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*Ecology*, Vol. 67, No. 2 (Apr., 1986), 534-544.

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## POPULATION DYNAMICS OF A MONTANE CONIFER FOREST, WESTERN CASCADE RANGE, OREGON, USA<sup>1</sup>

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**Abstract.** Size and age structure were used to reconstruct the population dynamics of two forested stands in the western Cascade Range, Oregon, USA. Trees with different growth rates and size-age relationships occurred in the same stand. The relationships between diameter and age of 939 aged trees of four species, although statistically significant, were often weak. Data on both age and spatial dispersion added critical information on stand dynamics not available from size alone.

The population structures and regeneration patterns described were strongly influenced by natural disturbances and species' life history characteristics. Periodic fires of variable intensity and extent have produced a mosaic of relatively even-aged patches of different conifer species. The early establishment and dominance by a species on a site was a determinant of subsequent forest regeneration. If *Pseudotsuga menziesii* dominated early, regeneration of *Tsuga heterophylla*, and often *Abies amabilis*, was rapid. If, however, *Tsuga heterophylla* established first, further regeneration of other species was absent or minimal until canopy openings formed.

**Key words:** *Abies amabilis*; *Abies procera*; age structure; disturbance; population dynamics; *Pseudotsuga menziesii*; size structure; spatial pattern; *Tsuga heterophylla*.

### INTRODUCTION

If a relationship between size (usually diameter) and age of trees can be established, size class frequency distributions can be used to infer age structures and, ultimately, to assess the population dynamics of forests (e.g., Harcombe and Marks 1978, Lorimer 1980). However, few studies have emphasized detailed age structure analysis, and age information has often been gathered from large tracts of forest (Hibbs 1979, Ross et al. 1982, Knowles and Grant 1983). The interpretation of age structures (and size structures) gathered in this way is difficult because of variability in growth rates caused by differences in stand structure and environment (cf. Parker and Peet 1984). Such a composite age structure, often derived from widely different stands, does not provide an understanding of the spatial arrangement of age classes in any particular spot (cf. Stewart and Veblen 1982). This investigation compares size and age structure analysis of individual stands as methods for studying the population dynamics of a small area of forest.

Many factors influence the shape of a population's age or size distribution. Foresters often distinguish between species they call "shade tolerant," which show a capacity for regeneration in shade and often an inverse-J age structure, and species they call "light demanding" or "shade intolerant," which have no individuals in the understory (Spurr and Barnes 1980). Many other characteristics of a species' life history may

affect population structures, but need to be considered in the context of physical and biological disturbances to the forest. For example, the creation of gaps in the forest canopy is important for the regeneration of many species (Runkle 1981). A second objective of this study, therefore, is to relate life history characteristics and the local disturbance regime to population age and size distributions.

### THE STUDY AREA

The evergreen true fir-hemlock forests characteristic of mid-elevations (1000–1300 m) in the western Cascade Range, Oregon (Pacific Northwest, USA) are dominated by Douglas-fir (*Pseudotsuga menziesii*), with a lower, multilayered canopy composed primarily of western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), and locally abundant western red cedar (*Thuja plicata*) (Franklin and Dyrness 1973). (Nomenclature follows Hitchcock and Cronquist [1973].) Above 1200 m, noble fir (*Abies procera*) can also be a conspicuous component of the main canopy (Franklin 1964a, b). These forests are considered to be in a transition zone between the upper climax forests of *Abies amabilis* and the lower elevation climax *Tsuga heterophylla* forests (Franklin and Dyrness 1973).

Two forest stands located west of Soapgrass Mountain in the Willamette National Forest, Linn County, Oregon (latitude 44°25' N, longitude 122°20' W; 1200 m altitude) were selected for study on the basis of differences in structure and disturbance history. These stands were located in areas to be logged for the first time in 1982.

Stand 1 was dominated by large, emergent *Pseudotsuga menziesii*, reaching heights of 50 m (Fig. 1a).

<sup>1</sup> Manuscript received 4 October 1984; revised 13 May 1985; accepted 16 May 1985.

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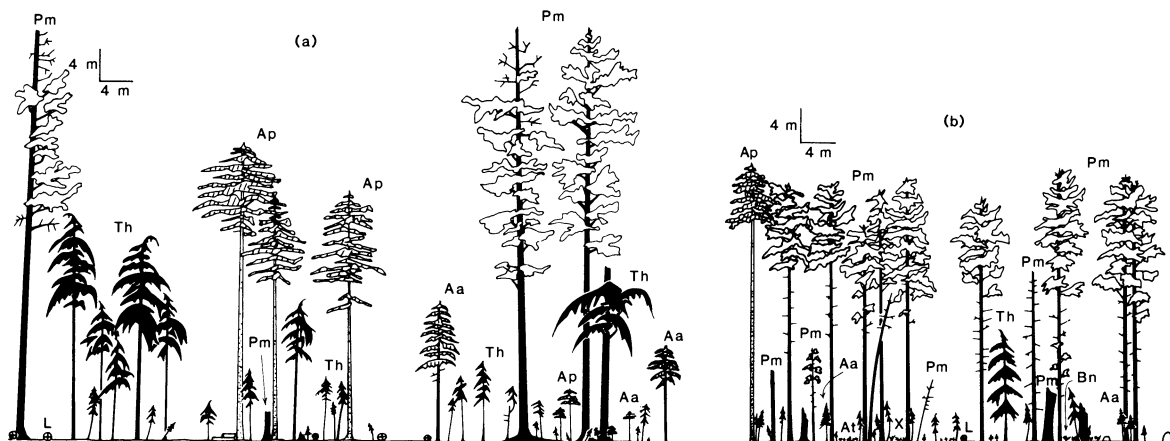


FIG. 1. Profiles of (a) Plot HY-1 (80 × 3 m), and (b) Plot HY-2 (50 × 3 m). Aa = *Abies amabilis*; Ap = *Abies procera*; At = *Achlys triphylla*; Bn = *Berberis nervosa*; L = log; Pm = *Pseudotsuga menziesii*; Th = *Tsuga heterophylla*; X = *Xerophyllum tenax*.

*Abies procera* formed a dominant main canopy in the central portion of the stand, but the most abundant tree was *Tsuga heterophylla*, both in the main (30–35 m) and lower canopy tiers (Table 1). The dense *Tsuga*-dominated canopy was broken where treefalls had created small canopy openings. Understory herbs and shrubs were rare or absent under *Tsuga*, but a few, small *Vaccinium alaskaense* occurred in openings or under *Abies procera*. Soils were deep and largely undifferentiated and sometimes had thick litter accumulations, especially near large *Pseudotsuga* trees.

In Stand 2, *Pseudotsuga menziesii*, some *Tsuga heterophylla*, and scattered individuals of *Abies procera* and *Abies amabilis* formed a relatively even canopy at 25–35 m (Fig. 1b, Table 1). The lower main canopy contained *Tsuga heterophylla* and suppressed *Pseudotsuga*. The subcanopy tiers included *Abies amabilis* and *Tsuga heterophylla*, with a few *Abies procera* and *Thuja plicata*. The shrubs *Vaccinium alaskaense*, *Acer circinatum*, and *Rhododendron macrophyllum* grew in canopy openings. Low shrubs and herbaceous plants were locally abundant and included *Achlys triphylla*, *Smilacina stellata*, *Berberis nervosa*, and *Xerophyllum tenax*.

