

## STAND DEVELOPMENT IN A 130-YEAR-OLD SPRUCE—HEMLOCK FOREST BASED ON AGE STRUCTURE AND 50 YEARS OF MORTALITY DATA

P.A. HARCOTBE

*Biology Department, Rice University, Houston, TX 77001 (U.S.A.)*

(Accepted 12 August 1985)

### ABSTRACT

Harcotbe, 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.

Influences on forest stand development were assessed using tree age and long-term mortality data in ten 0.4 ha permanent plots established in 1935. The stand originated following a major fire in the 1840s with a period of rapid invasion (1851–1870). This was followed by slower filling to full stand closure (1871–1900), recruitment suppression (1901–1930), reinitiation of hemlock recruitment (1931–1950), and continued slow recruitment (1951–present). Recruitment re-initiation was apparently associated with natural stand thinning and not with major disturbance. Large blowdown patches occurred in two plots in the 1960s, but the primary effect was release of hemlock advance regeneration rather than recruitment of new individuals. From 1935 to 1983 annual mortality (calculated from 5–10-years remeasurements) was 0.5–1.2% for both species. At this rate, continued thinning will likely allow a gradual transition to an all-aged forest, as population turnover time is short relative to frequency of intermediate or major disturbance.

### INTRODUCTION

Application of increasingly intensive methods to the analysis of forest stand development (e.g. Henry and Swan, 1974; Oliver and Stephens, 1977; Lorimer, 1980, 1983; Oliver, 1981) has led to renewed interest in the long-term dynamics of forests (Oliver, 1981), as have studies of the processes of tree population change (e.g. recruitment, growth, and mortality: Leak, 1970; Hartshorn, 1972; Harcombe and Marks, 1983). A question of particular interest is the role of disturbance in determining structure, composition, and spatial variation in forest communities. The role of fire has been clearly worked out in some systems (e.g. Heinselman, 1973; Hemstrom and Franklin, 1982; Grimm, 1984). Other disturbances are less clearly understood. White's (1979) major review catalogs the kinds of disturbance; in this paper I focus on effects of fire and wind in a coastal spruce—hemlock forest.

The goal is to assess forces and mechanisms influencing forest stand development through analysis of age structure and long-term mortality in a spruce—hemlock forest on the coast of Oregon. The system was chosen because its origin was known (a major fire in the 1940s), because long-term mortality data were available, and because the opportunity existed to evaluate the effects of wind as a major disturbance factor (Ruth and Yoder, 1953; Lynott and Cramer, 1966; Ruth and Harris, 1979). It is also of some interest that productivity in these forests is among the highest in the world (Briegleb, 1940; Fujimori, 1971; Grier, 1977). If stand structure and dynamics are related to productivity, then studies such as this may further the practical goal of understanding site productivity. Finally, old-growth forests in the Pacific Northwest are different in many ways from younger forests, and the nature of the transition to old-growth is poorly understood (Franklin et al., 1981). Documentation of the structure of these 130-year-old spruce—hemlock stands lays the groundwork for future observations regarding the development of old-growth characteristics.

The immediate objectives were to characterize the age distribution, to describe temporal and spatial variation in tree mortality over the period 1935—1983, and to assess prospects for long-term change. The particular questions of interest were:

- (1) Do coastal forests experience the same prolonged period of stand stocking as do some forests of the Cascades (Franklin and Hemstrom, 1981);
- (2) is there a period of recruitment suppression following initial stocking (see Connell and Slatyer, 1977; Alaback, 1982);
- (3) assuming recruitment suppression, when does recruitment eventually resume;
- (4) is mortality episodic due to wind storms, or continuous due to competition and small-scale windthrow; and
- (5) how do these results bear on current views of succession, stand development, and forest regeneration (see especially Connell and Slatyer, 1977; White, 1979; Oliver, 1981; Whitmore, 1982)?

#### SITE

The study was done at the Cascade Head Experimental Forest near Otis, Lincoln County, or (Lat. 45°03'N, Long. 123°55'W). The environment of the area is described by Grier (1978) and by Greene (1982), from which much of the following is abstracted. The forest is situated on an E—W ridge system which juts out as one of the characteristic headlands of the Pacific Northwest coast. A cool and wet climate prevails; annual precipitation is 3420 mm, coming mostly in the winter; mean January temperature is 4.6°C, and July temperature is 15.7°C. The ridge system ranges from 0 to 400 m elevation. Marine tuffaceous siltstone of the Tyee formation overlies a volcanic substrate (Baldwin, 1964; Snavely and Wagner, 1964). Soils are residual silt loams to silty clay loams, moderately well drained, strongly acid (pH about 4.0 at surface), and high in nitrogen (0.5%) and organic matter (28% in Al).

The forest is predominantly western hemlock and Sitka spruce (SAF cover types 223, 224, and 225 (Eyre, 1980); spruce—cedar—hemlock of Kuchler (1964); *Picea sitchensis* Zone of Franklin and Dryness (1973)). Much of it appears to have originated after a widespread catastrophic fire, the Nestucca burn of the mid-19th century (Morris, 1934; Munger, 1944). Other parts, especially those in the Neskowin Crest Research Natural Area contain scattered older trees (Greene, 1982; Quaye, 1982). Average tree height is about 45 m. Density ranges from 230 to 540 stems/ha ( $> 5$  cm dbh); basal area is 90–120 m<sup>2</sup>/ha. Important understory shrubs include *Menziesia ferruginea* Smith, *Vaccinium parvifolium* Smith, *Vaccinium ovalifolium* Smith, and *Oplopanax horridum* (J.E. Smith) Miq. The ground cover consists of ferns, especially *Polystichum munitum* (Kaulf.) Presl. and *Blechnum spicant* (L.) With., and herbs, especially *Tiarella trifoliata* L., and *Oxalis oregana* Nutt. ex T. & G. Poor regeneration has been noted in some stands of this type (McKee et al., 1979; Harmon and Franklin, 1983) though Quaye (1982) suggests that enough small individuals exist in old-growth stands on the Neskowin Crest to adequately replace canopy individuals as they die. This is supported by size distributions in Greene (1982).

#### METHODS

This study consisted of two parts, tree age determination in an area that blew down in 1981 and was salvaged in 1983, and analysis of periodic re-measurement data on tree populations tagged in 1935 as part of a growth and yield study (Meyer, 1935; Smith et al., 1984).

