

Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon

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Received July 8, 1985²

Accepted January 28, 1986

STEWART, G. H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. *Can. J. For. Res.* **16**: 558–568.

Size and age structure, and spatial pattern analysis were used to study the population dynamics of old-growth *Pseudotsuga menziesii* (Mirb.) Franco forests of the western Cascade Range, Oregon, U.S.A. Tree population structures confirmed that in the absence of fire, *Pseudotsuga* was replaced by *Tsuga heterophylla* (Raf.) Sarg. and (or) *Abies amabilis* (Dougl.) Forbes. Regeneration patterns of these species reflected establishment in canopy openings or under *Pseudotsuga*, but not under *Tsuga*. *Abies amabilis* occurred more frequently as seedlings and saplings in openings than did *Tsuga* because of favourable aspects of its life history. The composition and structure of the pioneer forest developing after fire was a determinant of subsequent regeneration. If *Pseudotsuga* dominated, *Tsuga* and *Abies* invaded the stand at an early stage. Regeneration in stands where *Tsuga* was a large component, however, was limited by dense canopies and the occurrence of canopy openings. These patterns demonstrate the importance of small-scale disturbances such as tree falls in the dynamics of Pacific Northwest conifer forests.

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Des analyses de la structure suivant l'âge et le diamètre, de même que suivant la répartition spatiale, ont servi à étudier la dynamique des forêts de première venue de *Pseudotsuga menziesii* (Mirb.) Franco de la partie occidentale des monts Cascade en Orégon, U.S.A. La structure de ces populations a confirmé qu'en l'absence d'incendies, le *Pseudotsuga* est remplacé par *Tsuga heterophylla* (Raf.) Sarg. et (ou) *Abies amabilis* (Dougl.) Forbes. Le pattern de régénération de ces essences résulte de leur établissement dans les trouées du peuplement ou sous les *Pseudotsuga*, mais non sous les *Tsuga*. *Abies amabilis* se trouvait plus fréquemment que *Tsuga* à l'état de semis ou de gaulis dans les trouées, à cause d'aspects favorables de son cycle vital. La composition et la structure de la forêt pionnière issue d'incendie était déterminante pour la régénération subséquente. Lorsque *Pseudotsuga* dominait, *Tsuga* et *Abies* envahissaient le peuplement très tôt. Cependant, dans les peuplements où *Tsuga* dominait, la régénération était limitée par un couvert dense et la présence de trouées. Ces observations montrent l'importance des petites perturbations telles que la chute d'arbres dans la dynamique des forêts de conifères de la région du Nord-ouest du Pacifique.

[Traduit par la revue]

Introduction

Regeneration in canopy openings of conifer forests of the Pacific Northwest (U.S.A.) has been noted by several authors. In the Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) zone, forests of the Cascade Range in Washington trees grew faster in openings than under a closed canopy, and gaps were considered necessary for *Abies amabilis* and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) to reach the main canopy (Kotar 1972; Long 1976). Canopy openings in coastal conifer forests (Oregon and Washington) allow the regeneration of both dominant species (*Picea sitchensis* (Bong.) Carr. (Sitka spruce) and *Tsuga heterophylla*) and may be essential for *Picea* (Quay 1982).

Extensive forests dominated by old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and, at higher elevations, noble fir (*Abies procera* Rehd.), have developed after periodic catastrophic fires in the western Cascade Range, Oregon, U.S.A. Two large fire episodes in the range in the last 5 centuries can be associated with the initiation of ca. 140- and 450-year-old *Pseudotsuga menziesii* (Franklin and Hemstrom 1981; Hemstrom and Franklin 1982). Without further fire episodes, the shade-intolerant *Pseudotsuga* would eventually be replaced by more shade-tolerant species such as western hemlock and Pacific silver fir (Franklin and Hemstrom 1981).

Various-sized patches of seedlings, saplings, and small diameter stems of *Abies amabilis* and *Tsuga heterophylla* are common in these old-growth forests (Franklin and Dyrness 1973; Franklin and Hemstrom 1981). Many are the result of partial burns (Stewart 1986), but others occur where fire apparently has been absent for several centuries. The regeneration processes by which *Abies amabilis* and *Tsuga heterophylla* replace *Pseudotsuga* in these "unburned" forests have not been investigated. This study describes and interprets forest regeneration in these forests.

Study sites

The area studied was in the South Santiam River catchment in the central western Cascade Range, Oregon (44°25' N, 122°20' W) at an elevation of ca. 1000–1300 m. Here, *Tsuga heterophylla* and *Abies amabilis* are both potential climax species and this area is a transition between the *Tsuga heterophylla* zone and the higher elevation *Abies amabilis* zone (Franklin and Dyrness 1973).

The two areas, Bear Pass (BP) and Squaw Creek (SC), selected for detailed study (Table 1) both contained old-growth, transition-zone forests, with large *Pseudotsuga* in a matrix of various-sized *Tsuga heterophylla* and *Abies amabilis*. *Pseudotsuga*-dominated stands of different age-classes indicated that fires had occurred over most of the two areas in the last 400–500 years. However, lack of *Pseudotsuga* and *Abies procera* regeneration and no evidence of fire scars over ca. 1 km² (Bear Pass) and ca. 2 km² (Squaw Creek) indicated that some areas had not been recently subjected to fires. Ages of dominant *Pseudotsuga* indicated that the fire free period was probably at least 4 to 5 centuries. Three *Pinus monticola* Dougl. ex D. Don, >1 m dbh, were the only other main canopy trees found in the two sample stands and probably

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²Revised manuscript received January 24, 1986.

TABLE 1. Study site characteristics

Location and plot	Canopy dominants	Stand age ^a (years)	Elevation (m)	Sample plot dimensions (m)	Aspect	Slope (°)
Bear Pass						
BP-1	<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	500	1170	80×100	Northeast	5–10
BP-2	<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	500	1200	30×120	Flat, northeast	0–5
Squaw Creek						
SC-1	<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i> , <i>Abies amabilis</i>	450,830 ^b	1260	60×100	East	10
SC-2	<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i> , <i>Abies amabilis</i>	800	1190	50×100	Northwest	5–10

^aApproximate age based on the emergent *Pseudotsuga menziesii*.

^bTwo age-classes present.

