tsuga with forest age (Oliver & Larson 1990), but it is not clear whether it is a response to widespread thinning in canopy density or to localized environments present in canopy gaps created by mortality of dominant trees. The loss and fragmentation of late-successional forests in the region has motivated proposals to promote greater structural and compositional diversity by manipulation of young stands within reserve areas (FEMAT 1993). Thus it is important to know how canopy gaps influence development of old-growth forests, how long it would take for old-growth structure to develop naturally, and whether selective tree harvest can mimic this process.

The gap partitioning hypothesis proposes that resource gradients from intact canopy areas into gaps are too broad to be dominated by any one species (Ricklefs 1977; Denslow 1980). Establishment and growth of different tree species should therefore be correlated with gap size and within-gap position and such patterns are seen in many forests (Minckler & Woerhide 1965; Runkle 1982; Brandani *et al.* 1988; Poulson & Platt 1989). In other forests, however, understorey plant density, abundance of specific substrates (e.g. logs or soil mounds), or high species diversity appear to prevent the development of consistent patterns (Ehrenfeld 1980; Veblen 1982; Denslow 1987; Uhl *et al.* 1988; Nakashizuka 1989).

The controls on tree seedling establishment in relation to canopy gaps within Pacific Northwest forests are poorly understood. The relatively shade-intolerant *Pseudotsuga menziesii* regenerates within forests on dry sites (Means 1982) but is rarely present in the forest understorey on more mesic sites (Franklin & Dyrness 1973). It is not known whether its establishment is limited by overstorey canopies or understorey vegetation. Although shade-tolerant *Tsuga heterophylla* and *Abies amabilis* seedlings are more abundant in canopy gaps than in closed-canopy areas (Thornburgh 1969; Long 1976; Stewart 1986; Harmon 1987; Spies *et al.* 1990; Alaback & Tappeiner 1991), many gaps are long-term features that may take 50–100 years to close (Spies *et al.* 1990; Lertzman 1992). In comparison, canopy closure may take as little as 2 years in moist tropical forests (Lorimer 1989) or 5 years in temperate deciduous forests (Runkle 1990).

The purpose of this paper is to (1) determine whether the establishment and growth of tree species of three different genera (*Abies*, *Pseudotsuga* and *Tsuga*) are affected by stand age, gap size and within-gap position, and (2) compare the same species' response patterns when seeds were sown in controlled experimental plots to those of naturally dispersed seeds within the same gaps. The latter objective will indicate the importance of gaps on tree seedling establishment compared to the added factors of seed dispersal, predation and microsite heterogeneity. The experiments described in this paper are part of a larger study; future papers will examine the importance of

substrate and resource levels for seedling establishment in forest canopy gaps.

Methods

SITE DESCRIPTION

Canopy gaps were created by cutting and removing trees in four forest stands in the *Tsuga heterophylla* Zone (Franklin & Dyrness 1973) of the west slope of the Cascade Mountains. Two stands were in old-growth forests (canopy trees ≈ 500 years in age) dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* in multiple canopy layers, and two stands were in mature forests (90–140 years in age) dominated by *Pseudotsuga* in a single canopy layer (Table 1). One old-growth stand (HJA) was located in the H. J. Andrews Experimental Forest in the Willamette National Forest of the central Cascades of Oregon; the other three stands, Trout Ck old (TCO), Martha Ck young (MCY) and Panther Ck mature (PCM), were located in the Wind River Experimental Forest in the Gifford-Pinchot National Forest of the southern Cascades of Washington. Old-growth stand HJA experienced a moderate-severity fire in 1836 (Teensma 1987) and was dominated by large *Pseudotsuga* and a dense *Tsuga* subcanopy with a sparse layer of understorey vegetation. The soil was a deep (depth to C horizon 1 m), well-drained, dark brown gravelly loam, classified as a loamy-skeletal, mixed, frigid Fluventic Dystrochrept (Brown 1975). Old-growth stand TCO was dominated by large *Pseudotsuga*, as well as *Tsuga* and *Abies* in all size classes, in a mosaic of open and closed canopy areas and a variety of understorey vegetation densities. The soil was a deep (typically 2 m to bedrock), well-drained, dark brown sandy loam classified as an Andic Haplumbrept (Franklin & DeBell 1988). Stand MCY established after the Yacolt fire of 1902 (Hofmann 1917), and was dominated by a fairly dense *Pseudotsuga* overstorey with abundant *Acer circinatum* Pursh. (vine maple) in the mid-storey and a high density of woody shrubs in the understorey. Stand PCM was dominated by *Pseudotsuga* about 140 years in age and had been selectively logged to remove trees killed by *Dendroctonus pseudotsugae* (Douglas-fir beetle) in the 1950s; the tree canopy was open with a high density of understorey *Acer*, herbs and shrubs. Soil classifications are unavailable for the mature stands, but textural classes were derived from particle size analyses (hydrometer method) on two soil samples from the upper 30 cm of soil from each stand (Table 1).