In the age study, basal diameters of all individuals in four 0.1-ha circular plots were determined, the stumps were identified, and disks were removed for age determination in the laboratory. In addition, seedlings and saplings were collected for age determination from two 0.1-ha circular plots in an adjacent undisturbed area.

The growth and yield study involved ten\* 0.4-ha plots distributed along the ridgetop 1–4.5 km from the Pacific Ocean on moderate S to SW facing slopes. All individuals greater than 5 cm dbh were tagged and measured in 1935 and classified by crown class (dominant, codominant, intermediate, suppressed). In each plot 10–20 of the largest trees were cored in 1935 at breast height for tree age determination. Trees were measured in 1935, and again in 1940, 1945, 1955, 1968, 1978 and 1983. Growth and yield data for the period 1935–1968 are presented in Smith et al. (1984). Mortality checks were made during re-measurement years, in 1950, 1961, and annually from 1979 to 1982 by the Forest Service. Ingrowth (individuals reaching 5 cm dbh between measurements) was not tagged until 1983. Density of saplings (0–5 cm dbh), small saplings (50–140 cm height), and seedlings (less than

---

\*Originally 13 plots were set up. However, most of the study is based on data from 10 plots (plot 11 is not included, as it was dominated by other species; plots 2 and 9 were destroyed by logging in the 1940s). In one case (Fig. 5) 11 plots appear. Here, plots 2 and 9 are included, but plot 13 is excluded due to loss of original data.

50 cm height) was estimated in 1983 using four 100-m<sup>2</sup> circular quadrats in each growth plot. Approximately 50 saplings were also collected near the growth plots for age determination. They were chosen to span the range of sizes present.

The measurement records were made available for this study by the U.S. Forest Service Pacific Northwest Forest and Range Experiment Station, Corvallis, OR.

## RESULTS

### *The relationship of size and age*

Early recruits (older stems) vary greatly in size (Fig. 1), as might be expected for a population experiencing the effects of site heterogeneity, genetic variation, and temporally and spatially varying competition. Though it was not within the scope of this study to sort out these influences, graphs of growth of the largest and smallest of the older recruits show some tendency for individuals to grow faster from the beginning (Fig. 2). Clear divergence occurs in the second interval (20–40 years), corresponding with the time of canopy closure.

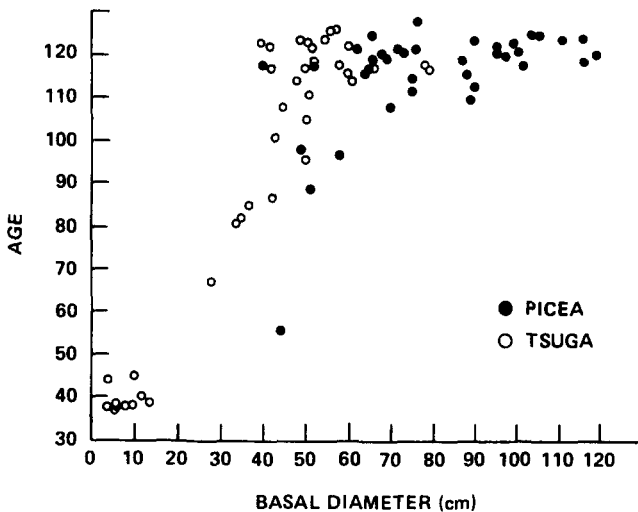


Fig. 1. Plot of age vs basal diameter for all stems of spruce (*Picea*) and hemlock (*Tsuga*) collected from four 0.1-ha plots in a 5-ha blowdown at Cascade Head Experimental Forest.

Later recruits show a reasonably close relationship between size and age (Fig. 1) and so for individuals less than 40 cm diameter, size might reasonably be used as a surrogate for age. The better correlation of size and age among younger individuals may indicate uniformly low light levels in the lower canopy. This is supported by the observation that ranges in growth are

lower among the younger individuals (mean annual diameter increments of 50-year-old stems range from 0.02 cm/year to 0.12 cm/year vs 0.33–1.10 cm/year for 120-year-old stems). The slowest of the 120-years-old trees grew at a mean annual rate nearly three times the most vigorous 50-year-old. If 0.33 cm/year were taken as the minimum long-term average growth rate required for successful entry into the canopy, then very few of the 50-year-olds would be expected to survive.

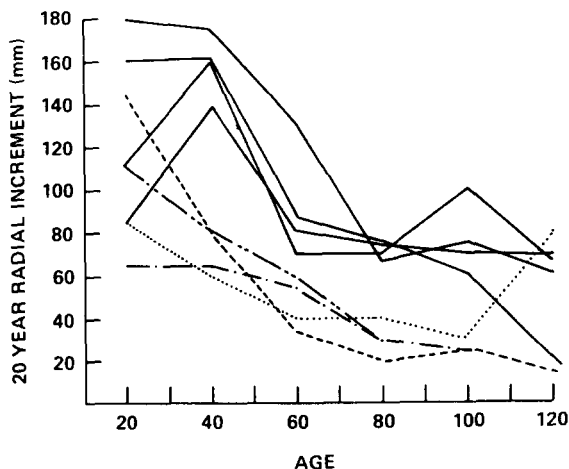


Fig. 2. Average growth in 20-year intervals (20-year radial increment) vs age for the four largest and the four smallest trees more than 100 years old.

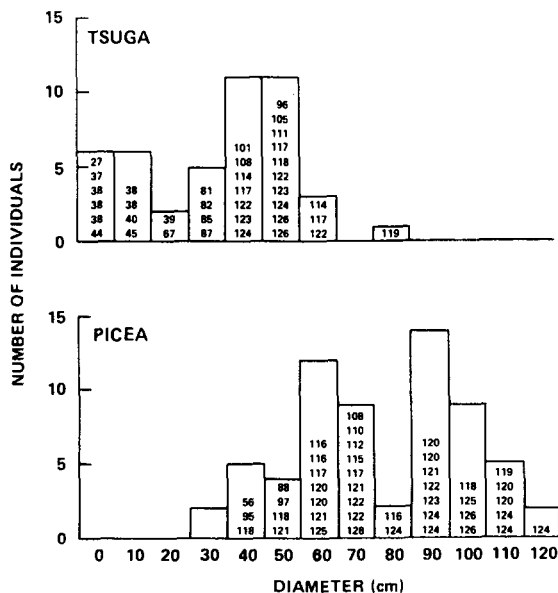


Fig. 3. Frequencies of stems by basal diameter class (class values denote lower limit of the size class). Numbers in bars are tree ages.