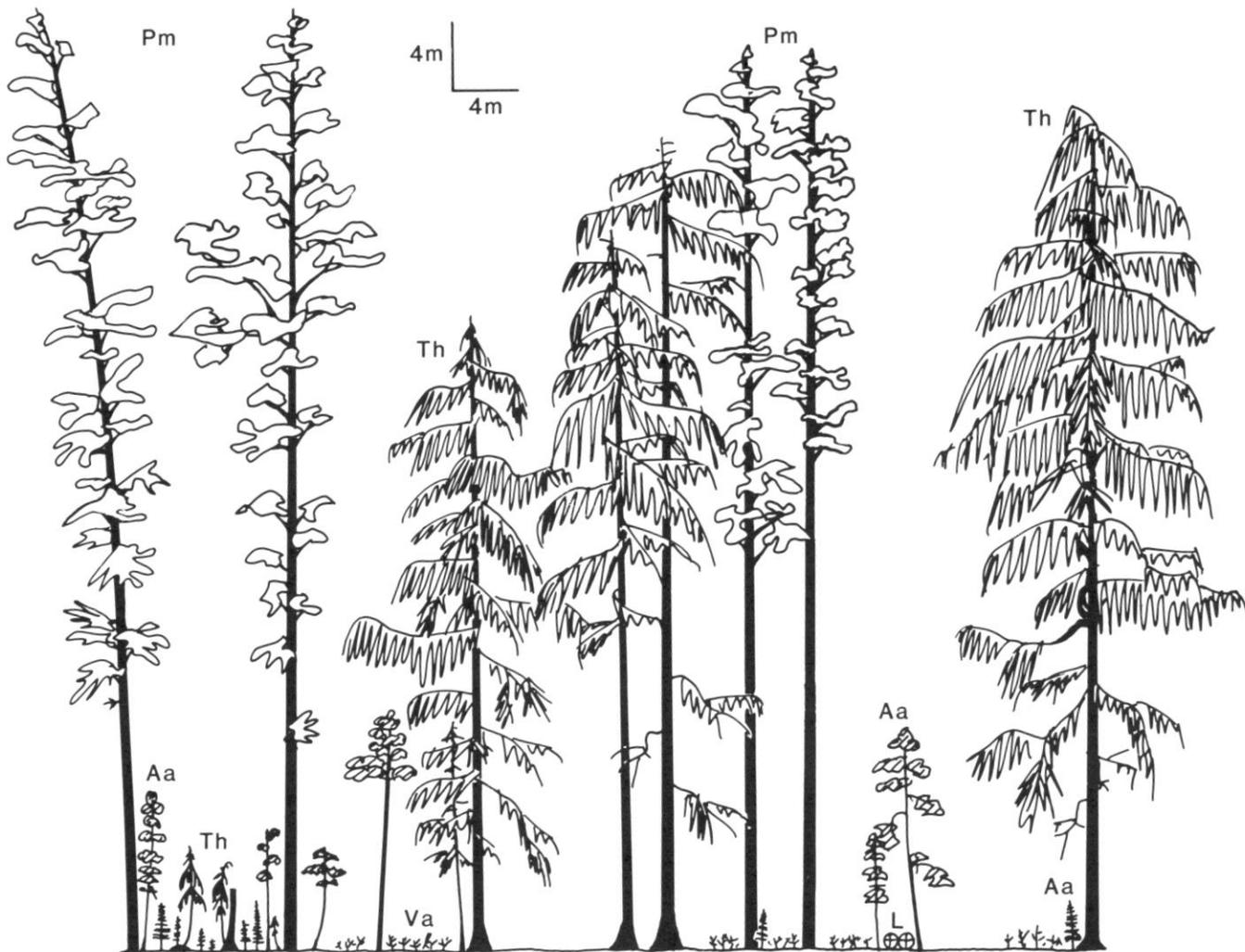


FIG. 1. Profile of plot BP-1. Aa, *Abies amabilis*; Ac, *Acer circinatum*; L, log; Oo, *Oxalis oregana*; Pm, *Pseudotsuga menziesii*; Rm, *Rhododendron macrophyllum*; Th, *Tsuga heterophylla*; Va, *Vaccinium alaskaense*.

established with *Pseudotsuga* after fire. Pacific yew (*Taxus brevifolia* Nutt.) and giant chinkapin (*Castinopsis chrysophylla* (Dougl.) A. DC.) were occasionally present in the subcanopy and a well-developed shrub tier (Alaska huckleberry (*Vaccinium alaskaense* Howell), vine maple (*Acer circinatum* Pursh), and Pacific rhododendron (*Rhododendron macrophyllum* D. Don ex G. Don)) was often present. Well-developed herbaceous communities were present in both areas.

Two rectangular plots were subjectively located and sampled in each area (Table 1), representing different structural types and, presumably, different fire histories.

Adjacent plots BP-1 and BP-2, located at the base of a glacial cirque, contained many main canopy *Pseudotsuga* and *Tsuga* that may have established together after fire (Fig. 1). Plot SC-1 was dominated by *Pseudotsuga* with fewer *Tsuga* in the upper main canopy (Fig. 2),

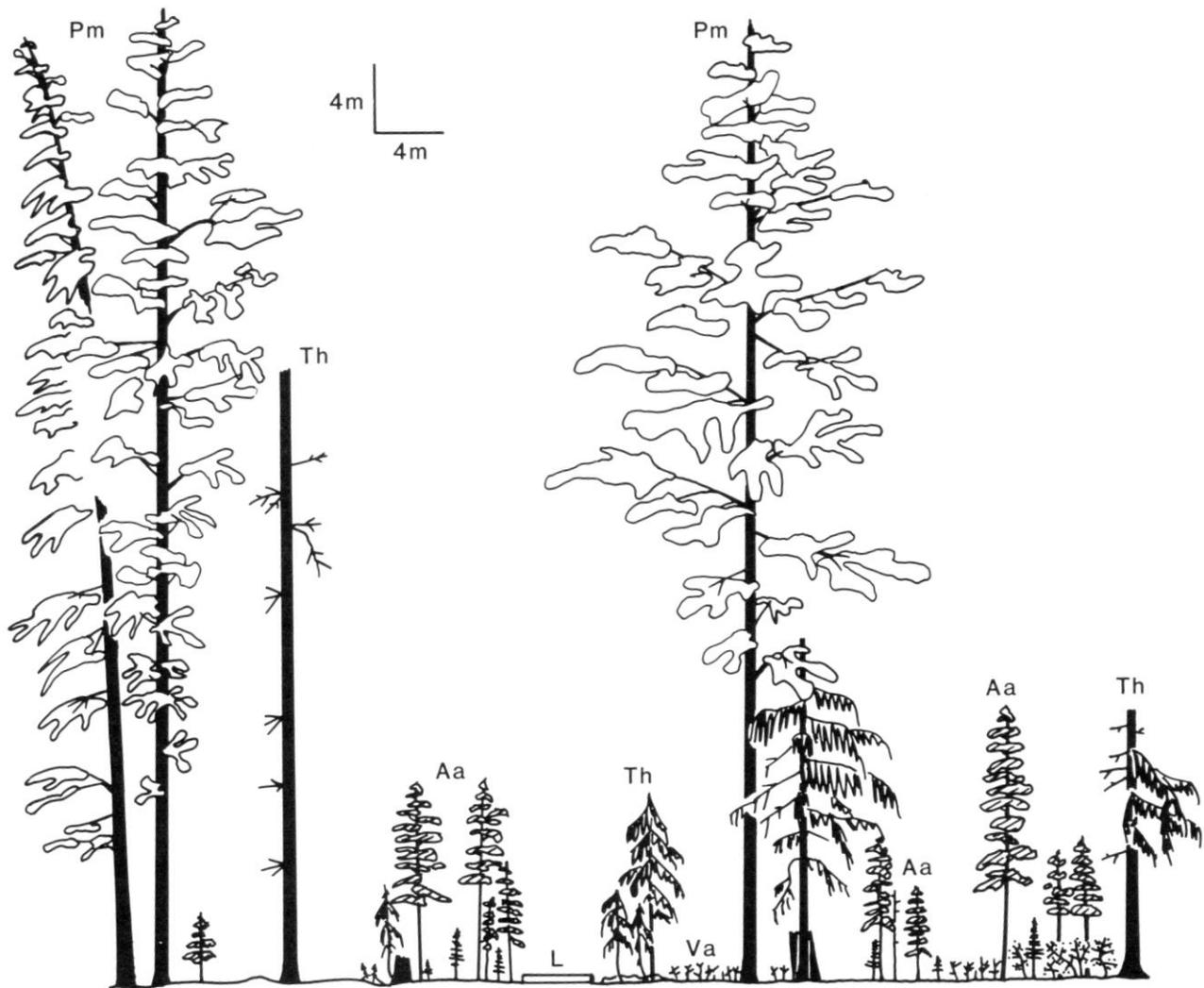


FIG. 2. Profile of plot SC-1. Abbreviations are as in Fig. 1.

suggesting that *Pseudotsuga* colonized first after fire and *Tsuga* established later. Plot SC-2, ca. 1 km distant from SC-1, contained few old-growth *Pseudotsuga* and the lower canopy was dominated by *Tsuga* and *Abies amabilis* (Fig. 3), suggesting prolonged succession without disturbance by fire.