Climatic regimes at meteorological stations in or near the two Experimental Forests are similar, with summer drought and high temperatures common from June to September, a pattern characteristic of the Pacific Northwest (Franklin & Waring 1980). Mean (15-year) annual precipitation was 224 and 208 cm at the H. J. Andrews and Wind River Exper-

Table 1 Characteristics of the four stands in the experimental gap study. *Pseudotsuga* refers to *Pseudotsuga menziesii*, 'tolerants' includes *Tsuga heterophylla*, *Thuja plicata*, *Abies amabilis* and *Abies grandis*. Covers are sums of individual species' cover estimates, with 'mid-canopy' referring to tree vegetation 1–5 m in height. Light was measured at 1.5 m at three points in control areas during summer 1991

	Old-growth		Mature	
	HJA	TCO	MCY	PCM
Location	44°15′N,	45°49′N,	45°47′N,	45°50′N,
	122°15′W	122°00′W	121°57′W	121°49′W
Elevation (m a.s.l.)	900	550	550	850
Soil texture	Loam	Loam	Clay loam	Sandy loam
Pseudotsuga age (years)	350–500	350–500	90	140
Mean canopy height (m)	50	50	35	50
Tree Basal Area (m² ha⁻¹)				
Pseudotsuga	73.5	39.2	58.5	83.3
tolerants	62.0	58.0	0.2	0.6
Vegetation Mean cover (%)				
bryophytes	7.3	8.1	9.6	5.0
herbs	4.9	9.3	0.8	26.7
shrubs	9.4	26.8	46.9	35.6
mid-canopy trees	4.2	5.8	43.4	34.6
total	25.8	50.0	100.7	101.9
Light (mol m⁻² day⁻¹ PAR)	1.17	1.22	1.03	1.47

imental Forests, respectively, with only 8% of annual precipitation falling between June and September. Annual mean, minimum and maximum air temperatures were 8.6, –3.1 and 27.0 °C at H. J. Andrews and 9.2, – 1.1 and 28.4 °C at Wind River, respectively. Winter snowpacks are often transient at 500–1000 m in the Cascades, with temporary accumulations occasionally exceeding 1 m in depth.

Within each stand, experimental gaps were located in areas with slopes less than 20% and with relatively dense tree canopies (to minimize interactions with recent gap events). Three sizes of circular gaps, with two replicates of each size, were created in each stand. Gap diameter (measured between tree crown edges) was scaled to the average height of dominant trees in each stand. The gap diameter to tree height ratios for the four gap sizes were 0.2, 0.4 and 1.0. Two control plots, equal in area to the 1.0 gap size, were established in undisturbed areas of each stand. Gaps were created in the fall of 1990 by cutting all trees over 2 m tall (except *Acer circinatum*) within the gap perimeter. Trees were stage-felled into the north-east or north-west quadrants, and skidders situated outside the gaps winched fallen tree boles from the gaps with cables. Removal of most of the felled trees was necessary to allow sampling of vegetation, soils and microclimate in intensive plots. Branches and foliage trimmed from felled trees were removed from the gaps to avoid localized differences in nutrient input and shading.

SEED-SOWING EXPERIMENT

The first experiment on seedling establishment in relation to gap size and within-gap position was a manipulative approach using known quantities of

sown seed and attempting to control variation from seedbed quality and understorey vegetation density. This study was conducted on a standardized substrate in control plots and 0.2, 0.4 and 1.0 gap sizes, using all replicates. Three within-gap positions (north, centre and south) were identified in each gap and control, except for the 0.2 gap size, in which only one position (centre) was used. North and south positions were within 2 m of gap edges, but not under overstorey tree canopies. For each position, three 0.25-m² seed-plots were created in the fall of 1991 by removing the forest floor and much of the A1 soil horizon, churning the upper 10 cm of remaining soil, and spreading a uniform layer of mixed A1 and B1 horizon soil (from a road-side in the TCO stand) in a 2.5-cm-deep surface layer. Soil surfaces were roughened slightly with a hand rake to discourage seed movement by raindrops (Lawrence & Rediske 1962).

One hundred *Abies amabilis*, 100 *Pseudotsuga menziesii* and 500 *Tsuga heterophylla* seeds were divided evenly between the three seed-plots of each gap position. Seed numbers were greater for *Tsuga* than for the other species because germination and early survival is usually much lower (Harmon & Franklin 1989). All seeds were sown during the first three weeks of November 1991. Seeds used at H. J. Andrews and Wind River were from local seed zones (seed provided by Wind River Nursery). Germination tests conducted by the Wind River nursery estimated seedlot viability for *Abies* at 95 and 93%, *Pseudotsuga* at 94 and 70% and *Tsuga* at 76 and 76% for the Wind River and H. J. Andrews seed zones, respectively. Natural seed rain also added large numbers of seed in the fall of 1991, primarily *Pseudotsuga* in the mature stands (MCY and PCM), and both *Pseudotsuga* and

Tsuga in the old-growth stands (HJA and TCO). Galvanized metal wire exclosures (12 mm mesh) were placed over each seed-plot to deter seed and seedling predation by rodents and birds. Exclosures reduced full-sunlight PAR quantum levels by 17.5%, but had no detectable effect on surface temperatures. Exclosure tops were removed from all seed-plots in July 1993 to avoid damage to fast-growing seedlings. Potentially shading understorey vegetation in and around the seed-plots was clipped or uprooted at regular intervals throughout the course of the study.

