MICROSITE CONTROLS ON TREE SEEDLING ESTABLISHMENT IN CONIFER FOREST CANOPY GAPS

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Abstract. Tree seedling establishment and growth were studied in experimental canopy gaps to assess the effect of heterogeneity of regeneration microsites within and among gaps in mature conifer forests. Seedlings were studied for two years in closed-canopy areas and in recently created gaps ranging in size from 40 to 2000 m² in four stands of mature (90–140 yr) and old-growth (>400 yr) Douglas-fir forest in the western Cascade Range of central Oregon and southern Washington, USA. We examined the relative importance of substrate type, shade from logs and shade cloth, density of understory vegetation, gap size, and forest age on the success of Pacific silver fir (*Abies amabilis*), Douglas-fir (*Pseudotsuga menziesii*), and western hemlock (*Tsuga heterophylla*). Seedlings originating from seed sown on experimental microsites were compared with seedlings regenerating naturally on a range of microsites.

Seedling establishment was greater on decayed wood than on forest floor or mineral soil in closed-canopy areas, particularly for *Tsuga*. Differences in establishment among substrates declined with increasing gap size, although establishment on the forest floor tended to be low in portions of large gaps exposed to direct solar radiation. In exposed areas, shade from woody debris and shade cloth facilitated establishment for all species, while shade from understory vegetation aided the establishment of *Pseudotsuga* but not that of *Tsuga*. Establishment in shaded portions of gaps declined with vegetation and shade-cloth cover. Seedling size increased with gap size, decreased with level of shade, and tended to be greatest on forest floor and lowest on decayed wood.

Establishment and growth of the different species was related to differences in seed mass and tolerance of environmental extremes. Heterogeneity at the seedling scale (<10 cm) often overrode larger-scale environmental gradients (>2 m) associated with gap size and within-gap position. Thus the gap partitioning hypothesis, which emphasizes gap size and within-gap position, may be too simple to account for the role of microsite heterogeneity and species' regeneration traits on the development of mature forests.

Key words: Abies amabilis; canopy gaps; disturbance; heterogeneity; microsites; old-growth forest; Pacific Northwest; Pseudotsuga menziesii; seedling establishment; succession; Tsuga heterophylla.

INTRODUCTION

Treefall gap disturbances are important to the species dynamics of many forest types (Pickett and White 1985, Platt and Strong 1989). Species composition on a disturbed site can be influenced by a great number of factors, ranging from the size and intensity of the disturbance itself to microclimate and the presence of competitors (Pickett et al. 1987). Gap size and shape are usually emphasized as determinants of species composition in gaps (Runkle 1982, Denslow 1987, Poulson and Platt 1989), but finer scale environmental heterogeneity within gaps can also be important (Brandani et al. 1988, Veblen 1989). Microsite environments at the scale of a few square centimeters often determine the germination and growth of individual plants, factors that govern compositional change in plant communities (Harper 1977). The multiplicity of factors affecting plant establishment can be considered in hierarchical arrangement (after Allen and Hoekstra 1992). Using light intensity as an example, forest structure and composition determine light penetration through the canopy, gap size and shape determine light penetration into gaps, and the density of understory vegetation and woody debris determine light levels on the forest floor where seedlings establish. Most work in forest gaps tends to stress the role of single factors in controlling species composition, without elucidating the importance of interactions among them, or their importance at different spatial scales.

The purpose of our study was to determine the role of within-gap heterogeneity, in conjunction with gap size and forest structure, on tree species establishment in mature and old-growth conifer forests of the Pacific Northwest. Most of the disturbance research in the region has focused on succession following relatively large disturbances like fire or clear-cutting (Isaac and

Meagher 1936, Dyrness 1973, Agee and Huff 1987, Halpern and Franklin 1990), but gap disturbances appear to have a site return interval similar to that of fire in these forests (Spies and Franklin 1989). Treefall gaps may be important for the transition of young stands dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) in a single canopy layer into multi-layer old-growth forests containing increasing amounts of shade-tolerant *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) (Spies and Franklin 1989). The importance of microsites such as nurse logs on seedling establishment has been identified in this region (Christy and Mack 1984, Harmon and Franklin 1989), but the relative importance of different microsites within gaps and across forest types is not known.

We also examine the gap-partitioning hypothesis, which proposes that tree seedlings should display distinct distributions over the resource gradients between closed-canopy forest and the edges and centers of canopy gaps (Ricklefs 1977, Denslow 1980). This concept is predicated on niche specialization among species, and is an extension of the competitive exclusion principle (Gause 1934). The multitude of factors determining plant regeneration ("regeneration niche"), however, may allow establishment of different species within similar portions of large-scale environmental gradients and subsequent survival in the face of competition (Grubb 1977). The importance of subtle fine-scale microsite conditions for the establishment of seedlings (Harper et al. 1965, Harper 1977) provides a mechanism for the establishment of many species on similar portions of the resource gradient from intact forests into canopy gaps, given sufficient microsite heterogeneity. For instance, in some forests the density of understory plants and presence of specific substrates (e.g., logs or windthrow mounds) are more important than gap size to tree species' establishment and long-term survival (Ehrenfeld 1980, Veblen 1985, Nakashizuka 1989).

Microsite heterogeneity within gaps in Douglas-fir forests is potentially important to tree seedling establishment and growth. Despite abundant winter precipitation, the climate of the Pacific Northwest is one of dry, warm weather during the summer growing season. Mortality of young tree seedlings is often associated with drought stress and high surface temperatures (>50°C) on substrates exposed to direct solar radiation (Haig et al. 1941, Livingston and Black 1988, Helgerson 1990). Shade from shrubs and logs may facilitate seedling establishment during the dry summers by providing moist or cool microsites. In high-light environments, establishment of the relatively shade-intolerant *Pseudotsuga menziesii* may be facilitated by shading from vegetation, woody debris, or live trees (Isaac 1943, Franklin 1963). *Pseudotsuga* often aggressively occupies early seral communities, but it can be excluded by dense non-tree vegetation (Isaac 1943). Es-

tablishment of *Pseudotsuga* is also sensitive to substrate type, usually being most successful on mineral soil in high-light environments (Isaac 1943, Hermann and Chilcote 1965). The shade-tolerant *Tsuga heterophylla* appears to be so sensitive to competition from understory plants at the seedling stage that establishment is usually limited to the surface of decayed *Pseudotsuga* logs (Scott et al. 1976, Christy and Mack 1984, Harmon and Franklin 1989). While the shade-tolerant *Abies amabilis* commonly establishes on the forest floor in closed-canopy forest, it also appears to be sensitive to overstory and understory canopy density (Wilson 1991, Zobel and Antos 1991).

Although shade-tolerant *Tsuga heterophylla* and *Abies amabilis* seedlings are more abundant in canopy gaps than under closed canopies (Thornburgh 1969, Long 1976, Stewart 1986, Harmon 1987, Spies et al. 1990, Alaback and Tappeiner 1991), many gaps are devoid of tree saplings even 50 yr or more after gap formation (Spies et al. 1990, Lertzman 1992). In comparison, canopy closure may take as little as 2 yr in moist tropical forests (Lorimer 1989) or 5 yr in temperate deciduous forests (Runkle 1990). It is unclear whether filling of gaps in the Pacific Northwest is limited by low light levels in narrow gaps surrounded by tall, deep tree crowns (Canham et al. 1990), or by lack of suitable microsites for tree establishment because of minimal disturbance to the forest floor and understory vegetation in most gaps, which are formed by standing dead trees (Spies et al. 1990).

The successional role of gaps in mature Douglas-fir forests has important implications for ecosystem management in the Pacific Northwest. The loss and fragmentation of late-successional (old-growth and mature) forests has been a contentious issue in the region for decades. Recent proposals for management of federal lands assume that young forests will develop greater structural and compositional diversity at rates high enough to compensate for continued cutting of old growth (FEMAT 1993). While this may be accomplished by passively allowing stands to age, selective harvest has been proposed as a way to achieve structural complexity more rapidly in young stands and allow some commodity extraction as well (Spies et al. 1991, McComb et al. 1993). For either the passive or active management strategy, 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 patch selection harvesting can mimic this process.

The objective of our paper is to examine the effect of microsite heterogeneity on tree seedling establishment in Douglas-fir forest canopy gaps. A companion study of seedling establishment on uniform microsites across a range of gap sizes (Gray and Spies 1996) found that gap size and within-gap position had modest effects on seedling establishment, but found differences between establishment of sown and naturally dispersed

seed, possibly due to finer scale variation in substrates and understory vegetation. This paper explores additional data to evaluate the importance of that fine-scale heterogeneity. Specific objectives of this study include: (1) to determine whether the establishment and growth of different tree species vary predictably with gap size or are affected by seedling substrates, (2) to determine whether shade near the ground (in the shrub and herb layer) affects species response within gaps (facilitation or inhibition), and (3) to compare species' response patterns on controlled experimental plots to the survival and density of naturally regenerated seedlings in different existing microsites within gaps. Tracking natural regeneration provided an opportunity to test the generality of patterns identified in the somewhat artificial experiments that used sown seed.

