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Age Structure Patterns in Abies amabilis Stands of the Cascade Mountains

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ABSTRACT.—The density and age structure of *Abies amabilis* younger than 50 yr were studied at 13 mature and old-growth forest stands in Oregon and Washington. All stands were within the *A. amabilis* vegetation zone, keyed to *A. amabilis* community types and had mature *A. amabilis* in the canopy. Density of individuals ≤50 yr (40 per ha to 47,680 per ha) was positively correlated with stand basal area of canopy *A. amabilis* and cover of woody understory plants. Density was negatively correlated with canopy and herbaceous cover. These results imply that local seed source is important for *A. amabilis* regeneration and that *A. amabilis* is partially intolerant of shade and competition with the herbaceous understory. *Abies amabilis* density was not significantly correlated with 13 other stand and microenvironmental characteristics.

Abies amabilis distributions were highly variable among stands. Age structures commonly associated with sustained regeneration were found at only four stands. Moreover, stand age structure type was unrelated to any of the measured stand and microenvironmental characteristics except cover of woody understory plants. Age structures were also unrelated to density of young *A. amabilis* individuals.

These observations of age distributions and densities of individuals ≤50 yr show that *Abies amabilis* can persist in late successional stands without maintaining continuous seedling establishment. *Abies amabilis* regeneration instead appears to be opportunistic, occurring when and where canopy and understory cover is disrupted.

INTRODUCTION

Two ecological processes can lead to the persistence of long-lived plant species in communities. First, a population may be able to sustain regeneration and growth in the presence of older plants of the same species. This tolerance model of persistence corresponds to the classical definition of a climax species (*e.g.,* Whittaker, 1975). A second way that populations can persist is in response to repeated disturbances. In this model, recently disturbed patches support abundant regeneration and other patches are dominated by older individuals (Bray, 1956; Forcier, 1975). As disturbance has become recognized as a widespread feature of many landscapes (White, 1979; Sousa, 1984), evidence has accumulated that the persistence of many species requires these repeated disturbances. In particular, an unresolved question is the extent to which even shade-tolerant species require disturbances for establishment and rapid growth (Aplet *et al.,* 1988; Canham, 1988; Swaine and Whitmore, 1988; Spies and Franklin, 1989).

In this study, populations of *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) were examined with respect to these two models of persistence. The density and age structure of young *A. amabilis* at several stands were studied to address three objectives: (1) to see if age structures were consistent with sustained reproduction within stands; (2) to determine if differences in age structures among *A. amabilis* populations corresponded to changes in stand and microsite conditions; and (3) to develop hypotheses about the importance of repeated, small-scale disturbances to the continued persistence of *A. amabilis*.

METHODS

Study species.—*Abies amabilis* is a prominent component of many forests from Oregon to southeast Alaska. Its climax status in midelevation stands on the west slope of the Cascade

Mountains (Franklin and Dyrness, 1973; Franklin and Hemstrom, 1981) is inferred from its prominence in old forest stands (Franklin and Dyrness, 1973), its apparent continuous regeneration on stands where it is present (Stewart, 1986b), its age structures (Stewart, 1986a, b) commonly associated with sustained regeneration (*e.g.*, Whipple and Dix, 1979), its moderate to high shade tolerance (Baker, 1949; Minore, 1979) and its long-term persistence in computer simulations of forest development based on the physiological properties of trees (Dale *et al.,* 1986).

Study sites.—*Abies amabilis* populations were sampled in 13 stands: 4 in western Oregon (within or near the H. J. Andrews Experimental Forest) and 9 at Mt. Rainier National Park, Washington. Each stand was part of the Reference Stand system of permanent plots administered at Oregon State University (Hawk *et al.,* 1978). All 13 stands were in the *A. amabilis* zone (Franklin and Dyrness, 1973), keyed to the *A. amabilis* community type (Dyrness *et al.,* 1974), had developed at least 135 years since major disturbance and had *A. amabilis* currently in the canopy. Thus, the stands were likely to support persistent populations of *Abies amabilis*. Slope and aspect were measured with a clinometer and compass. Information on additional stand characteristics [elevation, dominant overstory species, habitat type, age since last stand-initiating disturbance (estimated from ages of oldest trees), total basal area and basal area of *A. amabilis*] was obtained from the Forest Science Data Bank at Oregon State University.