Fire is the major natural disturbance in these forests,

and generally takes the form of catastrophic fires (as opposed to frequent light burns which recur at intervals of several centuries) (Franklin and Hemstrom 1981, Hemstrom and Franklin 1982). A general successional sequence after holocaustic fire for this lower montane zone involves initial colonization by *Pseudotsuga* or *Abies procera*, gradual replacement by *Tsuga heterophylla* and/or *Abies amabilis*, and eventual dominance by *Abies amabilis* (Franklin and Hemstrom 1981). Several recent major windstorms that must have strongly influenced forest structure have also been recorded, e.g., the Columbus Day storm in 1962, which felled 26 × 10<sup>6</sup> m<sup>3</sup> of timber in Oregon and Washington (Lynott and Cramer 1966).

METHODS

All sampling was done on two plots, one of 0.80 ha (100 × 80 m), HY-1, and one of 0.36 ha (60 × 60 m), HY-2. “Trees” were defined as ≥ 5 cm diameter at breast height (dbh); “saplings” as ≥ 1.4 m tall and < 5 cm dbh; and “seedlings” as < 1.4 m but ≥ 10 cm tall.

Forest structure

Size structure of tree species on the two plots was analyzed by size class frequency distributions. The dbh

TABLE 1. Number of trees ≥ 1.4 m tall in relative height classes in plots HY-1 and HY-2.

Species	Plot and height class									
	HY-1					HY-2				
	Over-topped	Below main canopy	Lower main canopy	Upper main canopy	Emer-gent	Over-topped	Below main canopy	Lower main canopy	Upper main canopy	Emer-gent
<i>Pseudotsuga menziesii</i>	1	3	3	5	62	19	18	33	100	1
<i>Tsuga heterophylla</i>	725	174	85	9	1	256	28	23	38	
<i>Abies procera</i>	49	17	26	26	2	7	1	2	5	
<i>Abies amabilis</i>	112	17	45	20		95	7	7	12	

of each tree  $\geq 5$  cm dbh was measured, and all seedlings and saplings were tallied by species. Signs of establishment on an elevated surface such as a log, stump, trunk buttress, or upturned root plate were recorded. Stumps, dead standing trees, and saplings were also measured and identified if possible. Trees  $\geq 1.4$  m tall were assigned to relative canopy-height categories: emergent, upper main canopy, lower main canopy, below main canopy (intermediate), and overtopped (less than half the height of the main canopy). Vegetation profiles of  $80 \times 3$  m (HY-1) and  $50 \times 3$  m (HY-2) were drawn to illustrate vertical structure (Fig. 1).

The age structure of the two plots was analyzed by age class frequency distributions. For HY-1, all seedlings, saplings, and trees  $\leq 10$  cm dbh were cut and discs taken at ground level. Increment cores were taken from trees 11–25 cm dbh at a height of 30 cm above ground level. Discs and cores were sanded with successively finer grades of sandpaper until annual rings could be easily distinguished under a binocular microscope. Numbered metal tags were attached to the bases of trees  $> 25$  cm dbh. After the area was logged in October–December 1982, the ages of tagged trees were determined by counting annual rings on the cut stumps. Because size class distributions of *Tsuga heterophylla* proved similar on both halves of HY-1, the ages of individuals on the northern half only were determined ( $n = 514$ ).

Time constraints limited detailed sampling in HY-2 to main canopy trees. Increment cores were removed at 30 cm above ground level from all stems of *Pseudotsuga menziesii*  $< 25$  cm dbh. All trees of this species, *Tsuga heterophylla*, *Abies amabilis*, and *Abies procera*  $> 25$  cm dbh were tagged, relocated after logging, and their ages determined from the cut stumps. The ages of an additional 20 *Abies amabilis*  $\leq 25$  cm dbh were determined from increment cores, and seven *Tsuga heterophylla*  $\leq 25$  cm dbh from annual ring counts on stumps.

It was not possible to relocate all tagged trees after logging, and a few trees were left standing. However, in HY-1, ages were determined for  $> 80\%$  of individuals of the four tree species. In HY-2, ages were determined for 93% of *Pseudotsuga menziesii*.

The number of years taken to reach core or stump height was calculated so that age determinations could be corrected for sampling height. Ages were determined at 30 cm above ground level for 30–35 saplings of each of the four main canopy tree species in an adjacent clearcut where conditions were relatively open, similar to those which probably prevailed in plots HY-1 and HY-2 after fire. The use of growth rates for seedlings or saplings within the two plots would have been inappropriate because many had established under closed forest conditions. Main canopy trees in the plots showed no signs of such suppression during establishment. Although most stumps were  $\approx 30$  cm tall, stumps of 30 large *Pseudotsuga menziesii* in plot HY-1 averaged

$54.7 \pm 1.7$  cm. Ages for *Pseudotsuga menziesii* saplings on the adjacent clearcut were therefore determined for both 30 and 55 cm above ground level. The following corrections for sampling height were added to age determinations from increment cores and stumps: *Pseudotsuga menziesii*, 5 yr (at 30 cm) and 7 yr (at 55 cm); *Tsuga heterophylla*, 6 yr; *Abies amabilis*, 5 yr; and *Abies procera*, 5 yr.

In plot HY-1, 22% of all *Abies amabilis* seedlings had been pressed to the forest floor by fallen trees and had produced roots from the prostrate part of their trunk. Because this layering could affect the age distribution of the population, a disc was removed for age determination from directly above the initial root-stock.

#### Stand history

Dates of past fire and treefall events were determined from increment cores and discs from scarred trees and from scars on stumps in situ. Many fire scars became apparent only after trees were cut, especially in HY-2.

#### Spatial pattern

Spatial distributions of species populations were assessed by mapping all individuals  $\geq 10$  cm tall in  $5 \times 5$  m (HY-1) and  $3 \times 3$  m (HY-2) contiguous quadrats (320 and 400 quadrats in the two plots, respectively). A variation of the nested-quadrat technique (Kershaw 1973, Greig-Smith 1983) was used to detect scales of pattern. Morisita's (1959) index was used to determine the departure from a random distribution (Veblen and Stewart 1982):

$$I_s = q \sum_{i=1}^q n_i(n_i - 1)/N(N - 1)$$

where  $q$  = number of quadrats,  $n_i$  = number of individuals of the species in the  $i^{\text{th}}$  quadrat, and  $N$  = the total number of individuals of the species in all quadrats.

The index,  $I_s$ , equals 1.0 when the population is randomly dispersed, where "random" implies an independent distribution of individuals into quadrats with an equal probability of each individual occurring in any one quadrat. If the individuals are aggregated,  $I_s$  will be  $> 1.0$ , and if evenly distributed or hyperdispersed,  $I_s$  will be  $< 1.0$ . The statistical significance of each  $I_s$  value was evaluated by an  $F$  test (Morisita 1959). Where the number of individuals is small (i.e.,  $< 20$ ),  $I_s$  can vary erratically and was computed only for the more abundant tree species populations.