Seedlings were counted in the seed-plots once each month from late April to October of 1992 and in June and October of 1993. Seedlings were considered 'emerged' and counted if they were erect and rooted and had mostly shed their seed coats. Seedlings were considered dead when they were missing, cut at the stem, or entirely lacking green colour. Seedlings were considered 'established' if they were alive at the end of the second growing season. At the end of the 1993 growing season, basal diameter and height were measured on up to five randomly selected seedlings of each species from each seed-plot in one replicate of each gap size per stand.

SURVIVAL AND GROWTH OF NATURAL REGENERATION

This study was designed to follow the fate of seedlings originating from natural seed rain in different natural microenvironments within a gap. In late May or early June of 1992, within two weeks of emergence of many of the seedlings in the gaps, one replicate of each gap size and control in each stand was searched and individuals of first-year *Pseudotsuga* and *Tsuga* were marked with small pin flags. Within each stand, a concerted effort was made to locate up to 15 seedlings in each combination of gap size (control, 0.2, 0.4 and 1.0), position (north, centre and south, but centre only in 0.2s), understorey cover level (0, 50 and 90%), and substrate (forest floor and decayed wood). Nevertheless, sample sizes varied considerably between treatment combinations, and *Tsuga* seedlings were rare in the mature stands (MCY and PCM). To avoid edge and east–west effects, most seedlings located were within 4–6 m of the north–south transect bisecting the gaps. Gap positions were delineated by dividing this north–south belt into three zones of similar area. Marked seedlings were revisited in September 1992 and July and October 1993 to assess survival. The term 'survival' is used for this experiment because the survival of individual seedlings was followed, the term 'establishment' is used for the seed-sowing experiment because individuals were not marked, so seedlings may have died and been replaced by new emergents between counts.

Size of naturally regenerated seedlings was measured in two 1.0 size gaps (one in stand PCM, one in stand TCO). Five sample points were established at

4-m intervals on east–west lines centred on the north–south transect through each gap; lines were spaced 4 m apart along the north–south transects. Seedlings within 2 m of each sample point were located, and basal diameter and height were measured on the three *Pseudotsuga* and three *Tsuga* seedlings from the 1992 cohort closest to each sample point.

DATA ANALYSES

The effects of the fixed factors of stand age, gap size, within-gap position, tree species, and of the interactions between them, on seedling establishment and seedling size were evaluated with split-split plot Analysis of Variance (ANOVA) for each experiment. Careful examination of the Type IV Sums of Squares linear contrasts (Milliken & Johnson 1984; Shaw & Mitchell-Olds 1993) indicated that this approach was appropriate. A separate single-factor ANOVA was conducted to analyse stand effects on seedling establishment in controls, using the three position treatments in both control areas per stand. Results of the analyses were considered significant if the probability of a Type I error was less than 0.05. Multiple comparisons of treatment means were conducted for significant factors using least-squared means and 95% confidence intervals, analogous to Fisher's Protected Least Significant Difference, calculated with the MIXED procedure in SAS 6.10 (SAS Institute Inc. 1987), although some factors could not be analysed due to the unbalanced design.

The response variable for the analysis of seedling establishment in the seed-sowing experiment was the fraction of the maximum number of emerged seedlings counted on a treatment that were still alive at the end of the second growing season (termed 'establishment'). Seedling counts were summed across the three seed-plots comprising a position 'treatment' within a gap, and establishment calculated on those sums. Establishment values were arcsin-square-root-transformed and the ANOVA was weighted by sample size (maximum number of seedlings per treatment). The response variable for the analysis of seedling size in the seed-sowing experiment was the mean size of the seedlings measured in a treatment (i.e. three seed-plots), where size was calculated as seedling height multiplied by basal area. Size data were log-transformed before analysis, and the ANOVA was weighted by the number of seedlings measured.

Due to the very low number of naturally regenerated *Tsuga* seedlings in the mature stands, separate ANOVAs were calculated for *Pseudotsuga* (using all four stands) and *Tsuga* (using the two old-growth stands) for the natural regeneration analyses. The response variable for these analyses was the fraction of the initial number of emerged seedlings marked in a within-gap position that were still alive at the end of the second growing season. Data were transformed

(arcsin-square root) and the analysis was weighted by the initial number of emergents.