### Tree size distributions

Size distributions of the two tree populations are offset (Fig. 3), probably due to inherently slower growth of hemlock, rather than age differences. Spruce shows a bimodal distribution, which is a well-recognized feature of thinning cohorts (Mohler et al., 1978); here it may be accentuated by slight age differences (mean age of 50–70 cm individuals is 118 years, mean age of 90–120 cm individuals is 122 years).

### Age structures

Age structures for both spruce and hemlock show relatively narrow peaks (Fig. 4) — 83% of all spruce and 68% of the big hemlocks (over 40 cm basal diameter) germinated within a 20-year period (1851–1970), suggesting that invasion was, in fact, rapid. Apparently seed sources were adequate, presumably due to presence of unburned remnants of the forest reported in the near vicinity (Munger, 1944; Juday, 1976; Quaye, 1982). The frequent and prolific seed production of spruce and hemlock (Ruth and Berntsen, 1955) undoubtedly also contributed to rapid regeneration. Reburning appears not to have been a problem, though it apparently seriously retarded tree recruitment further north in the Nestucca burn (Munger, 1944) and the Tillamook burn (Isaac and Meagher, 1938). Likewise, brush competition seems to have been unimportant, despite the strong tendency toward development of dense

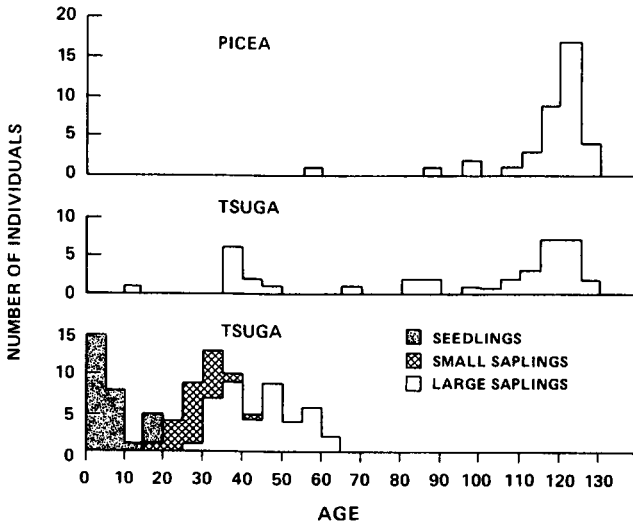


Fig. 4. Age-frequency distributions for spruce (*Picea*) and hemlock (*Tsuga*). Bars in the bottom panel represent individuals collected from the forest adjacent to the blow-down. Seedlings were defined as all individuals less than 50 cm tall. Small saplings were all individuals between 50 and 140 cm tall. Large saplings were all individuals greater than 140 cm tall and less than 5.0 cm dbh.

shrub communities dominated by *Rubus spectabilis*, *Sambucus racemosa* var. *arborescens*, and *Vaccinium* spp. during early succession in these forests (Franklin and Dyrness, 1973) and the observation of reduced establishment of spruce and hemlock (Bertsen, 1955) and lower growth and survivorship of spruce (Madison, 1959) under dense brush in clearcuts at Cascade Head Experimental Forest.

These data suggest early initiation and rapid completion of the tree establishment phase of stand development on a single site. To determine whether this occurred over a larger area, I obtained tree ages from field notes made in 1935 on the growth plots. The ages were based on breast-height cores from 10–20 dominant trees in each plot. Time of first arrival ranged from 1845 to 1861 (Fig. 5), and recruitment phases on individual plots ranged from a few years to as much as 24 years (these must be regarded as minimum estimates of recruitment phases, as only small samples of dominant trees were cored). The variation in time of first arrival suggests that at this large scale, brush competition and rates of seed input may have influenced the timing and duration of recruitment. As these plots appear to have been selected for their uniformity and as they occupy similar topographic positions, intrinsic site characteristics probably were a secondary source of variation. The plots are close together, so it seems unlikely that some would have escaped reburning if any had experienced it.

Peaks in the age structures for spruce and hemlock on the blowdown plot occurred at roughly the same point (Fig. 4) so it seems unlikely that earlier invasion could account for spruce dominance. Higher growth rates of seedlings and saplings of spruce in full sun (Minore, 1979) probably account for it.

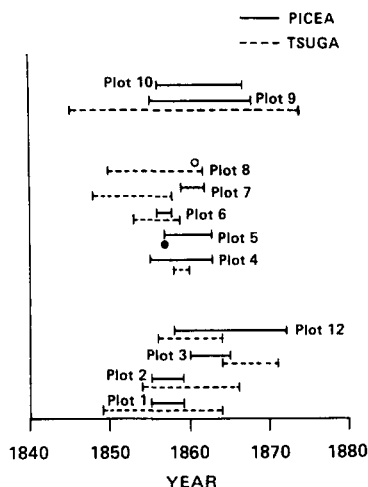


Fig. 5. Ranges in breast-height recruitment dates for 10–20 dominant trees one each of 11 0.4-ha plots set up in 1935. The vertical axis is order of proximity to ocean, from furthest (Plot 1: 4.5 km) to closest (Plot 10: 0.5 km).

Following the initial recruitment pulse, both species showed little regeneration between stand ages 20 and 90. Though spruce is often thought to require large openings it did continue to enter the stand in spite of the fact that canopy openings during this time would likely have been small. The secondary peak in the hemlock age structure for 30–50-year-old trees apparently represents reinitiation of recruitment. Ages of saplings (< 5 cm dbh) collected nearby (Fig. 4) indicate continued recruitment down to the present, with perhaps a slight reduction between 1950 and 1970.

The stages of stand development are perhaps most apparent in a time–frequency distribution (Fig. 6) which shows the accumulation of stems in the stand over time. It should be noted that this ignores any mortality that must have taken place, and hence is not an actual reconstruction of stand stocking. There is the suggestion of five stages in stand development: rapid invasion (1851–1870), slower filling to full stand closure (1871–1900), recruitment suppression (1901–1930), recruitment re-initiation (1931–1950), and a second period of slight suppression by later recruits (1951–present).