$I_s$  was computed for different species and different age and size classes for quadrats of increasing size by grouping the basic  $1 \times 1$  units. Thus, for HY-1, the quadrat sizes analyzed were 25, 100, 225, 400  $\text{m}^2$ , and so on. For quadrats  $< 8 \times 8$  units (HY-1) and  $< 10 \times 10$  units (HY-2), the original units were grouped into perfect squares to avoid fluctuations in  $I_s$  that may result from changes in the shape of the blocks of quad-

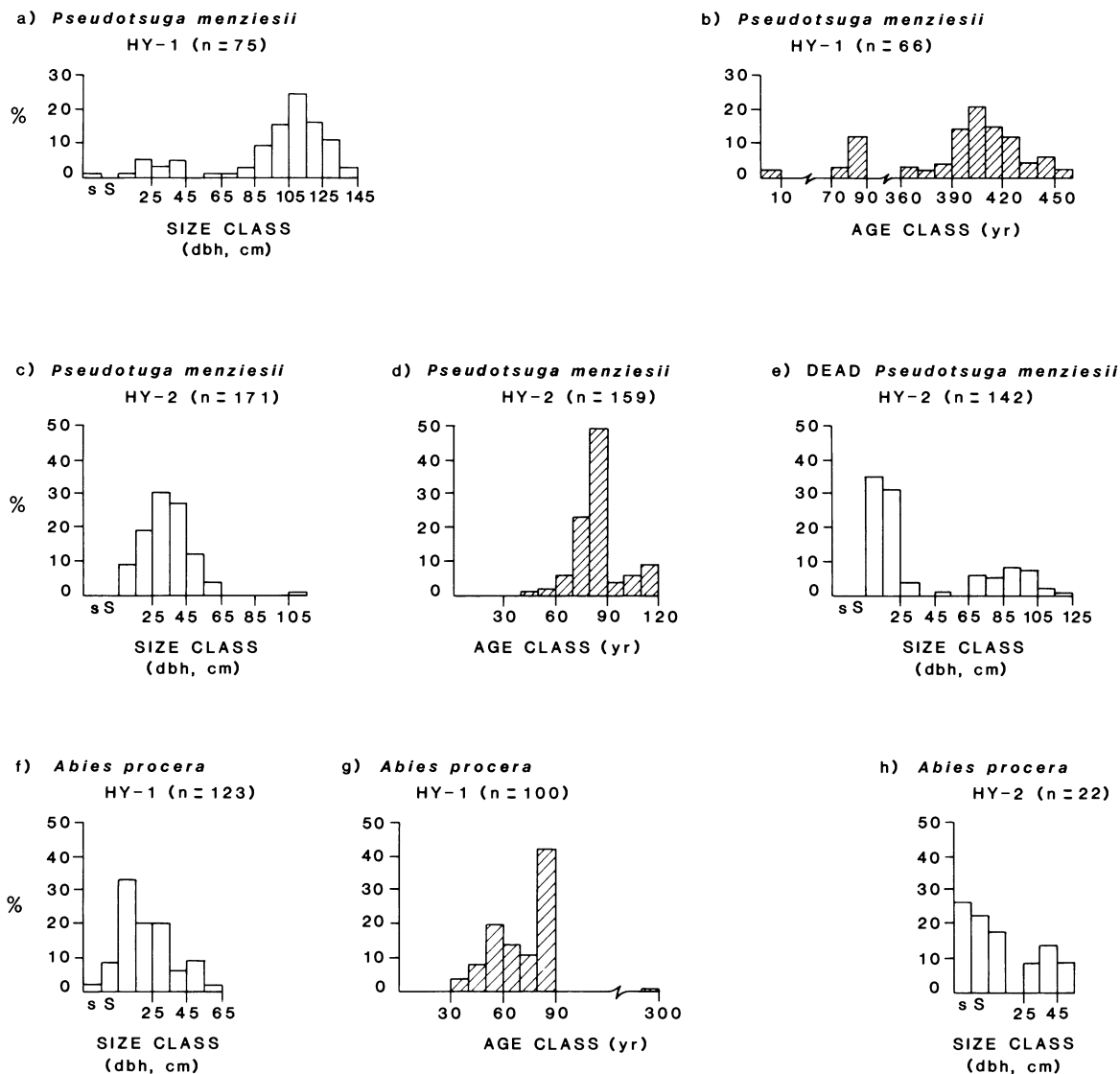


FIG. 2. Size class (□) and age class (▨) frequency diagrams for *Pseudotsuga menziesii* and *Abies procera* in plots HY-1 and HY-2. *n* = number of trees  $\geq 0.1$  m tall or number of trees aged. s refers to seedlings, S to saplings.

rais (Pielou 1977). Rectangles were used for larger blocks of quadrats.

The tendency for different pairs of species to occur together at various quadrat sizes was investigated by a chi-square test (Mueller-Dombois and Ellenberg 1974). The test was applied only to species sufficiently abundant to provide adequate cell frequencies in  $2 \times 2$  contingency tables, but not present in all quadrats.

## RESULTS AND INTERPRETATION

### Forest structure

Both size and age class distributions of *Pseudotsuga menziesii* showed at least two distinct populations in plot HY-1 (Fig. 2a, b). Trees of 5–44 cm dbh were equivalent to a younger age group of 71–90 yr old, and

the trees of 55–144 cm dbh spanned an establishment period of  $\approx 100$  yr from  $\approx 360$  to 460 yr ago. This long period of establishment concurs with other published accounts of the 450-yr-old age class in the central western Oregon Cascade Range (Franklin and Waring 1980, Franklin and Hemstrom 1981, Means 1982). In plot HY-2, however, the *Pseudotsuga* size distribution indicated a unimodal distribution of stems (Fig. 2c). In contrast, the age class distribution was bimodal, indicating two cohorts, one aged 90–120 yr and a more abundant group established 41–90 yr ago (Fig. 2d). The presence of an older age class could not have been determined from the size class information. Large numbers of standing dead *Pseudotsuga* ( $n = 99$ ) 5–34 cm dbh may reflect heavy thinning caused by density-dependent mortality (Fig. 2e). Stump diameters 65–