Results

SEED-SOWING EXPERIMENT

Establishment at the end of two growing seasons differed significantly among species and locations ('location' refers to one of the 10 combinations of gap size and within gap position). Gap size, within-gap position and species had significant effects on seedling establishment, as did all interactions between these factors (Table 2). Establishment in controls was relatively low for all species, and establishment was also low in 1.0 North locations for *Abies* and *Tsuga*, and in 0.4 North and 1.0 Centre locations for *Tsuga* (Fig. 1). Establishment was high for all species in 1.0 South, 0.4 Centre and 0.4 South locations. Despite their relatively small size, establishment in 0.2 gaps was significantly greater than in controls, and comparable to establishment in less exposed locations of larger gaps. Within 1.0 gaps, establishment of *Abies* and *Tsuga* increased from North to South.

The significance of the age–class interaction with position and with gap size and position (Table 2) appeared to be due to greater seedling establishment in exposed locations (1.0 North and Centre, 0.4 North) and deeply shaded locations (controls and 0.2 gaps), and lower establishment in lightly shaded locations (1.0 South, 0.4 Centre and South) in the old-growth age class than in the mature age class (Gray 1995). Most of the age class trends were due to differ-
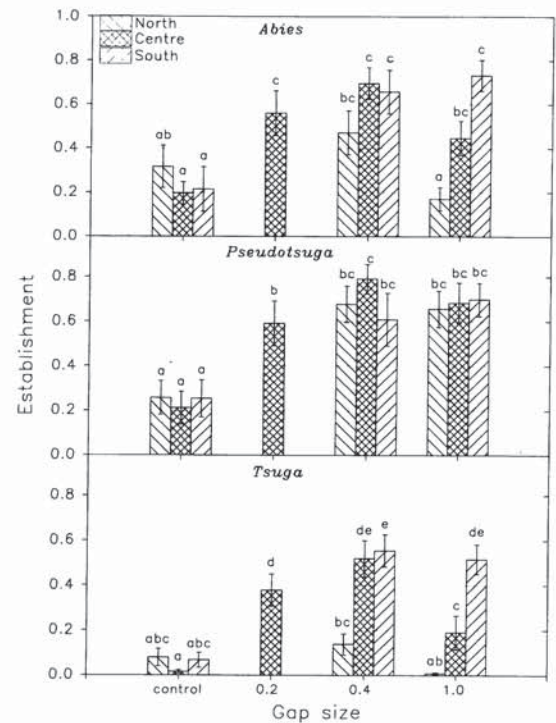
Fig. 1 Seedling establishment (fraction of maximum emerged) by gap size, within-gap position and species after two growing seasons in the seed-sowing experiment, showing means and standard errors ($n = 8$). Different letters indicate significantly different within-species means ($P < 0.05$).

ential establishment of *Abies* and *Tsuga*, rather than of *Pseudotsuga*.

Seedling establishment in closed-canopy control areas differed significantly among stands in single-

Table 2 Results of split-split plot ANOVA on seedling establishment (fraction of maximum count) for controlled seed-plot study. Factor abbreviations are: age = age class, gap = gap size, rep = gap-size replicate within stand, pos = position, spp. = species. Effects to the left of parentheses are nested within effects in parentheses. Significant effects ($P < 0.05$) are marked with asterisks (*)

Source	d.f.	Mean square	F-value	$P \geq F$	
age	1	0.942	0.19	0.7021	
Error: stand (age)	2	4.836			
gap	3	14.126	9.33	0.0112	*
age × gap	3	0.231	0.15	0.9242	
Error: stand × gap (age)	6	1.514			
rep (age × stand × gap)	16	0.812			
pos	2	3.804	21.52	0.0001	*
age × pos	2	0.953	5.39	0.0054	*
gap × pos	4	2.471	13.98	0.0001	*
age × gap × pos	4	0.441	2.50	0.0449	*
spp.	2	22.855	129.26	0.0001	*
age × spp.	2	0.257	1.46	0.2359	
gap × spp.	6	0.767	4.34	0.0004	*
pos × spp.	4	1.649	9.33	0.0001	*
age × gap × spp.	6	0.189	1.07	0.3817	
age × pos × spp.	4	0.215	1.22	0.3054	
gap × pos × spp.	8	0.679	3.84	0.0004	*
age × gap × pos × spp.	8	0.112	0.63	0.7476	
Error: rep (age × gap × stand × pos × spp.)	156	0.176			
Total	239				

Table 3 Means and standard errors of seedling establishment (fraction of maximum count) by stand and species for 1992 cohort on seed-plots in controls ($n = 6$). For each species, stand mean with different letters differed significantly ($P < 0.05$)

	Abies	*Pseudotsuga*	*Tsuga*
MCY	0.104 ± 0.047^a	0.106 ± 0.053^a	0.006 ± 0.004^a
HJA	0.173 ± 0.085^a	0.124 ± 0.072^a	0.013 ± 0.010^a
PCM	0.270 ± 0.096^{ab}	0.320 ± 0.066^b	0.032 ± 0.010^a
TCO	0.424 ± 0.116^b	0.413 ± 0.092^b	0.168 ± 0.044^b

factor ANOVAs for each species ($F_{3,23} = 3.66$, 4.52 and 9.20, $P = 0.03$, 0.014 and 0.0005 for *Abies*, *Pseudotsuga* and *Tsuga*, respectively). The rankings of stand establishment means were similar for all species, with MCY < HJA < PCM < TCO (Table 3).