Methods

Forest structure

Size-class analysis was used to describe and interpret forest structure and dynamics. Use of size-class analysis assumes a consistently positive relationship between diameter and age of different trees of the same species. To establish diameter-age relationships for *Tsuga* and *Abies* increment cores were taken at a height of 1 m for several trees in each 5 cm diameter class from 5 to 60 cm dbh, giving a sample of 26–33 trees for each species on each plot. Because plots BP-1 and BP-2 were adjacent, only one pooled sample was collected. To obtain a larger sample, some stumps aged in a recent clear-cutting adjacent to SC-2 were included in its age-diameter regression analysis. Age estimates for the main canopy trees in each area (Table 1) were also obtained from cut stumps on adjacent clear-cuttings.

The diameter of all trees ≥ 5 cm dbh and numbers of saplings (trees < 5 cm dbh, but ≥ 1.4 m tall) were recorded for each plot. Signs of establishment on elevated surfaces such as logs, stumps, tree buttresses, or upturned root plates were noted. Low snags and dead standing trees or saplings were also counted, measured, and identified to species level where possible.

The vertical component of the forest structure was assessed by assigning trees ≥ 1.4 m tall to relative canopy-height classes: emergent, upper main canopy, lower main canopy, below main canopy, and overtopped. Vertical structure was also depicted by vegetation profiles of 60×5 m strips of forest (Figs. 1–3).

Total cover of understory species (excluding tree species) was estimated in percentage cover classes of < 1 , 1–5, 6–25, 26–50, 51–75, and 76–100 on each 5×5 m unit quadrat (see next section) in all plots. Individual estimates were also made for *Acer circinatum* and *Rhododendron macrophyllum*, which were abundant in several plots.

Tree seedlings (> 5 cm tall, but < 1.4 m tall) were counted in 100 randomly located 2×1 m quadrats in plots SC-1 and SC-2.

Spatial dispersion and regeneration patterns

Because the spatial dispersion of trees often reflects the pattern of tree regeneration, all individuals ≥ 1.4 m tall were mapped in 5×5 m contiguous quadrats. A variation of the nested quadrat technique (Greig-Smith 1964; Kershaw 1973) and Morisita's (1959) index (I_8) were used to determine dispersion patterns. Morisita's index is given by

$$I_8 = \frac{\sum_{i=1}^q n_i(n_i - 1) + N}{N(N - 1)}$$

where q is the number of quadrats, n_i is the number of individuals in the i th quadrat, and N is the total number of individuals in all quadrats. If



FIG. 3. Profile of plot SC-2. Abbreviations are as in Fig. 1.

the population is randomly dispersed, $I_b = 1.0$; if the individuals are aggregated, $I_b > 1.0$; if individuals are evenly distributed or hyperdispersed, $I_b < 1.0$. The significance of values >1.0 was estimated by an F -test (Morisita 1959).

As spatial patterns of young trees often differ from those of older trees, different size-classes were assessed separately. Morisita's index was computed for quadrats of increasing size. Quadrat sizes for plot BP-1, for example, were 5×5 , 10×10 , 15×15 , 20×20 m, and so on. For quadrat sizes $<50 \times 50$ m (plot BP-1), $<25 \times 25$ m (plot SC-2), and $<30 \times 30$ m (plots BP-2 and SC-1), the original 5×5 m quadrats were grouped into perfect squares and larger blocks of quadrats were grouped into rectangles. Since the index may vary erratically if based on a few individuals, it was only calculated for populations ≥ 15 .

The size-class intervals used in the spatial analyses were chosen after considering age information and other structural attributes. For example, because *Tsuga heterophylla* >55 cm dbh formed a distinct group of large, main canopy trees in BP-1, their dispersion was analysed separately from the smaller *Tsuga* trees. Similarly, stems of *Tsuga* ≤ 10 cm dbh in the same plot frequently occurred in canopy openings, suggesting that their dispersion was produced by a different regeneration sequence. Usually, broad diameter-class intervals were chosen to reduce the influence of variation in the diameter-age relationship.

Association of different species was tested at various quadrat sizes

by a χ^2 test (Mueller-Dombois and Ellenberg 1974). Only species sufficiently abundant to provide adequate cell frequencies in 2×2 contingency tables (generally >5), but not present in all quadrats, were tested.

The relevance of canopy openings for tree regeneration in unburned old-growth stands was investigated using pairs of 10×10 m plots at Bear Pass. Of the 10 pairs established, one of each pair was in an opening and the other was under relatively closed canopy. Various sizes of openings from ca. 100 to 500 m² were sampled.

The plots in openings were subjectively sited in patches of seedlings and saplings because these were not distributed evenly throughout the opening. All saplings were counted in each plot and all seedlings were counted in five 2×1 m quadrats randomly located in each plot. The overstory dominant and the total understory cover of all species in percentage classes (<1 , 1–5, 6–25, 26–50, 51–75, and 76–100) were recorded for each quadrat. Signs of establishment on elevated surfaces were noted.

Tall forest canopies (≥ 50 m), variable crown forms, and irregularly shaped openings did not allow the accurate measurement of gap size. The effects of gap size on abundance and growth of seedlings and saplings was, therefore, investigated by two indirect methods. (i) Larger openings were presumed to transmit greater levels of radiation than smaller openings. Hemispherical fish-eye photographs were taken at a height of 1 m from the centre of each 10×10 m plot to assess differences in total diffuse and direct radiation. The percentage of total