Sampling methods.—Sampling for age structure and microenvironmental conditions was conducted in 5 m × 5 m quadrats located randomly within each Reference Stand. Overall sampling intensity varied between 125 m^2 and 4800 m^2 per stand (5–192 quadrats), depending on the spatial heterogeneity and seedling density. All young *Abies amabilis* ($\leq$50 yr) in each quadrat were aged. Because size is only an approximate index of age (in this study 50 yr *A. amabilis* ranged between between 47 cm and 144 cm in height), all individuals thought to be 50 yr or younger were aged and the data for trees over 50 yr discarded. Trees were aged by counting annual bud scale scars or by counting annual rings from increment cores taken at the base of the tree. For trees too small to bore and with obscured older bud scale scars, visible scars were counted as low on the stem as possible, then a correction factor was added for the uncounted height. The correction factor was calculated from regressions of age vs. height derived from smaller trees within the stand that were aged completely ($P < 0.01$ for all regressions). (In a subsample of sacrificed trees, ages calculated by counting visible scars and adding a correction factor agreed closely with ages calculated by counting annual rings at the base of the stem.) Ages of 336 of 3889 trees sampled required adjustment.

Microtopography within each 25 m^2 quadrat was assessed by estimating the proportion of each quadrat that was flat, in depressions or elevated. Depressions were defined as surfaces at least 10 cm below the general forest floor level. Elevated microsites were logs, trunk buttresses, rocks or upturned root plates. Substrate type (logs or stumps, organic soil, mineral soil and rock) was also recorded. Plant cover was estimated to the nearest 10% for three strata: herbaceous plants, woody plants with foliage 0–3 m above the ground and canopy cover (foliage >3 m in height, summed for all species). Canopy cover was visually estimated to the nearest 10% either directly in the field or from vertical fish-eye photographs.

Statistical analysis.—Relationships between density of young *Abies amabilis* and stand and microenvironmental characteristics were tested using Spearman's rank correlation analysis (Conover, 1980). Slope, aspect and latitude values were converted to potential solar insolation values (Buffo *et al.,* 1972), regarded as better indicators of relative evapotranspirational demand. Deviation from the middle of the elevational range of *A. amabilis* [1200 m in Washington (Franklin *et al.,* 1988), 1325 m in Oregon (Dyrness *et al.,* 1974)] was also used as a variable in the statistical analysis. For analysis with stand characteristics, total density (trees/ha) of young *A. amabilis* was calculated for each of the 13 stands. For analysis with microenvironmental characteristics, density was calculated for individual quadrats. Because stands 13, 21 and 22 were more intensively sampled than the other stands, correlation analysis used a random subset of 10 quadrats within each of these stands.

The general shape of the age distribution curve of *Abies amabilis* within a stand was obtained by fitting a smoothed curve to the histogram of frequencies of individuals within age classes. The smoothing algorithm, symbolized "4253H,twice" by Velleman and Hoaglin (1981), is based on running medians and is robust in the face of the year-to-year variability common in age distributions.

The shapes of age distribution curves and the average age of trees ≤50 yr were used to assign each stand to an age structure category. The "balanced" age structure category was defined as having abundant seedlings in a range of age classes, but with decreasing numbers of older trees; average age in this age structure is between 10 and 15 yr. This category corresponds to the inverse-J age distribution type of Whipple and Dix (1979) and others. The "intermediate" age structure category was defined as intermediate between the balanced and mostly-very-young age structure categories, with average ages between 5 and 7 yr. The "mostly-very-young" age structure category was defined as having under-represented older age classes, with average ages <5 yr. The "mostly older" age structure category was defined as having more trees in the 25–50 yr age class than in the 0–25 yr age class; hence average ages are >25 yr. The "irregular" age structure category was defined as one with no clear age structure.

Relationships between age structure category and stand and microenvironmental conditions were tested using the Multi-Response Permutation Procedure (MRPP) technique (Mielke *et al.,* 1981; Zimmerman *et al.,* 1985; McCune, 1987). MRPP is analogous to multivariate analysis of variance, but does not assume that the response variables have multivariate normal distributions or that variances are homogeneous. The null hypothesis tested by MRPP was that average stand and microenvironmental characteristics were the same for stands having different categories of age structures. Stand and microenvironmental characteristics were standardized for the MRPP analysis.

The association of single stand and microenvironmental characteristics with age structure categories was tested with a Kruskal-Wallis nonparametric analysis of variance (Conover, 1980). For tests of microenvironmental characteristics, quadrats were assigned to the age structure category of the stand as a whole. Because quadrats within a stand were always in the same category and so were not independent of each other, published statistical tables for the Kruskal-Wallis test could not be used. Therefore, statistical significance levels were calculated by randomization methods (Sokal and Rohlf, 1981), using 1000 random permutations of the stand classification based on age structure category. If a stand or microenvironmental characteristic was significantly related to age structure category, differences among categories were tested by nonparametric multiple comparisons tests (Conover, 1980).