Seedling size after two growing seasons (i.e. growth since emergence) differed significantly among gap sizes ($F_{3,6} = 17.8$, $P = 0.002$), within-gap positions ($F_{2,32} = 23.5$, $P = 0.0001$), species ($F_{2,32} = 84.4$, $P = 0.0001$), and the gap size by within-gap position interactions ($F_{4,32} = 13.7$, $P = 0.0002$). Seedling size increased significantly with gap size, and the largest seedlings in the 0.4 and 1.0 gap sizes were usually found in Centre positions (Fig. 2). The few *Tsuga* surviving in 1.0 North locations grew as well, on average, as those in 1.0 Centre locations, however. *Pseudotsuga* seedlings were the largest of the three species, and *Tsuga* were the smallest, in all locations. Species
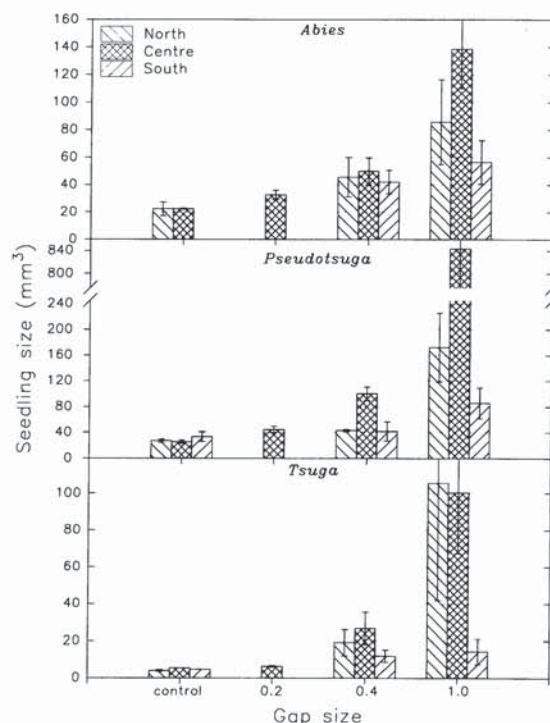
Fig. 2 Seedling size (basal area × height) after two growing seasons in seed-sowing experiment by gap size, within-gap position and species, showing means and standard errors ($n \leqslant 4$).

differences were also apparent in the changes in seedling size with gap size ($P = 0.12$ for gap size by species interaction). *Pseudotsuga* size was relatively small in all locations except for the 1.0 Centre location, *Tsuga* size appeared to increase dramatically in the larger gaps and *Abies* size increased more steadily with gap size.

SURVIVAL AND GROWTH OF NATURAL REGENERATION

The abundance of naturally seeded tree species varied significantly between forest age classes. Large numbers of *Pseudotsuga* emergents were found in both forest age classes, whereas large numbers of *Tsuga* emergents were found in the old-growth stands but only a few (13 individuals) in the mature stands; few *Abies* emergents were found at all and then only in the old-growth stands (total number of marked seedlings was 1443, 2202 and 11, respectively, for the three species). Survival of naturally regenerated individuals after two growing seasons differed significantly by gap size and within-gap position for *Pseudotsuga* ($F_{3,18} = 37.4$, $P = 0.0001$ and $F_{4,18} = 6.26$, $P = 0.009$, respectively), and by within-gap position for *Tsuga* ($F_{2,6} = 9.52$, $P = 0.014$). The gap size effect and gap size by within-gap position interaction were almost significant for *Tsuga* ($F_{3,4} = 5.44$, $P = 0.068$ and $F_{4,6} = 3.65$, $P = 0.077$, respectively). Multiple comparison of gap size means indicated that *Pseudotsuga* survival was significantly greater in 0.4 and 1.0 gaps than in controls. Survival of *Pseudotsuga* tended to decrease from South to Centre to North positions within the larger gaps (Fig. 3). Survival of *Tsuga* was very low in controls, greater in 0.2 and 0.4 gap sizes, and then declined somewhat in the 1.0 gap size. A strong gradient of decreasing survival from South to North positions was evident for *Tsuga* in the 0.4 and 1.0 gap sizes.