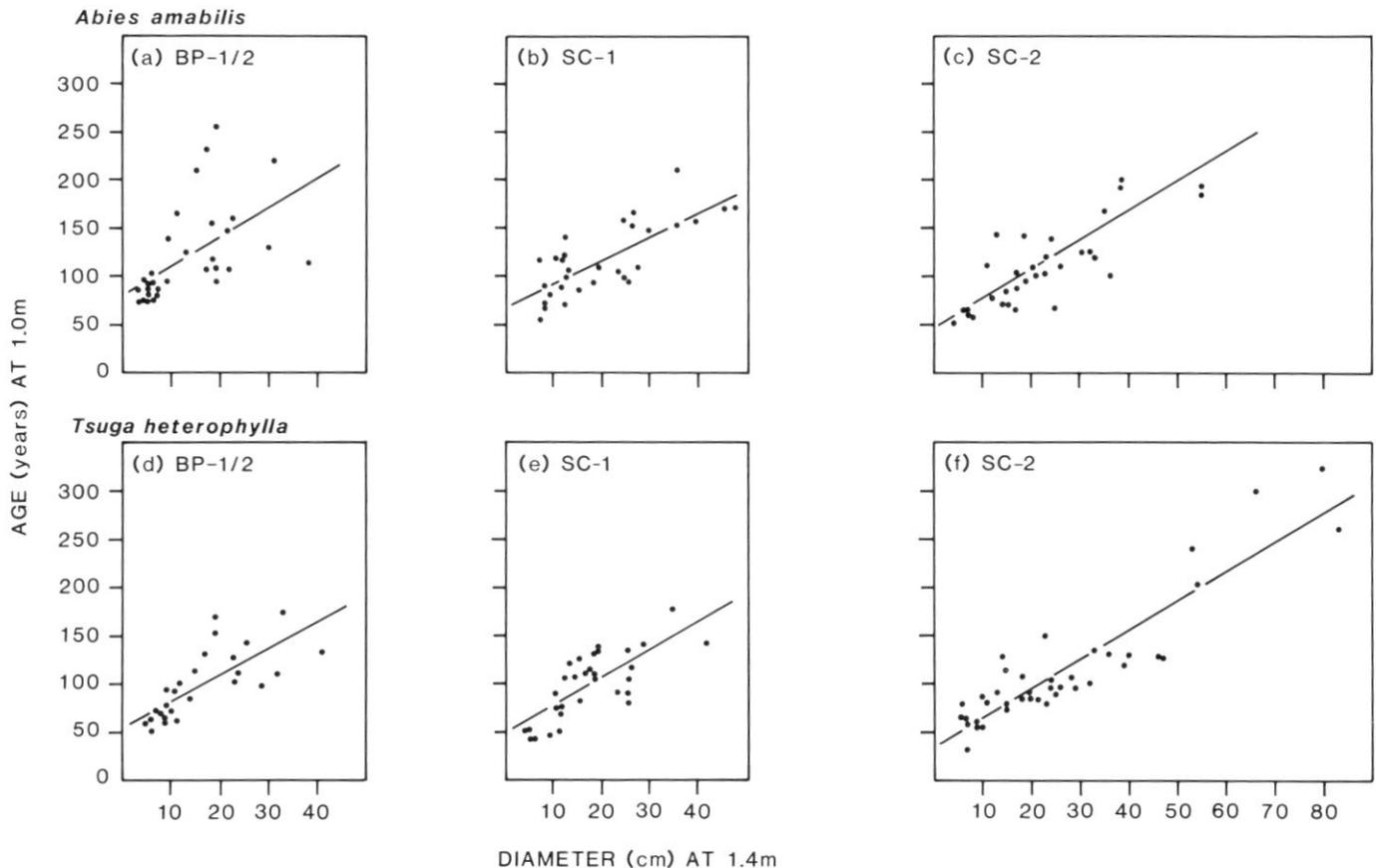


FIG. 4. Relationship of age to diameter at a height of 1 m for *Abies amabilis* and *Tsuga heterophylla* in the study plots. Least-squares linear regressions are as follows: (i) *Abies amabilis*: (a) $y = 76.0 + 3.0x$, $r = 0.56$, $n = 33$; (b) $y = 68.4 + 2.5x$, $r = 0.76$, $n = 30$; (c) $y = 51.3 + 2.6x$, $r = 0.81$, $n = 32$; (ii) *Tsuga heterophylla*: (d) $y = 56.2 + 2.6x$, $r = 0.73$, $n = 26$; (e) $y = 49.4 + 2.9x$, $r = 0.75$, $n = 31$; (f) $y = 34.8 + 3.0x$, $r = 0.91$, $n = 41$. For all equations, $P < 0.001$.

potential diffuse and direct radiation at a given site (i.e., compared with total radiation in the open over the same period) was assumed to be approximately equal to the percentage of visible sky ("total site factor" of Anderson, 1964). The percentage of direct potential radiation ("direct site factor" of Anderson, 1964), was estimated by computing the percentage intercept of visible sky along the sun's tracks. Since heavy snowpacks of 1–2 m are common in these forests from December to May and bury most seedlings and saplings, percentage direct radiation was calculated only for the growing season (May–September). (ii) Plants in small openings are more influenced by adjacent main canopy trees than plants in larger openings. The basal area of all trees >10 cm dbh was, therefore, measured in a circle of 15 m radius from the center of each canopy opening plot to give an indirect measure of the influence of adjacent canopy trees as gap size increased.

Height growth of seedlings and small stems of *Abies amabilis* and *Tsuga heterophylla* was observed to be greater in canopy openings than under relatively closed canopies. This was quantified by measuring the last 5 years height growth on 6–11 small *Abies* in each canopy opening plot. *Abies* was chosen because each year's growth finished with a whorl of branches and a terminal bud scar, so that height increments were easily measured.

Results

Forest structure

Age was significantly correlated with increasing diameter for *Tsuga heterophylla* and *Abies amabilis* (Fig. 4). However, groups of *Abies amabilis* of similar age but different diameter, which reflected periods of suppression and release, weakened the correlation, especially for the Bear Pass plots. Because of

this, broad class intervals of diameter (i.e., 10 cm dbh) were used to reduce the influence of variation when illustrating age structures of the tree populations.

Size-class distributions and the age–diameter relationships indicated that all-aged populations of *Tsuga heterophylla* were present in all plots (Figs. 5a–5d). Only plot BP-1 contained large numbers of large, main canopy *Tsuga* (Fig. 5a, Table 2), which ranged in age from at least 452 to 488 years (calculated by measuring stumps of similar diameter on an adjacent 12-year-old clear-cutting). In all plots, there were some stems in all size classes up to 1 m dbh (and sometimes greater), but at least 50% of stems in all plots were <15 cm dbh and often grew in canopy openings.

Abies amabilis was represented by many saplings and small stems, with few larger individuals (Figs. 5e–5h). The size-class distributions of this species and *Tsuga* in all plots were reverse J-shaped and indicated continuously regenerating populations (Hett and Loucks 1976; Whittaker 1974).

Size-class distributions of *Pseudotsuga menziesii* (Fig. 6) were similar to those of other old-growth stands in the central western Cascade Range and probably represented populations that established over several decades after catastrophic fire (Franklin and Hemstrom 1981). Stumps of similar-sized (>100 cm dbh) *Pseudotsuga* on adjacent clear-cuttings were ca. 450–500 (BP-1, BP-2), ca. 425–470 (SC-1), and ca. 790–830 years old (SC-2). Many trees in some populations had recently died, as in BP-1 (Fig. 6b). Thus, the *Pseudotsuga* populations in all plots belonged to the 450-year-old age-class which is