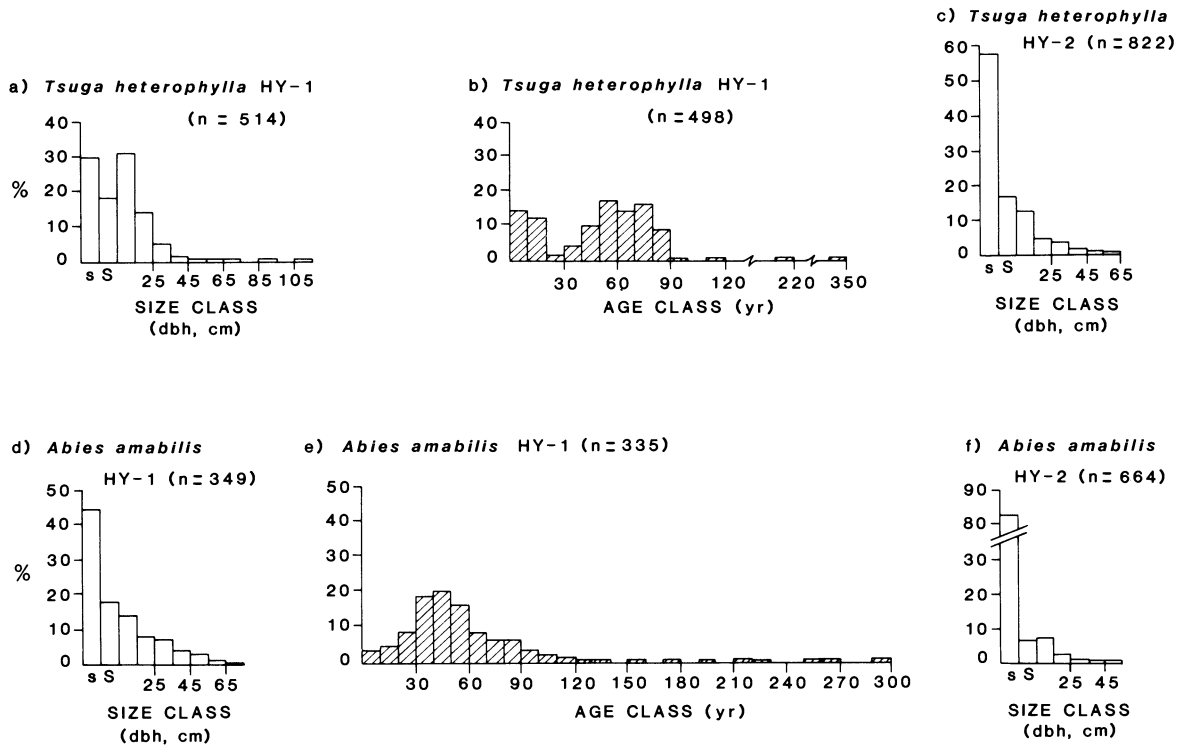


FIG. 3. Size class (□) and age class (▨) frequency diagrams for *Tsuga heterophylla* and *Abies amabilis* in plots HY-1 and HY-2.  $n$  = number of trees  $\geq 0.1$  m tall or number of trees aged. s refers to seedlings, S to saplings.

124 cm dbh suggest that before this mortality the population could have been similar in structure to that in HY-1, 100 m away.

*Abies procera* was represented by many stems in all height classes and all size classes  $\geq 5$  cm dbh in HY-1, although 71% were 5–34 cm dbh (Table 1, Fig. 2f). This size class distribution indicated a relatively even-aged population, and age analysis confirmed that 42% of trees that were aged established 81–90 yr ago (Fig. 2g). An initial pulse of recruitment was followed by a reduction in successful establishment, a second peak of recruitment  $\approx 51$ –60 yr ago, and then little recent establishment. This species was not abundant in HY-2, but occurred sporadically as seedlings, saplings, and main canopy trees (Table 1, Fig. 2h). Seven main canopy *Abies procera* were 81–100 yr old.

There were many stems 5–24 cm dbh of *Tsuga heterophylla* in HY-1, with declining numbers in larger size classes and a few scattered large individuals (Fig. 3a). The age class distribution for *Tsuga* differed from the size class distribution (Fig. 3b). A few larger and older individuals were apparent in both distributions, but almost half of the total tree population aged (47%) was established between 51 and 80 yr ago. Low numbers of individuals  $< 30$  yr old may reflect a marked decline in establishment or high mortality in this young population (84 dead individuals present were  $\leq 34$  cm dbh). In contrast to HY-1, *Tsuga* in HY-2 was well represented by seedlings and saplings with lower num-

bers in larger size classes (Fig. 3c). Ages of 60 individuals 10–63 cm dbh ranged from 44 to 117 yr, 75% being 71–90 yr old, and a further 10 trees were 101–120 yr old. This paralleled the ages of cohorts of *Pseudotsuga* in this plot. It is likely that a large group of *Tsuga* seedlings and saplings ( $n = 619$ ) formed a third age cohort  $< 40$  yr old in this stand (Fig. 3c).

*Abies amabilis* showed even greater differences between size and age class distributions than did *Tsuga* in HY-1 (Fig. 3d, e). There were a few trees 100–292 yr old, a range in age not evident from the size class distribution. Much of the population (54%) established 31–60 yr ago, after the main period of *Tsuga* regeneration (Fig. 3b, e). Few trees, including seedlings, were younger than 30 yr. Interpretation of the regeneration pattern of *Abies amabilis* on the basis of size alone would have been incorrect. *Abies amabilis* in HY-2 (Fig. 3f) had a similar size class distribution to *Tsuga* in the same plot (Fig. 3c).

#### Size-age relations

Least squares linear, exponential, logarithmic, and power function regression models were fitted to the diameter and age data for each species and to the height and age data for *Abies amabilis* and *Tsuga heterophylla* seedlings in HY-1. In almost all cases, the best fit was obtained using the power function regressions.

Although the use of power function regression showed good correlations of size and age, examination of the