METHODS

Site description

The studies of microsite and gap size effects on tree seedling establishment were conducted in four forest stands: two old-growth stands, ~500 yr of age, dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* in multiple canopy layers; and two mature stands, 90 and 140 yr of age, dominated by *Pseudotsuga* in a single canopy layer. All stands were on relatively flat ground (slopes < 20%) in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973) on the west slope of the Cascade Range. One old-growth stand was located in the H. J. Andrews Experimental Forest in the central Oregon Cascades, and the other three stands were located in the Wind River Experimental Forest in the southern Washington Cascades. These sites represent the drier southern end of the geographic range for both *Tsuga heterophylla* and *Abies amabilis*. Four sizes of circular gaps were created in the fall of 1990 with two replicates of each size and two closed-canopy control plots in each stand. The gap diameter to tree height ratios for the four gap sizes were 0.2, 0.4, 0.6, and 1.0, and the control plots were equal in area to the 1.0 gap size (dominant tree heights were 50 m in three of the stands and 35 m in the fourth). The 0.2 gap size corresponded to the removal of a single dominant tree. Details of stand characteristics and gap creation methods are provided in Gray and Spies (1996). The weather varied during the two years of study, with 1992 being relatively dry and 1993 slightly wetter than average (October–September precipitation = 214, 170, and 228 cm; May–September precipitation = 29, 17, and 31 cm; for mean, 1992, and 1993, respectively).

Substrate experiment

This study was conducted on three standardized substrates in three gap sizes (0.2, 0.4, and 1.0) and in closed-canopy controls, using both replicates of each gap size per stand. Three 0.25-m² seed plots were cre-

ated for each mineral soil, forest floor, and decayed wood substrate in the center of each gap and control. The mineral soil ("soil") substrate was created 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 (dug from a roadside in one of the old-growth stands) in a 2.5 cm deep surface layer. This soil disturbance probably reduced root density, but was believed to have little effect on the availability of mycorrhizal inocula (R. Molina, *personal communication*). Forest-floor ("litter") seed plots were located on relatively flat areas with an intact litter layer over mineral soil. The mean depth of litter layer to mineral soil was calculated from measurements at two points next to each forest-floor seed plot. Decayed wood ("wood") plots were created by chopping up large pieces of well-decayed *Pseudotsuga* logs (decay class IV; Maser et al. 1979) and placing them in 60 × 60 cm boxes made with 15 cm high boards on the sides and window screen on the bottom. Smaller pieces of wood were packed around the larger pieces and a fine wood powder was spread over the top for a uniformly soft surface to retain seed. Because of a lack of class IV logs in the mature stands, wood from the Wind River old-growth stand was used for the seed plots in the mature stands. Seed-plot surfaces were roughened slightly with a hand rake to discourage seed movement by raindrops (Lawrence and Rediske 1962).

One hundred *Abies amabilis,* 100 *Pseudotsuga menziesii,* and 500 *Tsuga heterophylla* seeds were divided evenly between the three seed plots of each substrate treatment. Seed was used in greater quantities for *Tsuga* than for the other species because germination and early survival is usually much lower for *Tsuga* (Harmon and Franklin 1989). All seeds were sown during the first three weeks of November 1991 to approximate the natural time of seed dispersal. The seeds used at the H. J. Andrews and Wind River sites were from local seed zones (all seed lots were obtained from the Wind River Nursery, Carson, Washington). Germination tests conducted by the Wind River Nursery estimated seed-lot 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 lots, respectively. Natural seed rain also added large numbers of seed in the fall of 1991, primarily *Pseudotsuga* in the mature stands, and both *Pseudotsuga* and *Tsuga* in the old-growth stands. Seed rain was monitored with 0.19-m² seed traps placed in the centers and along the north-south transects of one replicate of each gap size and control in each stand. 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 photosynthetically active radiation (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. Shrubby and herbaceous vegetation that might have cast shade over the seed plots was clipped or uprooted at regular intervals throughout the course of the study; this treatment probably also reduced root density.

Seedlings were counted in the seed plots once each month from late April to October of 1992 and during June and October of 1993. Seedlings were considered "emerged" and were 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 lacked green color. Seedlings were considered "established" if they were alive at the end of the second growing season (1993). 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.

Surface temperatures were monitored in August 1992 on the three substrates in the center of a 1.0 size gap using thermocouple wire (TT-E-24S chromel-constantan, Omega Engineering Incorporated, Stamford, Connecticut) with single-strand sensor ends and dataloggers (CR-10, Campbell Scientific Incorporated, Logan, Utah), which stored 10-min averages and maxima of 1-min samples. One thermocouple each was placed on two soil, litter, and wood seed plots, and pinned with wire "staples" so that sensor ends were within 3 mm of the surface.

Understory shade experiment

This study was designed to examine the effect of understory shade on seedling survival and growth. The effects of 0, 40, and 90% shade over forest floor were investigated in the centers of both replicates of the closed-canopy controls and 0.4 and 1.0 gap sizes in the mature stands. The "litter" seed plots from the substrate experiment comprised the unshaded treatment for this experiment. Shade cloth stapled to 1 × 1 m square wooden frames, set on stakes 30 cm above the forest floor (the average height of tall herb and low shrub canopies in these stands), comprised the shaded treatments. To approximate the partial shade of understory vegetation, "40% shade" and "90% shade" treatments were created by removing 60 and 10%, respectively, of the black (96% opaque) shade cloth in regularly spaced 5 cm diameter holes. The same Wind River seed lots used in the substrate study were sown at the same densities and in the same manner, and seedlings were counted and measured at the same intervals. Placement of exclosures and removal of potentially shading vegetation was done in the same manner as for the substrate experiment. Shade-cloth frames were removed over winter (November to April) to avoid destruction by snow. Surface temperatures were measured on shade plots in the same gap and manner as done for the substrate study. One thermocouple was placed on each of two litter plots, and two thermocouples were placed on each of two 40% and 90% shade plots.

Log shade experiment

This study was designed to characterize the effect of proximity to large logs on seedling survival by planting germinants on north and south sides of large log pieces in different positions inside large gaps. Log pieces ~50 cm in diameter and 1.5 m long were placed in north, center, and south positions within the two 1.0 gap sizes of the Wind River old-growth stand. The long axes of the logs were oriented east–west, and *Pseudotsuga* and *Tsuga* germinants were each planted in five north–south transects (5 cm apart) on the north and south sides of each log. Using the vertical projection from the log edge as a reference point, seedlings were planted at 3-cm intervals along each transect, beginning 6 cm under to 30 cm beyond the edge of the log. Equations of radiation, gap, and log geometry indicated that a log length of 1.5 m was sufficient to prevent morning or afternoon direct radiation (other than sunflecks) from irradiating seedlings that were otherwise shaded by the logs.

Seedlings were grown from the same Wind River seed lots that were used in the substrate and shade experiments by stratifying seed for one month at 4°C and sowing seed in a peat–vermiculite mixture in transportable flats at a greenhouse in Corvallis, Oregon. Seedlings were taken to the field and planted within two weeks of emergence in early June 1993 (seedlings were roughly the same age as naturally germinating seedlings in the gaps). All understory vegetation in the seedling plots and any from around the logs that might have cast shade was removed, which probably reduced root density. At each seedling position, a steel spike was used to create a planting hole and seedlings were quickly transferred from the planting mix into the holes, which were closed by inserting the spike 1 cm away and pushing toward the seedling. Each planted plot was immediately watered with 2 L of water to mitigate planting shock. Exclosures similar to those used in the seed-plot experiments were placed around each plot. Plots were revisited periodically throughout the summer and early fall of 1993 to assess seedling survival.

Measurements of PAR, surface temperature, and soil moisture were made next to the seedling transects outward from three logs in one of the gaps using calibrated quantum sensors (LI-190SZ, LI-COR Incorporated, Lincoln, Nebraska), thermocouples (as described for the *Understory shade experiment*), and time domain reflectometry (TDR) soil moisture probes (method and calibration described in Gray and Spies 1995) placed at 6-cm intervals on the north and south sides of each log. Quantum sensor surfaces were 2 cm above the forest floor, thermocouple sensors were placed within 3 mm of the surface, and soil moisture probes sampled to a depth of 15 cm from the top of the litter layer.

Two microclimate stations were used, one each at the north and center logs in July, one of which was used again on the south log in August. Exclosure tops were removed while microclimate sensors were running. Over the entire period, additional light and temperature sensors were operating in the center of the gap. Dataloggers sampled the quantum sensors and thermocouples every 10 s and stored 10-min averages, while soil moisture was sampled monthly with TDR.

Survival of natural regeneration

Survival of seedlings originating from natural seed rain was monitored across a range of existing natural microsites within the closed-canopy and different gap size treatments. In addition to exploring the effects of substrate and understory vegetation cover, this study examined the effect of within-gap position on survival. 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 (except size 0.6) and control in each stand was searched and individuals of first-year *Pseudotsuga* and *Tsuga* were marked with small pin flags. A concerted effort was made to locate up to 15 seedlings in each combination of gap size treatment (control, 0.2, 0.4, and 1.0), position (north, center, and south; center only in the 0.2 size class), shrub and herb layer cover level (0, 50, and 90% cover of shrubs and herbs within 28 cm diameter circular plot rings), and substrate (forest floor and class III and IV decayed wood). Nevertheless, sample sizes varied considerably among treatment combinations, and *Tsuga* seedlings were rare in the mature stands. To avoid edge effects and any east-west effects, most marked seedlings 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 in July and October 1993 to assess survival.

Statistical analysis

The effects of the fixed factors (e.g., forest age, gap size, substrate) in the substrate, understory shade, and natural regeneration experiments 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 for unbalanced experiments (Milliken and Johnson 1984, Shaw and Mitchell-Olds 1993) indicated that they were appropriate. Lack of balance in the analysis of seedling size in the shade experiment resulted from missing observations (lack of survivors), and lack of balance in the natural regeneration experiment resulted from missing treatments (only one within-gap position in gap size 0.2). The different treatments within each gap size (e.g., substrate, shade, or vegetation cover) were technically "repeated measures" of gap size, and could be treated as split-plot levels only if the covariance matrices sat-

isfied the Huynh-Feldt condition (Huynh and Feldt 1970). The Huynh-Feldt condition was assessed by conducting sphericity tests on these factors for each species in repeated-measures ANOVAs (SAS Institute 1987); none of the datasets violated this condition at the $P = 0.05$ level. The analyses for the substrate and shade experiments had two possible sub-plot error terms, one for the variation of gaps within stands, and one for the variation of gap-size replicates within stands; the term with the largest mean square was used as the error term. Results of the analyses were considered significant if the probability of a Type I error was <0.05. Multiple comparisons of treatment means were conducted for significant factors using least-squares means and 95% confidence intervals, analogous to Fisher's protected least significant difference, calculated with the Mixed procedure in SAS 6.10 (SAS Institute 1987), although some factors could not be analyzed because of unbalanced design.