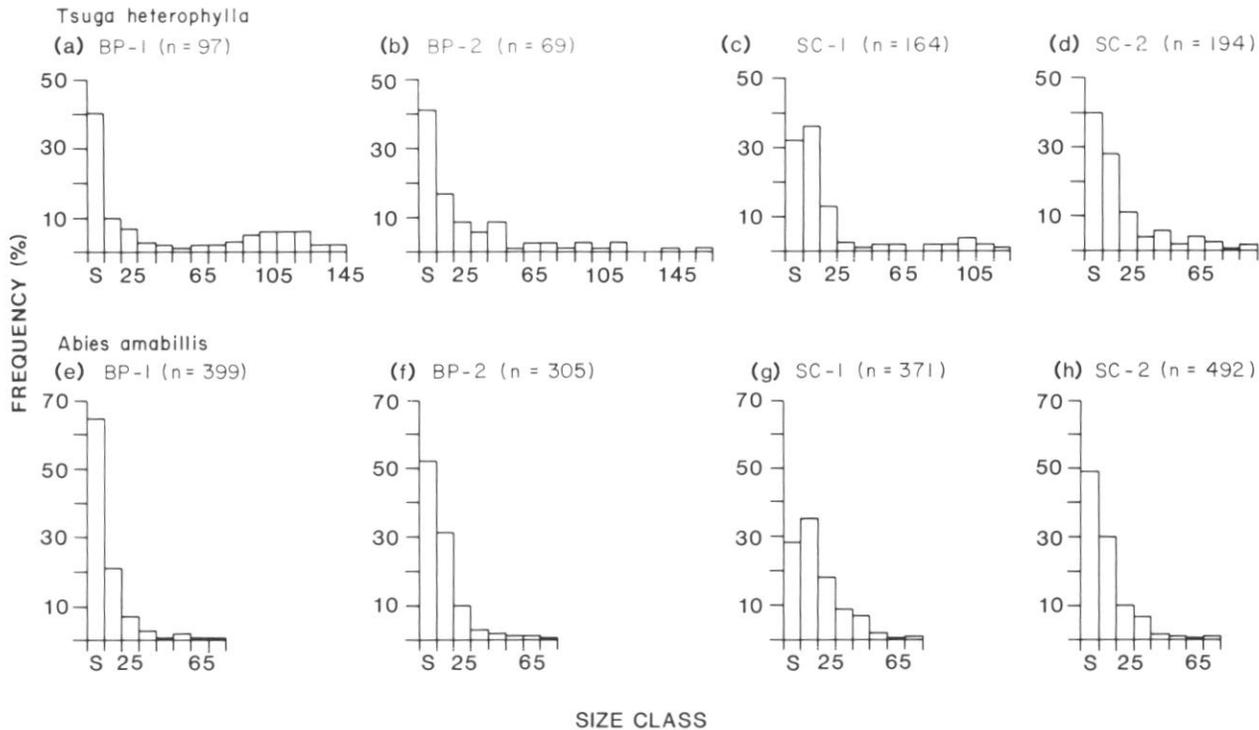


FIG. 5. Size-class frequency histograms for *Tsuga heterophylla* and *Abies amabilis* in the four study plots: *n*, number of trees ≥ 1.4 m tall; S, saplings.

TABLE 2. Percentage of trees ≥ 1.4 m tall in relative height classes in the study plots

Species	Height class	Plot			
		BP-1	BP-2	SC-1	SC-2
<i>P. menziesii</i>	Upper main canopy	11	5	14	45
	Emergent	89	95	86	55
	<i>n</i> ^a	37	22	22	11
<i>T. heterophylla</i>	Overtopped	53	64	85	79
	Below main canopy	11	12	6	9
	Lower main canopy	4	12	7	7
	Upper main canopy	30	12	2	5
	Emergent	2			
<i>n</i>	97	69	164	194	
<i>A. amabilis</i>	Overtopped	90	87	68	85
	Below main canopy	6	9	20	9
	Lower main canopy	4	4	11	4
	Upper main canopy	<1	<1	1	2
	<i>n</i>	399	305	271	492

^aNumber of trees.

widespread in the western Cascade Range, but at Squaw Creek an older age-class of ca. 800 years was also present.

In all plots, >80% of *Tsuga heterophylla* had established on elevated surfaces (Table 3). Fewer *Abies amabilis* and *Taxus brevifolia* regenerated on these microsites (Table 3).

There were almost twice as many seedlings of both *Tsuga* and *Abies* in plot SC-2 as in SC-1. Almost all *Tsuga* seedlings in both plots and most *Abies* seedlings in SC-1 were found on elevated surfaces, but only 38% of seedlings of the latter species were found on such surfaces in SC-2 (Table 4). In plot SC-2,

TABLE 3. Percentages of saplings and stems ≥ 5 cm dbh of important tree species established on elevated surfaces (logs, stumps, trunk buttresses, or upturned root plates) in the four plots

Species	Plot			
	BP-1	BP-2	SC-1	SC-2
<i>Tsuga heterophylla</i>	88	94	80	81
<i>Abies amabilis</i>	16	35	35	18
<i>Taxus brevifolia</i>	—	—	—	22

seedling density was higher in an area that contained most of the old-growth *Pseudotsuga* (SC-2A) than in an area where the canopy was dominated by *Tsuga* and *Abies* (SC-2B).

The mean understory cover in all plots was >50%, but the understory shrub cover was much greater in the Squaw Creek plots (Table 5). In plot SC-2, more *Rhododendron* and *Acer* grew beneath the *Pseudotsuga* canopy (SC-2A) than beneath the *Abies*-*Tsuga* canopy (SC-2B) (Table 5). These shrubs occurred in dense clumps, interspersed with relatively open areas where seedlings of *Tsuga* and *Abies* were abundant.

Spatial dispersion and regeneration patterns

No regeneration of *Pseudotsuga* has occurred in any of the plots, so spatial analyses were confined to canopy trees. Large *Pseudotsuga menziesii* were uniformly distributed at a quadrat size of 25 m² in all plots (Fig. 7), reflecting a tendency towards even spacing between trees in old, even-aged populations. In plots BP-1 and SC-2, trees were randomly distributed at quadrat sizes >225 m² (Fig. 7, top). Clumps seemed to form at 400–625 m² in plot BP-2 and at 100 and 400 m² in plot SC-1, indicating patches of main canopy *Pseudotsuga* (Fig. 7, bottom).

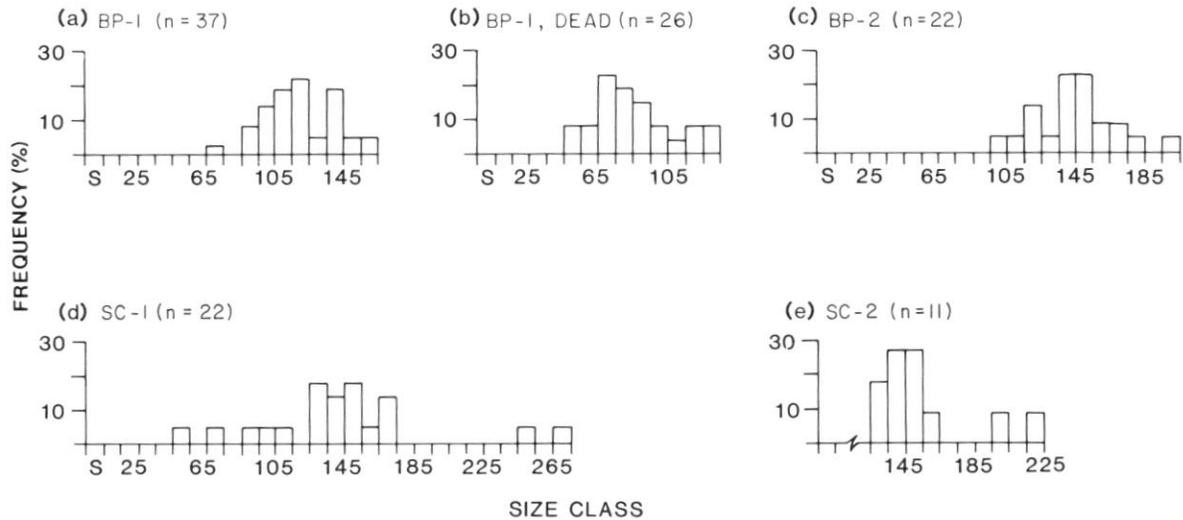


FIG. 6. Size-class frequency histograms for *Pseudotsuga menziesii* in the four study plots: *n*, number of trees ≥ 1.4 m tall; S, saplings.