Seedling survival patterns for naturally regenerated seedlings differed from those found for the seed-sowing experiment in several ways. Establishment percentages of both *Pseudotsuga* and *Tsuga* were greater in the seed-plot study (Fig. 1) than survival percentages in the study of naturally regenerated emergents (Fig. 3). Establishment trends among locations also differed between these studies. Although survival of naturally regenerated *Pseudotsuga* was generally lower in 0.2 gaps than in larger gaps, establishment of *Pseudotsuga* in seed-plots was similar among gaps. The north–south gradient in survival of naturally regenerated *Pseudotsuga* in the larger gaps was also not evident in the seed-plot study. Trends in *Tsuga* survival across locations were similar between the two studies, although establishment was relatively greater in 1.0 Centre locations in the seed-plot study. Variability in establishment within locations tended to be greater in the natural regeneration experiment than in the seed-sowing experiment.
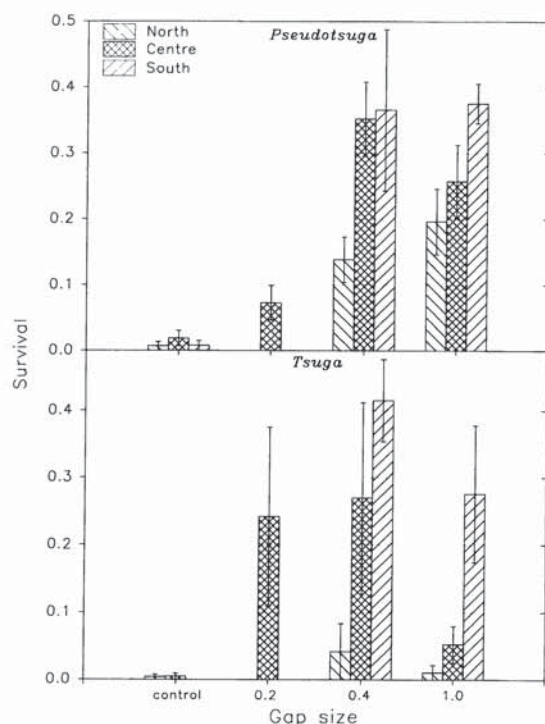
Fig. 3 Survival (fraction of initial marked) of natural regeneration after two growing seasons by gap size and within-gap position, showing means and standard errors ($n = 4$ for *Pseudotsuga*, $n = 2$ for *Tsuga*).

The size of naturally regenerated seedlings varied greatly along the north–south transect of the 1.0 size gap in stand TCO, but not in stand PCM. In stand TCO, seedling height peaked just north of gap centre and declined towards the north and south edges, although the trend for *Tsuga* was more variable than the trend for *Pseudotsuga* (Fig. 4). Heights of *Pseudotsuga* seedlings varied little across the gap in stand PCM.
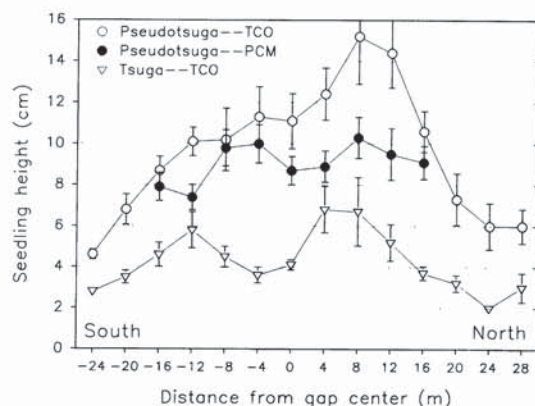

Fig. 4 Heights of naturally regenerated seedlings after two growing seasons by stand and species on north–south transects in 1.0 size gaps, showing means and standard errors ($n \leqslant 15$).

Discussion

GAP SIZE AND WITHIN-GAP POSITION EFFECTS

Although differences within and among forest canopy gaps are often cited as a mechanism for coexistence of different species within mature forests (e.g. Ricklefs 1977; Denslow 1980; Orians 1982; Runkle 1982), this is the first study that examined the process of seedling establishment for three common species over a range of gap sizes. Emergence and establishment of all three species was greater in gaps than in closed-canopy areas. Expected patterns of establishment success based on species' shade-tolerance were not observed, however. Although *Pseudotsuga menziesii* would be expected to have the lowest survival in closed canopy forest because it is considered the least shade-tolerant of the three species (Minore 1979), establishment of *Pseudotsuga* in control areas was similar to that of *Abies* and greater than that of *Tsuga*. High mortality of *Tsuga* in some closed-canopy forests is caused by burial of young seedlings by litter during snow-melt (Thornburgh 1969), yet most of the *Tsuga* mortality in our study occurred during the first summer after emergence (Gray 1995). Differential ability to extract soil moisture during the summer drought may have been more critical for survival in closed-canopy forest than shade-tolerance or resistance to burial; both *Abies* and *Pseudotsuga* have larger seed than *Tsuga* (seed weights are 22 and nine times greater, respectively; Schopmeyer 1974), enabling them to develop deeper rooting systems and conferring an advantage for early survival (Haig *et al*. 1941; Scott *et al*. 1976; Zobel & Antos 1991).