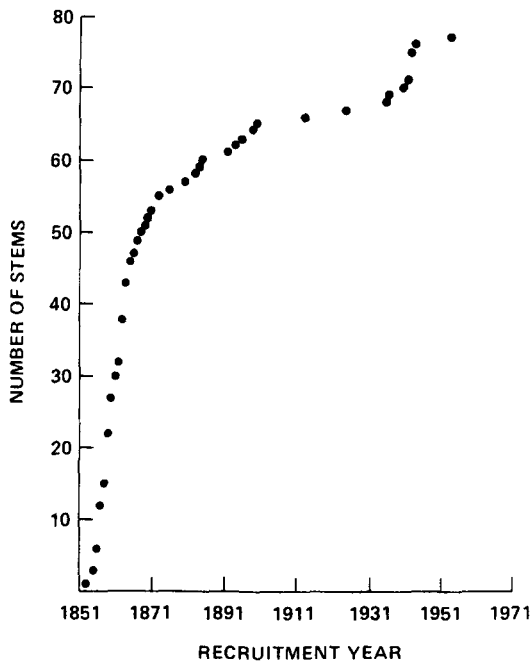


Fig. 6. Cumulative time–frequency distribution of stems present in four 0.1-ha plots at the time of blowdown in 1981.

### *Mortality*

The average mortality rates (number of dead trees in 48 years) were 0.99% per year for hemlock and 1.03% per year for spruce); these are in the range



of rates for other species in the eastern United States (see Harcombe and Marks, 1983) and are also quite similar to those calculated from normal yield tables for spruce-hemlock forest of similar ages (0.91%; Barnes, 1962) and to estimates for western conifers. For example, Hamilton and Edwards (1976) estimated mortality rates of 1.36% per year for western hemlock and 0.63–0.95% per year for other conifers in Idaho, and normal yield tables for Douglas-fir (McArdle et al., 1949) show 0.80% mortality between 80 and 130 years.

There was some variation among time intervals and among plots in mortality (Table 1), but declines in numbers of tagged individuals from 1935 to 1983 were relatively continuous over the 48 years for all but hemlock in three of the plots (Figs. 7 and 8, plots 6, 10, and 13). Of these three stands, one was blown down by a major wind storm on 12 October 1962 (plot 6); this plot was in a vulnerable position, being in a saddle just above a clearcut area (see Ruth and Harris, 1979). Another stand was opened up by wind some time after 1968, and has continued to lose individuals at a high rate (plot 13), a gap enlargement phenomenon reminiscent of fir waves (Sprugel, 1976) in the northeastern United States. High losses in the remaining plot

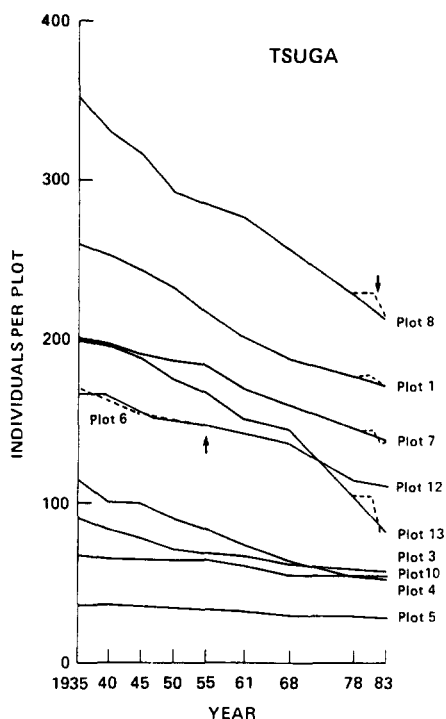


Fig. 7. Number of hemlock individuals each 0.4-ha plot at each census time (multiply by 2.47 for numbers per ha). Note that the line for plot 6 (dashed) ends in 1955. The plot was apparently entirely blown down in 1962. The arrow above plot 8 denotes the 1981 windstorm.

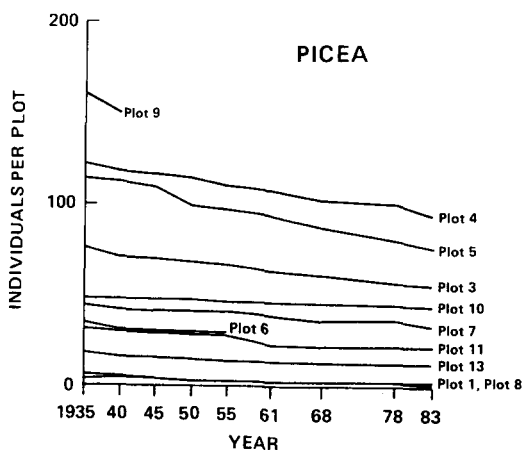


Fig. 8. Number of spruce individuals in each 0.4-ha plot at each census time (multiply by 2.47 for numbers per ha). Plot 9 was destroyed by road building activity in the late 1940s. Plot 6 was blown down in 1962.

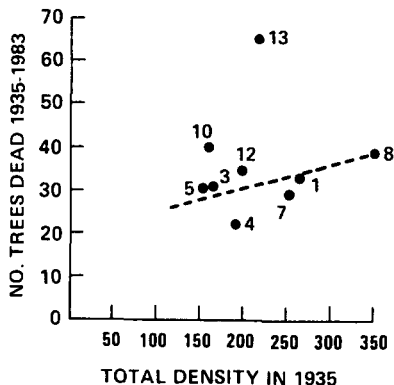


Fig. 9. Plot of number of trees dying between 1935 and 1983 vs total initial density (spruce plus hemlock) in each of the nine 0.4-ha plots that survived to 1983.

(plot 10) are undoubtedly related to exposure to wind and salt spray as this plot is nearly 3 km closer to the ocean than the others. It is noteworthy that spruce survivorship was highest in this plot, perhaps due to greater salt tolerance (Cordes, 1972) and reduced competition.