TABLE 4. Numbers of seedlings per hectare (mean \pm SE) in the two study plots at Squaw Creek

Species	Plot ^a			
	SC-1	SC-2	SC-2A	SC-2B
<i>Tsuga heterophylla</i>	2450 \pm 780 (95.9) ^b	4750 \pm 1602 (98.9)	6400 \pm 2955	3100 \pm 1236
<i>Abies amabilis</i>	2250 \pm 548 (71.1)	4400 \pm 683 (38.6)	6100 \pm 1091	2700 \pm 759

^aSC-2A is the *Pseudotsuga*-dominated half of plot SC-2; SC-2B is dominated by *Tsuga* and *Abies amabilis*.

^bValues in parentheses are percentages of seedlings on elevated surfaces.

TABLE 5. Mean understory cover (percent) excluding *Rhododendron macrophyllum* and *Acer circinatum* for the four study plots and mean cover (percent) of *Rhododendron* and *Acer*

	Plot ^a				
	BP-1 (320) ^b	BP-2 (144)	SC-1 (240)	SC-2A (100)	SC-2B (100)
Mean understory cover	50.8	65.9	62.7	48.8	69.6
Mean <i>Rhododendron</i> cover	+ ^c	+	+	30.6	11.2
Mean <i>Acer</i> cover	+	+	13.2	12.4	1.8

^aSC-2A is the *Pseudotsuga*-dominated half of plot SC-2; SC-2B is dominated by *Tsuga* and *Abies amabilis*.

^bThe values in parentheses are the numbers of 25-m² quadrats assessed.

^c+, <1% mean cover.

Three types of dispersion pattern were found for *Tsuga heterophylla*. As for *Pseudotsuga*, uniform distributions of large *Tsuga* at small quadrat sizes and randomness at larger quadrat sizes indicated more even spacing in main canopy populations (plots BP-1 and SC-1; Fig. 8a). Intermediate-sized *Tsuga* were clumped at small quadrat sizes (Fig. 8b), but the highest degree of contagion was found in stems ≤ 10 cm (Fig. 8c). Clumps of stems ≤ 10 cm reflected patches of *Tsuga* that had established in canopy gaps, especially on elevated substrates. Smaller clumps of intermediate-sized stems resulted from mortality in these patches. These last two dispersion patterns were found in all plots.

Clumped patterns were found for *Abies amabilis* in all plots. Stems ≤ 10 cm dbh occurred in clumps at various quadrat sizes up to 1600 m² (Fig. 8d), indicating various-sized patches. Larger stems of *Abies* were aggregated in small patches, but tended to randomness at larger quadrat sizes (Fig. 8d).

Composition and association were tested in patches of *Abies* and *Tsuga* identified by spatial analysis. In plots BP-1 and SC-2, where there was a large component of *Tsuga* in the main canopy, *Tsuga* and *Abies* ≤ 10 cm dbh did not grow under main canopy *Tsuga*, giving a consistently negative association ($\chi^2 = 4.0-14.7$, $P < 0.05$ to $P < 0.001$). Single species patches (*Tsuga* or *Abies*) were common, as indicated by some negative

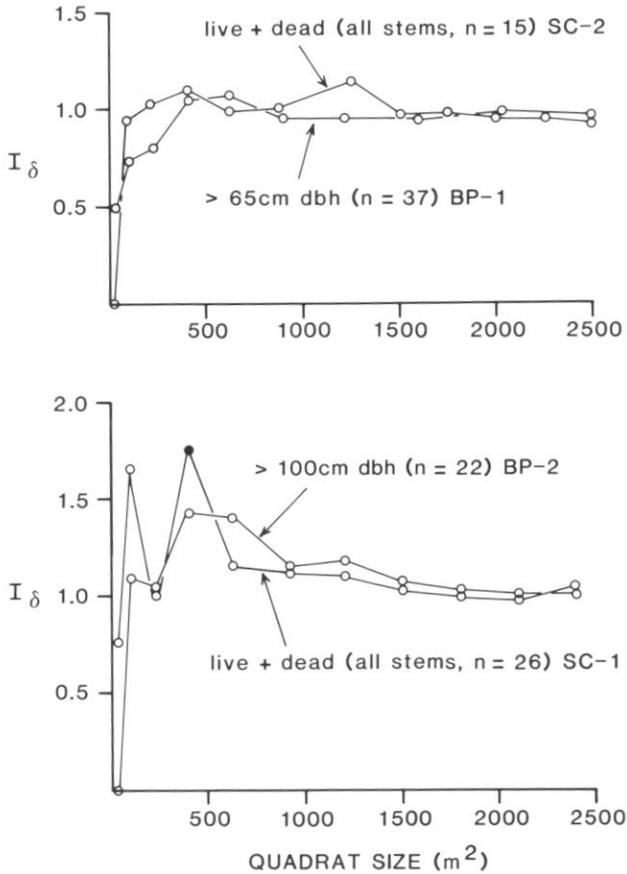


FIG. 7. Values of Morisita's index, I_{δ} , at different quadrat sizes for *Pseudotsuga menziesii* in the four study plots. ●, I_{δ} value significantly greater than 1.0 ($P < 0.05$) according to an F -test of Morisita (1959).

associations, e.g., *Abies* and *Tsuga* ≤ 10 cm dbh in plot SC-2 ($\chi^2 = 4.0$ at 225 m^2 , $P < 0.05$) and *Abies* and *Tsuga* > 10 cm dbh in plots BP-2 and SC-2 ($\chi^2 = 4.2$ at 100 m^2 , $P < 0.05$; $\chi^2 = 10.1$ at 25 m^2 , $P < 0.005$, respectively). Occasionally, small *Tsuga* were found under the less dense crowns of main canopy *Pseudotsuga* ($\chi^2 = 4.6$ and 14.3 at 25 m^2 , $P < 0.05$; plots BP-2 and SC-1, respectively).

Canopy openings were common in all stands. At Bear Pass and at Squaw Creek, 36–40 and 53–60% of all $5 \times 5 \text{ m}$ quadrats were in openings, respectively. At Bear Pass, the understory under a *Pseudotsuga* canopy and in canopy openings was much denser than under a *Tsuga* canopy and there were more tree seedlings in canopy openings (Table 6). Seedlings and saplings of *Tsuga* and *Abies* were more abundant in openings than under closed canopies (Table 7). Success to the sapling stage, especially for *Tsuga*, also appeared to be related to the abundance of elevated substrates. The percentages of saplings on these surfaces was greater than percentages of seedlings (Table 7).

There was more total direct and diffuse plus direct radiation in canopy openings than beneath a relatively close canopy (Table 8). Openings transmitted twice as much direct beam radiation during the growing season as did closed canopies (Table 8). Numbers of tree seedlings and saplings were greater in larger openings that transmitted higher levels of direct beam radiation during the growing season (Figs. 9a and 9b). A corresponding increase in height growth occurred for saplings and small stems of *Abies amabilis* (Fig. 9c). Large canopy openings with lower surrounding basal areas contained greater numbers of seedlings

TABLE 6. Relationship between overstory dominant (or canopy opening) and mean understory cover (percent) and mean number of seedlings per quadrat for seedling plots at Bear Pass

Overstory dominant	n^a	Mean understory cover	Mean no. of seedlings
<i>Pseudotsuga menziesii</i>	18	64a	3a
<i>Tsuga heterophylla</i>	50	28b	2a
Canopy opening	30	68a	9b
<i>Abies amabilis</i> ^b	2	88	2

NOTE: Values within a column followed by a different letter are significantly different according to Duncan's new multiple-range test ($P < 0.01$).

