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TREE SEEDLINGS ON LOGS IN *PICEA-TSUGA* FORESTS OF OREGON AND WASHINGTON¹

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Abstract. Logs are the major seedbed for trees in coastal *Picea sitchensis*–*Tsuga heterophylla* forests. Field experiments were conducted at Cascade Head, Oregon, and Hoh River, Washington, to examine pathogens, predation, competition, and standing water as causes for this close seedling–log association.

More seedlings survived on log blocks than on soil blocks, regardless of whether the blocks were raised or placed flush with the soil surface. Standing water was therefore an unlikely cause of the seedling–log association. Comparisons of plots protected from and exposed to predation revealed that predation was minor and of equal intensity on soils and logs. Sterilizing soils did not consistently increase seedling survival above controls. Clearing ground-layer vegetation from soil plots significantly increased the survival of conifer seedlings compared with that on uncleared soils. The seed penetration rates through moss mats indicated that <1% of the seedlings germinated within moss mats.

Competition with herbs and mosses on the forest floor therefore appears to be responsible for the disproportionate number of tree seedlings found on logs. Recently fallen logs represent sites where competition is low enough for tree seedling recruitment within many *Picea*–*Tsuga* forests.

Key words: bryophytes; competition; logs; nurse logs; Pacific Northwest; regeneration; seedbeds; seedlings; temperate rain forest.

INTRODUCTION

Far from being uniform, forest floors are a mosaic of microsites with differing rates of plant growth, survival, and reproductive output (Harper 1977, Whitaker and Levin 1977). Common forest microsites include pits and mounds associated with windthrown trees (Hutnik 1952, Beatty 1984), rotten wood (Harmon et al. 1986, Scott and Murphy 1987), light gaps (Runkle 1981), as well as variations in soil depth (McVaugh 1943, Bratton 1976), depth to the water table (Menges and Waller 1983, Huenneke and Sharitz 1986), and litter depth (Sydes and Grime 1981, Knapp and Smith 1982). Differential survival of tree seedlings in microsites can influence the composition and spatial pattern of forests. The cause of these patterns may not be readily apparent, however, because the environmental scale of seedlings and trees differs markedly. Understory plants, for example, rarely outcompete mature trees, but may shade and outcompete young seedlings (Shirley 1945, Maguire and Forman 1983). An interesting example of the effect of microsites on spatial pattern occurs in the Pacific Northwest, where tree

seedlings are often restricted to logs (Franklin and Dyrness 1973). The close link between tree seedlings and logs in some forests in this region indicates that tree recruitment may be limited by the areal extent of logs (Harmon 1988). Our study was designed to test the causes of this pattern through field and laboratory experiments.

When tree seedlings become established on the surface of a fallen dead tree, a nurse log develops. Nurse logs are found in many forests throughout North America, but perhaps are most abundant in the *Picea sitchensis* zone of the Pacific Northwest (Harmon et al. 1986). Nurse logs and stilt-rooted trees (often formed when logs or stumps completely decompose from beneath established trees) are conspicuous components of these forests (Sharpe 1956). McKee et al. (1982) estimate that 88–97% of the tree seedlings in alluvial *Picea sitchensis*–*Tsuga heterophylla* forests in Olympic National Park, Washington, grow on logs. This proportion is remarkable because only 6–11% of the ground surface in these forests is covered by logs (Graham and Cromack 1982).

Many hypotheses have been proposed for the preponderance of tree seedlings growing on logs in *Picea*–*Tsuga* forests. Sharpe (1956) felt that tree seedlings

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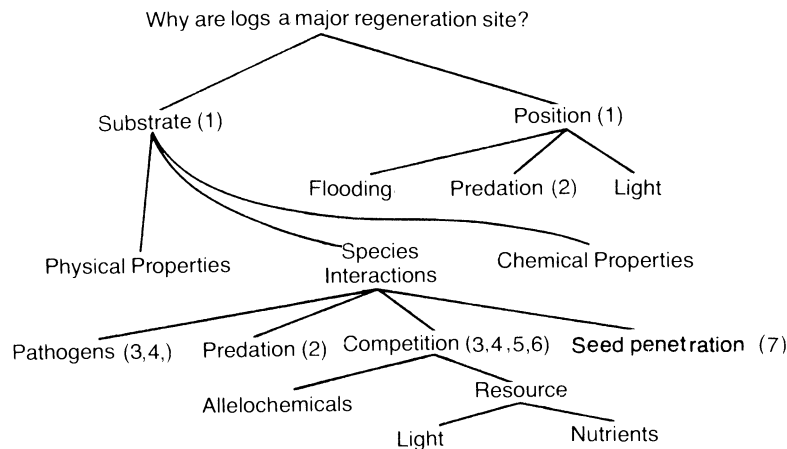


FIG. 1. Flowchart of hypotheses explored during the study of tree-seedling establishment on log substrates in *Picea-Tsuga* forests. The numbers next to each hypothesis indicate the relevant experiments.

growing on logs were subject to less moss and herb competition. McKee et al. (1982) hypothesized that soil pathogens or excessively long periods of standing water excluded seedlings from the soil. The importance of standing water was also emphasized by Graham and Cromack (1982). Minore (1972) hypothesized that logs, with their deep accumulations of litter and duff, might have better nutrient availability than soils. Quayle (1982) felt the soil was too poor in Mg and P to support the growth of *Picea* and *Tsuga* seedlings beyond the first few years. The nutrient deficiency hypothesis seems unlikely given that wood, even when rotten, is low in nutrients (Harmon et al. 1986). Christy and Mack (1984) hypothesized that 1st-yr seedlings growing on soils in *Pseudotsuga menziesii-Tsuga heterophylla* forests were buried by litter. Logs were safe sites because they sloughed litter; however, surfaces that slough litter are also poor in retaining seeds (Harmon 1986). This indicates that the litter-sloughing hypothesis is unlikely. Logs may also be safe sites in terms of seed and seedling predation. Leslie (1982) found that 19–44% of the diet of Roosevelt elk (*Cervus canadensis* var. *roosevelti*) was composed of *Tsuga*, and seedlings growing in elevated positions on logs might escape browsing. Although ungulates kill tree seedlings, the seedling-log linkage seems to develop when seedlings are too small to be browsed. Allelochemicals released by ground vegetation might also restrict seedlings to logs. del Moral and Cates (1971) state that many species occurring in the Pacific Northwest are potentially allelopathic. We feel this hypothesis is also unlikely given that vegetation of logs and the forest floor in these forests is quite similar (Sharpe 1956). Thus, of the major hypotheses offered to explain this phenomenon, competition, standing water, and pathogens would appear to be the most likely.

The purpose of our study was to identify the major factors deterring establishment of tree seedlings on the forest floor in *Picea-Tsuga* forests in Washington and Oregon. Because of the many possible explanations for

the strong relation between tree seedlings and logs in *Picea-Tsuga* forests, we thought it best to proceed from general to specific hypotheses (Fig. 1). Seven experiments were conducted during 2 yr. The broadest hypothesis was that the substrate quality differed between logs and soils in a characteristic such as vegetative cover. Because logs are above the soil, we posed an alternative hypothesis that substrate position might cause differences in seedling survival. Within each general hypothesis were a number of subhypotheses; for example, position effects could be caused by differences in standing water, light, or predation. Substrate quality differences might be caused by chemical or physical properties or by species interactions such as amensalism (one population is inhibited, but the other is not affected), competition, pathogens, or predation. Once the effects of position and substrate quality differences were assessed, experiments were designed to test the most likely of the subhypotheses.