The fixed effects in the ANOVA for the substrate experiment were stand age, gap size, substrate, and tree species. The response variable for the analysis of establishment was the fraction of the maximum number of emerged seedlings counted in each 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 substrate treatment within a gap, and establishment was calculated on those sums. Establishment values were transformed with an arcsine square-root equation and the analysis was weighted by the sample size (the maximum number of seedlings per treatment). The term "establishment" is used for the substrate and shade experiments because individuals were not marked, so seedlings may have died and been replaced by new emergents between counts. The term "survival" is used for the log shade and natural regeneration experiments because the survival of individual seedlings was followed. The response variable for the analysis of seedling size for the substrate experiment was the mean size of the seedlings measured in a treatment, 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.

The fixed effects in the ANOVA for the shade experiment were gap size, shade level, and tree species. The response variable for the analysis of establishment was calculated and transformed as for the substrate analysis. The analysis was weighted by the maximum number of counts in a treatment. In addition, establishment was calculated as a fraction of total seed (seed rain plus sown seed). The analysis of seedling size was calculated and transformed as for the substrate analysis.

Because of high mortality from predation of seedlings in one of the gaps in the log shade experiment (most likely by cutworms, family Noctuidae; Overhulser 1990), log effects were assessed for one log in

TABLE 1.   Results of split-split plot ANOVA on seedling establishment (fraction of maximum number emerged) for substrate study. Factor abbreviations are: Age = age class, Gap = gap size, Rep. = gap replicate within stand, Subs. = substrate, Spp. = species.

Source	df	MS	F	P
Age	1	1.726	0.35	0.6138
Error: Stand(Age)	2	4.922		
Gap	3	15.108	3.41	0.0940
Age × Gap	3	0.972	0.22	0.8797
Error: Stand × Gap(Age)	6	4.434		
Rep.(Age × Stand × Gap)	16	1.515		
Subs.	2	11.465	52.40	0.0001*
Age × Subs.	2	0.744	3.40	0.0355*
Gap × Subs.	6	1.940	8.87	0.0001*
Age × Gap × Subs.	6	0.286	1.31	0.2566
Spp.	2	10.428	47.66	0.0001*
Age × Spp.	2	0.253	1.16	0.3172
Gap × Spp.	6	1.859	8.50	0.0001*
Subs. × Spp.	4	3.122	14.27	0.0001*
Age × Gap × Spp.	6	0.326	1.49	0.1840
Age × Subs. × Spp.	4	0.348	1.59	0.1788
Gap × Subs. × Spp.	12	0.147	0.67	0.7786
Age × Gap × Subs. × Spp.	12	0.067	0.30	0.9880
Error: Rep(Age × Stand × Gap × Sub. × Spp.)	189	0.219		
Total	284			

* $P < 0.05$.

each position from one gap only. Lack of replication therefore precluded statistical analyses. The number of surviving seedlings of each species is presented by distance from log edge and side of log (e.g., north or south side). Light and surface temperature data were averaged over several hot and sunny days, defined as those during which maximum surface temperatures exceeded 60°C at the gap center microclimate station (16 d for the north and center logs and 7 d for the south log). Volumetric soil moisture data sampled on 9 July 1993 (by which time most seedling mortality had occurred) are also presented.

The survival of naturally germinated seedlings was analyzed with separate split-plot ANOVAs for the effects of cover and substrate (despite thorough searches, few seedlings were found on decayed wood across the range of other factor levels). The response variable was the fraction of the initial number of emerged seedlings counted for a treatment combination (e.g., cover level within a position) that were still alive at the end of the second growing season. Survival data were transformed with an arcsine square-root equation, and analyses were weighted by sample size. Because of the very low number of *Tsuga* seedlings in the mature stands, separate analyses were done for *Pseudotsuga* (all four stands) and *Tsuga* (two old-growth stands).

RESULTS

Substrate effects

Seedling establishment at the end of two growing seasons differed significantly among species and substrates, but the gap size effect was only marginally significant ($P = 0.094$). Interactions of substrate with age class and gap size, and of species with gap size and substrate, were also significant (Table 1). Establishment on wood was significantly greater than establishment on soil and litter in closed-canopy controls and in 0.2 gaps, while establishment on litter tended to be lower than on the other substrates in 1.0 gaps (Table 2, Fig. 1). Seedling establishment patterns in 1.0 gaps were similar to surface temperature patterns; maximum surface temperatures commonly exceeded 50°C, with highest temperatures on litter and lowest temperatures on wood (Table 3). Although establishment of *Abies amabilis* and *Tsuga heterophylla* was greater in 0.2 and 0.4 gaps than in controls and 1.0 gaps, establishment of *Pseudotsuga menziesii* only differed between gaps and controls. In addition, *Tsuga* establishment was significantly lower than that of the other species in 1.0 gaps. The significance of the substrate by species interaction was primarily caused by similar establishment of *Pseudotsuga* across substrates and greater establishment of *Abies* and *Tsuga* on wood than on soil and litter (Table 2). The age class by substrate interaction was caused by lower establishment on wood in old-growth compared to mature stands, but consistent patterns across species and gap size were not apparent (Gray 1995).

Seedling size after two growing seasons differed significantly by age class ($F_{1,8} = 9.9, P = 0.014$), gap size ($F_{3,8} = 83.4, P = 0.0001$), substrate ($F_{2,46} = 13.2, P = 0.0001$), species ($F_{2,46} = 126.5, P = 0.0001$), and the interactions of gap size by substrate ($F_{6,46} = 5.6, P = 0.0002$), gap size by species ($F_{6,46} = 5.0, P = $

TABLE 2. Separation of means for significant interactions in ANOVA on substrate effects on seedling establishment. Values are least-square means (with standard errors in parentheses) of arcsine-transformed establishment data. Means within an interaction with different superscript letters differed significantly ($P < 0.05$). Gap size is the ratio of gap diameter to tree height, and control plots were equal in area to the 1.0 gap size.

	Control	Gap size 0.2	Gap size 0.4	Gap size 1.0
Gap size × substrate				
Soil	0.321[a] (0.101)	0.798[cde] (0.101)	0.952[ef] (0.101)	0.711[cd] (0.102)
Litter	0.396[ab] (0.103)	0.774[cde] (0.103)	0.850[de] (0.102)	0.594[bc] (0.105)
Wood	0.804[de] (0.098)	1.072[f] (0.098)	0.960[ef] (0.099)	0.788[cde] (0.099)
Gap size × species				
Abies	0.648[bc] (0.105)	0.971[e] (0.104)	0.970[e] (0.103)	0.753[cd] (0.106)
Pseudotsuga	0.506[ab] (0.100)	0.885[de] (0.102)	0.953[de] (0.101)	0.931[de] (0.103)
Tsuga	0.367[a] (0.098)	0.817[cde] (0.097)	0.839[cde] (0.097)	0.411[a] (0.099)

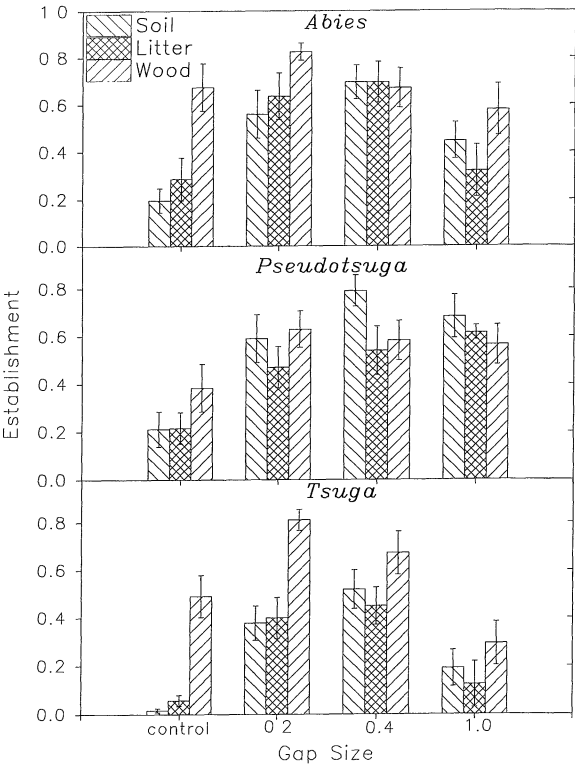|	Soil	Litter	Wood
Substrate × species			
Abies	0.754[b] (0.066)	0.737[b] (0.067)	1.015[c] (0.060)
Pseudotsuga	0.851[b] (0.060)	0.746[b] (0.064)	0.836[b] (0.057)
Tsuga	0.482[a] (0.055)	0.477[a] (0.059)	0.867[b] (0.053)

FIG. 1. Seedling establishment (fraction of maximum number emerged) after two years on substrate seed plots by species, gap size, and substrate. Gap size is the ratio of gap diameter to tree height, and control plots were equal in area to the 1.0 gap size. Data are means and standard errors ($n = 8$).