The low variation in the remaining six plots may be attributable to the relative uniformity of these stands; they were roughly even-aged, reasonably well-stocked, and on sites with limited topographic and geographic variation. There is some evidence for weak density dependence (Fig. 9) — the densest plot showed highest loss (39%) and the sparsest plots showed lowest losses (21 and 22%) — but mortality was not related to stand basal area or volume either among plots or over time. Aside from the periods of high mortality in plots 6 and 13 mentioned above, annualized interval mortality was remark-

TABLE 1

Annualized interval mortality of spruce and hemlock on growth plots at Cascade Head Experimental Forest (fraction of trees present at start of interval that died during the interval, divided by interval length)

Plot	1936-40	1951-45	1946-50	1951-55	1956-61	1962-68	1969-78	1979-83	Mean
<i>Hemlock</i>									
1	0.005	0.007	0.008	0.013	0.012	0.008	0.005	0.006	0.008
3	0.015	0.012	0.017	0.005	0.004	0.010	0.004	0.003	0.009
4	0.003	0.000	0.003	0.000	0.007	0.014	0.001	0.007	0.005
5	0.000	0.005	0.005	0.005	0.005	0.008	0.003	0.006	0.005
7	0.003	0.006	0.004	0.003	0.012	0.008	0.009	0.012	0.007
8	0.013	0.007	0.015	0.004	0.004	0.009	0.010	0.013	0.010
10	0.024	0.002	0.018	0.015	0.020	0.019	0.014	0.003	0.015
12	0.002	0.013	0.005	0.003	0.005	0.005	0.016	0.008	0.008
13	0.003	0.008	0.013	0.009	0.015	0.005	0.028	0.044	0.016
Mean	0.008	0.007	0.010	0.007	0.010	0.010	0.010	0.012	0.009
<i>Spruce</i>									
1	0.033	0.040	0.050	0.000	0.000	0.000	0.000	0.000	0.015
3	0.013	0.002	0.005	0.002	0.007	0.004	0.008	0.003	0.006
4	0.004	0.003	0.003	0.006	0.004	0.006	0.002	0.012	0.006
5	0.003	0.003	0.020	0.004	0.003	0.010	0.009	0.010	0.008
7	0.009	0.004	0.000	0.000	0.008	0.010	0.000	0.016	0.006
8	0.000	0.000	0.000	0.050	0.000	0.000	0.000	0.066	0.015
10	0.000	0.000	0.000	0.004	0.000	0.003	0.002	0.000	0.011
12	0.006	0.006	0.000	0.013	0.024	0.006	0.000	0.000	0.007
13	0.022	0.000	0.012	0.026	0.000	0.000	0.007	0.000	0.009
Mean	0.010	0.007	0.010	0.012	0.005	0.005	0.003	0.012	0.008

ably constant over the measurement period for both species (Table 1). Though these 5-10-year averages are slightly misleading, as indicated by the variation evident in annual mortality data for 1979-1983 (Figs. 7 and 8), they do set an upper bound for the proportion of trees that might die in any given year.

It is doubtful that the temporal uniformity of mortality rate applies to the first 80 years of stand development. One way of evaluating this is to estimate initial hemlock and spruce densities by projecting back in time from present stocking levels assuming a constant exponential mortality rate equal to that computed for the period 1935-1983. This was done graphically using semi-logarithmic paper (Fig. 10) to obtain an estimate of 540 hemlock and 250 spruce recruits per plot (1350 and 625 per ha, respectively) (using the most densely stocked plots). Modern studies at Cascade Head Experimental Forest (Berntsen, 1955) showed establishment of approximately 5000 spruce and 5000 hemlock per ha after logging. Shaw (1953) found natural regeneration after the Forks (Wn) burn of 2250-3250 hemlocks per ha. The low recruitment estimate must be due to a combination of low recruitment rate following the Nestucca fire and high mortality rates in these stands during the first 80 years. Plots of number of stems from normal yield tables (Barnes, 1962) suggest the latter is more important (Fig. 10).

Causes of death were not uniformly recorded. Field notes on the 61

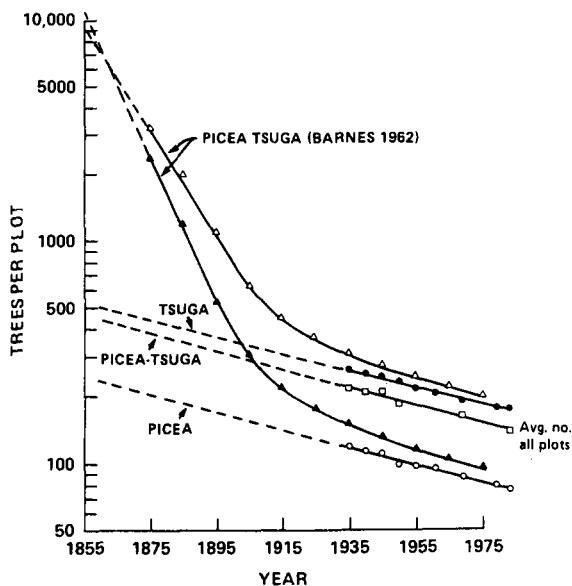


Fig. 10. Estimates of pre-1935 stocking rates based on assumed constant mortality rates over the entire period (dashed lines) and on normal yield tables for spruce and hemlock in western Oregon and Washington (solid lines) (multiply by 2.47 for number of trees per ha).

trees found dead in the 1950 mortality check show suppression (50) and wind (4) as death causes. In the 1983 remeasurement, 26 dead trees were found, half windthrown and half standing. Though Grier (1978) suggests that wind is the major cause of mortality, these observations suggest that standing death has always been more common. A gradual shift from suppression to wind as the chief agent of mortality seems entirely reasonable; as the stand ages, fewer suppressed trees remain, and a larger proportion of the trees are in the upper canopy where susceptibility to wind damage is higher.

### *Recruitment*

Notes made during establishment of the growth plots and again during remeasurement indicate presence of hemlock seedlings on the plots since 1935. The recruits were mostly 1–1.5 m tall in 1940; they approached 3 m by 1950, and were not much taller in 1983. Apparently changes have occurred in the understory since 1935, culminating in 1983 in presence of a substantial amount of ingrowth (stems greater than 5 cm dbh). Early field notes suggest that the large numbers of 5 cm stems recorded in plots 5 and 8 in 1983 (Table 2) are related to road construction nearby in the 1940s. Large ingrowth numbers in plot 13 are undoubtedly due to sapling release by the wind-related stand opening that began in 1968.