STUDY AREAS

Hoh River

The Hoh River experimental site is located in Olympic National Park, Washington (47°50' N, 123°53' W). The climate is mild and extremely wet. Annual average precipitation is 320 cm at the Hoh River Ranger Station, with mean, maximum, and minimum temperatures of 10°, 36°, and -11°C, respectively.

In Olympic National Park, forests dominated by *Picea* and *Tsuga* occur on old river terraces in the Quinalt, Queets, Hoh, and Bogachiel River Valleys (Franklin and Dyrness 1973). The outstanding features of these forests are (1) a tall, open canopy layer often taller than 80 m; (2) dominance by large *Picea* and *Tsuga*; (3) large aboveground biomass (640–810 Mg/ha); and (4) low tree densities (64 to 142 trees/ha) (Fonda 1974, McKee et al. 1982). Other notable features include abundant nurse logs and related phenom-

ena (e.g., stilt-rooted trees), luxurious cover of bryophytes and herbs on the forest floor, and an abundance of epiphytic bryophytes and pteridophytes.

Soils of the area are fluvial in origin (Fonda 1974, McCreary 1975). The Queets series occurs on older terraces, and the Hoh series is found on lower, younger terraces. Soils of the Queets series are strongly acidic, of silt-loam texture, and moderately well drained with a winter water table 1–2 m below the surface. The soils of the Hoh series are well drained, have a silt-loam to fine sandy texture, and are strongly acidic. The water table in the Hoh series tends to be slightly shallower than that in the Queets series at 1.3–1.6 m below the surface during winter. Tree roots penetrate to depths > 1.5 m in both soil series.

The 0.5-ha experimental plot at the Hoh River was at 150 m elevation on an upper terrace (equivalent to Fonda's [1974] level 4) in a mature *Picea-Tsuga* forest. We selected this area because it was representative of forests in which tree seedlings seemed to be restricted to logs. Charcoal found near the site indicated that the stand had originated after fire > 300 yr ago. Tree basal area was 65.7 m²/ha and was composed of *Tsuga* (51%), *Picea* (38%), and *Pseudotsuga* (11%). Total tree density was 346 trees/ha that were > 1 cm diameter at breast height (dbh); 62% were *Picea* and 37% were *Tsuga*. Herb, bryophyte, and shrub cover were 49, 52, and 14%, respectively (Harmon 1986). Logs covered 9% and undisturbed soil covered 82% of the forest floor. Soil disturbed by root throw covered 8% of the plot, but only 0.8% of the soil was bare (Harmon 1986). The maximum and minimum water table depths within the experimental plot were measured biweekly to monthly from summer 1981 to summer 1982 using three wells (Minore 1969). The water table did not rise into the wells in 1982 or 1983, which indicated that the water table was at least 1 m below the surface (Harmon 1986).

Cascade Head

The second experimental site was in the Cascade Head Experimental Forest near Otis, Lincoln County, Oregon (45°03' N, 123°59' W). The climate at this site is also wet and mild. Mean annual precipitation at the Experimental Forest headquarters (13.5 km northwest of the experimental plot) is 232 cm. Mean, maximum, and minimum temperatures of 10°, 21°, and –7° were recorded between October 1981 and October 1982 in the experimental plot. The forests at Cascade Head are also dominated by *Picea* and *Tsuga* and developed after a catastrophic fire in the 1840s (Morris 1934). Unlike the alluvial forests at Hoh River, Cascade Head forests grow on an extremely dissected basaltic headland adjacent to the Pacific Ocean. The soils of the area are unclassified but have been described by Franklin et al. (1968) as strongly acidic, of silt-loam to silty clay-loam texture, moderately well drained, with a high cation exchange capacity, and high nitrogen and or-

ganic matter content. Tree roots rarely penetrate > 1 m in most soils.

The 0.5-ha experimental plot at Cascade Head was near a ridgetop on a west-facing and slightly convex surface. We selected this area because it represented areas where tree seedlings were restricted to logs. The plot had a gradient of 20% at 400 m in elevation and was ≈ 0.6 km from the ocean. Tree density (trees > 1 cm dbh) was 226 trees/ha; 79% were *Tsuga* and the remainder *Picea*. Total basal area was 104 m²/ha, of which 83% was *Tsuga*. Bryophyte, herb, and shrub cover were 43, 58, and 22%, respectively. Logs, undisturbed soil, and soil disturbed by root throw covered 6, 87, and 7% of the forest floor, respectively. Ground-water fluctuations were observed at this site in four wells similar to those used at Hoh River. The water table was often near the surface during fall, winter, and early spring, but not when seeds germinated (Harmon 1986).

METHODS

Experiment 1: Substrate vs. position

Logs and soils differ in two basic ways, position and substrate. Position effects cause differences in seedling survival because logs usually lie above the soil surface. Substrate effects cause higher survival on logs because of inherent differences in factors such as bulk density, nutrient content, and vegetative cover. In experiment 1, we examined the degree to which position and substrate affected seedling abundance on logs.

At Hoh River, reciprocal transplants of soil and logs were used to test the effects of substrate and position. Four treatments were used: (1) soil left at the ground level, (2) log placed at ground level, (3) log left on logs, and (4) soil placed on logs. We used a completely randomized factorial design with two types of substrate, two levels of position, four species of seedlings, and five replicates. Each experimental log was chosen randomly after a complete log inventory. Only logs in decay classes II–V (Graham and Cromack 1982) were used. The position of an experimental unit on a selected log was determined randomly. Soil treatment units were selected by randomly choosing *X* and *Y* coordinates in the 50 × 100 m plot. The experimental units were circular sections of soil or log, 45 cm in diameter and 15 cm thick. Each unit was removed intact by sliding a board underneath before moving the unit. Soil and log pieces left in their original positions were removed in the same way as transplanted pieces and then replaced, to control for effects of handling. To reduce the number of seeds and seedlings eaten by small animals, a wire-screen collar (12-mm mesh) was placed around each plot 15 cm below the soil surface, and a wire cone was placed over each plot. During November 1981, 100 seeds were scattered on the surface of each experimental plot. Seeds of one of the following four species were placed in each plot: *Picea*, *Pseudotsuga*, *Tsuga*,

and *Thuja plicata*. Live and dead seedlings were counted on each plot on 28 June 1982 and on 25 March 1983. These counts were adjusted for the presence of naturally recruited seedlings. The dependent variable for the analysis of variance tests was the angularly transformed percentage of seeds that germinated and survived to a given date. In these and all subsequent experiments, the results were considered significant if $.01 < P < .05$ and highly significant if $P < .01$.

At Cascade Head, the reciprocal transplant approach was not used, but pieces of logs were placed at ground level to compare with plots of soil left at ground level. The soil plots were removed and replaced as at Hoh River to control for effects of handling. The design was otherwise similar to the Hoh River design, but with seeding during January 1982. The experimental design was a completely randomized factorial with two substrates, four species, and five replicates. Seedlings were counted on 1 July 1982 and 29 January 1983.