RESULTS

Stand and microenvironmental characteristics.—Basal areas of *Abies amabilis* varied between 0.3 m^2 per ha and 50.1 m^2 per ha, averaging 23% of total stand basal area (Table 1). Slopes ranged between 6° and 39° and a wide variety of slope aspects was represented. The youngest stand apparently arose from a disturbance 135 yr ago and the oldest stand was approximately 1000 yr old (data on file in the Forest Science Data Bank, Stafford *et al.,* 1984).

Stands varied in amount of vegetative cover (Table 2). Canopy cover ranged between 27% and 88%. Six stands had woody understory cover >50%. The relative contribution of

TABLE 1.—Study stand characteristics. Habitat type labels are from the Oregon State University Forest Science Data Bank (Stafford *et al.*, 1984). Elev. dev. refers to the deviation from the middle of *Abies amabilis*'s elevational distributions. PSI is potential solar insolation. BA is basal area. Density and average age are for *Abies amabilis* individuals ≤50 yr

Reference stand number	Dominant species	Habitat type	Lat. (deg)	Stand. age (yr)	Elev. (m)	Elev. dev. (m)	Slope (deg)	Aspect (deg)	PSI (kcal/ cm²/ day)	Abam BA (m²/ha)	Total BA (m²/ha)	Sample area (m²)	Abam density (stems/ha)	Aver. Abam age (yr)
2	Abam/Tshe	Abam/Vaal	47	1000	850	350	11	130	194	36.3	80.4	250	7320	11.7
3	Abam/Tshe	Abam/Opho	47	1000	850	350	9	110	185	38.9	102.0	250	1360	3.1
5	Abam/Tshe	Abam/Gash	47	650	950	250	13	336	144	30.0	83.2	125	47,680	12.7
6	Abam/Tshe	Abam/Vaal	47	750	1060	140	9	190	199	23.6	50.4	125	35,040	11.7
7	Chno/Abam	Abam/Rhal	47	300	1430	230	39	100	173	31.2	78.9	125	38,640	6.8
8	Tshe/Psme	Abam/Bene	47	750	1050	150	10	292	167	0.4	76.6	250	1160	15.5
10	Abam/Chno	Abam/Ermo	47	300	1430	230	30	150	222	50.1	94.0	250	42,960	4.4
13	Abpr/Psme	Abam/Tiun	44	135	1325	0	14	195	217	3.1	77.7	1025	3317	3.7
15	Tshe/Psme	Abam/Xete	47	150	1030	170	14	80	169	0.3	72.4	250	40	4.0
16	Abam/Chno	Abam/Mefe	47	600	1195	5	6	246	184	13.4	62.6	250	10,920	6.7
21	Psme/Tshe	Abam/Tiun	44	450	1190	135	10	200	209	7.2	106.6	4800	294	35.1
22	Abpr/Psme	Abam/Vame	44	275	1290	35	9	148	205	11.0	89.7	500	4320	3.7
23	Tshe/Psme	Abam/Vaal	44	450	1020	305	19	10	134	0.3	67.6	250	4400	10.2

Species codes are as follows: Abam, *Abies amabilis*; Abpr, *Abies procera*; Bene, *Berberis nervosa*; Chno, *Chamaecyparis nootkatensis*; Ermo, *Erythronium montanum*; Gash, *Gaultheria shallon*; Mefe, *Menziesia ferruginea*; Opho, *Oplopanax horridum*; Psme, *Pseudotsuga menziesii*; Rhal, *Rhododendron albiflorum*; Tiun, *Tiarella uniflora*; Tshe, *Tsuga heterophylla*; Vaal, *Vacccinium alaskense*; Vame, *Vaccinium membranaceum*; Xete, *Xerophyllum tenax*

TABLE 2.—Summary of average vegetative cover (%) within study stands. Canopy = foliage > 3 m in height, Woody = woody plant foliage 0–3 m in height, Herb. = herbaceous cover

		Reference stand												
Cover (%)		2	3	5	6	7	8	10	13	15	16	21	22	23
Canopy	mean	29	64	48	56	38	55	49	71	88	27	82	52	46
	SE	10.2	8.1	10.7	17.5	8.0	4.5	6.4	2.2	3.9	10.4	1.2	5.4	7.8
Woody	mean	60	15	88	64	70	26	40	8	18	59	26	30	65
	SE	8.2	6.9	3.7	13.6	10.5	4.5	6.8	2.5	6.6	9.2	1.6	3.9	8.9
Herb.	mean	0	81	2	10	4	10	14	26	13	45	21	31	11
	SE	0.0	5.5	2.0	0.0	2.4	2.1	7.6	1.8	2.6	12.1	1.2	5.0	1.0