Some evidence for gap partitioning by different species of regenerating seedlings was found. Establishment of *Pseudotsuga* on mineral soil seed-plots varied the least among gap sizes and within-gap positions, while establishment of *Abies* tended to be low in northern portions of large gaps and establishment of *Tsuga* was lowest in control areas and in northern portions of large gaps. Seedling survival in exposed clear-cut microsites also declines from *Pseudotsuga* to *Abies* to *Tsuga* (Minore 1986). The northern edges of 0.4 gaps and the northern halves of 1.0 gaps were the only zones that received substantial amounts of direct solar radiation in this study (Gray 1995). Seedling mortality in exposed environments is commonly associated with high surface temperatures that can kill the cambium at the soil line (Silen 1960; Helgerson 1990) or lead to high transpiration rates and desiccation (Livingston & Black 1988). Differences in establishment among gaps were greater on natural substrates (Fig. 3) than on mineral soil seed-plots (Fig. 1), possibly due to more rapid drying and greater surface temperatures on forest floor than on mineral soil seedbeds (Haig *et al*. 1941; Silen 1960) and greater root competition from surrounding plants on natural

microsites than on disturbed seed-plots. Nevertheless, the greatest establishment for all species occurred in the same locations on natural and disturbed microsites: the moist, shaded environments in 0.2 gaps and southern portions of larger gaps (0.4 and 1.0 sizes). A study of seedling physiology of three species of *Acer* in different gap sizes and within-gap positions likewise found little partitioning among species (Sipe & Bazzaz 1994). The lack of specialization among species for establishment in distinct gap environments in this study indicates broad overlap in species' regeneration niches (Grubb 1977).

The natural regeneration and seed-plot studies provided complementary information on seedling establishment in gaps. The controlled seed-plot study provided greater precision in defining differences among locations, as well as the ability to study species which had no natural seed crop in a given year (e.g. *Abies*, or *Tsuga* in the mature stands). The natural regeneration study provided greater generality by examining seedling establishment on natural microsites that varied in terms of substrate quality and vegetation cover, and that were exposed to predation. Both studies showed greater seedling establishment occurring in gaps, although the lower establishment rates for natural regeneration may partly reflect seedling predation by birds and rodents (Gashwiler 1967). Differences in establishment among within-gap positions were greater in the natural regeneration study than in the seed-plot study, suggesting an interaction between position and substrate and/or vegetation cover.

There appeared to be a relationship between forest canopy structure and seedling establishment in closed-canopy areas. We expected to find greater seedling establishment under higher light levels in mature, *Pseudotsuga*-dominated stands than in multilayered old-growth stands which contained large proportions of shade-tolerant *Tsuga* in the canopy (Spies *et al.* 1990). Instead, the lowest seedling establishment occurred in the youngest stand and the old-growth stand with a relatively dense, intermediate layer of *Tsuga* that originated after a moderate-intensity fire about 150 years ago; both stands had tree cohorts with dense canopies relatively close to the forest floor. Canham *et al.* (1994) found that understorey light levels are correlated more with crown depth and the distance from the forest floor to the base of the crown than with canopy composition. The lack of a stronger relationship between canopy structure and measured light levels in the closed-canopy areas in this study (Table 1) may be due to the inherent difficulty of capturing the temporal and spatial variability of light regimes under forest canopies (Chazdon 1988). General age-related forest classifications, which do not reflect the variation in stand disturbance histories and development, do not adequately describe the variation in forest structure important for tree seedling establishment.

Growth after germination increased with gap size

for all species, particularly in gap centre positions, a common pattern for trees in canopy gaps (Minckler & Woerhide 1965; Runkle & Yetter 1987; Uhl *et al.* 1988; Denslow *et al.* 1990). Seedling growth response appeared to differ among species, however, with *Pseudotsuga menziesii* growth relatively low in all locations except for the 1.0 Centre location, *Tsuga heterophylla* growth increasing substantially with gap size, and *Abies amabilis* growth responding the least to gap size. Although *Abies* seedlings are initially larger than *Tsuga* seedlings, *Tsuga* growth rates are greater (Herman 1967; Kotar 1972; Long 1976; Harrington & Murray 1982), and the difference in growth rates increases with decreasing canopy cover (Zobel & Antos 1991). Some of the patterns in seedling growth among species and gap positions were related to length of growing season, with *Abies* typically setting buds before the other species, and seedlings in the centres of the largest gaps being the last to set buds (Gray 1995). Within the 1.0 size gap in stand TCO, size of *Pseudotsuga* and *Tsuga* tended to be greatest just north of gap centre (Fig. 4), possibly due to high light levels and low influence from gap edges (e.g. soil moisture depletion). The lack of pattern in *Pseudotsuga* seedling height across the 1.0 size gap in stand PCM may be due to the dense shrub and herb layer in that stand. Understorey vegetation can override or modify species establishment patterns in gaps in other forests (Veblen 1982; Nakashizuka 1989).

Locations with the greatest survival often had relatively low growth, and vice-versa. In control areas, low resource levels (e.g. light and moisture) may have limited survival as well as growth. Moderate resource levels in shaded gap locations may have been sufficient to ensure survival, but not high growth rates. High light levels in exposed gap locations may have led to stress and mortality of emergent seedlings, but also contributed to high growth rates of established seedlings. Competition among seedlings in high survival areas probably did not contribute to low seedling size; even on the densest seed-plots, each seedling had, on average, 35 cm^2 of surface space available. It is more likely that differences between survival and growth are due to different seedling response thresholds with respect to light.