Experiment 2: Predation

Predation of seeds and seedlings was examined on undisturbed substrate at both sites. Unprotected plots, similar in size and shape to those of experiment 1, were compared with protected plots. Because the mesh size was 12 mm, insects could enter protected plots. At Cascade Head, protected and unprotected soil plots were compared; at Hoh River both substrates were compared. The methods used to place the plots and the seeds were the same as those used in experiment 1. At Cascade Head, the experimental design was a completely randomized factorial with two levels of protection, four species, and five replicates of each. At Hoh River, the completely randomized factorial design had two levels of protection, two substrates, four species, and five replicates of each. Surviving seedlings were counted on 28 June 1982 and 25 March 1983 at Hoh River and on 1 July 1982 and 29 January 1983 at Cascade Head.

Experiment 3: Soil pathogens vs. competition

Our first field experiment on soil pathogens vs. competition was done at both Cascade Head and Hoh River; it compared seedling survival on sterilized-cleared, unsterilized-cleared, and unsterilized-uncleared plots. A complete, randomized factorial design was used with three levels of sterilization-clearing treatment, four species, and five replicates. During March 1982, 15 cm of soil from 20 randomly selected, 45 cm diameter plots was removed intact at each site and placed in plastic bags. Methyl bromide was injected into each soil block twice over 24 h at 6 g/kg dry soil. Methyl bromide is most effective when soils are at least 5°C and wetted to field capacity, conditions that prevailed during the sterilization process. After fumigation, blocks were aired for 24 h, then replaced in their original positions and protected from predation by a wire-cloth collar and cone. Before the seeds were scattered on the

soil surface in March, the vegetation, which had been killed by fumigation, was removed. To assess the effect of competition at both sites, soil plots similar to those used in experiment 1 were cleared of surface vegetation. The plots were periodically cleared of vegetation. During July 1983, a modified version of this experiment was done at Cascade Head by comparing the number of naturally occurring *Tsuga* seedlings found in cleared plots with the number on adjacent, uncleared plots. The experimental design of this modification was a randomized complete block with two levels of clearing treatment and 12 blocks.

The second field experiment on pathogens and competition was done at Hoh River; we used a split-plot version of a randomized complete block design, with the comparison of sterilized-cleared, unsterilized-cleared, and unsterilized-uncleared effects as the main plot treatment and two species as the subplot treatment. Ten blocks were randomly located along a 100-m transect within the experimental site. At each location, a 40 × 70 cm plot was divided into three treatments: (1) a control with no clearing or sterilization, (2) an unsterilized area that had the surface vegetation removed, and (3) a sterilized area with the surface vegetation removed. The sterilization procedure followed the methods described above, except that fumigation was done the first week of July 1982. Each of the sterilization-clearing treatments was divided in half, and 20 seeds of *Picea* or *Pseudotsuga* were planted in a randomly chosen half. Stratified seeds were planted in July 1982. Seedlings were watered every 3 d during the first 2 wk of the experiment. Each block was protected from predation by a cage of 6-mm wire mesh. Seedlings were counted periodically in 1982 and 1983.

Experiment 4: Soil pathogens and shading

In experiment 4, the effects of sterilization and shading on seedlings were investigated by using a growth chamber. The experimental design was a completely randomized factorial with two levels of sterilization, three levels of shading, and three replicates of each treatment. The top 5 cm of mineral soil was removed from three locations near the Hoh River experimental plot. This soil was thoroughly mixed, screened, and placed into 10 × 10 × 10 cm plastic pots. One-half of the pots were randomly selected and sterilized by means of steam pasteurization twice for 1 h during a 24-h period. Nylon shade screens that removed 50 and 75% of the light were placed over some of the pots. This gave photosynthetically active radiation (PAR) quantum flux densities of 50, 25, and 12.5 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; these values correspond to 2.5, 1.2, and 0.6% of full sunlight on a clear day, respectively (Cambell 1977: 47). Screens were placed over both sterilized and unsterilized pots. Twenty *Picea* seeds were planted in each of the pots. Growth chamber conditions were a 12-h day length, 20° day temperature, and a 10° night temperature. The soil was watered every other day to keep

it very moist. Living and dead seedlings were counted periodically until 90 d after planting, when seedlings were harvested to determine the length of shoots and roots and the number of needles > 1 mm long.

Experiment 5: Competition with mosses

The importance of mosses in excluding tree seedlings from the soil was explored in experiment 5 by using a growth chamber. The experimental design was a completely randomized factorial with six levels of moss depth, two seedling species, and two replicates. Soil from Hoh River was collected, screened, mixed, and placed in plastic pots as in experiment 4. Moss was added to pots so that dry biomasses of 0, 1, 2, 3, 4, and 5 g (which corresponded to 0, 100, 200, 300, 400, and 500 g/m²) were replicated four times. The mosses *Hylocomium splendens* and *Rhytidiadelphus loreus* were collected at Hoh River. Twenty seeds of *Picea* were planted in each of 12 randomly chosen pots, and 20 seeds of *Tsuga* were planted in each of the remaining pots. Growth conditions were 12-h day length, a day temperature of 20°, and a night temperature of 10°. After 30 d, germination rate was determined; at 90 d, survivors and needles longer than 1 mm were counted, and root and stem lengths were measured.

Experiment 6: Competition on logs

The effect of moss depth on seedling establishment on logs was tested at Hoh River. Four logs, each with a homogeneous moss depth but representing a different depth class, were located, and pieces of these logs were transplanted to four-sided wooden boxes, 60 cm long and 35 cm wide, each nailed to a recently fallen log. The bottom of the box was formed by the fallen log itself. Each box was divided into quarters, and one of four moss depths (1.4, 3.7, 7.8, or 11 cm) was assigned randomly to each of the quarters. The boxes were protected from predation by a 6-mm wire mesh cage.

Three trials of experiment 6 were done. In the first trial, a split-plot of a complete randomized block design was used with four moss depths and two seedling species yielding eight blocks. Fifty seeds of *Tsuga* and 50 seeds of *Picea* were scattered on one-half of each of the moss treatments during March 1982. Seedlings were counted in July 1982. In the second trial, seedlings that survived the first trial were removed and replaced by *Picea* seeds on 19 July 1982. These seeds had been stratified at 1° for 2 mo and were germinating when planted. Forty seeds were planted on each moss depth. The experimental design of trial 2 was a randomized complete block design with eight blocks and four moss depth treatments. Surviving *Picea* seedlings were counted periodically throughout 1982 and 1983. In the third trial, the *Tsuga* seedlings that had established naturally within the boxes by July 1983 were counted. This trial also used a randomized complete block design with eight blocks and four moss-depth treatments.

Experiment 7: Seed penetration rate

The mechanisms whereby mosses affect tree-seedling establishment depend, in part, on the rate at which seeds penetrate moss mats. If a seed completely penetrates a deep moss mat and germinates, the roots are in contact with the soil, but the leaves are shaded. But if the seed germinates before fully penetrating, the roots are in a nutrient-poor medium prone to drying.