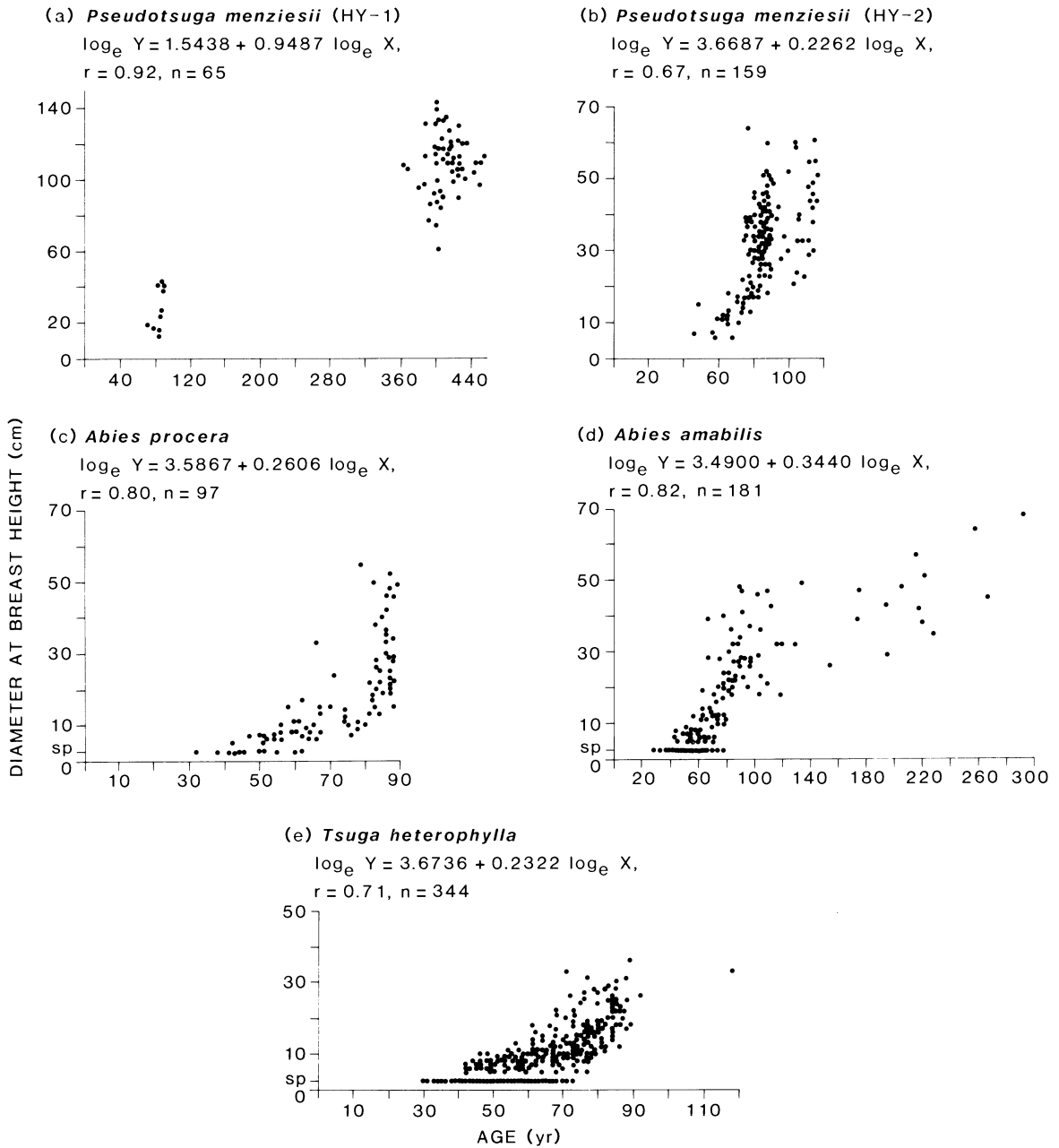


FIG. 4. Relationship of age to breast height diameter for main canopy tree species in plot HY-1 and for *Pseudotsuga menziesii* in plot HY-2. One *Abies procera* (dbh = 56 cm, age = 299 yr) and three *Tsuga heterophylla* (dbh = 25, 55, 66 cm; age = 217, 220, 348 yr, respectively) are not shown. Regression equations are included,  $P < .001$  in all cases.  $n$  = number of trees aged.

size-age scattergrams indicated that such correlations were often spurious. Regression equations of size and age for *Pseudotsuga menziesii* in HY-1 and HY-2 indicated that the variables were correlated (Fig. 4a, b). However, no apparent relationship existed between size and age for the older cohort of *Pseudotsuga* in HY-1 ( $\log_e Y(\text{age}) = 5.86 + 0.33 \log_e X(\text{dbh})$ ,  $n = 55$ ,  $r = 0.12$ , NS). If the group of 10 younger trees is added to the equation, a significant relationship can be obtained by

joining the two groups of points (Fig. 4a). The HY-2 population of *Pseudotsuga* also had two distinct age cohorts (45–89 and 90–116 yr old), both with a large range in diameter for a narrow range in age (Fig. 4b). Power function regressions for *Abies procera*, *Abies amabilis*, and *Tsuga heterophylla* also showed that size and age were correlated ( $r = 0.71\text{--}0.82$ ,  $P < .001$ ), but examination of the size-age scattergrams revealed weaknesses in the relationships. Many of the 81–90 yr

old *Abies procera* in HY-1 grew rapidly and attained main canopy dominance, resulting in diameters 3–4 times those of other trees of similar age (Fig. 4c, Table 1). Trees that established subsequently under this canopy grew more slowly. Thus, although size and age were statistically correlated (Fig. 4c), there was considerable variation in the relationship. Thirty percent of *Abies amabilis* trees >90 yr old in HY-1 showed periods of release from suppressed growth (as seen in wider annual rings) either at 85–90 or 110–115 yr ago (Fig. 4d). These trees had different size-age relationships than trees that grew rapidly to similar diameters in the last 90 yr. The high degree of shade tolerance of saplings of this species was apparent as they ranged in age from 27 to 77 yr (Fig. 4d). There was considerable range in ages for *Tsuga heterophylla* of similar diameters in HY-1 (Fig. 4e). For example, saplings ranged in age from 30 to 73 yr and trees  $\approx$ 10 cm dbh ranged from 45 to 80 yr old. Only a few, large, fire-scarred trees that were older than 90 yr (Fig. 5) showed markedly different growth rates.

Differences in the size-age relations of *Tsuga heterophylla* and *Abies amabilis* suggest possible differences in relative shade tolerance. There were 43 dead *Abies amabilis* 5–14 cm dbh (47% of all stems 5–14 cm dbh), but only about one-fifth of the *Tsuga heterophylla* of that size were dead (43 of 201). The lack of individuals of *Abies amabilis* of intermediate size may be caused by an inability to persist as a subcanopy tree. An ability to persist as seedlings or saplings and an apparent inability to survive as a tree under a dense canopy may explain the large differences between the size and age structures for this species (Figs. 3d, e). Compared to *Abies amabilis*, *Tsuga* had more representatives of intermediate height (Table 1), which showed a wide range in age (Fig. 4e), suggesting that *Tsuga heterophylla* may be shade tolerant at all tree heights.

Power function regressions of seedling height and age for *Tsuga heterophylla* and *Abies amabilis* in HY-1 indicated that the two variables were correlated ( $n = 154$ ,  $r = 0.81$ ,  $P < .001$ ;  $n = 154$ ,  $r = 0.82$ ,  $P < .001$ , for *Tsuga* and *Abies*, respectively). However, the occurrence of relatively even-aged groups of seedlings of different growth rates (especially for *Tsuga*) caused extreme variability in the age-height relationship.

#### Disturbance history

The frequency and pattern of fires in the two stands were different from those documented for other areas in the western Cascade Range. For example, fires in the study area have been more frequent and less destructive than described for Mount Rainier National Park (Franklin and Hemstrom 1981, Hemstrom and Franklin 1982). Dates determined from scarred trees indicated that at least four fires have significantly affected the study area during the last four and a half centuries. A fire that occurred  $\approx$ 450 yr ago appears to

have initiated the old-growth *Pseudotsuga*. Another occurred  $\approx$ 320 yr ago, as aged from scars on nine *Pseudotsuga* in HY-1. A third fire at  $\approx$ 120 yr ago ( $\approx$ 1860 AD) gave rise to the oldest cohort of trees in HY-2, and 12 trees in HY-1 and HY-2 had scars from a fire  $\approx$ 90 yr ago ( $\approx$ 1890 AD). Many codominant *Abies amabilis* and *Tsuga heterophylla* showed large increases in annual ring widths at  $\approx$ 120 and 90 yr BP, further verifying the two most recent fires. Two scars dated at  $\approx$ 210 and 250 yr ago may indicate localized fires or lightning strikes.

Eight large *Pseudotsuga*, seven at the southern end of HY-1, had been recently windthrown, all falling from south to north. Treefall scars on small *Abies amabilis* and *Tsuga heterophylla* indicated that all eight trees were blown over in 1962, probably as a result of the Columbus Day storm.

#### Spatial pattern

The distributional patterns of tree species in HY-1 illustrated the effects of periodic disturbance. In HY-1 *Pseudotsuga menziesii* 362–455 yr old were distributed widely over the plot, and although uniformly distributed up to block sizes of 100 m<sup>2</sup>, were randomly distributed at all larger block sizes (Fig. 5a, c). Dead *Pseudotsuga*  $\geq$ 65 cm dbh were distributed randomly at all block sizes, but analysis of live and dead stems together showed a similar pattern to that for live trees only. These patterns may have reflected sporadic mortality and intense competition over a long period of time in a large, old, even-aged population. *Tsuga heterophylla* and *Abies amabilis* >90 yr old were clumped at all quadrat sizes up to and including 625 m<sup>2</sup> (Fig. 5b, d). This was the result of survival in clumps after the  $\approx$ 1890 fire. Several of these trees and *Pseudotsuga* had fire scars dated to that event (Fig. 5a, b).