Sapling ages range from about 15 to 55 years, suggesting relatively continuous recruitment. Though field observations suggest that a dense canopy of saplings can suppress later recruitment, sapling distribution is sufficiently irregular that seedlings are abundant, and so it seems most reasonable to regard the seedling-sapling population as a continuously turning-over pool of recruits. Presence of numerous dead stems is evidence of the turnover.

The number of hemlock ingrowth stems tallied in 1983 (Table 2) more than compensates for the loss of stems due to mortality over all the plots, though there is considerable variation among the plots. Overall, hemlock population density is clearly increasing, giving promise that regeneration is adequate for long-term perpetuation of the forest. Spruce is declining, as it did in an Alaska chronosequence (Alaback, 1982), but recruits are still entering the stand.

TABLE 2

1983 Size distribution of seedlings and saplings in growth plots (number of individuals per plot)<sup>a</sup>

Plot	50 cm tall	50-140 cm height	dbh 2.5 cm	dbh 2.5-5 cm	dbh 5 cm (tagged ingrowth)
1	172	810	1630	466	29
3	314	375	253	111	0
4	101	121	506	375	54
5	54	40	142	395	304
7	1397	617	921	405	42
8	202	506	1761	627	126
10	1994	20	10	0	0
12	1568	91	202	324	120
13	4454	202	202	263	200

<sup>a</sup>Multiply by 2.47 to obtain number of individuals per ha.

Continued decline in spruce on the 130-year-old growth plots seems likely in light of the overwhelming dominance of hemlock in the understory. Such a decline has been suggested by others (e.g. Franklin and Dyrness, 1973; Alaback, 1982) and Hines (1971), Cordes (1972), and Quaye (1982) all speculate that spruce must persist by gap-phase regeneration. However, low adult mortality (and great longevity — Franklin et al., 1981) undoubtedly contributed to persistence of spruce in these forests despite apparently low recruitment.

## DISCUSSION

The stands described here were initiated by a crown-destroying fire, and their age structure is quite clearly a consequence of the nature of the initiat-

ing disturbance. Regarding the role of fire in these systems, Hemstrom and Franklin (1982) suggest that it is the most important stand-initiating event in the Pacific Northwest, even in the Coast Range. They calculate a mean fire rotation of 434 years, but point out that it is highly variable (226–2583), depending on topography and the time span involved. Viers (1982), on the other hand, found no evidence of canopy fires for the coast redwoods of northern California in a habitat much like that of Cascade Head. There, ground fires occur at 250–1000-year intervals. In the Coast Range, the major fires of the late 19th and early 20th centuries were all thought to be man-caused (Morris, 1934; Munger, 1944); they were all crown fires. It seems plausible therefore, that though large-scale fires may well be major stand initiation events in the spruce–hemlock zone, the natural return interval is long.

Restocking, which may take more than 75 years in drier forests of the Cascades (Franklin and Hemstrom, 1981; Hemstrom and Franklin, 1982) is as rapid here as in spruce (McCulloch, 1929) or spruce–hemlock forests (Alaback, 1982) in Canada and Alaska. At Cascade Head, Berntsen (1955) found a logged area near plot 7 to be 81% stocked 6 years after logging. The rapid restocking can be attributed in part to frequent and prolific seed production by both spruce and hemlock (Ruth and Berntsen, 1955).

Initiation of recruitment following the period of suppression seems to have been related, as often as not, to events occurring outside the stands, suggesting that increases in diffuse light are as important as increases in direct beam radiation that might occur under discrete canopy gaps. There is little evidence, either in the mortality pattern or recruitment under the canopy, of the cyclic regeneration in even-aged stands postulated by Hett and Loucks (1976) for eastern hemlock (*Tsuga canadensis*) in Wisconsin. However, Meyer (1937), on finding frequent evidence of suppression during the first 30–50 years of growth in even-aged stands, explained the widespread occurrence of even-aged stands in western Oregon as follows: “Suddenly the overstory was removed, perhaps by windthrow, less probably by looper — and within a few years the stagnant stand developed into a vigorous second-growth stand.”

Very large blowdowns are known to occur in some forests (e.g. a 61-ha blowdown in central Wisconsin on 4 July 1978; Canham and Loucks, 1984), and wind damage is common in spruce–hemlock forests (Ruth and Harris, 1979). Two extensive blowdowns are known to have occurred in western Oregon since about 1880, one in 1951 and another in 1962 (responsible for the blowdown in plot 6); a third storm blew down approximately 5 ha of timber at Cascade Head in 1981 (the blowdown stand in which the age determinations reported here were made). Greeley et al. (1953) attributed a loss of more than 10 billion board feet (23.6 million m<sup>3</sup>) to blowdown and subsequent bark beetle attack following the 1951 storm. They noted that “in the recorded history of the forests of the two states (Oregon and Washington), only the Tillamook fire of 1933 has caused more damage at a single stroke.”

Concentrated blowdown (more than 10% of the stems in a stand) occurred on about 200 000 acres (81 000 ha), which is roughly 2% of the area surveyed. Overall, about 70% of the volume loss occurred as scattered trees. Mortality of Douglas-fir in one of the areas most heavily damaged by blowdown and insects was only 0.96% per year over the period 1945–1955 (Wright and Lauterbach, 1958). This pattern of damage is reminiscent of that reported by Lorimer (1980) in western North Carolina, where storm episodes were apparent in ring-width records, but evidently did not completely destroy the canopy. Aside from the blowdown of plot 6, none of the recent major Pacific Northwest storms is particularly evident in the growth plot survivorship figures (Figs. 7 and 8). Though wind is certainly an important cause of mortality, its effect on landscape patterns is apparently more diffuse than wind in other areas, e.g. fir waves in the mountains of the northeastern United States (Sprugel, 1976) or the large-area blowdown in Wisconsin. Consequently it may not generate a distinct mosaic of regeneration patches like fire does in mixed conifer trees of the western United States (see Bonnicksen and Stone, 1982).