An experiment at Cascade Head measured the effect of moss species, moss biomass, and time on seed penetration rate. The experimental design was a split-split-plot of complete, randomized-block design with three blocks, five moss biomass treatments, and two species of moss (*R. loreus* and *H. splendens*) in each biomass treatment. Each experimental unit was a 35 × 80 cm wooden box, 15 cm deep, with the top and the bottom covered with 12-mm wire mesh. The box was mounted 20 cm above the soil. Wooden panels divided each box into 10 15 × 15 cm compartments. The moss was packed loosely to mimic natural conditions. Fifty dewinged *P. sitchensis* seeds were added at six separate times for penetration times of 0, 21, 42, 63, 84, and 105 d. Seeds were painted a different color for each time they were added. A preliminary experiment using a similar method indicated that seed form did not have a significant effect on seed penetration rate (Harmon 1986). Thus, the use of dewinged seeds (which made handling easier) probably gave realistic values. At the end of the experiment, the moss was harvested and oven dried, and seeds that had not penetrated the moss mats were recovered.

Seed viability

The seeds used in these experiments were tested for viability after stratification at 1° for 30 d. The percentages of germinated seeds after 30 d, based on 200 seeds, were 99, 99, 88, and 89% for *Picea*, *Pseudotsuga*, *Thuja*, and *Tsuga*, respectively (Harmon 1986).

RESULTS

Experiment 1: Substrate vs. position

At Hoh River, more seedlings survived on logs than on soils in June 1982, but this difference was not significant. Highly significant differences occurred among tree species, with *Thuja* $>$ *Picea* $>$ *Tsuga* $>$ *Pseudotsuga*. Survival rates for all species were low during this early phase of establishment; the maximum value was 13% for *Thuja* growing on logs.

By March 1983, the substrate effect had markedly increased, with few seedlings surviving on soil in either position. *Pseudotsuga* did not survive on any of the treatments and was excluded from the analysis. Significantly more seedlings survived on log substrates, with a mean survival of 3% on logs and 0.1% on soils. No significant effects could be attributed to position, species, or any of the interaction terms.

Seedling survival at Cascade Head was substrate de-

TABLE 1. Establishment of tree seedlings at the Cascade Head site on three different substrate/position treatments (experiments 1 and 2). Each 45-cm diameter plot was planted with 100 seeds. $N = 5$ replicates.

Treatment and date	Seedling species			
	<i>Picea sitchensis</i>	<i>Pseudotsuga menziesii</i>	<i>Thuja plicata</i>	<i>Tsuga heterophylla</i>
	No. seedlings per plot ($\bar{X} \pm \text{SE}$)			
Soil left on ground and protected				
1 Jul 1982	1.8 \pm 0.49	0.2 \pm 0.20	3.0 \pm 1.84	3.4 \pm 2.23
29 Jan 1983	0 \pm 0	0 \pm 0	0.6 \pm 0.60	1.2 \pm 0.97
Log placed on ground				
1 Jul 1982	1.6 \pm 1.13	0.6 \pm 0.40	4.4 \pm 2.23	4.6 \pm 1.81
29 Jan 1983	1.0 \pm 1.00	0.6 \pm 0.24	2.2 \pm 1.11	3.2 \pm 1.02
Soil left on ground and unprotected				
1 Jul 1982	4.2 \pm 2.85	0 \pm 0	2.0 \pm 2.00	2.2 \pm 1.15
29 Jan 1983	1.6 \pm 1.03	0 \pm 0	1.0 \pm 1.00	0 \pm 0

pendent and, as at Hoh River, took a long time to develop. The initial sample in July 1982 at Cascade Head did not reveal significant differences in seedling survival caused by substrates, species, or their interactions (Table 1). The mean seedling survival rate for all species and substrates in July 1982 was 2.5%. By January 1983, a highly significant interaction between species and substrate had developed. The main effects of species and substrate were also highly significant. Only *Thuja* and *Tsuga* were able to establish on soil left at the ground level; all species were able to survive and establish on the log surfaces at ground level.

Experiment 2: Predation

Predation had a significant effect on seedling survival early during the growing season, but substrate differences masked this later in the year. In June 1982 at Hoh River, significantly more seedlings were growing on protected soil and log plots than on unprotected plots. The differences were not large, however; protected soil plots had an average survival rate of 2.45%, and the unprotected soil plots had a survival rate of 0.45%. Differences in survival rates among species and between substrates were not significant, nor were any of the interactions significant. By March 1983, significantly more seedlings were growing on logs than on soils at Hoh River. No significant effects could be attributed to species, protection treatment, or any of the interactions. The mean survival rates were 1.95% for log surfaces and 0.03% for soil surfaces.

At Cascade Head during July 1982, no significant differences in seedling survival were found among species or between protected vs. unprotected soils (Table 1). As in the other experiments, survival was low on all the treatments, with a mean survival rate on soils of 2.1%. Neither the main effects (i.e., species or protection) nor the interaction term were significant as of January 1983, when the mean survival rate on soils was 0.55%.

Experiment 3: Soil pathogens vs. competition

Seedling survival should have been higher on sterilized soil than on unsterilized soil if pathogens were killing seedlings growing on soil. Under field conditions, sterilization kills vegetation, which, in turn, releases nutrients unless the dead vegetation is removed. Because an increase in seedling survival might be associated with vegetation clearing, we compared the effects of the three treatments on seedling survival. Pathogens would be indicated if the sterilized-cleared treatment had greater seedling survival than either the control or the cleared treatment. For pathogens to be acting alone, the clearing and control treatments should have equivalent effects. Competition would be indicated if the sterilized-cleared and the cleared plots were equal and had greater survival rates than the control.

Pathogens appeared potentially important at Hoh River because the sterilization-clearing increased survival over the other two treatments. A significant interaction between species and soil treatments occurred in the June 1982 Hoh River data (Fig. 2). All species had low survival on the control plots, with values of 0.4, 5.2, 3.4, and 0.8% for *Picea*, *Pseudotsuga*, *Thuja*, and *Tsuga*, respectively. On the cleared plots, survival was greater than on the control for *Picea* and *Thuja* but not for *Pseudotsuga*, which had no living seedlings on this treatment. By March 1983, a highly significant interaction between species and soil treatments occurred. None of the species had survived on the control plots. Survival on cleared soils was 8.4, 5.4, and 0.2% for *Picea*, *Thuja*, and *Tsuga*, respectively. Survival on the sterilized-cleared plots was similar to the 28 June values for all four species. Although this experiment indicated the potential presence of pathogens, the results were confounded by two factors. First, seeds on sterilized plots were applied 2 to 3 mo later than those on the other two treatments; this may have influenced germination and survival. Second, the seeds on sterilized soils germinated later than those on other treat-