0.0005), and substrate by species ($F_{4,46} = 5.7$, $P = 0.0008$). Seedlings in old-growth stands were 50% larger on average than those in mature stands, with the greatest differences found in gap size 1.0. Seedlings in closed-canopy controls and 0.2 gaps were similar in size, but seedling size increased with gap size, with the largest seedlings in 0.4 and 1.0 gaps usually found on litter (Fig. 2). Although the smallest Pseudotsuga seedlings in a gap were usually those growing on wood, seedling size was similar on wood and soil for Abies in 0.4 and 1.0 gaps and for Tsuga in 1.0 gaps. Seedling size increased in all treatments from Tsuga to Abies to Pseudotsuga. Seedling height/diameter ratios tended to decrease with increasing gap size for Pseudotsuga and to some extent for Abies, but not for Tsuga (Table 4).

Understory shade effects

Seedling establishment after two growing seasons as a fraction of maximum emerged seedlings differed significantly by shade level ($F_{2,24} = 6.7$, $P = 0.005$), species ($F_{2,24} = 17.3$, $P = 0.0001$), and the gap size by shade level and gap size by species interactions ($F_{4,24}$

TABLE 3. Surface temperatures (°C) measured in seed plots in a 1.0 size gap over five hot days in mid-August 1992. Daily maximum temperatures for each sensor were averaged for the five days; means and maxima for each substrate or shade treatment are shown (two sensors were used for soil, litter, and wood; four sensors were used for 40% and 90% shade).

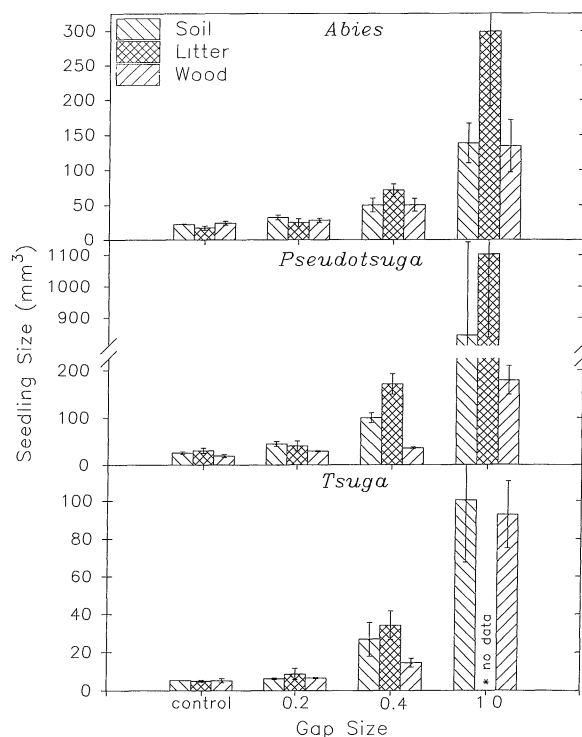|	Soil	Litter	Wood	40% shade on litter	90% shade on litter
Mean	55.5	61.8	49.7	52.5	46.5
Maximum	57.2	65.3	53.7	57.5	56.7

FIG. 2. Seedling size (basal area × height) on substrate seed plots by species, gap size, and substrate. Note the break in the y-axis for *Pseudotsuga*. No *Tsuga* were present on measured litter plots in the 1.0 gap size. Data are means and standard errors (n = 4).

TABLE 4. Mean seedling height/diameter ratios by substrate, species, and gap size. Data are means (with standard errors in parentheses) of treatments in each stand (n ≤ 4, depending on presence of seedlings within a treatment). Gap size is the ratio of gap diameter to tree height, and control plots were equal in area to the 1.0 gap size.

Gap size	Substrate	*Abies*	*Pseudotsuga*	*Tsuga*
Control	soil	37 (1)	93 (11)	54
Control	litter	37 (2)	89 (8)	52 (5)
Control	wood	41 (2)	78 (2)	49 (3)
0.2	soil	39 (2)	88 (5)	49 (2)
0.2	litter	38 (3)	82 (6)	58 (8)
0.2	wood	42 (2)	80 (6)	55 (2)
0.4	soil	35 (1)	73 (14)	61 (7)
0.4	litter	39 (4)	74 (10)	69 (7)
0.4	wood	37 (1)	65 (4)	58 (5)
1.0	soil	28 (2)	69 (9)	58 (12)
1.0	litter	33 (5)	61 (6)	...
1.0	wood	30 (2)	55 (5)	62 (5)

Log shade experiment

Seedling survival was greatly affected by proximity to large logs in the 1.0 size gap, and the effect varied by within-gap position (Fig. 3). Survival of *Pseudotsuga* and *Tsuga* was greatest within 15 cm of the north sides of logs in the north and center of the gap. No *Tsuga* survived beyond this zone on the north sides, or anywhere on the south sides of the north and center logs. Some *Pseudotsuga* did survive outside of the 15 cm north side zone; survival in these areas was greater for the log at gap center than for the log at the north end of the gap. Almost all dead seedlings at north and center logs were either standing brown or withered and faded. At the south log, seedling survival was generally high regardless of proximity to the log; almost all mortality that did occur was identified as clipping of stems by predators.

Patterns of seedling survival next to logs corresponded well with some measures of microclimate. Positions within 12 cm of the north sides of all logs received less light than other positions, and light levels at unshaded positions decreased from north to south log location within the gap (Fig. 3). Temperature maxima paralleled light levels closely, with positions beyond 12 cm of the north sides and all positions on the south sides of the north and center logs experiencing surface temperatures in excess of 40°C. In contrast, near the south log, temperature maxima did not exceed 30°C. No obvious soil moisture patterns with distance from logs were found, although moisture tended to be greatest at the south log and lowest at the north log. We found little evidence of an expected zone of increased temperature and moisture stress near the south sides of logs in high-light areas, although survival of *Pseudotsuga* appeared to increase at distances >15 cm from the south side of the gap-center log.

= 6.0, P = 0.001 and $F_{4,24}$ = 6.0, P = 0.001, respectively). Establishment under 90% shade was lower than establishment under 40% or no shade in closed-canopy controls and in 0.4 gaps (Table 5). Establishment in 1.0 gaps tended to be greatest under 90% shade, particularly for *Abies*. We expected a more dramatic effect from the 90% shade treatment caused by amelioration of the extreme surface temperatures on litter in gap size 1.0, but temperatures commonly exceeded 50°C on shade treatments, despite the much shorter duration of solar "sunflecks" (Table 3). The shade treatments in 1.0 gaps did allow for greater emergence of seedlings, however, because establishment as a fraction of total seed tended to be greater under shade than without shade (Table 5).

Seedling size after two growing seasons differed significantly by gap size ($F_{2,16}$ = 41.7, P = 0.0001), shade level ($F_{2,16}$ = 12.8, P = 0.0004), and species ($F_{2,16}$ = 40.5, P = 0.0001). Seedling size decreased from *Pseudotsuga* to *Abies* to *Tsuga* in most treatments and with level of shade in all gaps (no *Tsuga* survivors were present in the unshaded plots in the measured 1.0 gaps, however) (Table 6). Seedling height/diameter ratios tended to increase with shade level for *Pseudotsuga*, particularly in 1.0 gaps (Table 6).

TABLE 5. Mean establishment by gap size and artificial shade level, expressed as percentage of total seed and percentage of maximum emerged seedlings. "Ctl." refers to closed-canopy controls. Standard errors are in parentheses ($n = 4$).

Gap size	Shade (%)	Abies		Pseudotsuga		Tsuga	
		Emergents (%)	Seed (%)	Emergents (%)	Seed (%)	Emergents (%)	Seed (%)
Ctl.	0	37.2 (15.3)	2.3 (0.9)	25.8 (9.5)	1.6 (1.0)	5.1 (3.1)	0.5 (0.4)
Ctl.	40	26.0 (11.0)	2.8 (1.0)	19.1 (10.8)	2.8 (1.6)	0.0 (0.0)	0.0 (0.0)
Ctl.	90	1.8 (1.8)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
0.4	0	86.0 (6.6)	13.0 (4.1)	46.7 (19.7)	4.4 (1.9)	52.2 (8.2)	7.3 (2.4)
0.4	40	73.2 (6.7)	11.5 (3.4)	62.0 (13.3)	4.8 (0.8)	70.4 (9.8)	5.2 (1.2)
0.4	90	59.1 (9.5)	10.8 (1.3)	15.0 (10.2)	1.3 (0.7)	14.4 (6.7)	1.0 (0.3)
1.0	0	39.7 (14.7)	6.0 (4.7)	66.1 (4.2)	2.7 (0.3)	19.1 (19.1)	0.8 (0.8)
1.0	40	36.5 (16.1)	9.5 (5.9)	59.4 (17.7)	3.9 (1.9)	22.1 (8.9)	1.5 (1.0)
1.0	90	62.0 (8.3)	9.8 (5.0)	69.6 (10.1)	5.4 (2.1)	23.2 (3.6)	1.5 (0.4)

Survival of natural regeneration

Survival of naturally regenerated *Pseudotsuga* after two growing seasons differed significantly by gap size ($F_{3,6} = 10.6$, $P = 0.008$), within-gap position ($F_{2,46} = 3.83$, $P = 0.029$), and substrate ($F_{1,29} = 6.33$, $P = 0.031$), but survival of *Tsuga* differed significantly only by gap size ($F_{3,15} = 17.2$, $P = 0.010$). The effect of understory vegetation cover was not significant for either species, although the gap size by within-gap position by cover interaction was marginally significant for *Tsuga* ($F_{7,52} = 2.66$, $P = 0.057$). Low sample sizes for some of the crossed factors may have precluded greater significance in these analyses. Seedling survival tended to be greater on decayed wood than on litter for both *Pseudotsuga* and *Tsuga*, although not in controls, nor for *Tsuga* in gap size 0.2 and in north and center positions of gap size 1.0 (Fig. 4). Survival of *Tsuga* and *Pseudotsuga* on litter was low in controls, with no survivors under high levels of understory vegetation cover (Fig. 5). *Pseudotsuga* survival tended to be greater under high cover than low cover in exposed locations (e.g., 0.4 and 1.0 north, and 1.0 center), while the opposite tended to occur in shaded parts of gaps (e.g., 0.4 and 1.0 south). Survival of *Tsuga* also tended to be lowest in high-cover microsites in open parts of gaps, but did not appear to benefit from understory cover in exposed locations (0.4 and 1.0 north).