Another way of assessing the role of wind is to ask what proportion of the individuals initially present was removed in major events. Nine percent of the individuals were lost in storms blowing down more than an acre at a time, 4% were lost in multiple-tree blowdowns of less than an acre, and 42% died standing or were blown down in smaller patches. If large storms were the major force affecting forest dynamics, canopy turnover time would be 550 years (9% in 50 years). Adding in the blowdown in plot 13 gives 13% in 50 years, or a 384-year turnover time. Turnover time based on small scale events alone is 119 years. A turnover time of 400–500 years is short compared to return intervals for catastrophic disturbances reported for other systems, e.g. approx. 1200 years for large-area blowdowns (greater than 0.5 ha) in Wisconsin (Canham and Loucks, 1984) or 800 years for forest fires in Maine (Lorimer, 1977).

Large fires and blowdowns do occur, but the results of this study suggest that less spectacular events may be equally important forces in community dynamics in spruce–hemlock forests. Clearly, however, the relative importance of large- or small-scale events depends very strongly on the temporal and spatial scale of the investigation and also on the perspective of the observer. Certainly canopy openings occur in all sizes, and it may be premature to generalize by trying to evaluate the relative importance of “catastrophic” events. This study emphasizes the need for a broad perspective and caution in attempting to fit the results into the prevailing general models of forest development, as such models are, of necessity, often oversimplified. Only through accumulation of a larger body of case histories of long-term forest dynamics at several spatial scales, will the true picture of the role of disturbance in determining structure and dynamics emerge.

## ACKNOWLEDGEMENTS

This research was carried out while the author was Visiting Scientist in the Department of Forest Sciences, Oregon State University, on sabbatical leave from Rice University. It was funded by National Science Foundation Grant DEB 8012162-04. Professor J.F. Franklin provided the plot records, which were collected as part of a long-term growth and yield study by the Pacific Northwest Forest and Range Experiment Station, USDA Forest Service. Thanks are due Professor Franklin, Sarah Greene and Jack Booth for help in collecting the tree disks, for thoughtful comments, and for their enthusiastic support. Tom Spies, Joe Means, Mark Harmon, Miles Hemstrom, P.L. Marks, J.S. Glitzenstein, and D.R. Streng provided many helpful comments.

## REFERENCES

- Alaback, P.B., 1982. Forest community structural changes during secondary succession in southeast Alaska. In: J. Means (Editor), *Forest Succession and Stand Development Research in The Northwest*. For. Res. Lab., Oregon State Univ., Corvallis, OR, pp. 70-79.
- Alaback, P.B., 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology*, 63: 1932-1948.
- Baldwin, E.M., 1964. *Geology of Oregon*. Univ. Oregon Coop Bookstore, Eugene, OR, 2nd edn, 165 pp.
- Barnes, G.H., 1962. Yield of even-aged stands of western hemlock. USDA For. Serv. Tech. Bull. 1273, Washington, DC.
- Berntsen, C.M., 1955. Seedling distribution on a spruce-hemlock clearcut. USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Res. Note 119, 7 pp.
- Bonnicksen, T.M. and Stone, E.C., 1982. Reconstruction of a presettlement giant sequoia-mixed conifer forest community using the aggregation approach. *Ecology*, 63: 1134-1148.
- Briegleb, P.B., 1940. Spruce-hemlock forest shows prodigious growth. USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Res. Note 31, 2 pp.
- Canham, C.D. and Loucks, O.L., 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology*, 65: 803-809.
- Connell, J.H. and Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.*, 111: 1119-1144.
- Cordes, L.D., 1972. An ecological study of the Sitka spruce forest on the west slope of Vancouver Island. Ph.D. Thesis, Univ. British Columbia, Vancouver, BC, 452 pp.
- Dunn, C.P., Guntenspergen, G.R. and Dorney, J.R., 1983. Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. *Can. J. Bot.*, 61: 211-217.
- Eyre, F.H. (Editor), 1980. *Forest Cover Types of The United States and Canada*. Society of American Foresters, Washington, DC, 148 pp.
- Franklin, J.F. and Dyrness, C.T., 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, 417 pp.
- Franklin, J.F. and Hemstrom, M.A., 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: D.C. West, H.H. Shugart and D.B. Botkin (Editors), *Forest Succession*. Springer-Verlag, New York, pp. 212-219.
- Franklin, J.F., Cromack, K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F. and Juday, G., 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118, 48 pp.
- Fujimori, T., 1971. Primary productivity of a young *Tsuga heterophylla* stand and some speculations about biomass of forest communities on the Oregon coast. USDA For. Serv. Res. Pap. PNW-123, 11 pp.