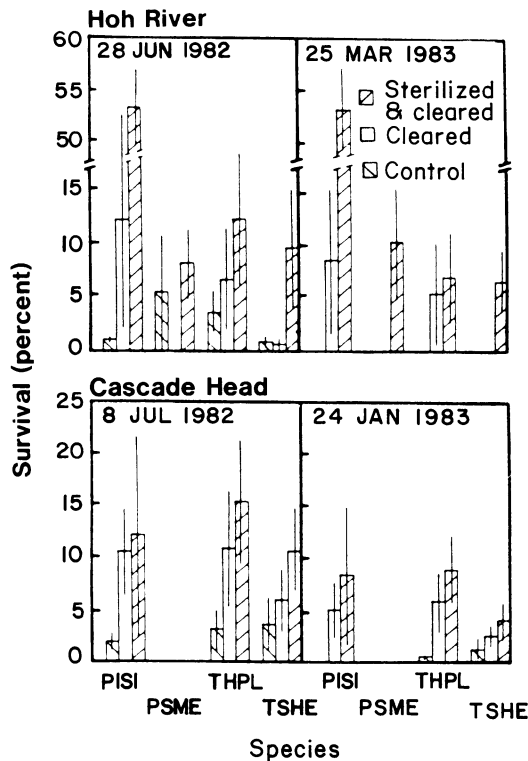


FIG. 2. Results at two sampling dates for the competition vs. pathogen experiment (experiment 3) conducted at the Hoh River and Cascade Head sites. Each histogram bar represents the mean of five observations and vertical lines are ± 1 SE. The species codes are Pisi, *Picea sitchensis*; Psme, *Pseudotsuga menziesii*; Thpl, *Thuja plicata*; and Tshe, *Tsuga heterophylla*.

ments; this may have allowed more individuals to survive a drought in May and June 1982.

The cleared and sterilized-cleared plots at Cascade Head were very similar, in contrast to those at Hoh River. The results from both sampling times at Cascade Head indicated that competition, not pathogens, had been responsible for excluding seedlings from the soil. In July 1982, highly significant differences in seedling survival were associated with species and soil treatments (Fig. 2). The main species distinction was that *Pseudotsuga* failed to survive on all treatments. By January 1983, a highly significant species and soil treatment interaction had developed. Control plots had the lowest survival rates, with no individuals of *Picea* or *Pseudotsuga* surviving. Although *Thuja* and *Tsuga* had some living seedlings at this time, the survival rates were very low, with values of 0.6 and 1%, respectively. Seedling survival, with the exception of *Pseudotsuga*, was higher on cleared plots than on the controls but slightly lower than on the sterilized-cleared treatments.

Clearing of vegetation also significantly increased the number of naturally established *Tsuga* seedlings at Cascade Head. In cleared plots, the mean seedling den-

sity was 146 ± 2.6 seedlings/m²; on the control plots, the density was 14 ± 0.98 seedlings/m².

Seedling survival on cleared plots in the second field experiment conducted at Hoh River exceeded that on sterilized-cleared and on control treatments almost from the start, and these differences became more pronounced with time (Fig. 3). *Pseudotsuga* survival was higher initially than that of *Picea* for all treatments, but after 250 d the situation reversed. At 370 d, highly significant differences in survival were associated with sterilization-clearing treatments; *Picea* had significantly higher survival than *Pseudotsuga* on all treatments. No significant effects were attributed to species-treatment interactions. The lower survival rate of the sterilized-cleared plots relative to the cleared plots developed early in the experiment; explanations for this might be a reduction of mycorrhizal activity or a modification of the soil during sterilization.

Few *Picea* seedlings were able to overtop the moss or the herb layers growing in the Hoh River experimental plots; *Pseudotsuga* overtopped the moss on a few plots but was always below the herb layer. The mean (\pm SE) heights of mosses and herbs were 5.7 ± 0.41 cm and 12.1 ± 0.87 cm, respectively ($N = 10$). Herb and moss cover on the control plots indicated potentially severe competition; cover was $63 \pm 7\%$ for herbs and $95 \pm 3\%$ for mosses. The cover and height of the vegetation on the soil and the increases in survival of planted seedlings associated with vegetation clearing indicated that competition, not pathogens, had excluded seedlings from the soil at Hoh River.

Clearing of vegetation also significantly increased the success of unplanted *Tsuga* seedlings on soil in the second pathogen-competition field experiment conducted at Hoh River. *Tsuga* density was lowest in the control plots (mean \pm SE, 197 ± 62 seedlings/m²), higher in cleared plots (855 ± 179 seedlings/m²), and

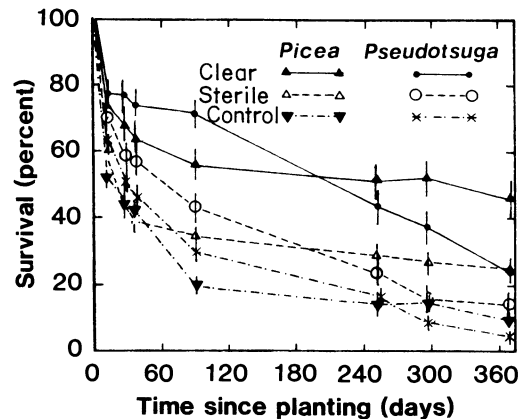


FIG. 3. Survival of *Picea sitchensis* and *Pseudotsuga menziesii* seedlings as a function of time on cleared, sterilized-cleared, and control plots (experiment 3). Each point is a mean, and vertical lines show ± 1 SE ($N = 10$).

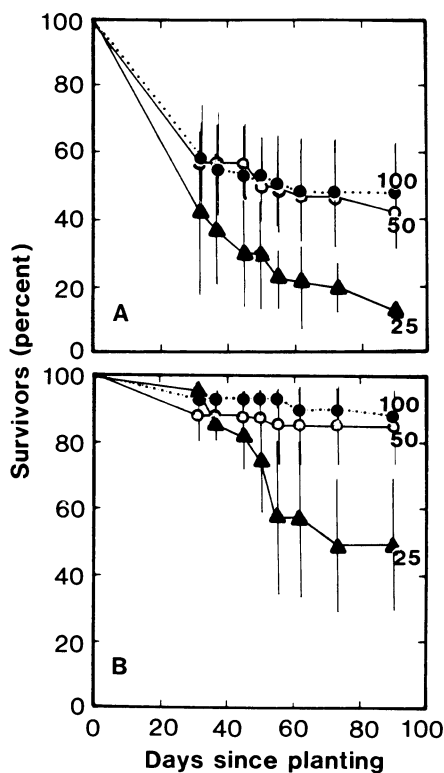


FIG. 4. Changes in *Picea sitchensis* survival over time on (A) sterilized and (B) unsterilized soils (control) that had been shaded (experiment 4). The quantum flux density of photosynthetically active radiation (PAR) was $50 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and the shade treatments allowed 100, 50, and 25% of this flux to reach the seedlings. Each point represents a mean, and vertical lines show ± 1 SE ($N = 3$).

highest in the sterilized-cleared plots (1010 ± 200 seedlings/ m^2).