^aNumber of $1 \times 2 \text{ m}$ quadrats located under each overstory dominant.

^bNo statistical comparisons were made with this species.

and saplings than small openings (Y (number of seedlings and saplings per plot) = $99.8 - 6.4 \times$ basal area (square metres per hectare); $r = -0.76$, $P < 0.01$).

There was no apparent relationship between total diffuse plus direct radiation and numbers of seedlings and saplings. This, as well as the strong relationship between direct beam radiation and numbers of seedlings and saplings, suggests that the configuration of canopy openings and not size alone influences the amount of regeneration present. It may explain why seedlings and saplings were often absent from the center of openings and located to one side.

Abies amabilis seedlings and saplings were generally more abundant than those of *Tsuga*, especially in areas of relatively closed canopy that received $< 10\%$ direct radiation during the growing season (Table 9). *Tsuga* seedlings were as abundant as *Abies* in large openings, although saplings were almost always *Abies amabilis*.

The composition of the main canopy and emergent tiers also affected the numbers of *Abies* vs. *Tsuga* in the understory. In plots BP-1 and BP-2, where there were approximately equal numbers of *Pseudotsuga* and *Tsuga* in these tiers (*Pseudotsuga*, 37; *Tsuga*, 35; and *Pseudotsuga*, 22; *Tsuga*, 17; plots BP-1 and BP-2, respectively), there were 7 (BP-1) and 6 (BP-2) times more *Abies* in the overtopped tier than *Tsuga*. In contrast, in plot SC-1, where there were 22 emergent and main canopy *Pseudotsuga* and only 3 upper main canopy *Tsuga*, there were only 2 times as many *Abies* in the overtopped tier as *Tsuga*.

Discussion

Regeneration of shade-tolerant *Tsuga* and *Abies* in patches of old-growth, transition-zone forests unaffected by fire for several centuries occurs in canopy openings or under *Pseudotsuga*. Patterns of regeneration are determined by the composition and structure of the pioneer vegetation developing after fire. If regeneration after fire is largely of *Pseudotsuga*, *Tsuga* usually invades the stand within the 1st century of development (Franklin and Hemstrom 1981; plot SC-1, this study). If *Pseudotsuga* and *Tsuga* establish together after fire (e.g., plot BP-1), subsequent regeneration of *Tsuga* and *Abies* may be limited because of dense *Tsuga* canopies (also see Stewart 1986). Canopy openings may not form until the shorter lived *Tsuga* die and topple over, which may take 300–400 years.

The proportions of *Tsuga* and *Pseudotsuga* in the canopy influence conditions in the understory environment. The widespread crowns of *Tsuga* create larger openings than *Pseudotsuga* of similar height when they die standing or are wind-thrown. They also intercept more precipitation (Rothacher 1963; Voigt 1960), reducing available soil moisture in the

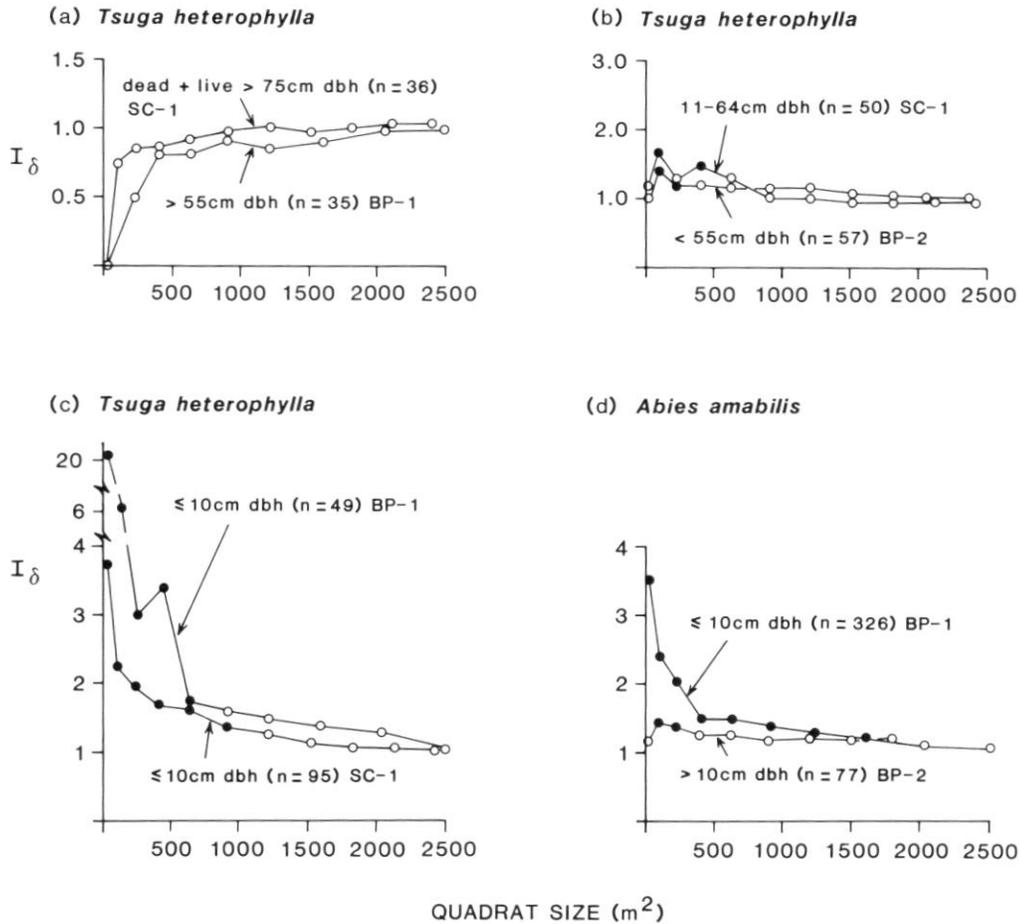


FIG. 8. Values of Morisita's index, I_{δ} , at different quadrat sizes for *Tsuga heterophylla* and *Abies amabilis* in plots BP-1, BP-2, and SC-1. ●, I_{δ} values significantly greater than 1.0 ($P < 0.05$) according to an F -test of Morisita (1959).

TABLE 7. Mean numbers of tree seedlings (per 10 m²) and saplings (per 100 m²) in 10 canopy openings and under 10 adjacent closed canopies at Bear Pass

Species	Seedlings		Saplings	
	Canopy opening	Closed canopy	Canopy opening	Closed canopy
<i>T. heterophylla</i>	14.4(77.8) ^a	1.5(46.7)	1.8(94.4)	0.2(100.0)
<i>A. amabilis</i>	20.9(26.8)	5.7(10.5)	9.5(45.3)	0.4(0.0)

NOTE: Numbers of seedlings and saplings in canopy openings are significantly greater than under a closed canopy ($P < 0.02$, t -test).
^aValues in parentheses are percentages on elevated surfaces.