DISCUSSION

Substrate effects

Tree seedling establishment varied dramatically by species, with interactions among substrates and gap size. In closed-canopy areas, establishment on decayed wood seed plots was greater than establishment on forest floor and mineral soil, and the difference was greatest for *Tsuga heterophylla* and least for *Pseudotsuga menziesii*. Other studies have similarly found that decayed wood is typically the only substrate on which *Tsuga heterophylla* establishes in closed-canopy forests (Minore 1972, Christy and Mack 1984, Harmon and Franklin 1989). In the gaps in this study, however, seedling establishment was much less restricted to wood than in closed-canopy areas. For *Tsuga* in particular, the relative advantage of decayed wood over the other substrates declined with increasing gap size. Greater establishment on decayed wood than on the forest floor in closed-canopy areas of these summer-dry forests is most likely a result of the greater moisture content of wood (Harmon et al. 1986, Gray 1995). Establishment of *Tsuga heterophylla* seems to be particularly sensitive to substrate moisture (Williamson 1976). Avoidance of drought mortality depends on a species' ability to establish roots below the progressively deeper drying front in the soil (Haig et al. 1941,

TABLE 6. Mean seedling size (basal area × height) and height/diameter ratios in response to artificial understory shade by species, gap size, and shade level. Data are means (with standard errors in parentheses) of treatments in each stand ($n \leq 2$, depending on presence of seedlings within a treatment).

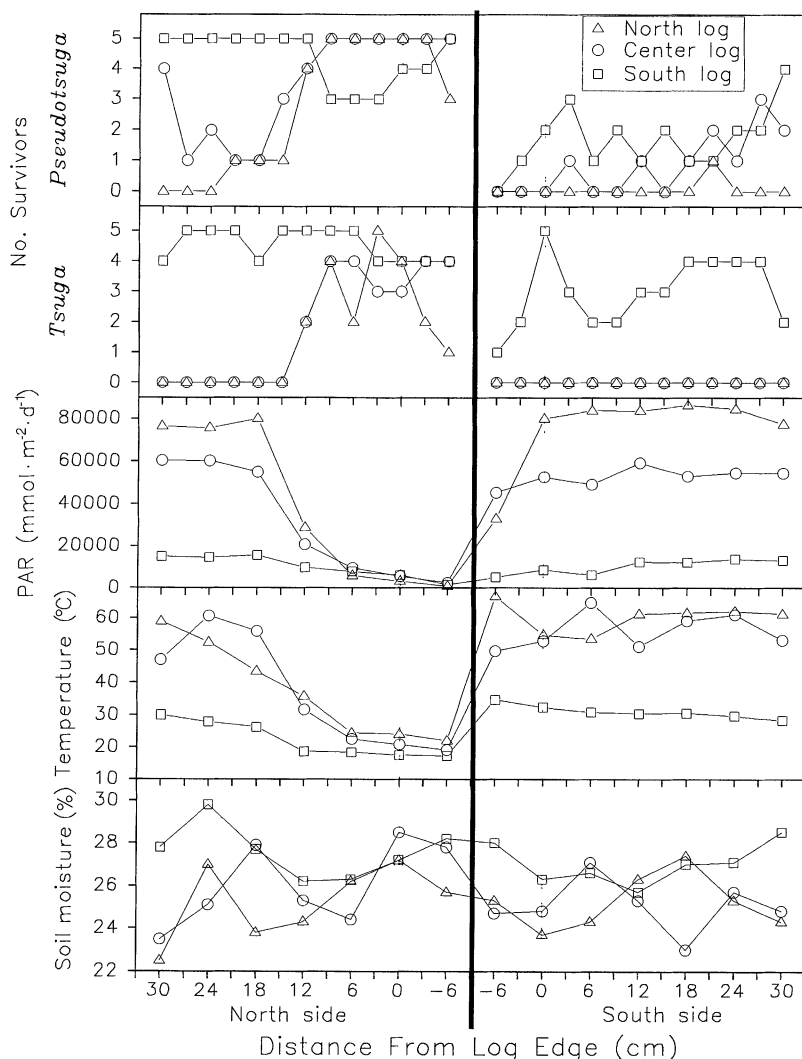| Gap size	Shade (%)	Abies		Pseudotsuga		Tsuga	
		Size (mm³)	Height/diam. ratio	Size (mm³)	Height/diam. ratio	Size (mm³)	Height/diam. ratio
Control	0	14	35	25	82	5	47
Control	40	15	39	17	80	...	...
Control	90	24	42	...	...	...	...
0.4	0	59 (8)	44 (1)	182 (43)	69 (22)	28 (7)	62 (2)
0.4	40	38 (5)	39 (2)	138 (80)	69 (20)	20 (7)	65 (4)
0.4	90	22 (5)	48 (7)	25 (2)	109 (4)	7 (1)	54 (1)
1.0	0	174 (44)	32 (8)	676 (154)	65 (10)	...	...
1.0	40	108 (23)	32 (1)	494 (144)	87 (13)	129	86
1.0	90	50 (6)	41 (1)	108 (17)	112 (16)	13 (3)	61 (2)

FIG. 3. Seedling survival (from a total of five seedlings planted per position) and microclimate with distance from logs in three positions within a large (1.0 size) gap. Mean daily quantum flux of photosynthetically active radiation (PAR) and mean daily temperature maxima are from dry sunny days, and volumetric soil moisture measurements (by volume; 0–15 cm depth) were taken in mid-July.

Ruth 1976, Scott et al. 1976), but root growth can be limited by low light levels (Haig et al. 1941). The larger seed of *Abies amabilis* (41 mg) and *Pseudotsuga menziesii* (12 mg) compared to *Tsuga* (1.7 mg) (Schopmeyer 1974) and their deeper rooting habit (Scott et al. 1976, Minore 1979, Zobel and Antos 1991) may give these species an advantage over *Tsuga* in developing adequate root systems in low light environments. Drought mortality of *Tsuga* on the forest floor is common (Christy and Mack 1984), and establishment of *Abies* in deep shade is usually greater than that of *Tsuga* (Thornburgh 1969, Minore 1972, Long 1976). The greater similarity in establishment between wood and litter in gaps than in controls may be due to greater soil moisture content in gaps than in controls (A. N. Gray and T. A. Spies, *unpublished manuscript*). Minore

(1972) also found no difference in seedling survival between wood and litter substrates (or lower survival on wood for some species) in greenhouse studies where moisture levels were kept high.

Drought may also have affected seedling establishment on substrates exposed to high levels of solar radiation in the largest gaps. *Tsuga* and *Abies* establishment on all substrates was lower in the largest gap size than in smaller gaps, with the lowest establishment tending to occur on forest-floor substrates. *Tsuga* seedlings in particular were relatively rare on forest floor in north and center positions of 1.0 gaps. Substrate type affects germination of different sizes of seeds by influencing seed moisture status (Smith 1951, Harper et al. 1965); moisture content in litter in exposed areas can fluctuate greatly, making germination difficult for
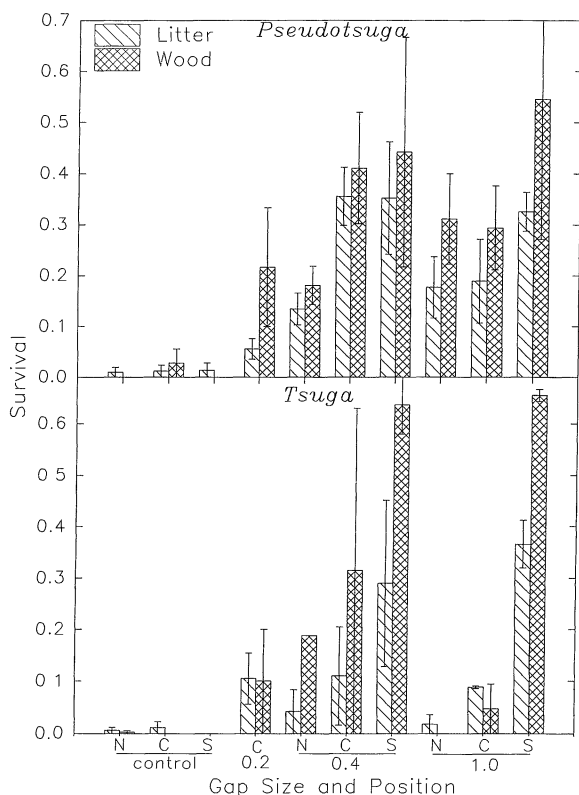
FIG. 4. Survival of natural regeneration (fraction of marked emergents) by substrate type. Data are means and standard errors from all stands for *Pseudotsuga* and old-growth stands for *Tsuga* ($n \leq 4$ or 2, respectively, depending on presence of seedlings). For within-gap position, N = north, C = center, S = south.
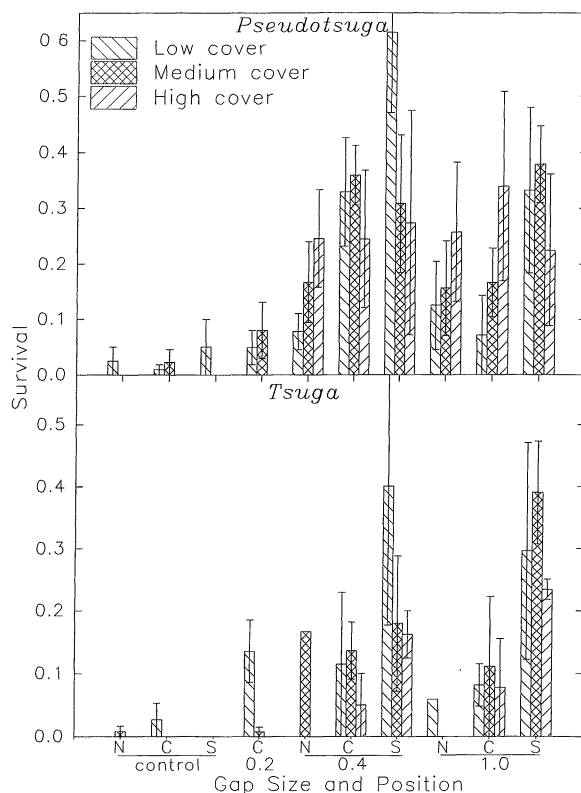
FIG. 5. Survival of natural regeneration (fraction of marked emergents) on forest floor by vegetation cover level, species, gap size, and within-gap position (N = north, C = center, S = south). Data are means and standard errors from all stands for *Pseudotsuga* and old-growth stands for *Tsuga* ($n \leq 4$ or 2, respectively, depending on presence of seedlings).