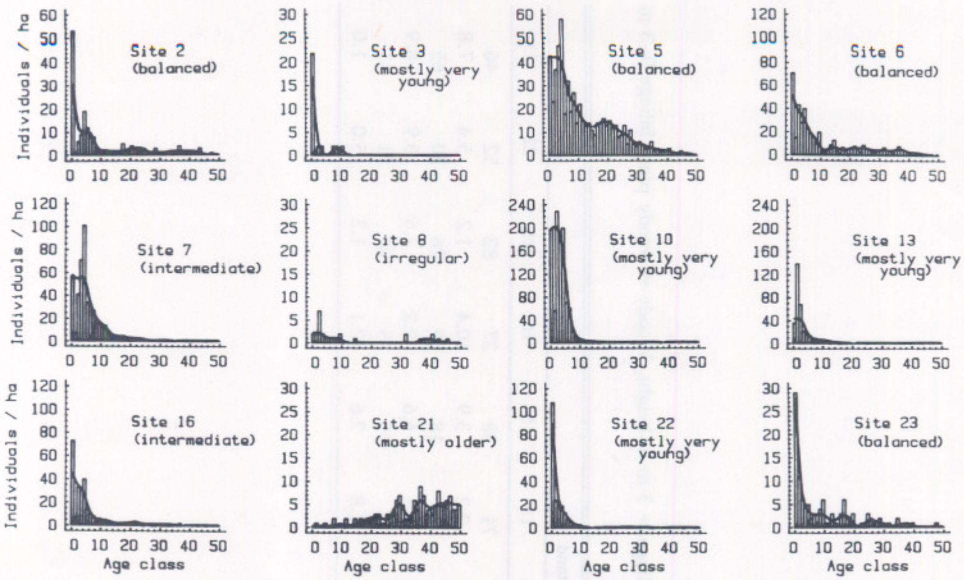

FIG. 1.—Age structures of *Abies amabilis* younger than 50 yr at 12 study locations. (Stand 15, in which only a single individual was encountered, is not shown.) Shown are both age distributions and smoothed curves fit to the age-frequency data. Note the different scales on the Y-axis, reflecting different overall densities within stands

young *Abies amabilis* to overall woody understory cover was almost always below 10%. The herbaceous stratum varied most, ranging between 0% and 81% cover.

Microtopography varied little, with all stands having mostly flat surfaces (70%–96% of the ground surfaces). Stands differed only in the proportion of elevated microsites (2%–22%). Organic substrates were most prominent, constituting at least 83% of the ground surfaces within quadrats. No exposed mineral soil was encountered in any quadrats in the 13 study stands.

Density and age structure.—Overall density of individuals ≤50 yr varied between 40 per ha in stand 15 and about 48,000 per ha in stand 5 (Table 1). Density was significantly correlated (Spearman's rank correlation) with four of the 17 stand and microenvironmental characteristics: basal area of *Abies amabilis* ($r_s = 0.63$, $n = 13$, $P < 0.03$), woody plant cover ($r_s = 0.53$, $n = 115$, $P < 0.001$), canopy cover ($r_s = -0.36$, $n = 115$, $P < 0.001$) and herbaceous cover ($r_s = -0.22$, $n = 115$, $P < 0.02$).

Stands 2, 5, 6 and 23 had "balanced" age structures (Fig. 1). Younger age classes were substantially under-represented on stand 21: only 17% of the *Abies amabilis* between 0 and 50 yr were younger than 25 yr. In contrast, stands 3, 10, 13 and 22 fitted the mostly-very-young category, with few or no trees between 25 and 50 yr. Stands 7 and 16 were intermediate between the balanced and mostly-very-young categories of age structures (Fig. 1). Stand 8 had an irregular age structure, and a single *Abies amabilis* individual was encountered in stand 15.

There was no consistent relationship between stand age structure and density of young *Abies amabilis* individuals. For example, the density of young individuals varied tenfold both among stands with balanced age structure (4320 per ha to 47,680 per ha) and among stands under-represented in trees 25–50 yr (1360 per ha to 42,960 per ha) (Tables 1, 2).