Experiment 4: Soil pathogens and shading

At the end of 90 d, significantly greater survival of *Picea* was noted in growth chambers on the unsterilized and unshaded treatments than on the other treatments (Fig. 4). Lack of a significant shading-sterilization interaction indicated that pathogens did not selectively kill seedlings weakened by shading. The differences in sterilization treatments reflected lower rates of seedling emergence on sterilized soils during the 1st mo of the experiment. Significantly more seeds germinated and emerged on the unsterilized soil (94%) than on the sterilized soil (62%). The steam-pasteurized soil had a hard and massive structure, which made radicle penetration of the soil surface difficult; this may have reduced successful germination and emergence. Damping-off symptoms were noted on only 1 seedling out of 360 during this experiment, indicating that these pathogens were not an important source of mortality. The high rate of survival on unshaded and unsterilized Hoh River soils also indicated that soil pathogens were

of minor importance under the given conditions. The shading treatments provided a dramatic contrast. The 100% and 50% light treatments were very similar; on unsterilized soils, the mean survival rates were 88% under full light and 85% under 50% light. Reducing the light to 25% reduced survival at 90 d to 13% on sterilized soil and 50% on the unsterilized soil.

Experiment 5: Competition with mosses

Increasing moss biomass decreased the survival and growth of *Picea* and *Tsuga* seedlings in the growth chamber. Germination was not significantly affected by moss biomass or seedling species and averaged 73.5%. At 90 d, survival decreased significantly as a linear function of moss biomass (Fig. 5). Analysis of covariance indicated no significant difference in survival for the two species based on moss biomass.

Increasing moss biomass also decreased root growth and needle formation of both species. Mean root length declined significantly from 50–61 mm/seedling with no moss to 10–20 mm with a moss biomass of 500 g/m^2 . The number of needles per seedling also declined as a significant function of moss biomass. The mean numbers of needles that formed on *Picea* and *Tsuga* when mosses were not present were 9 and 4, respectively; however, when moss biomass was 500 g/m^2 , the mean numbers of needles formed were 4 and 1 for *Picea* and *Tsuga*, respectively.

Experiment 6: Competition on logs

All three trials of this experiment concerning competition on logs at Hoh River indicated that deep moss mats excluded tree seedlings. In the first trial, differences in survival among moss depths and species were highly significant. *Picea* had higher survival than *Tsuga* at all moss depths. The mean survival rates for *Picea* species were 9% at 1.4 cm, 13% at 3.7 cm, and 1% at both 7.8 and 11.0 cm moss depths. In contrast, *Tsuga*

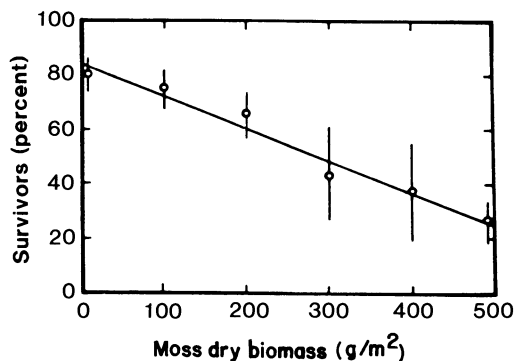


FIG. 5. *Picea sitchensis* and *Tsuga heterophylla* seedling survival 90 d after planting, as a function of moss biomass (moss depth) (experiment 5). Each point is the mean of the two species combined, and the vertical lines show the standard error ($N = 4$). The regression equation is $Y = 83.6 - 0.115 X$, where Y is the percentage of seedlings surviving at 90 d, and X is the moss dry biomass in g/m^2 .

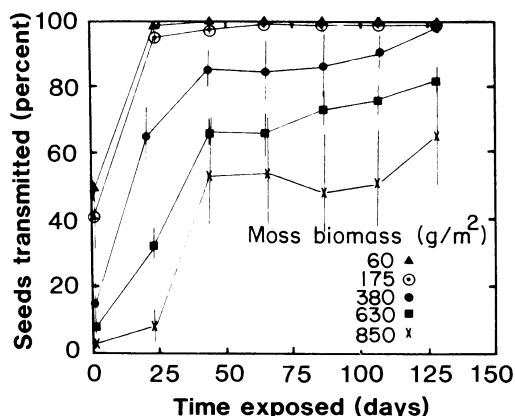


FIG. 6. Penetration of *Picea sitchensis* seeds through *Rhizidiadelphus loreus* and *Hylocomium splendens* mats in experiment 7 as a function of moss biomass and time. Each point represents a mean, and the vertical lines show ± 1 SE ($N = 6$).

did not survive at the two deepest moss depths. At the 1.4 cm moss depth, the survival rate of this species was 6%; at 3 cm, it was 7%.

In the second trial, a highly significant difference in survival was associated with moss depth. At the end of 370 d, survival for planted *Picea* was 30% at 1.4 cm, 35% at 3.7 cm, 2% at 7.8 cm, and 1% at 11.0 cm moss depths.

The third trial, in which naturally recruited *Tsuga* seedlings were used, revealed patterns similar to those of planted seeds. The effect of moss depth on density of naturally established *Tsuga* seedlings was highly significant. *Tsuga* density was 675 seedlings/m² at 1.4 cm, 780 seedlings/m² at 3.7 cm, 65 seedlings/m² at 7.8 cm, and 15 seedlings/m² at 11.0 cm moss depths.

Experiment 7: Seed penetration rate

Even though mosses temporarily suspended seeds above the soil, the measured rates of penetration were rapid enough for most seeds to penetrate mats of <400 g/m² within 3 mo (Fig. 6). Penetration of dewinged *Picea* seeds was significantly affected by moss biomass (moss depth), time, and the interaction between time and moss biomass. No significant effects were due to moss species. The proportion of *Picea* seeds that penetrated moss mats increased with decreasing moss biomass and increasing time. Where moss biomass was 175 g/m², which is most similar to the value measured on the forest floor, 40% of the *Picea* seeds penetrated the artificial moss mat within a few minutes of landing on the mat. After 23 d, 95% of the seeds had penetrated; by 65 d, almost all of the seeds (99%) had penetrated the mats. When the moss biomass was 380 g/m², 128 d were required for 98% of the seeds to penetrate the moss mat. These results indicated that natural moss mats in *Picea-Tsuga* forests are generally not deep enough to prevent seeds from reaching the soil.

DISCUSSION

Factors that exclude tree seedlings from the forest floor

The substrate vs. position experiments conducted at Hoh River and Cascade Head indicated that substrate and species-substrate interactions are responsible for differences in seedling establishment. Position (i.e., elevated on log) is of minor importance. The differences among logs and soils in the experiments would have been even more dramatic had moss depth and cover on logs been controlled. The absence of moss or litter from some log surfaces used in experiment 1 probably drastically reduced seed retention (Harmon 1986). Other logs used in this experiment had deep moss mats that excluded seedlings. Lack of any effect from position indicated that standing water was probably not important in creating the close link between tree regeneration and logs. Furthermore, the slow development of the seedling-log relation indicated that causal factors kill seedlings gradually, and generally not within the 1st mo of growth. This makes pathogenic and allelochemical mechanisms of doubtful importance.

The standing water hypothesis was not supported by field observations. Wells indicated that standing water and saturated soils were absent when the seedlings were germinating or growing during the summer (Harmon 1986). The lack of any position effect in experiment 1 indicated a lack of standing water at the study sites. Even so, standing water may be important in some areas within the *Picea-Tsuga* forest type. Minore and Smith (1971) found, for example, that *Picea* and *Tsuga* are both absent from soils with a mean water table <5 cm from the surface. Sites with standing water during winter often have *Carex obnupta* and *Scirpus microcarpus* growing on them (Minore 1969). This cover type did not occur in the experimental plots. That standing water could be restricting tree seedlings to logs within most of this forest type seems unlikely.