small-seeded species like *Tsuga* (Haig et al. 1941). For seeds that do germinate, the ability to establish deep roots can be critical to survival, since litter dries out more readily than soil in the open (Hermann and Chilcote 1965, Helgerson 1990). Once dry, litter also gets hotter than mineral soil when exposed to direct sunlight. Heat is often thought to kill seedlings by killing the cambium at ground level (Silen 1960, Helgerson 1990), but little of that type of mortality was noted in this study. Mortality in exposed areas, which was greatest for *Tsuga* and lowest for *Pseudotsuga,* was probably caused by desiccation. High temperatures create greater evaporative demand and greater levels of photorespiration in seedlings (Waring and Schlesinger 1985). *Abies amabilis* and *Tsuga heterophylla* transpire more under stress than *Pseudotsuga menziesii* (Hinckley et al. 1982, Livingston and Black 1988), becoming prone to desiccation, and *Tsuga* also tend to close stomata later in the day than the other species (Livingston and Black 1987).

Survival of naturally regenerated seedlings on the existing natural substrates in the gaps differed substantially from seedling establishment on seed plots in several instances. There was little or no apparent dif-

ference between survival on decayed logs and on forest floor in closed-canopy areas in the natural regeneration study. The relatively high establishment on the wood seed plots may be a result of easy penetration of seedling radicles in the uniformly soft plot surface, and to lack of competition from previously established vegetation. The quality of naturally occurring decayed logs, however, was highly variable, often containing patches of hard outer wood and bark. The suitability of wood for seedling establishment has been found to vary with species, decay class, and log origin (e.g., from standing snag or blowdown) (Thornburgh 1969, Minore 1972, Christy and Mack 1984). In addition, soft areas of decayed logs in this study were often densely occupied by previous cohorts of *Tsuga* seedlings (up to 800 seedlings/m²; Gray 1995) and woody shrubs (e.g., *Vaccinium* spp.), and older (class IV and V) logs were often permeated with roots; all of these factors may have precluded establishment of new seedling cohorts in closed-canopy areas. In gaps, however, survival of natural regeneration on logs tended to be greater than on the forest floor. Greater survival of natural regeneration in gaps compared to controls on both substrates may be caused by a surplus of resources (light

and moisture) in gaps that had not been appropriated by existing vegetation. Greater survival on logs than on forest floor in gaps may have been due to the fact that naturally occurring logs in gaps were relatively unoccupied by roots compared to soil in gaps; decayed logs tend to be occupied by tree roots much more than by non-tree roots (Harvey et al. 1987, Vogt et al. 1995), and conifer root density declines after gap formation (Parsons et al. 1994, Vogt et al. 1995) while understory vegetation density increases.

Although *Pseudotsuga* is often said to require mineral soil to establish (Ruth 1976, Stewart 1978), density of natural regeneration on the forest floor seemed adequate in this study (1 seedling/m²; Gray 1995), even in exposed portions of large gaps. *Pseudotsuga*'s "requirement" for mineral soil may be an exaggeration, or may be sensitive to site conditions and annual weather. Adequate *Pseudotsuga* regeneration on litter in exposed areas has also been reported in other studies (Hermann and Chilcote 1965, Williamson 1973).

Patterns of seedling growth by the end of the second year often differed from patterns of survival on different substrates and in different gap sizes. Seedling size generally increased with gap size, with the largest seedlings of each species found in the 1.0 gap size. The largest seedlings were usually those growing on litter, while those on wood tended to be the smallest. Other studies have also found greater seedling growth on forest floor than on mineral soil (Radwan 1992, Kotar 1972). Low growth rates on wood may be caused by the relatively low nitrogen content of decayed wood (Minore 1972), while high growth rates on litter may be due to mineralization of organic nitrogen in the forest floor. *Pseudotsuga,* which had the greatest reduction in growth on wood, tends to be less tolerant of low nitrogen levels than *Tsuga* (Minore 1979); similar comparisons with *Abies* are not available.

Substrates are important in the gap dynamics of other forest types as well. Logs are important for tree establishment in Appalachian spruce–fir forests (White et al. 1985), tropical forests (Lawton and Putz 1988), and South American temperate forests (Veblen 1985), particularly for pioneer species. Mineral soil is also important for establishment of pioneer or small-seeded species in gaps (Putz 1983, Lawton and Putz 1988, Nakashizuka 1989). The importance of these substrates for tree establishment is often tied to the exclusion of seedlings from the forest floor by dense vegetation (Veblen 1985, Nakashizuka 1989).

The relatively high establishment of shade-tolerant *Abies amabilis* and *Tsuga heterophylla* on forest floor as well as on wood in 0.2 gaps, the most common gap size in Pacific Northwest forests, suggests that the slow occupation of gaps in these forests by saplings (Spies et al. 1990, Lertzman 1992) is not due to lack of appropriate substrates for seedling establishment. Slow occupation of gaps may instead be due to slow seedling growth and subsequent mortality. *Abies* and *Tsuga*

seedling sizes after two years in the 0.2 gaps were small and only slightly greater than seedling sizes in closed-canopy control areas, despite doubled light levels and greater soil moisture (A. N. Gray and T. A. Spies, *unpublished data*). The generally low light levels in these small gaps, caused by the narrow crowns of gap-maker trees and the tall, deep crowns of gap edge trees (Canham et al. 1990), may be the primary cause of slow tree growth and slow gap closure by regenerating trees. This crown and gap geometry suggests that gap effects on light levels (and seedling growth) may be spatially diffuse; a recent study found little relationship between spatial patterns of understory trees and locations of existing canopy gaps in these forests (Van Pelt 1995). Even in forest types that tend to reach gap closure much faster than Douglas-fir forests, shade-tolerant trees usually require relatively large disturbances for tree recruitment (Oliver and Stephens 1977) and need multiple gaps to attain canopy status (White et al. 1985, Runkle and Yetter 1987, Uhl et al. 1988).

Vegetation and understory shade effects

Understory shade inhibited and facilitated seedling establishment in different gap sizes and within-gap positions. Artificial understory shade over the forest floor reduced seedling establishment in closed-canopy areas and 0.4 size gaps, most likely caused by reduced light levels. Shade appeared to aid establishment in 1.0 size gaps, primarily through higher germination rates rather than through greater survival of emerged seedlings. The similarity in survival of emergents among shade treatments in large gaps may have been caused by the high surface temperatures from "sunflecks" penetrating the 5-cm openings in the shade-cloth treatments. The reduction in total light levels under shade apparently reduced seedling growth in all gap sizes.

Shade provided by large logs facilitated seedling survival in exposed portions of large gaps, especially for *Tsuga heterophylla.* Similar effects on natural regeneration of *Tsuga* in exposed locations were noted on north sides of small logs (e.g., 10 cm diameter), old snags, and cut stumps (Gray 1995). Although the zone of enhanced survival on north sides of logs was narrow, a low amount of woody debris could greatly change the species composition in large openings by facilitating establishment of *Tsuga* where it might otherwise not establish. Studies in clearcuts have also found that shade by coarse woody debris and stumps enhances seedling survival, often more effectively than shade from live vegetation (Isaac 1943, Thornburgh 1969, Minore 1986).

Understory vegetation creates shaded microsites on the forest floor, but may locally deplete soil moisture and nutrients as well. *Pseudotsuga* establishment in relation to understory vegetation cover was similar to establishment in relation to dead shade: establishment tended to decrease with increasing cover in closed-canopy areas, 0.2 size gaps, and shaded portions of

large gaps, and tended to increase with increasing cover in exposed portions of larger gaps. Facilitation of seedling establishment by vegetation in exposed areas has previously been noted anecdotally for *Pseudotsuga* (Isaac 1943) and *Abies* (Thornburgh 1969). Establishment of *Tsuga* seedlings apparently was not increased by shade of vegetation: establishment tended to decline with increasing cover regardless of gap size or within-gap position. Indeed, Harmon and Franklin (1989) found that understory vegetation in closed-canopy areas of *Picea sitchensis*-dominated coastal forests was the primary cause for the lack of *Tsuga* establishment on the forest floor. Although *Tsuga* survival was reduced by vegetation cover in gaps in this study, densities under high cover in southern portions of large gaps were still >40 seedlings/m² (Gray 1995). However, gaps in some forests in the Oregon Coast Range have no more *Tsuga* seedlings than do closed-canopy areas (Holah 1991), possibly a result of the generally greater shrub cover or the different assemblage of understory species compared to forests in the Cascade Range (Spies and Franklin 1991).