At small block sizes, *Tsuga heterophylla*  $\leq$ 30 yr old were extremely clumped, as they had established on logs in canopy openings formed, in part, from windthrow in 1962 (Fig. 5c, e; Table 2). Clumping occurred up to quadrat sizes of 2000 m<sup>2</sup>, reflecting the presence of several large patches of this age group (Fig. 5c). Trees of this species 31–90 yr old also occurred in clumps up to 2000 m<sup>2</sup>, and this was related to regeneration in openings created by fire ( $I_s = 1.32$  at 25 m<sup>2</sup>,  $I_s = 1.11$  at 2000 m<sup>2</sup>). The lower values of  $I_s$  for older stems probably reflected heavy thinning of patches as they aged, which resulted in a tendency towards a random distribution within each patch. *Tsuga heterophylla*  $\leq$ 30 yr old and *Tsuga* 31–90 yr old were negatively associated with *Tsuga* and *Abies amabilis* >90 yr old ( $\chi^2 = 4.6$  at 225 m<sup>2</sup> and  $\chi^2 = 12.1$  at 25 m<sup>2</sup>, respectively,  $P < .05$ ; also see Fig. 5b, e), verifying the regeneration patterns described above. In addition, *Tsuga*  $\leq$ 30 yr old were often positively associated with dead *Pseudotsuga*  $\geq$ 65 cm dbh ( $\chi^2 = 7.1$  at 100 m<sup>2</sup>,  $P < .01$ ).

*Abies amabilis* in HY-1 had clumped distributions similar to *Tsuga heterophylla*. Clumped distributions



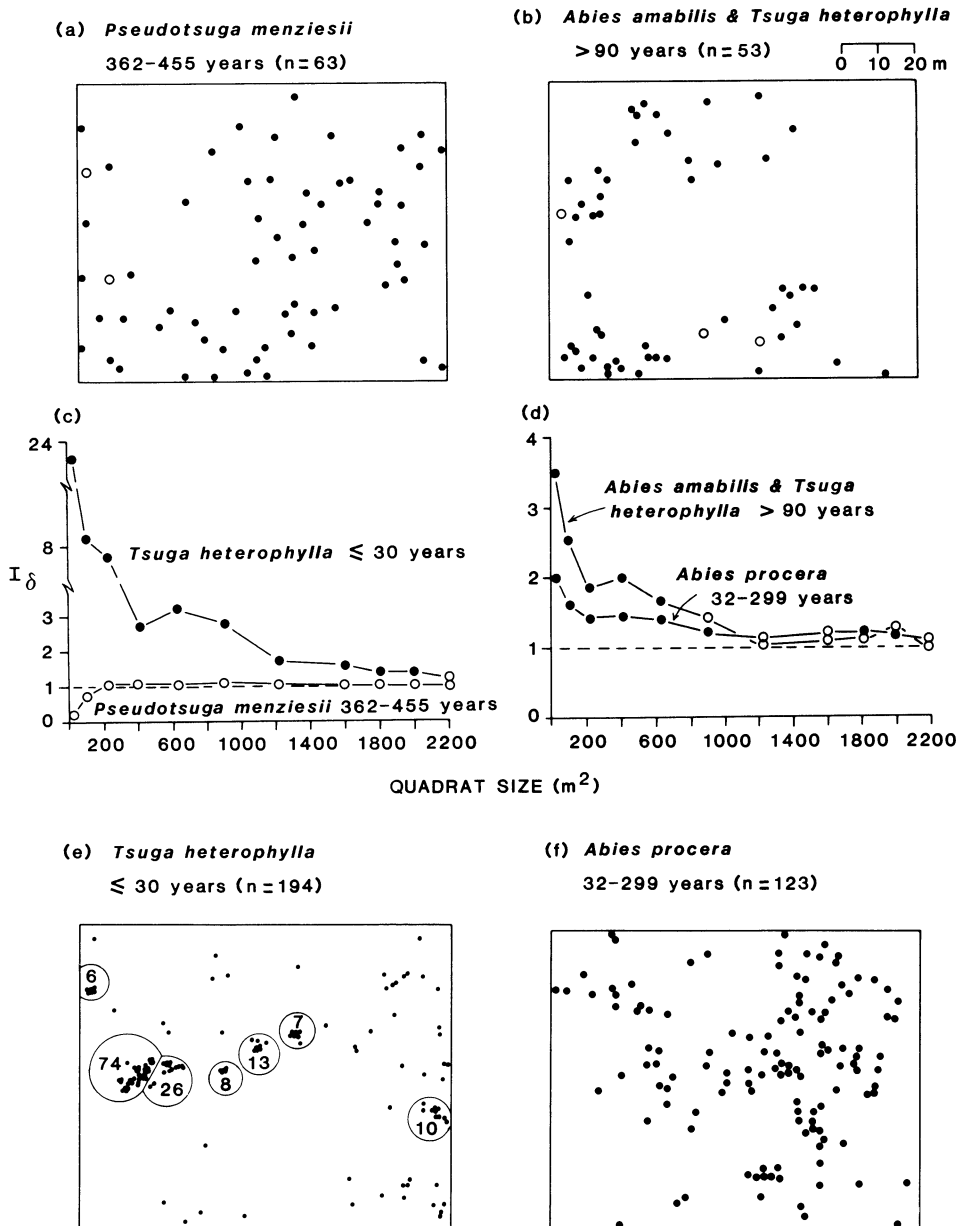


FIG. 5. Maps of species of different age classes in plot HY-1 [(a), (b), (e), and (f)] and their values of Morisita's index,  $I_s$ , at different quadrat sizes [(c) and (d)]. Solid symbols in (c) and (d) are  $I_s$  values significantly  $> 1.0$  ( $P < .05$ ) according to an  $F$  test of Morisita (1959). The dashed lines at  $I_s = 1$  represent the index values for random spatial distributions. Open circles in (a) and (b) are trees that had scars from the 1890 fire.

of  $\leq 30$ -yr-old *Abies amabilis* ( $I_s = 11.5$  at  $25 \text{ m}^2$ ) and a positive association with *Tsuga*  $\leq 30$  yr old ( $\chi^2 = 14.8$  at  $25 \text{ m}^2$ ,  $P < .001$ ) indicated co-establishment in canopy gaps. Patches of *Abies amabilis* 31-90 yr old also formed in openings created by the  $\approx 1890$  fire, as indicated by clumped distributions up to  $900 \text{ m}^2$ .

The third species to establish in the canopy openings formed by the  $\approx 1890$  fire was *Abies procera* (Fig. 5d, f). *Tsuga heterophylla* 31-90 yr old and *Abies procera*  $< 90$  yr old were positively associated as a result ( $\chi^2 = 4.6$  at  $25 \text{ m}^2$ ,  $P < .05$ ).

Spatial patterns of trees in HY-2 illustrated other regeneration patterns. Combining dead and live *Pseudotsuga menziesii*  $\leq 64$  cm dbh revealed that the trees present several decades ago were clumped up to  $144 \text{ m}^2$  (Fig. 6a). Subsequent thinning of these patches left clumps of live trees at  $144 \text{ m}^2$ , but with fewer trees in each patch ( $I_s = 1.11$  at  $144 \text{ m}^2$ , Fig. 6a). The occurrence of clumps of two or three *Pseudotsuga* stumps  $\geq 65$  cm dbh suggests that mortality in the original population was influenced by fire or windthrow, resulting in the death of trees in some areas but not in

TABLE 2. Seedling (0.1–1.4 m tall) and tree density in plots HY-1 and HY-2.