Greater differentiation in establishment among species may occur with time, due to differences in growth rates, competitive ability and mortality from suppression or low vigour. Spies *et al.* (1990) found that seedling density in Cascade forest gaps was better related to gap age than to gap size, and Poulson & Platt (1989) found that patterns of species composition in hardwood forest gaps changed over time due to competition and morphological differences among species. Initial establishment patterns and seedling growth rates from our study suggest that differences in species composition among gap environments will increase over time. Early differences in growth rates among species may be a useful

measure of long-term survival, since many species are able to establish in areas that eventually prove unsuitable for survival (Shmida & Wilson 1985).

Although the experimental gaps differed in some ways from natural gaps in the Pacific Northwest (e.g. removal of tree boles), they were similar in several ways. Natural gaps formed by standing dead or wind-snapped trees, which cause minimal disturbance to the forest floor and understorey vegetation, account for 58–87% of the tree mortality in Cascade forests (Franklin & DeBell 1988; Spies *et al.* 1990). Experimental gaps were created in autumn, when tree-fall from wind-storms tends to be greatest. The sizes of the experimental gaps also reflect the range in size of natural tree-fall gaps (Spies *et al.* 1990). Differences between natural gaps and experimental gaps may be important to seedling establishment. Natural tree mortality and changes in resource levels in gaps, may not be as abrupt as mortality caused by cutting (e.g. mortality caused by root pathogens). Some large natural gaps form through expansion of smaller gaps, either due to wind exposure or root pathogen spread. Variation in topography and shape of natural gaps could modify within-gap environments and seedling establishment patterns. Environments within natural gaps would also tend to be modified somewhat by shading from snags and logs, effects that were considered in a companion study (Gray 1995).

GAPS AND FOREST DEVELOPMENT

This study suggests that canopy gaps in Douglas-fir forests are important sites for establishment of shade-tolerant tree seedlings, thus providing a mechanism for forest development from stands dominated by *Pseudotsuga menziesii* to stands containing multiple size classes and canopy layers of different species. Change in forest structure following establishment of shade-tolerant seedlings in these forests may be slow, however: seedling growth rates in this study were quite low in 0.2 gaps, the most common gap size in Cascade forests (Spies *et al.* 1990). Nevertheless, early establishment in small gaps may have lasting effects on stand development, since both *Abies amabilis* and *Tsuga heterophylla* can survive with little growth for many decades in shaded environments and resume growth into the canopy in response to subsequent disturbance (Van Pelt 1995). Larger gaps are not naturally as common as the 0.2 gap size in Pacific Northwest forests, but may be important sites for forest development by allowing abundant establishment and relatively high growth rates of established seedlings.

The largest experimental gaps in this study were important sites for establishment and growth of shade-intolerant *Pseudotsuga menziesii*. Most regional observations in mesic forest types indicate that the presence of *Pseudotsuga* saplings in natural stands is rare (Munger 1940; Franklin & Dyrness 1973), possibly due to the rarity of large gaps (Spies

et al. 1990) or exclusion of this species from gaps by *Phellinus weirii* ((Murrill) Gilbertson), a common fungal pathogen (Holah *et al.* 1993). The common perception that *Pseudotsuga* is unable to germinate in the shade or establish on intact forest floor (Ruth 1976; Stewart 1978) was not supported by this study. *Pseudotsuga* can develop multiaged stands in mesic forests in response to moderate- or variable- intensity fire (Means 1982; Morrison & Swanson 1990). In contrast to tree-fall gaps, moderate-intensity fire tends to impact entire stands at one point in time, create larger gaps, remove much of the litter layer, and kill most of the above-ground portions of understorey vegetation.

Although canopy gaps may not strictly be required for the establishment of shade-tolerant trees in *Pseudotsuga*-dominated forests, the initial results of this study suggest that development of secondary canopy layers, one criterion for the transformation from mature forests to old-growth forests, may be more rapid where gaps do occur. At least two important factors must be considered, however. The very low levels of seed rain and natural establishment of *Abies* and *Tsuga* in the mature stands in this study underscores the importance of seed sources in forest development. Forest development under such conditions will probably be slow and limited by infrequent establishment and the time required for established trees to begin producing on-site sources of seed. Gap size and within-gap position are also important considerations for any silvicultural strategy to accelerate development of old-growth Douglas-fir forests. Single-tree gaps are suitable locations for seedling establishment, but development of mature shade-tolerant trees may not occur without subsequent disturbance. Substantial portions of large gaps, however, may be unsuitable for establishment of late-successional species. In addition, sapling development in 1.0 and 0.4 gap sizes may result in even-aged, single canopy-layered patches rather than the multilayered canopy structure usually associated with old-growth forests. Thus there may be a trade-off between the speed of structural change and the heterogeneity of canopy structure resulting from gap formation in mature forests.

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