Microsite heterogeneity and gap dynamics

Although the importance of microsite heterogeneity for plant establishment in gaps has been recognized (Orians 1982, Denslow 1987, Veblen 1989), this is the first study that systematically examines the process of seedling establishment in different microsites over a range of gap sizes. Many interactions, or potential interactions, were found among species, substrates, coarse woody debris, vegetation cover, gap size, and within-gap position. In the face of such complexity, it is natural to ask whether microsite heterogeneity is simply "noise" that is "averaged out" at greater scales (e.g., gap), or whether there is variation in the linkage between micro- and macro-scale features (Baker 1989); that is, do micro-scale features matter more in some gaps than in others? Definitive answers to this question require study of a much larger portion of the tree life cycle than that covered in this paper. Nevertheless, results from the early stages of establishment provide several insights concerning the importance of heterogeneity for different species.

Establishment of *Tsuga heterophylla* appears to be quite sensitive to microsite heterogeneity on a scale of ~10 cm or less; the relative importance varies with gap size. Logs, often of a single species in a particular stage of decay (*Pseudotsuga,* class III or IV) are important for successful establishment of *Tsuga* seedlings (Christy and Mack 1984). Indeed, most *Tsuga* saplings in mature forests are found on wood or organic "skirts" of bark and litter that accumulate around *Pseudotsuga* stems, and many adult *Tsuga* are stilt-rooted, suggesting establishment on logs or windthrow mounds (A. N. Gray, *personal observation*). Logs on the forest floor also provide shaded microsites for *Tsuga* establishment in exposed areas within large openings. Although es-

tablishment is frequent on the forest floor in shaded portions of gaps, the negative effect of vegetation cover suggests that woody microsites may still be important in many forests. Thus previous establishment, mortality, and decay of *Pseudotsuga* could be important for the establishment of *Tsuga* in mature stands. Mature forests with little decayed wood or with large openings lacking dead shade may also have low establishment of *Tsuga.*

Establishment of *Pseudotsuga menziesii* appears to be much less sensitive to microsite heterogeneity than establishment of *Tsuga heterophylla. Pseudotsuga* was able to germinate regardless of light levels, its survival was similar regardless of substrate, and although sensitive to understory cover, its establishment in gaps was plentiful even in stands with high densities of understory vegetation. Establishment of *Pseudotsuga* does appear to be limited by exposure on the forest floor, however, and benefits from shade by woody debris, understory vegetation, or residual trees in large openings (Fig. 3; Franklin 1963, Minore 1986). Sensitivity of *Abies amabilis* establishment to a broad range of microsite types is unclear because of a lack of natural regeneration in the gaps, but *Abies* appears to be relatively insensitive to substrate, able to establish in closed-canopy areas, and more sensitive to exposure than *Pseudotsuga.* Species' sensitivities to microsite heterogeneity may be closely tied to seed size; *Tsuga,* with the smallest seed, is most prone to desiccation prior to germination and has the fewest carbohydrate reserves to expand its initial roots or leaves into favorable environments.

Since the process of seedling establishment begins with the arrival of seed in a microsite, the abundance of seed-producing adults in a landscape can dramatically affect species establishment in gaps. Very few *Tsuga* or *Abies* established naturally in otherwise suitable gaps in the mature stands of this study because of a lack of seed. Since none of the principal tree species in the Pacific Northwest have seed banks in the soil (Isaac 1935, Ingersoll and Wilson 1990), the timing of seed production can be important as well. The results for natural regeneration in this study may have differed if copious seed crops of *Tsuga heterophylla* and *Pseudotsuga menziesii* had not been shed one year after gap formation. The dramatic increase in understory cover and the decrease in soil moisture with time since gap formation (A. N. Gray and T. A. Spies, *unpublished data*) suggests that the abundance of suitable regeneration microsites decreases with time since disturbance; favorable timing of establishment of less competitive species can overwhelm another species' competitive superiority (Harper 1977). *Tsuga,* which appears to be most sensitive to understory competition and moisture, usually produces at least some seed every year, which is probably an advantage for early arrival in suitable microsites. *Pseudotsuga* and *Abies,* on the other hand, shed seed in mast years, often separated

by 3–5 yr intervals (Schopmeyer 1974); the larger seed of these species compared to *Tsuga* may confer an advantage for establishing on less than ideal microsites. Low abundance of suitable microsites may not be critical, however, if large seed crops ensure that at least some seed disperse to suitable microsites. Thus, seed size and the abundance and timing of seed dispersal could greatly influence species composition in gaps.

Microsite heterogeneity has important implications for the gap-partitioning hypothesis, which is usually cast in terms of coarser scale (>2 m) environmental gradients than those associated with seedling regeneration microsites (<10 cm). Rather than simply modifying the effect of gap size and within-gap gradients, microsite heterogeneity appears to allow species to transcend the constraints of those environments. Given a forest with sufficient heterogeneity, *Tsuga heterophylla* is able to establish in dense closed-canopy forest as well as in large openings prone to environmental extremes. The gap-partitioning hypothesis is based on niche separation among species along resource gradients at a particular spatial scale, but it may be too simple or too limited in scale to capture the many variables affecting seedling establishment. The gap-partitioning hypothesis may be a restricted case of regeneration niche theory. Resources and microclimate could be considered the primary factors in niche partitioning; both gaps and microsites are structural "filters" determining resource patterns at different spatial scales. While many studies have found predictable differences in seedling and sapling species composition with gap size and position (Minckler and Woerhide 1965, Runkle 1982, Brandani et al. 1988, Poulson and Platt 1989, Phillips and Shure 1990), several others have not (Ehrenfeld 1980, Denslow 1987, Uhl et al. 1988, Nakashizuka 1989, Spies et al. 1990). Under the concept of regeneration niche (Grubb 1977), which has no implicit spatial scale, species response to general resource levels is a single trait that must be considered in concert with timing and amount of seed production, seed size, seed dispersal, specific environmental requirements for germination, suitability of different substrates, effects of timing and severity of weather, susceptibility to predation, and effects of specific species of neighboring plants. The interaction of microsite heterogeneity with these species-specific characteristics provides a wide array of potential outcomes for species establishment in canopy gaps that seldom fit into the one or two-dimensional categorizations of environment implicit in the gap-partitioning hypothesis.

LITERATURE CITED

Agee, J. K., and M. H. Huff. 1987. Fuel succession in a western hemlock/Douglas-fir forest. Canadian Journal of Forest Research 17:697–704.

Alaback, P. B., and J. C. Tappeiner II. 1991. Response of western hemlock (*Tsuga heterophylla*) and early huckleberry (*Vaccinium ovalifolium*) seedlings to forest windthrow. Canadian Journal of Forest Research 21:534–539.

Allen, T. F. H., and T. W. Hoekstra. 1992. Toward a unified ecology. Columbia University Press, New York, New York, USA.

Baker, W. L. 1989. Macro- and micro-scale influences on riparian vegetation in western Colorado. Annals of the Association of American Geographers 79(1):65–78.

Brandani, A., G. S. Hartshorn, and G. H. Orians. 1988. Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. Journal of Tropical Ecology 4: 99–119.

Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20:620–631.

Christy, E. J., and R. N. Mack. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. Journal of Ecology 72:75–91.

Denslow, J. D. 1980. Gap partitioning among tropical rainforest trees. Biotropica 12(supplement):47–55.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18: 431–451.

Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54:57–69.

Ehrenfeld, J. G. 1980. Understory response to canopy gaps of varying size in a mature oak forest. Bulletin of the Torrey Botanical Club 107:29–41.

FEMAT (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic, and social assessment. USDA Forest Service Pacific Northwest Region, Portland, Oregon, USA.

Franklin, J. F. 1963. Natural regeneration of Douglas-fir and associated species using modified clear-cutting systems in the Oregon Cascades. USDA Forest Service Pacific Northwest Research Station Research Paper **PNW-3**.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Pacific Northwest Research Station General Technical Report **PNW-8**.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore, Maryland, USA.

Gray, A. N. 1995. Tree seedling establishment on heterogenous microsites in Douglas-fir forest canopy gaps. Thesis, Oregon State University, Corvallis, Oregon, USA.

Gray, A. N., and T. A. Spies. 1995. Water content measurement in forest soils and decayed wood using time domain reflectometry. Canadian Journal of Forest Research 25(3): 376–385.

Gray, A. N., and T. A. Spies. 1996. Gap size, within-gap position, and canopy structure effects on seedling establishment of conifer species in forest canopy gaps. Journal of Ecology 84(5):635–645.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review 52:107–145.

Haig, I. T., K. P. Davis, and R. H. Weidman. 1941. Natural regeneration in the western white pine type. USDA Technical Bulletin 767.

Halpern, C. B., and J. F. Franklin. 1990. Physiognomic de-

velopment of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. Journal of Vegetation Science 1:472–482.

Harmon, M. E. 1987. The influence of litter and humus accumulations and canopy openness on *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. seedlings growing on logs. Canadian Journal of Forest Research 17:1475–1479.

Harmon, M. E., and J. F. Franklin. 1989. Tree seedlings on logs in *Picea–Tsuga* forests of Oregon and Washington. Ecology 70:48–59.

Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.

