 43 to 47 %. Hemlock had higher recruitment, but mortality was also higher, so hemlock stems were turning over at two to three times the rate of spruce. Thus, the differences in size distributions and recruitment rates do not necessarily indicate replacement of spruce by hemlock. Rather, 10 yr of demographic data suggest that spruce is a stable component of this forest, in spite of its low recruitment rate. Persistence of spruce was also found in forests dominated by hemlock regeneration in SE Alaska (Alaback 1982; Deal, Oliver & Bormann 1991). This situation is similar to that of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) in the Rocky Mountains (Veblen 1986). Veblen's static estimates of population turnover suggest coexistence between a species with high recruitment and mortality and a species with low recruitment and low mortality. Our data on population dynamics provided even stronger support for the coexistence of two species with different life histories.

Harcombe (1986) attributed persistence of spruce in the CHEF plots to low mortality and longevity of the species. The importance of longevity to persistence is graphically illustrated by Franklin & DeBell (1988), who calculated that Douglas-fir - another shade-intolerant, large, long-lived species - can persist for over 1000 yr. An additional factor favoring spruce persistence in this study may be shade tolerance, spruce being somewhat tolerant in the southern end of its range (Ruth & Harris 1979). Finally, according to Taylor (1990) spruce can colonize and even dominate large gaps in this forest. Hence, the high rate of blowdown further contributes to spruce persistence in competition with hemlock.

Biomass dynamics

Over the last decade the biomass dynamics of NCRNA and the CHEF plots have been very different: biomass at NCRNA has declined approximately 7 % to 460 Mg/ha, while CHEF plots have remained at about 750 Mg/ha (Harcombe, Harmon & Greene 1990). Given the similarity in species and climate, why are these adjacent areas so different? Site quality is frequently offered as an explanation for differences in stand production and biomass. However, a 1935 timber cruise (DeGroote & Isaac 1938) indicated that NCRNA biomass was only 5 - 10 % less than that of the CHEF biomass, suggesting that site quality differences were not large. Moreover, the measured *NPPB* over the last decade on the two sites is very similar (4.9 Mg ha^{-1} yr^{-1} at NCRNA vs 5.2 Mg ha^{-1} yr^{-1} at CHEF).

Although the two sites are very similar in NPPB, mortality loss rates over the last decade (8.7 Mg ha^{-1} yr^{-1} vs 6.3 Mg ha^{-1} yr^{-1} at CHEF) have been different. This difference, if it persisted over a long period, could cause the observed difference in biomass. A higher frequency and intensity of winds at NCRNA than at CHEF would explain the difference in mortality loss rates between the two sets of plots. The NCRNA plots are adjacent to the Pacific Ocean where winter winds can be severe. In contrast, the CHEF plots are more protected from wind by virtue of their location 2-4 km inland.

Many models of vegetation dynamics, e.g. ALLOCATE of Tilman (1988), JABOWA/FORET of Botkin, Janak & Wallace (1972; Shugart 1984) assume biomass accumulation is limited by mortality. The evidence presented here supports the assumption. It also supports the argument that mortality can determine maximum stand biomass (Harcombe, Harmon & Greene 1990).

The observed decline in biomass over the last decade is consistent with the observation that mortality exceeds production. However, it raises the question of how long biomass has been declining at NCRNA. We attempted to answer this question by evaluating three possible scenarios of stand biomass change over time.