- Greeley, A.W., Wright, K.H. and Pope, R.B., 1953. Final report on the 1952 blowdown-bark beetle survey in the Douglas-fir region of Oregon and Washington. USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Portland For. Insect Lab.
- Greene, S.E., 1982. Neskowin Crest Research Natural Area. Supplement No. 13 to: J.F. Franklin et al. (1972), Federal Research Natural Areas in Oregon and Washington: A Guidebook for Scientists and Educators. USDA For. Serv., Pac. Northwest For. and Range Exp. Stn., 17 pp.
- Grier, C.C., 1977. Biomass, productivity, and nitrogen-phosphorous cycles in hemlock-spruce stands of the central Oregon coast. In: R.J. Zasoski and W.A. Atkinson (Editors), Proc., Conf. on Intensive Management of Western Hemlock. Univ. Washington, Seattle. Inst. For. Prod. Bull., 21: 71-78.
- 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.
- Grimm, E.C., 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. Ecol. Monogr., 54: 291-511.
- Hamilton, D.A., Jr. and Edwards, B.M., 1976. Modeling the probability of individual tree mortality. USDA For. Serv. Res. Pap. INT-185, 22 pp.
- Harcombe, P.A. and Marks, P.L., 1983. Five years of tree mortality in a *Fagus*-*Magnolia* forest, southeast Texas (USA). Oecologia, 57: 49-54.
- Harmon, M.E. and Franklin, J.F., 1983. Age distribution of western hemlock and its relation to Roosevelt elk populations in South Fork Hoh River Valley, Washington. Northwest Sci., 57: 249-255.
- Hartshorn, G.S., 1972. The ecological life history and population dynamics of *Pentaclethra macroloba*, a tropical wet forest dominant, and *Stryphnodendron excelsum*, an occasional associate. Ph.D. Thesis, Univ. Washington, Seattle, WA, 118 pp.
- Heinselman, M.L., 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. NY, 3: 329-382.
- Hemstrom, M. and Franklin, J.F., 1982. Fire and other disturbances of the forests in Mt. Rainier National Park. Quat. Res. NY, 18: 32-51.
- Henry, J.D. and Swan, J.M.A., 1974. Reconstructing forest history from live and dead plant material - an approach to the study of forest succession in southwest New Hampshire. Ecology, 55: 772-783.
- Hett, J. and Loucks, O.L., 1976. Age structure models of balsam fir and eastern hemlock. J. Ecol., 64: 1029-1044.
- Hines, W.W., 1971. Plant communities of the old-growth forests of north coastal Oregon. MS Thesis, Oregon State Univ., Corvallis, OR.
- Isaac, L.A. and Meagher, G.S., 1938. Natural reproduction on the Tillamook Burn four years after the fire. Pac. Northwest For. Exp. Stn., Portland, OR, 15 pp. (mimeo).
- Juday, G.P., 1976. The location, composition, and structure of old-growth forests of the Oregon Coast Range. Ph.D. Thesis, Oregon State Univ., Corvallis, OR, 206 pp. illus.
- Kuchler, A.W., 1964. Manual to accompany the map of potential natural vegetation of the conterminous United States. Am. Geogr. Soc. Spec. Publ. 36, 116 pp.
- Leak, W.B., 1970. Successional changes in northern hardwoods predicted by birth and death simulation. Ecology, 51: 794-801.
- Lorimer, C.G., 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. Ecology, 58: 139-148.
- Lorimer, C.G., 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology, 61: 1169-1184.
- Lorimer, C.G., 1983. Eighty-year development of Northern Red Oak after partial cutting in a mixed-species Wisconsin forest. For. Sci., 29: 371-383.
- Lynott, R.E. and Cramer, O.P., 1966. Detailed analysis of the 1962 Columbus Day wind-storm in Oregon and Washington. Mon. Weather Rev., 94: 105-117.
- Madison, R.W., 1959. Growth and survival of a Sitka spruce plantation of coastal Oregon. USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Res. Note 178, 6 pp.
- McArdle, R.E., Meyer, W.H. and Bruce, D., 1949 (Rev. 1961). The yield of Douglas-fir in the Pacific northwest. USDA For. Serv. Tech. Bull. 201, 71 pp.

- McCulloch, W.F., 1929. Natural regeneration of Sitka spruce in the Queen Charlotte Islands. *For. Chron.*, 5: 21–27.
- McKee, A., LaRoi, G. and Franklin, J.F., 1979. Structure, composition and reproductive behavior of terrace forests, South Fork Hoh River, Olympic National Park. In: *Proc. Second Conf. Sci. Res. Nat. Parks*, San Francisco, CA, Vol. 7, pp. 64–79.
- Meyer, W.H., 1935. First report on sixteen permanent plots located on the Cascade Head Experimental Forest. *Pac. Northwest For. and Range Exp. Stn.*, Portland, OR, Type-written, Dec. 15, 1935, 37 pp. plus tables.
- Meyer, W.H., 1937. Yield of even-aged stands of Sitka spruce and western hemlock. *USDA Tech. Bull.* 544, Washington, DC, 86 pp.
- Minore, D., 1979. Comparative autecological characteristics of Northwest tree species — a literature review. *USDA For. Serv. Gen. Tech. Rep.* 87, 72 pp.
- Mohler, C.L., Marks, P.L. and Sprugel, D.G., 1978. Stand structure and allometry of trees during self-thinning of pure stands. *J. Ecol.*, 66: 599–614.
- Morris, R.F., 1934. Forest fires in western Oregon and Washington. *Oreg. Hist. Quart.*, 35: 313–339.
- Munger, T.T., 1944. Out of the ashes of the Nestucca. *Am. For.*, 50: 342–347.
- Noble, I.R. and Slatyer, R.P., 1980. The use of vital attributes to predict successional change in plant communities subject to recurrent disturbance. *Vegetatio*, 43: 5–21.
- Oliver, C.D., 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.*, 3: 153–168.
- Oliver, C.D. and Stephens, E.P., 1977. Reconstruction of a mixed species forest in central New England. *Ecology*, 58: 562–572.
- Quaye, E., 1982. The structure and dynamics of old-growth sitka spruce (*Picea sitchensis*) forest of the Oregon Coast Range. Ph.D. Thesis, Oregon State Univ., Corvallis, OR, 109 pp.
- Ruth, R.H. and Berntsen, C.M., 1955. A four-year record of Sitka spruce and western hemlock seed fall. *USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Res. Pap.* 12, 13 pp.
- Ruth, R.H. and Harris, A.S., 1979. Management of western hemlock—Sitka spruce forests for timber production. *USDA For. Serv. Gen. Tech. Rep.* PNW-88, 195 pp.
- Ruth, R.H. and Yoder, R.A., 1953. Reducing wind damage in the forests of the Oregon Coast Range. *USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Res. Pap.* 7, 30 pp.
- Shaw, E.W., 1953. Direct seeding experiments on the 1951 Forks burn. *USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Res. Pap.* 9, 19 pp.
- Smith, S.H., Bell, J.F., Herman, F.R. and 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, 30 pp.
- Snavely, P.D., Jr. and Wagner, H.E., 1964. Geologic sketch of northwest Oregon. *USGS Bull.* 1181M, 17 pp.
- Staebler, G.R., 1953. Mortality estimation in fully stocked stands of young growth Douglas-fir. *USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Res. Pap.* 4, 17 pp.
- Sprugel, D.G., 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. *J. Ecol.*, 64: 889–911.
- Viers, S.D., Jr., 1982. Coast redwood forest: stand dynamics, successional status, and the role of fire. In: J. Means (Editor), *Forest Succession and Stand Development Research in The Northwest: Proceedings of A Symposium*. *For. Res. Lab.*, Oregon State Univ., Corvallis, OR, pp. 119–141.
- White, P.S., 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.*, 45: 229–299.
- Whitmore, T.C., 1982. On pattern and process in forests. In: E.I. Newman (Editor), *The Plant Community as A Working Mechanism*. Blackwell, Oxford, pp. 45–59.
- Wright, K.H. and Lauterbach, P.G., 1958. A 10-yr study of mortality in a Douglas-fir sawtimber stand in Coos and Douglas Counties, Oregon. *USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. Res. Pap.* 27.