Harper, J. L., J. T. Williams, and G. R. Sagar. 1965. The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. Journal of Ecology 53:273–286.

Harvey, A. E., M. F. Jurgesen, M. J. Larsen, and R. T. Graham. 1987. Relationships among soil microsite, ectomycorrhizae, and natural conifer regeneration of old-growth forests in western Montana. Canadian Journal of Forest Research 17:58–62.

Helgerson, O. T. 1990. Heat damage in tree seedlings and its prevention. New Forests 3:333–358.

Hermann, R. K., and W. W. Chilcote. 1965. Effect of seedbeds on germination and survival of Douglas-fir. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.

Hinckley, T. M., R. O. Teskey, R. H. Waring, and Y. Morikawa. 1982. The water relations of true firs. Pages 85–92 in C. D. Oliver and R. M. Kenady, editors. Proceedings of the Biology and Management of True Fir in the Pacific Northwest Symposium. College of Forest Resources, University of Washington, Seattle, Washington, USA.

Holah, J. C. 1991. Effects of *Phelinus weirii* on plant community composition and succession of mature and old-growth Douglas-fir forests. Thesis. Oregon State University, Corvallis, Oregon, USA.

Huynh, H., and L. S. Feldt. 1970. Conditions under which mean square ratios in repeated measurements designs have exact *F*-distributions. Journal of the American Statistical Association 65:1582–1589.

Ingersoll, C. A., and M. V. Wilson. 1990. Buried propagules in an old-growth forest and their response to experimental disturbances. Canadian Journal of Botany 68:1156–1162.

Isaac, L. A. 1935. Life of Douglas-fir seed in the forest floor. Journal of Forestry 33:61–66.

———. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Foundation, Washington, D.C., USA.

Isaac, L. A., and G. S. Meagher. 1936. Natural reproduction on the Tillamook Burn two years after the fire. USDA Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.

Kotar, J. 1972. Ecology of *Abies amabilis* in relation to its altitudinal distribution and in contrast to its common associate *Tsuga heterophylla*. Dissertation. University of Washington, Seattle, Washington, USA.

Lawrence, W. H., and J. H. Rediske. 1962. Fate of sown Douglas-fir seed. Forest Science 8:210–218.

Lawton, R. O., and F. E. Putz. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology 69:764–777.

Lertzman, K. P. 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. Ecology 73:657–669.

Livingston, N. J., and T. A. Black. 1987. Stomatal characteristics and transpiration of three species of conifer seed-

lings planted on a high elevation south-facing clear-cut. Canadian Journal of Forest Research 17:1273–1282.

Livingston, N. J., and T. A. Black. 1988. The growth and water use of three species of conifer seedlings planted on a high elevation south-facing clear-cut. Canadian Journal of Forest Research 18:1234–1242.

Long, J. N. 1976. Forest vegetation dynamics within the *Abies amabilis* zone of a western Cascades watershed. Dissertation. University of Washington, Seattle, Washington, USA.

Lorimer, C. G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. Ecology 70:565–567.

Maser, C., R. G. Anderson, K. Cromack, Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Pages 78–95 in J. W. Thomas, editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service, Washington, D.C., USA.

McComb, W. C., T. A. Spies, and W. H. Emmingham. 1993. Douglas-fir forests: managing for timber and mature-forest habitat. Journal of Forestry 91:31–42.

Milliken, G. A., and D. E. Johnson. 1984. Analysis of messy data. Volume 1. Designed experiments. Van Nostrand Reinhold, New York, New York, USA.

Minckler, L. S., and J. D. Woerhide. 1965. Reproduction of hardwoods 10 years after cutting as affected by site and opening size. Journal of Forestry 63:103–107.

Minore, D. 1972. Germination and early growth of coastal tree species on organic seed beds. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Research Paper PNW-135.

———. 1979. Comparative autecological characteristics of northwestern tree species: a literature review. USDA Forest Service Pacific Northwest Forest and Range Experiment Station General Technical Report PNW-87.

———. 1986. Germination, survival, and early growth of conifer seedlings in two habitat types. Pacific Northwest Research Station, Portland, Oregon. USDA Forest Service Research Paper PNW-348.

Nakashizuka, T. 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology 70:1273–1278.

Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed-species forest in central New England. Ecology 58:562–572.

Orians, G. H. 1982. The influence of tree-falls in tropical forests in tree species richness. Tropical Ecology 23:255–279.

Overhulser, D. L. 1990. Cutworms: Noctuidae. Pages 46–47 in P. B. Hamm, S. J. Campbell, and E. M. Hansen, editors. Growing healthy seedlings: identification and management of pests in northwest forest nurseries. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.

Parsons, W. F. J., D. H. Knight, and S. L. Miller. 1994. Root gap dynamics in lodgepole pine forest: nitrogen transformations in gaps of different size. Ecological Applications 4:354–362.

Phillips, D. L., and D. J. Shure. 1990. Patch-size effects on early succession in southern Appalachian forests. Ecology 71:204–212.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms, and pathways of succession. Botanical Review 53:335–371.

Pickett, S. T. A., and P. S. White. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3–13 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Platt, W. J., and D. R. Strong. 1989. Gaps in forest ecology. Ecology 70:535.

Poulson, T. L., and W. J. Platt. 1989. Gap light regimes influence canopy tree diversity. Ecology **70**:553–555.

Putz, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology **64**:1069–1074.

Radwan, M. A. 1992. Effect of forest floor on growth and nutrition of Douglas-fir and western hemlock seedlings with and without fertilizer. Canadian Journal of Forest Research **22**:1222–1229.

Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. American Naturalist **111**: 376–381.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology **63**:1533–1546.

———. 1990. Gap dynamics in an Ohio *Acer–Fagus* forest and speculations on the geography of disturbance. Canadian Journal of Forest Research **20**:632–641.

Runkle, J. R., and T. C. Yetter. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. Ecology **68**:417–424.

Ruth, R. H. 1976. Harvest cuttings and regeneration in young-growth western hemlock. Pages 41–74 *in* A. B. Berg, editor. Managing young forests in the Douglas-fir region. School of Forestry, Oregon State University, Corvallis, Oregon, USA.

SAS Institute. 1987. SAS/STAT guide for personal computers. Version 6 edition. SAS Institute, Incorporated, Cary, North Carolina, USA.

Schopmeyer, C. S., technical coordinator. 1974. Seeds of woody plants in the United States. Agriculture handbook 450. USDA, Washington, D.C., USA.

Scott, D. R. M., J. N. Long, and J. Kotar. 1976. Comparative ecological behavior of western hemlock in the Washington Cascades. Pages 26–33 *in* W. A. Atkinson and R. J. Zasoski, editors. Western hemlock management. College of Forest Resources, University of Washington, Seattle, Washington, USA.

Shaw, R. G., and T. Mitchell-Olds. 1993. ANOVA for unbalanced data: an overview. Ecology **74**:1638–1645.

Silen, R. R. 1960. Lethal surface temperatures and their interpretation for Douglas-fir. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Smith, D. M. 1951. The influence of seedbed conditions on the regeneration of eastern white pine. Connecticut Agricultural Experiment Station Bulletin **545**.

Spies, T. A., and J. F. Franklin. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology **70**:543–545.

Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests. Pages 91–110 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-GTR-285**.

Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research **20**:649–658.

Spies, T. A., J. Tappeiner II, J. Pojar, and D. Coates. 1991. Trends in ecosystem management at the stand level. Pages 628–639 *in* Transactions of the 56th North American Wildlife and Natural Resources Conference.

Stewart, G. H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Canadian Journal of Forest Research **16**: 558–568.

Stewart, R. E. 1978. Site preparation. Pages 99–129 *in* B. D. Cleary, R. D. Greaves, and R. K. Hermann, editors. Regenerating Oregon's forests. Oregon State University Extension Service, Corvallis, Oregon, USA.

Thornburgh, D. A. 1969. Dynamics of the true fir-hemlock forests of the west slope of the Washington Cascade Range. Dissertation. University of Washington, Seattle, Washington, USA.

Uhl, C., K. Clark, N. Dezzeo, and P. Maquirino. 1988. Vegetation dynamics in Amazonian treefall gaps. Ecology **69**: 751–763.

Van Pelt, R. 1995. Understory tree response to canopy gaps in old-growth Douglas-fir forests of the Pacific Northwest. Dissertation. University of Washington, Seattle, Washington, USA.

Veblen, T. T. 1985. Forest development in tree-fall gaps in the temperate rain forests of Chile. National Geographic Reports Spring 1985:162–183.

———. 1989. Tree regeneration responses to gaps along a transandean gradient. Ecology **70**:541–543.

Vogt, K. A., D. J. Vogt, H. Asbjornsen, and R. A. Dahlgren. 1995. Roots, nutrients and their relationship to spatial patterns. Plant and Soil **168–169**:113–123.

Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, Orlando, Florida, USA.

White, P. S., M. D. MacKenzie, and R. T. Busing. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce–fir forests. Canadian Journal of Forest Research **15**:233–240.

Williamson, R. L. 1973. Results of shelterwood harvesting of Douglas-fir in the Cascades of western Oregon. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Research Paper **PNW-161**.

———. 1976. Natural regeneration of western hemlock. Pages 26–33 *in* W. A. Atkinson and R. J. Zasoski, editors. Western hemlock management. College of Forest Resources, University of Washington, Seattle, Washington, USA.

Wilson, M. V. 1991. Age structure patterns in *Abies amabilis* stands of the Cascade Mountains. American Midland Naturalist **125**:331–339.

Zobel, D. B., and J. A. Antos. 1991. Growth and development of natural seedlings of *Abies* and *Tsuga* in old-growth forest. Journal of Ecology **79**:985–998.