The first and simplest scenario assumes that biomass increased at the same rate as at CHEF and then began to decline uniformly at the present rate. The date and value for peak biomass were obtained by extending the line connecting 1979 and 1989 biomass back in time until it crossed the CHEF biomass curve. This occurred in the mid 1950s at a peak biomass of 600 Mg/ha. That is, NCRNA biomass has declined by as much as 25 % in the last 40 yr. The second scenario assumes that biomass declined at a uniform rate from the 1930s when NCRNA and CHEF had similar bole biomass (530 Mg/ha estimated from volume data in DeGroote & Isaac 1938). That is, biomass declined by 13 % over 60 yr. This scenario implies low mortality of 0.7 Mg ha^{-1} yr^{-1} between 1935 and 1979, followed by a 5-fold increase after 1979. Either of these scenarios is consistent with National Weather Service records which document five major storms along the Oregon coast since 1940 (Anon. 1951; 1962; 1963; 1967; 1971) and our observation that two major storms occurred in the last 10 yr. The third, and most unlikely scenario is that biomass at NCRNA increased until the 1970s, as it did at CHEF, and then declined rapidly from about 760 Mg/ha to about 460 Mg/ha, a 60 % reduction in just a few years.

Although we cannot eliminate any of the three scenarios with the data presented in this paper, the accumulation of dead wood in these plots may hold the key to answering these questions. For example, a large mortality pulse in the late 1970s should have left a large number of dead trees on the forest floor. No such accumulations of fresh wood were apparent at the time of plot establishment, suggesting that the third scenario is incorrect. A more detailed examination of amount and decay state of dead trees at NCRNA should make it possible to distinguish among the remaining two scenarios.

Our data suggest that biomass accumulation may be limited by wind disturbance and that biomass may actually decline due to a positive feedback of blowdown upon canopy opening. The canopy of the forest apparently began to break up earlier at NCRNA than in the CHEF plots, increasing surface roughness that in turn made the forest more vulnerable to the effects of future windstorms, and causing a progressive increase in mortality rate, exactly as predicted (Ruth & Harris 1979; Bormann & Likens 1979; Foster 1988). Our simple stand projections suggest that the biomass decline may have approached 25% at NCRNA, a value greater than we previously predicted for the more protected CHEF spruce-hemlock plots nearby (Harcombe, Harmon & Greene 1990). Though we find support for the conclusion that the biomass decline at NCRNA is part of a longer-term trend, the scenarios we propose must be regarded as hypotheses to be tested through further stand dynamics studies, continued long-term data collection at NCRNA, and measurements of coarse woody debris.

Conclusions

In a coastal *Picea sitchensis - Tsuga heterophylla* forest wind disturbance was very important, not only killing a majority of trees but determining the location and extent of canopy recruitment as well as the dynamics of biomass accumulation during stand development. Although disturbance regimes in mature forests are often classified as small-scale or large-scale, disturbance can span the full range from individual tree gaps to large blowdown areas. An initial small canopy opening may expand and join adjacent small openings to form eventually a larger, indistinct patch. A consequence of this process, characteristic of forests exposed to chronic wind storms, may be an early peak in biomass at a relatively low value, followed by a decline in biomass.

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References

Anon. 1951. *Climatological data: Oregon. San Francisco, CA.* 57(12): 228. US Department of Commerce.

Anon. 1962. *Climatological data: Oregon. San Francisco, CA.* 68(10): 174-175. US Department of Commerce.

Anon. 1963. *Climatological data: Oregon. San Francisco, CA.* 69(3): 40. US Department of Commerce.

Anon. 1967. *Climatological data: Oregon. San Francisco, CA.* 73(10): 184. US Department of Commerce.

Anon. 1971. *Climatological data: Oregon. San Francisco, CA.* 77(3): 42. US Department of Commerce.

Anon. 1988. *SAS/STAT User's Guide, Release 6. 03 Edition.* Cary, NC: SAS Institute Inc.

Abrell, D. B. & Jackson, M. T. 1977. A decade of change in an old-growth beech-maple forest in Indiana. *Am. Midl. Nat.* 98: 22-32.

Alaback, P. B. 1982. Forest community structural changes during secondary succession in southeast Alaska. In: Means, J. (ed.) *Forest succession and stand development research in the Northwest,* pp. 70-79. For. Res. Lab., Oregon State Univ., Corvallis, OR.