Predation could remove a large fraction of tree seeds and seedlings (Place 1955, Lawrence and Rediske 1962, Radvanyi 1966, Gashwiler 1967), but only a small portion of the seedlings were eaten by vertebrates in our study. In light of the ability of the *Picea-Tsuga* forests to produce seeds, predation is unlikely to be important in the long run; during good seed years, 5–35 × 10⁶ seeds/ha may be produced (Ruth and Berntsen 1955). Even with high predation rates (e.g., 90%), recruitment during good seed years would greatly exceed the number required to maintain stand density.

Damping-off fungi can influence conifer seedling populations. Fungi can kill as many as 20–38% of seedlings <1 mo old (Duncan 1954, Place 1955, Lawrence and Rediske 1962). Although damping-off fungi may have killed some seedlings in this study, few cases of hypocotyl shriveling were observed. Fungi other than the damping-off type may also exclude seedlings from the forest floor (Florence 1965). Results of the present

study indicated that pathogens were not a primary factor in the close link between rotting wood and seedlings. Furthermore, although shade may increase the susceptibility of conifer seedlings to damping-off fungi (Smith 1951, Vaartaja 1962, Taher and Cooke 1975), these effects were not seen in experiment 4.

Deep moss mats, other than *Sphagnum*, are poor seedbeds because they dry rapidly and prevent contact between the seedling and soil (LeBarron 1948, Smith 1951, Place 1955, Johnston 1971). At the moss biomass levels observed in our study some seedlings could be killed by germinating in the moss mat. Calculations including penetration rate and time between seedfall and germination showed otherwise. In *Picea-Tsuga* forests, 90% of seeds fall between October and February (Ruth and Berntsen 1955), and germination ranges from March to June. If the Ruth-Berntsen (1955) pattern of seedfall is typical, then the fraction of seeds that penetrated a moss mat of 175 g/m² can be calculated. If germination occurs in June, virtually all seeds reach the soil before germination. If germination occurs in March near the end of seedfall, then 99% of the seeds reach the soil before germination. Even if a moss mat had 380 g/m² of biomass, 91% of the seeds could penetrate the moss mat by the March germination date. Although these are hypothetical examples, they indicate that few seeds will germinate within the moss mat and die because of subsequent desiccation.

The evidence from the field pathogen-competition experiments indicated that competition excludes tree seedlings from the forest floor. In the substrate-position experiment, the factor responsible was shown to be transferable and related to substrate quality, but not to position. Clearing of surface vegetation improved survival of planted and natural seedlings dramatically at both experimental sites. Deep moss mats were also associated with low seedling survival on logs in experiment 6, adding weight to the competition hypothesis, for there is no reason why competition would occur on soils and not on logs. Shading both by screens and by mosses in a growth chamber (experiments 4 and 5) reduced seedling survival and growth. Furthermore, the mosses at the study sites occurred at biomass values large enough to dramatically reduce available light. When biomass reaches 230 g/m², only 5% of the PAR is predicted to be transmitted through the moss mat (Harmon 1986). This moss biomass is quite similar to the 220 g/m² ($N = 20$) on the forest floor at Hoh River (Harmon 1986). Finally, potential competitors overtop young tree seedlings. The mean hypocotyl length of 100 naturally occurring *Tsuga* seedlings at the Hoh River site was 14 mm; in contrast, the mean heights of the moss and herb layers at this site were 44 and 39 mm, respectively.

Seedlings could be excluded from the forest floor by allelopathic inhibition. Aqueous extracts of *Tsuga canadensis* litter were allelopathic to *T. canadensis* seedlings (Ward and McCormick 1982). *T. heterophylla*

could have similar effects on its seedlings; but seedling germination and survival on cleared plots indicated that *T. heterophylla* allelopathy is not critical. Both logs and soils are exposed to similar amounts of canopy throughfall and litterfall. Mosses and herbs may exclude seedlings from soil via allelopathic mechanisms. Allelopathic action has been hypothesized for some nonvascular plants (Fisher 1979), although the mosses found in our study are yet to be implicated. Germination was not affected by moss biomass (experiment 5), which indicated that allelopathy must affect the later stages of seedling survival. If an allelopathic mechanism is involved, the toxin is not stored in litter because clearing alone increased survival; moreover, the toxin must be potent because it operates under conditions of abundant and constant precipitation.

The evidence for competition is strong. The abundance of precipitation, which makes the allelopathic mechanism so doubtful, is partially responsible for the luxuriant moss and herb understories found in *Picea-Tsuga* forests. The negative effects of mosses on conifer seedlings are noted for other North American forests (LeBarron 1948, Smith 1951, Duncan 1954, Place 1955). Because mosses derive their nutrition from precipitation, dust, and rainsplash (Tamm 1953), their main competitive effect is light removal. Our study centered on mosses, but in some *Picea-Tsuga* stands (e.g., Cascade Head) herbs are probably also major competitors of conifer seedlings. The importance of herb competition in reducing conifer seedling survival has been observed in other forests (Shirley 1945, Maguire and Forman 1983). Another form of competition that might exclude seedlings from the forest floor is root competition with canopy trees (Korstian and Coile 1938). Low densities of seedlings on soil at the experimental sites were probably not due to competition from tree roots because experiments 1–3 involved trenching tree roots to a depth of at least 15 cm, and seedlings still survived poorly on uncleared surfaces. Indirect resource competition with mosses and herbs offers a simple, yet adequate explanation of the close link between seedlings and rotting wood in many *Picea-Tsuga* forests.

Substrate-limited recruitment of seedlings

The close link between conifer seedlings and rotten wood in the *Picea-Tsuga* type indicated that tree recruitment might, in fact, be limited by seedbed availability. Given the high degree of competition on the forest floor and old log surfaces, freshly fallen logs appear to be one of the few sites where tree recruitment can occur. Colonization of the log by bryophytes initially increases recruitment (Harmon 1986), but this competition-free "window" closes once the moss layer exceeds 5 cm in depth. Further recruitment occurs on older logs when the surfaces are disturbed by bark sloughing and bole fragmentation (Harmon 1988). Disturbance of the soil surface also reduces competitive

effects and allows seedling recruitment. One of the few places where seedlings are consistently observed growing on soil is on mounds and pits associated with windthrown trees. These sites are less extensive than logs and are, therefore, even more limited for tree recruitment.

Modeling 1st-yr survival of *Tsuga* seedlings in a *Picea-Tsuga* forest indicates that seedling survival is very low on soils (0.02%) (Harmon 1986). Given the heavy rain of seeds in these forests (Ruth and Berntsen 1955), even this low degree of survival on soils means a recruitment rate of 10^3 seedlings/ha on soils during a good seed year (Harmon 1986). If seedlings growing on soil occur in safe sites where mortality agents are less effective, long-term survival may be high. In contrast, mortality rates on logs increase with age because competition among seedlings is high and logs are unstable, subject to bark sloughing and bole fragmentation (Harmon 1988). The long-term recruitment of canopy trees from soils may therefore be greater than suggested by the proportion of seedlings on the two seedbeds. A resolution of whether tree recruitment is seedbed-limited within *Picea-Tsuga* forests may require long-term study of seedling demography on soils and logs within these forests.