Species	Seedlings/ha		Trees/ha	
	HY-1	HY-2	HY-1	HY-2
<i>Tsuga heterophylla</i>	288 (78.0)*	1325 (82.0)	1231 (50.3)	958 (63.5)
<i>Abies amabilis</i>	194 (15.0)	1514 (29.0)	244 (23.6)	331 (33.6)
<i>Abies procera</i>	4 (100.0)	17 (33.0)	144 (25.2)	44 (31.3)
<i>Pseudotsuga menziesii</i>	1 (100.0)		93 (0.0)	475 (45.6)

\* Numbers in parentheses refer to percentages of seedlings and trees that were on elevated surfaces (logs, stumps, trunk buttresses, or upturned root plates).

others. The similarity in dispersions for live *Pseudotsuga*  $\leq 64$  cm dbh and dead trees  $\geq 65$  cm dbh also suggests that many of the live trees could have established on the stumps of the trees of the previous population (also see Table 2).

Spatial patterns of *Tsuga heterophylla* and *Abies amabilis* in HY-2 reflected establishment in patches; *Abies amabilis* only is illustrated (Fig. 6b). For both species, seedlings were clumped (up to 900 m<sup>2</sup>) as were larger stems (up to 300 m<sup>2</sup>; Fig. 6b). Seedlings of *Tsuga* and *Abies* and stems  $\leq 10$  cm dbh occurred in similar situations, as indicated by positive associations ( $\chi^2$  seedlings = 15.3 at 9 m<sup>2</sup>,  $P < .001$ ;  $\chi^2 \leq 10$ -cm stems = 5.4 at 36 m<sup>2</sup>,  $P < .025$ ). The importance of elevated surfaces for the establishment of *Tsuga* was apparent from a positive association between  $\leq 10$ -cm dbh stems and dead *Pseudotsuga*  $\geq 65$  cm dbh ( $\chi^2 = 4.0$  at 9 m<sup>2</sup>,  $P < .05$ ).

The regeneration patterns of *Tsuga* and *Abies amabilis* after different disturbances can be clarified further from the association tests. *Tsuga*, *Abies amabilis*, and *Abies procera* established in canopy openings created by the  $\approx 1890$  fire in HY-1. In contrast, *Tsuga* and *Abies amabilis* established with *Pseudotsuga* in HY-2, indicated by a positive association of *Tsuga* and *Abies*  $\leq 10$  cm dbh with live *Pseudotsuga*  $\leq 64$  cm dbh ( $\chi^2 = 5.9$  at 9 m<sup>2</sup>,  $\chi^2 = 4.2$  at 9 m<sup>2</sup>,  $P < .05$ , for *Tsuga* and *Abies*, respectively). After establishment of a tree canopy in both plots, regeneration of *Tsuga* and *Abies* was most abundant in canopy openings. Seedlings of *Tsuga* and *Abies* were consistently rare or absent under *Tsuga*  $> 10$  cm dbh, as indicated by negative associations in HY-1 ( $\chi^2 = 5.6, 5.4$ , at 25 m<sup>2</sup>,  $P < .025$ , for *Tsuga* and *Abies* seedlings) and in HY-2 ( $\chi^2 = 8.3, 10.5$  at 9 m<sup>2</sup>,  $P < .005$  for *Tsuga* and *Abies* seedlings).

#### DISCUSSION

Both size and age class frequency distributions provided useful information for the interpretation of past population dynamics in the two plots. However, because trees of different growth rates and size-age relationships occurred in the same stand, size class analysis alone was insufficient to interpret forest development. Several authors have suggested that size is more important than age in studies of tree population dynamics (e.g., Buchholz and Pickering 1978, Knowles and Grant 1983). However, for the forests studied,

direct age determination revealed patterns not obvious from the diameter distributions (cf. Ross et al. 1982).

The two forest plots described had similar recent fire disturbance histories but different stand structures. Plot HY-1, with emergent, old-growth *Pseudotsuga menziesii*, was dominated by main canopy *Tsuga heterophylla* and *Abies procera*. In contrast, plot HY-2, subjected to the same fire in  $\approx 1890$ , was dominated by *Pseudotsuga menziesii*. Although it was impossible to reconstruct the pattern of older fires, the approximate area and probable nature of the 1890 fire can be inferred.

In stand HY-1, the 1890 fire must have been of variable intensity; in some areas all trees were killed, but in others trees were only scarred. Individuals of all four canopy species survived, providing seed for invasion of the openings created. These openings remained sheltered by a scattered *Pseudotsuga* canopy, and *Tsuga heterophylla* and *Abies procera* were the most successful invaders. Certain life history characteristics may have favored *Tsuga* and *Abies procera*; both have rapid growth rates and can quickly attain dominance on a site (Franklin 1964a, Kotar 1972). Conversely, *Abies amabilis* must reach a certain height in the canopy before it produces much seed (Long 1976). Because, at the time of the 1890 fire, most *Abies amabilis* in the area would have been suppressed individuals  $< 100$  yr old, they probably produced very little seed. Regeneration of all species was limited beneath the dense *Tsuga* canopy. Even though *Tsuga* and *Abies amabilis* are extremely shade tolerant, they established only in canopy openings. Since many of the old-growth *Pseudotsuga* survived the 1890 fire, the availability of log substrates for seedling establishment may have been limited. As noted by Christy and Mack (1984), the age class structures of *Tsuga heterophylla* juveniles may be related to the amount of fallen wood of an appropriate decay class on the forest floor.

Regeneration after the same fire in HY-2 followed a different pattern. The  $\approx 1860$  fire probably destroyed the previous old-growth *Pseudotsuga*. The 1890 fire destroyed most of the resulting young stand, and created large openings which were invaded primarily by *Pseudotsuga*. The large numbers of small *Abies amabilis* may have resulted from highly favorable conditions under the *Pseudotsuga* canopy and seed input from a few trees that survived the last fire. Woody

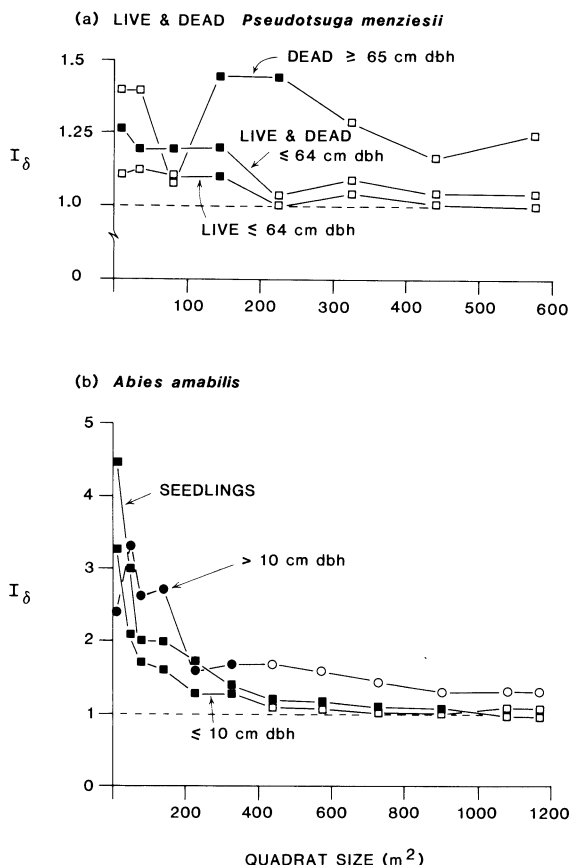


FIG. 6. Values of Morisita's index,  $I_\delta$ , at different quadrat sizes for (a) *Pseudotsuga menziesii* and (b) *Abies amabilis* of different size classes in plot HY-2. Solid symbols are  $I_\delta$  values significantly  $> 1.0$  ( $P < .05$ ) according to an  $F$  test of Morisita (1959). The dashed lines at  $I_\delta = 1$  represent random spatial distributions.

material would have decomposed sufficiently after the  $\approx 1860$  fire to provide an ideal substrate for establishment of many of the most recent populations after the 1890 fire (Table 2). Seedling populations were also favored by the decomposition of trees killed by the 1890 fire. Therefore, in contrast to HY-1, abundant regeneration was possible because of the greater availability of suitable substrates.