Avery, C. C., Larson, F. R. & Schubert, G. H. 1976. *Fifty-year record of virgin stand development in southwestern ponderosa pine.* USDA For. Serv. Gen. Tech. Rept., RM 22.

Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.* 2: 49-53.

Bormann, F. H. & Likens, G. E. 1979. *Pattern and process in a forested ecosystem.* Springer-Verlag, New York.

Botkin, D. B., Janak, J. F. & Wallis, J. R. 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60: 849-873.

Deal, R. L., Oliver, C. D. & Bormann, B. T. 1991. Reconstruction of mixed hemlock-spruce stands in coastal southeast Alaska. *Can. J. For. Res.* 21: 643-654.

DeGroote, L. H. & Isaac, L. A. 1938. *Cascade Head Experimental Forest: topographic and timber survey.* USDA For. Serv., Forestry Sciences Laboratory, Corvallis, OR.

Fonda, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecology* 55: 927-942.

Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England. U. S. A. *J. Ecol.* 76: 135-151.

Franklin, J. F. & DeBell, D. S. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. *Can. J. For. Res.* 18: 633-639.

Franklin, J. F. & Dyrness, C. T. 1988. *Natural vegetation of Oregon and Washington.* Oregon State Univ. Press, Corvallis, OR.

Franklin, J. F., Shugart, H. H. & Harmon, M. E. 1987. Tree death as an ecological process. *BioScience*. 37: 550-556.

Fujimori, T., Kawanabe, S., Saito, H., Grier, C. C. & Shidei, T. 1976. Biomass and primary production in forests of three major vegetation zones of the northwestern United States. *J. Jap. For. Soc.* 58: 360-373.

Glitzenstein, J. S. & Harcombe, P. A. 1987. Effects of the December 1983 tornado on forest vegetation of the Big Thicket, Southeast Texas, U.S.A. *For. Ecol. Manage.* 25: 269-290.

Greene, S. 1982. *Neskowin Crest Research Natural Area.* Guidebook Supplement 13. USDA For. Serv., Pac. Northwest Res. Stn., Portland, OR.

Grier, C. C. 1976. Biomass, productivity, and nitrogen-phosphorous cycles in hemlock-spruce stands of the central Oregon coast. In: Atkinson, W. A. & P. J. Zasaki (eds.) *Western hemlock management*, pp. 71-78. Univ. Washington, Inst. For. Prod. Contrib. 21.

Grier, C. C. 1978. A *Tsuga heterophylla-Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Can. J. For. Res.* 8: 198-206.

Grosenbaugh, L. R. 1963. Optical dendrometers for out-of-reach diameters, a conspectus and some new theory. *For. Sci. Monogr.* 4.

Harcombe, P. A. 1986. Stand development in a 130-year-old spruce-hemlock forest based on age structure and 50 years of mortality data. *For. Ecol. Manage.* 14: 41-58.

Harcombe, P. A., Harmon, M. E. & Greene, S. E. 1990. Changes in biomass and production over 53 years in a coastal *Picea sitchensis-Tsuga heterophylla* forest approaching maturity. *Can. J. For. Res.* 20: 1602-1610.

Harmon, M. E. et al. 1986. Ecology of coarse woody debris in ecosystems. *Adv. Ecol. Res.* 15: 133-302.

Hemstrom, M. A. & Franklin, J. F. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. *Quat. Res.* 18: 32-51.

Hitchcock, C. L. & Cronquist, A. 1973. *Flora of the Pacific Northwest.* University of Washington Press, Seattle.

Hoyer, G. & Swanzy, J. D. 1986. *Growth and yield of western hemlock in the Pacific Northwest following thinning near the time of initial crown closing.* USDA For. Serv., Pac. Northwest Res. Stn. Res. Pap. PNW-356. Portland, OR.

Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G. S. 1985. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *J. Ecol.* 73: 915-924.