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LITERATURE CITED

- Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* **65**:1406-1419.
- Bratton, S. P. 1976. Resource division in an understory herb community: response to temporal and microtopographic gradients. *American Naturalist* **110**:679-693.
- Cambell, G. S. 1977. Introduction to environmental biophysics. Springer-Verlag, New York, New York, USA.
- 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.
- del Moral, R., and R. G. Cates. 1971. Allelopathic potential of the dominant vegetation of western Washington. *Ecology* **52**:1030-1037.
- Duncan, D. P. 1954. A study of some of the factors affecting the natural regeneration of tamarack (*Larix laricina*) in Minnesota. *Ecology* **35**:498-521.
- Fisher, R. F. 1979. Possible allelopathic effects of reindeer moss on jack pine and white spruce. *Forest Science* **25**:256-260.
- Florence, R. G. 1965. Decline of old-growth redwood forests in relation to some soil microbiological processes. *Ecology* **46**:52-64.
- Fonda, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecology* **55**:927-942.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. United States Forest Service General Technical Report PNW-8. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- Franklin, J. F., C. T. Dyrness, D. G. Moore, and R. F. Tarrant. 1968. Chemical properties under coastal Oregon stands of alder and conifers. Pages 157-172 in J. M. Trappe, J. F. Franklin, R. F. Tarrant, and G. M. Hansen, editors. Biology of alder. Symposium, Northwest Scientific Society 40th Annual Meeting. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- Gashwiller, J. S. 1967. Conifer seed survival in a western Oregon clearcut. *Ecology* **48**:431-433.
- Graham, R. L., and K. Cromack, Jr. 1982. Mass, nutrient content and decay rate of dead boles in rain forests of Olympic National Park. *Canadian Journal of Forest Research* **12**:511-521.
- Harmon, M. E. 1986. Logs as sites of tree regeneration in *Picea sitchensis*-*Tsuga heterophylla* forests of coastal Washington and Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- . 1988. Effects of bark fragmentation on plant succession on conifer logs in *Picea-Tsuga* forest of Olympic National Park, Washington. *American Midland Naturalist*, in press.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregorgy, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 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.
- Huenneke, L. F., and R. R. Sharitz. 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. *American Midland Naturalist* **115**:328-335.
- Hutnik, R. J. 1952. Reproduction on windfalls in a northern hardwood stand. *Journal of Forestry* **50**:693-694.
- Johnston, W. F. 1971. Management guide for the black spruce type in the lake states. United States Forest Service Research Paper NC-64. North Central Forest Experiment Station, St. Paul, Minnesota, USA.
- Knapp, A. K., and W. K. Smith. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. *Canadian Journal of Botany* **60**:2753-2761.
- Korstian, C. F., and T. S. Coile. 1938. Plant competition in forest stands. Bulletin 3. Duke University School of Forestry, Durham, North Carolina, USA.
- Lawrence, W. H., and J. H. Rediske. 1962. Fate of sown Douglas-fir seed. *Forest Science* **8**:210-218.
- LeBarron, R. K. 1948. Silvicultural management of black spruce in Minnesota. Circular 791. United States Department of Agriculture, Washington, D.C., USA.
- Leslie, D. M. 1982. Cervid-habitat interactions in Olympic National Park. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Maguire, D. A., and T. T. Forman. 1983. Herb cover effects on tree seedling patterns in a mature hemlock-hardwood forest. *Ecology* **64**:1367-1380.
- McCreary, F. R. 1975. Soil survey of Jefferson County Area, Washington. United States Soil Conservation Service, Washington, D.C., USA.
- McKee, A., G. LaRoi, and J. F. Franklin. 1982. Structure, composition and reproductive behavior of terrace forests, South Fork Hoh River, Olympic National Park. Pages 22-29 in E. E. Starkey, J. F. Franklin, and J. W. Matthews, editors. Ecological research in national parks of the Pacific

- Northwest. Oregon State University, Forest Research Laboratory, Corvallis, Oregon, USA.
- McVaugh, R. 1943. The vegetation of the granite flatrocks of the southeastern United States. *Ecological Monographs* **13**:120–166.
- Menges, E. S., and D. M. Waller. 1983. Plant strategies in relation to elevation and light in floodplain herbs. *American Naturalist* **122**:454–473.
- Minore, D. 1969. Yellow skunk-cabbage (*Lysichitum americanum* Hult and St. John)—an indicator of water-table depth. *Ecology* **50**:737–739.
- . 1972. Germination and early growth of coastal tree species on organic seed beds. United States Forest Service Research Paper PNW-135. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- Minore, D., and C. E. Smith. 1971. Occurrence and growth of four northwestern tree species over shallow water tables. United States Forest Service Research Note PNW-160. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- Morris, R. F. 1934. Forest fires in western Oregon and Washington. *Oregon Historical Quarterly* **35**:313–339.
- Place, I. C. M. 1955. The influence of seed-bed conditions on the regeneration of spruce and balsam fir. Bulletin 117. Canadian Forestry Branch, Ottawa, Ontario, Canada.
- Quaye, E. 1982. The structure and dynamics of old-growth Sitka spruce (*Picea sitchensis*) forest of the Oregon Coast Range. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Radvanyi, A. 1966. Destruction of radio-tagged seeds of white spruce by small mammals during summer months. *Forest Science* **12**:307–315.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* **62**:1041–1051.
- Ruth, R. H., and C. M. Berntsen. 1955. A 4-year record of Sitka spruce and western hemlock seed fall on the Cascade Head Experimental forest. Station Research Paper 12. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- Scott, M. L., and P. G. Murphy. 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. *American Midland Naturalist* **117**:10–16.
- Sharpe, G. W. 1956. A taxonomical–ecological study of vegetation by habitats in eight forest types of the Olympic rain forest, Olympic National Park, Washington. Dissertation. University of Washington, Seattle, Washington, USA.
- Shirley, H. L. 1945. Reproduction of upland conifers in the lake states as affected by root competition and light. *American Midland Naturalist* **33**:537–612.
- Smith, D. M. 1951. The influence of seedbed conditions on the regeneration of eastern white pine. Bulletin 545. Connecticut Agricultural Experiment Station, New Haven, Connecticut, USA.
- Sydes, C., and J. P. Grime. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. *Journal of Ecology* **69**:237–248.
- Taher, M. M., and R. C. Cooke. 1975. Shade-induced damping-off in conifer seedlings. I. Effects of reduced light intensity on infection by necrotrophic fungi. *New Phytologist* **75**:567–572.
- Tamm, C. O. 1953. Growth, yield and nutrition in carpets of a forest moss (*Hylocomium splendens*). *Meddelanden fran Statens Skogsforskningsinstitut* **43**:1–140.
- Vaartaja, O. 1962. The relationship of fungi to survival of shaded tree seedlings. *Ecology* **43**:547–548.
- Ward, H. A., and L. H. McCormick. 1982. Eastern hemlock allelopathy. *Forest Science* **28**:681–686.
- Whittaker, R. H., and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* **12**:117–139.