The differential stand development between HY-1 and HY-2 illustrates important aspects of forest succession in the region. The relatively shade-intolerant *Pseudotsuga menziesii* and *Abies procera* (Minor 1979) usually regenerate in relatively even-aged stands after major fires. The shade-tolerant species *Abies amabilis* and *Tsuga heterophylla* (Fowells 1965) regenerate in even-aged patches after catastrophic events, but also in canopy openings created by lesser disturbances, such as partial burns and small windfalls. These differences in regeneration result in patches of different sizes and ages within an area of forest; the forest is therefore a "mosaic of more or less even-aged aggregations" (cf.

Bonnicksen and Stone 1981). Similar interactions of large- and small-scale disturbances in the successional pattern of forests have been documented elsewhere (e.g., Oliver and Stephens 1977, Veblen et al. 1981). The patterns described also suggest that the initial colonizers after disturbance have important effects on subsequent tree regeneration (cf. "initial floristic composition" of Egler [1954]). If *Pseudotsuga* establishes first, regeneration of *Tsuga* and often *Abies amabilis* may occur (as in HY-2). If, however, *Tsuga* dominates early after fire (as in HY-1), regeneration may be excluded or remain at a low level until canopy openings are formed.

#### ACKNOWLEDGMENTS

I am grateful to Drs T. T. Veblen and J. A. Antos for discussions on this theme and suggestions for improvement of the original manuscript; to Drs D. B. Zobel, J. F. Franklin, and F. Swanson for critical review of the manuscript; J. Orwin for editorial assistance; and to M. A. Stewart for assistance in data collection. The study was supported by a New Zealand National Research Advisory Council Postgraduate Fellowship.

#### LITERATURE CITED

- Bonnicksen, T. M., and E. C. Stone. 1981. The giant sequoia-mixed conifer forest community characterized through pattern analysis as a mosaic of aggregations. *Forest Ecology and Management* 3:307-328.
- Buchholz, K., and J. L. Pickering. 1978. DBH—distribution analysis: an alternative to stand age analysis. *Bulletin of the Torrey Botanical Club* 105:282-288.
- Christy, E. J., and R. N. Mack. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *Journal of Ecology* 72:75-91.
- Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition—a factor in old-field vegetation development. *Vegetatio* 4:412-417.
- Fowells, H. A. 1965. *Silvics of forest trees of the United States*. United States Department of Agriculture Handbook Number 271.
- Franklin, J. F. 1964a. Some notes on the distribution and ecology of noble fir. *Northwest Science* 38:1-13.
- . 1964b. Ecology and silviculture of the true fir-hemlock forests of the Pacific Northwest. *Proceedings of the Society of American Foresters* 1964: 28-32.
- Franklin, J. F., and C. T. Dyrness. 1973. *Natural vegetation of Oregon and Washington*. United States Forest Service General Technical Report PNW-8.
- Franklin, J. F., and M. A. Hemstrom. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. Pages 212-229 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession*. Springer-Verlag, New York, New York, USA.
- Franklin, J. F., and R. H. Waring. 1980. Distinctive features of the northwestern coniferous forest: development, structure and function. Pages 59-86 in R. H. Waring, editor. *Forests: fresh perspectives from ecosystem analysis*. Oregon State University Press, Corvallis, Oregon, USA.
- Greig-Smith, P. 1983. *Quantitative plant ecology*. Third edition. University of California Press, Berkeley, California, USA.
- Harcombe, P. A., and P. L. Marks. 1978. Tree diameter distributions and replacement processes in southeast Texas forests. *Forest Science* 24:153-166.
- Hemstrom, M. A., and J. F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. *Quaternary Research* 18:32-51.

- Hibbs, D. E. 1979. The age structure of a striped maple population. *Canadian Journal of Forest Research* **9**:504–508.
- Hitchcock, C. L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, Washington, USA.
- Kershaw, K. A. 1973. *Quantitative and dynamic plant ecology*. Second edition. American Elsevier, New York, New York, USA.
- Knowles, P., and M. C. Grant. 1983. Age and size structure analyses of Engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. *Ecology* **64**:1–9.
- Kotar, J. 1972. *Ecology of Abies amabilis in relation to its altitudinal distribution and in contrast to its common associate Tsuga heterophylla*. Dissertation. University of Washington, Seattle, Washington, USA.
- Long, J. N. 1976. *Forest vegetation dynamics within the Abies amabilis zone of a western Cascades watershed*. Dissertation. University of Washington, Seattle, Washington, USA.
- Lorimer, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* **61**:1169–1184.
- Lynott, R. E., and O. P. Cramer. 1966. Detailed analysis of the 1962 Columbus Day windstorm in Oregon and Washington. *Monthly Weather Review* **94**:313–339.
- Means, J. E. 1982. Development history of dry coniferous forests in the central western Cascade range of Oregon. Pages 142–158 in J. E. Means, editor. *Forest succession and stand development research in the Northwest*. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Minore, D. 1979. *Comparative autecological characteristics of Northwestern tree species—a literature review*. United States Forest Service General Technical Report PNW-87.
- Morisita, M. 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. *Memoirs of the Faculty of Science of Kyushu University, Series E, Biology* **2**:215–235.
- Mueller-Dombois, D., and H. Ellenberg. 1974. *Aims and methods of vegetation ecology*. Wiley, New York, New York, USA.
- Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed-species forest in central New England. *Ecology* **58**:562–572.
- Parker, A. J., and R. K. Peet. 1984. Size and age structure of conifer forests. *Ecology* **65**:1685–1689.
- Pielou, E. C. 1977. *Mathematical ecology*. Wiley, New York, New York, USA.
- Ross, M. S., T. L. Sharik, and D. W. Smith. 1982. Age-structure relationships of tree species in an Appalachian oak forest in southwest Virginia. *Bulletin of the Torrey Botanical Club* **108**:287–298.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* **62**:1041–1051.
- Spurr, S. H., and B. V. Barnes. 1980. *Forest ecology*. Second edition. J. Wiley and Sons, New York, New York, USA.
- Stewart, G. H., and T. T. Veblen. 1982. Regeneration patterns in southern rata (*Metrosideros umbellata*)–kamahi (*Weinmannia racemosa*) forest in central Westland, New Zealand. *New Zealand Journal of Botany* **20**:55–72.
- Veblen, T. T., Z. C. Donoso, F. M. Schlegel, and B. Escobar, R. 1981. Forest dynamics in south-central Chile. *Journal of Biogeography* **8**:211–247.
- Veblen, T. T., and G. H. Stewart. 1982. On the conifer regeneration gap in New Zealand: the dynamics of *Libocedrus bidwillii* stands on South Island. *Journal of Ecology* **70**:413–436.