Lieberman, M., Lieberman, D. & Peralta, R. 1989. Forests are not just swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70: 550-552.

Liu Qinghong & Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *J. Veg. Sci.* 2: 391-402.

Maeglin, R. R. & Wahlgren, H. E. 1972. *Western wood densities survey.* USDA For. Serv. For. Prod. Lab. Report No. 2. Res. Pap. FPL-183.

McKee, A. W., LaRoi, G. & Franklin, J. F. 1982. Structure, composition and reproductive behavior of terrace forests, South Fork Hoh River, Olympic National Park. In: Starkey, E. E., Franklin, J. F. & Matthews. J. W. (eds.) *Ecological Research in National Parks of the Pacific Northwest*, pp. 22-29. For. Res. Pub., For. Res. Lab., Oregon State Univ., Corvallis, OR.

Morris, W. G. 1934. Forest fires in western Oregon & western Washington. *Oreg. Hist. Quart.* 35: 313-339.

Morrison, P. H. & Swanson, F. J. 1990. *Fire history and pattern in a Cascade Range landscape.* USDA For. Serv. Pac. Northwest Res. Stn., Portland, OR, PNW-GTR-254.

Munger, T. T. 1944. Out of the ashes of the Nestucca. *Amer. For.* 50: 342-345, 366-368.

Ogden, J., Fordham, R. A., Pilkington, S. & Serra, R. G. 1991. Forest gap formation and closure along an altitudinal gradient in Tongariro National Park, New Zealand. *J. Veg. Sci.* 2: 165-172.

Parker, G. R., Leopold, D. J. & Eichenberger, J. K. 1985. Tree dynamics in an old-growth, deciduous forest. *For. Ecol. Manage.* 11: 31-57.

Peet, R. K. 1981. Changes in biomass and production during secondary forest succession. In: West, D. C., Shugart, H. H. & Botkin, D. B. (eds) *Forest Succession: Concepts and Approaches*, pp. 325-338. Springer-Verlag, New York.

Pickett, S. T. A. & White, P. 1985. Patch dynamics: a synthesis. In: Pickett, S. T. A. & White, P. (eds) *The ecology of natural disturbance & patch dynamics*, pp. 371-384. Academic Press, New York.

Ruth, R. H. & Harris, A. S. 1979. *Management of western hemlock-Sitka spruce forests for timber production.* USDA For. Serv. Gen. Tech. Rept. PNW-88. Portland, OR.

Shugart, H. H. 1984. *A theory of forest dynamics.* Springer-Verlag, New York.

Smith, J. G. H. & Kozak, A. 1971. Thickness, moisture content, and specific gravity of inner and outer bark of some Pacific Northwest trees. *For. Prod. J.* 21: 38-40.

Smith, S. H., Bell, J. F., Herman, F. R. & See, T. 1984. *Growth and yield of Sitka spruce and western hemlock at Cascade Head Experimental Forest, Oregon.* USDA For. Serv. Res. Pap. PNW-325.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* 12: 18-28.

Sprugel, D. G. 1985. Changes in biomass components through stand development in wave-regenerated balsam fir forests. *Can. J. For. Res.* 15: 269-278.

Stewart, G. H. 1986. Population dynamics of a montane conifer forest, western Cascades Range, Oregon, USA. *Ecology* 67: 534-544.

Taylor, A. H. 1990. Disturbance and persistence of Sitka spruce [(*Picea sitchensis* (Bong. Carr.)] in coastal forests of the Pacific Northwest, North America. *J. Biogeogr.* 17: 47-58.

Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities.* Princeton Univ. Monographs in Population Biology 26. Princeton University Press, Princeton, NJ.

Veblen, T. T. 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology* 67: 644-649.

Veblen, T. T., Hadley, K. S., Reid, M. S. & Rebertus, A. J. 1989. Blowdown and stand development in a Colorado subalpine forest. *Can. J. For. Res.* 19: 1218-1225.

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