Multi-Response Permutation Procedure analysis indicated a statistically significant relationship ($|T| = 1.92$, $P < 0.05$) between age structure category (Fig. 1) and the environmental conditions and vegetative cover of the stands (Tables 1, 2). That is, the environments of stands having the same *Abies amabilis* age structure were more similar to each other than might be expected by chance. This relationship was due largely to the patterns of woody understory cover, which was the only single characteristic significantly related to age structure category (Kruskal-Wallis test, $P < 0.01$). Stands with balanced and intermediate age structures tended to have quadrats with higher cover of woody understory plants, which were almost entirely *Tsuga heterophylla* and *A. amabilis* older than 50 yr. Stands with mostly very young and irregular age structures tended to have lower cover of woody understory plants.

DISCUSSION

The stands sampled were chosen because they appeared likely to support persistent populations of *Abies amabilis*. Each stand was within the *A. amabilis* zone recognized by Franklin and Dyrness (1973), keyed to a *A. amabilis*-dominated habitat type (Dyrness *et al.*, 1974), had developed at least 135 years since major disturbance, and contained *A. amabilis* in the overstory (Table 1). Yet the pattern of *A. amabilis* regeneration was highly variable among stands. Only four stands had the balanced age structure associated with sustained regeneration (Whipple and Dix, 1979; Parker and Peet, 1984). Moreover, balanced age structures were not consistently related to prime *A. amabilis* elevations or to late successional conditions (Table 1).

In addition, the significant negative correlation between canopy cover and density of *Abies amabilis* individuals younger than 50 yr indicates that *A. amabilis* establishment rates are higher in light gaps. Stewart (1986b) likewise found a positive response of *A. amabilis* to reduced canopy, with *A. amabilis* seedlings and saplings in greater abundance in canopy gaps than under intact canopies. Herbaceous cover (which was generally much greater than the cover of young *A. amabilis* individuals) appears to be detrimental to *A. amabilis* regeneration ($r_s = -0.22$). On the other hand, woody-plant cover was positively correlated with density of *A. amabilis* individuals younger than 50 yr. Since much of this woody cover was contributed by *A. amabilis* saplings older than 50 yr, this positive correlation with density and the association of woody understory cover with balanced and intermediate age structures probably reflect the common response of these two age groups to other factors, such as lower canopy cover and herbaceous cover.

The other significant positive correlation, between density of young *Abies amabilis* and the basal area of canopy *A. amabilis,* probably is from higher establishment rates because of increased seed availability or because stands suitable for past establishment continue to be good today.

The majority of the *Abies amabilis* populations did not exhibit sustained regeneration. Instead, abundant *A. amabilis* regeneration appears irregularly in time and space, during those periods in which conditions were particularly favorable for reproduction and establishment.

Events that could lead to such conditions temporarily favorable for *Abies amabilis* regeneration include disturbance partially disrupting the canopy and normal variability in climate. Small-scale canopy gaps left by the death of large *Pseudotsuga menziesii* can harbor higher densities of *Abies amabilis* seedlings and saplings in western Oregon (Stewart, 1986b). This pattern of dependence of dominant, late successional species on canopy gaps for successful recruitment and growth has also been suggested for *Tsuga heterophylla* (Spies and Franklin, 1989) and *Acer saccharum* (Canham, 1988).

Enhanced establishment conditions for *Abies amabilis* could also be provided by a less dramatic but more uniform reduction in canopy cover. For example, insect or pathogen outbreaks could open the canopy of a stand sufficiently to allow *A. amabilis* regeneration. Since at least 1954, the balsam wooly adelgid (*Adelges piceae*) has been infesting some stands suitable for *A. amabilis* (U.S. Forest Service, 1954–72; I. Ragenovich, pers. comm.). Unfortunately, detection surveys cannot pinpoint infestations to particular stands, so the role of the balsam woody adelgid in producing the age structures reported in this study cannot be tested.

Annual temperature (Graumlich and Brubaker, 1986) and winter snow accumulation (George and Haglund, 1973) varied significantly within the geographical range of *Abies amabilis* in the past 50 yr. Such variation in climate or weather can effectively allow or prevent *A. amabilis* regeneration (J. A. Henderson, pers. comm.). These microenvironmental fluctuations in canopy cover or climate could cause the heterogeneous age structures found in this study if the degree of change and its ecological effects varied from stand to stand, allowing *Abies amabilis* regeneration to flourish on some stands but be temporarily unsuccessful on others.

The data presented here suggest that *Abies amabilis* may maintain its long-term dominance without continuous seedling establishment. *Abies amabilis,* as a more opportunistic species than has been recognized heretofore, may depend on sporadic periods of environment favorable for regeneration. If these periods of opportunity were repeatedly available at different times and locations within the landscape, however, a long-lived species like *A. amabilis* could persist and remain dominant (Cooper, 1913; Loucks, 1970; Bormann and Likens, 1979).

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