TABLE 8. Mean light conditions for canopy openings and adjacent closed canopies at Bear Pass

	% diffuse and direct beam radiation	% direct beam radiation
Canopy openings ($n = 10$) ^a	53 ^a	18 ^a
Closed canopies ($n = 10$)	42 ^b	9 ^b

NOTE: Values in a given column followed by a different letter are significantly different according to a Mann-Whitney U -test ($P < 0.01$).
^aNumber of photographs analysed.

surrounding area, a factor that may be critical for seedling establishment, especially for *Tsuga* (Christy 1982; Kotar 1972). Main-canopy *Tsuga* were more abundant in the Bear Pass plots than at Squaw Creek and may explain the greater abundance of *Tsuga* seedlings and saplings at Squaw Creek. A similar lack of seedlings and forest floor herbs under *Tsuga heterophylla* has been noted in southeast Alaska (Alaback 1982) and under eastern hemlock (*Tsuga canadensis* (L.) Carr.), where it has been attributed to a lack of soil moisture (Daubenmire 1930). Root competition has been implicated as the main cause of seedling inhibition in a number of studies (Christy 1982; Korstian and Coile 1938; Toumey and Kienholz 1931).

The amount of radiation intercepted at the forest floor also influences regeneration. Numbers of seedlings, saplings, and small stems of *Tsuga* and *Abies* were greater in openings where radiation levels were generally higher than in the surrounding forest (Table 8). In addition, twice the levels of direct radiation are intercepted by openings than by closed canopies. This may be important, since occasional sun flecks are necessary for photosynthesis and, thus, direct light may be more critical for the development of understory plants, including tree seedlings, than the amount of total light (cf. Emmingham and Waring 1973; Hodges 1967).

Greater successful establishment of *Abies* compared with *Tsuga* in these forests is related to individual differences in life history. *Abies* seedlings and saplings are more abundant in openings because (i) *Tsuga* seedlings are more susceptible to damage by snow (Kotar 1972; Long 1976; Thornburgh 1969), (ii) *Tsuga* establishes on rotten logs and, thus, suitable

TABLE 9. Numbers of seedlings and saplings of *Abies amabilis* and *Tsuga heterophylla* under different light conditions at Bear Pass

Species	% direct radiation ^a (May–September)																			
	5.1	5.4	6.8	7.7	8.0	8.3	8.9	10.0	10.0	10.0	11.1	14.9	15.4	16.3	17.7	20.0	20.4	22.4	22.9	29.2
	No. of seedlings (per 100 m ²)																			
<i>T. heterophylla</i>					2	3				4	5	5	17	40		20	24	15	11	13
<i>A. amabilis</i>	1	10	3	8	12	4	3	1	5	22	10	8	21	56	7	13	27	13	8	34
	No. of saplings (per 100 m ²)																			
<i>T. heterophylla</i>			1	1				1								2	4		4	7
<i>A. amabilis</i>			1	1	1		1		1	1		5	4	17	12	3	5	14	33	

^aValues for percent direct radiation are for 10 openings and 10 closed canopies.

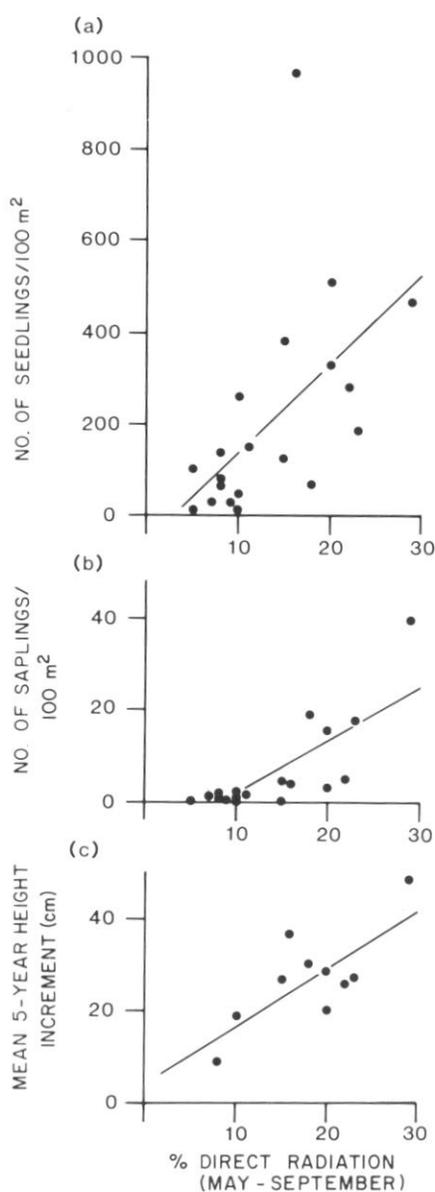


FIG. 9. Relationship of percentage direct beam radiation (May–September) at Bear Pass to (a) numbers of seedlings of all tree species, (b) numbers of saplings of all tree species, and (c) mean 5-year height increment of *Abies amabilis* saplings and small stems. The regression equations are as follows: (a) $y = 19.3x - 48.3$, $r = 0.56$, $P < 0.02$; (b) $y = 1.2x - 9.9$, $r = 0.79$, $P < 0.001$; (c) $y = 1.3x + 4.0$, $r = 0.76$, $P < 0.02$.

microsites may be limiting (Christy and Mack 1984; Kotar 1972), and (iii) *Tsuga* seedlings are susceptible to conditions of low soil moisture in summer (Kotar 1972). In many old-growth western Cascade Range forests, including those in this study, *Rhododendron macrophyllum*, *Acer circinatum*, and several *Vaccinium* species are abundant shrubs, especially where stands have not been severely disturbed by fire for centuries (e.g., plot SC-2). Here, the availability of surfaces elevated above the competing understory, such as rotten logs, may be critical for successful establishment, especially for *Tsuga*.

Tsuga and *Abies amabilis* are very shade tolerant and can persist in the understory as suppressed individuals for many years (Franklin and Hemstrom 1981; Minore 1979), increasing growth when the canopy thins or is removed. Although the proportions of newly established compared with suppressed seedlings, saplings, and small stems were not assessed in this study, it is likely that most individuals (especially *Abies amabilis*) in canopy openings were present before the openings were formed. Trees 3–7 cm dbh were 70–90 years old in openings that had only been created over the last 10–20 years. Several clumps of small *Abies* were also observed under closed canopies and their lack of measurable height growth in recent years indicated that they had established in small openings that had subsequently closed. Since numbers of seedlings in openings were similar for *Abies* and *Tsuga* (Table 9) and growth rates of both species were approximately the same (Fig. 4), it seems likely that other factors are responsible for the greater success of *Abies*. The nature of the substrate (*Tsuga* vs. *Pseudotsuga* logs) may be critical for *Tsuga*, and this is worthy of further study.

The variability in structure and spatial pattern, and the relationship of canopy openings to tree regeneration described in the present study demonstrate the importance of small-scale disturbances, such as tree falls, in the dynamics of old-growth conifer forests that have not been subjected to fire for several centuries. Furthermore, it suggests that the species that dominates a site after disturbance strongly affects subsequent regeneration (cf. "initial floristic composition," Egler 1954). These subtle interactions between small and large disturbances demonstrate the need for any successional scheme devised for these forests to include the effects of different canopy species, in addition to various disturbances, as factors controlling the rate and nature of forest succession (cf. Drury and Nisbet 1971; Runkle 1981).

Acknowledgments

I am grateful to J. Antos, J. Franklin, R. Frenkel, F. Swanson, T. Veblen, and D. Zobel for critical review of the

original manuscript; T. Pearson for drawing the figures; J. Orwin for editorial assistance; and M. Stewart for assistance in data collection. The study was supported by a New Zealand National Research Advisory Council Postgraduate Fellowship.

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