AN ABSTRACT OF THE THESIS OF

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Title: LOGS AS SITES OF TREE REGENERATION IN PICEA SITCHENSIS-TSUGA HETEROPHYLLA FORESTS OF COASTAL WASHINGTON AND OREGON

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Abstract Approved: ______________________________

Jerry F. Franklin

Logs are seedbeds for trees in many *Picea sitchensis*-*Tsuga heterophylla* forests of Washington and Oregon. Factors affecting this close association, including seed retention and seedling establishment on logs and successional changes in log characteristics, are explored in this study.

Field and laboratory experiments indicated that competition with vegetation on the forest floor favored tree seedling development on logs. Reciprocal transplants of soil and log blocks revealed

differences in substrate quality and not position effects, such as standing water, produced the "nurse-log" phenomenon. Clearing vegetation significantly increased survival of planted and natural conifer seedlings above survival on uncleared plots. Experiments on the effects of predation and soil pathogens indicated these interactions were of minor importance. Logs are therefore sites where competitive effects are sufficiently small to allow abundant seedling recruitment.

Log surfaces vary widely in their ability to retain seeds and needles. Moss- and litter-covered surfaces retained 48-98% of seeds and needles, whereas sound and rotten wood and bare bark retained 0-8%. A model of seedling establishment on log surfaces in *Picea*-*Tsuga* forests, which incorporated the effects of seed retention and seedling survival rates, indicated 1.3% of the seed crop would produce one-year-old seedlings on logs but only 0.02-0.18% on undisturbed forest floor.

Surficial litter accumulations enable *Picea* and *Tsuga* seedlings to establish and grow rapidly on slightly decayed logs. Survival rates for the first two years of both species increased asymptotically with litter biomass with a maximum of 62% for *Picea* and 34% for *Tsuga*. Seedling growth was fastest when canopy openness and litter biomass were high, but slow when either factor was low.

Successional development influences tree seedling recruitment and survival on logs. Changes in bark, bryophytes, humus and trees were examined for a chronosequence of *Picea*, *Pseudotsuga* and *Tsuga* logs.

Bark fragmentation was a critical process; it removed plants and humus, reinitiated succession and was responsible for major differences in successional patterns among log species. Although a large proportion of tree seedlings establish on logs in *Picea*-*Tsuga* forests, high mortality rates caused by competition, bark fragmentation and toppling from logs indicated long-term survival on logs was very low and possibly equivalent to the forest floor.

Logs as Sites of Tree Regeneration in *Picea sitchensis*-*Tsuga heterophylla* Forests of Coastal Washington and Oregon

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I. INTRODUCTION

Logs serve a variety of functions within ecosystems as part of nutrient cycles and energy flow, as an influence on geomorphic and soil processes and as a habitat for organisms (Harmon *et al*. 1986). Although often considered to be a habitat and food source for decomposers (Frankland *et al*. 1982, Käärik 1974) and other heterotrophs (Swift 1977, Thomas 1979), logs also serve as habitat for many terrestrial autotrophs including lichens, bryophytes and vascular plants (Dennis and Bateson 1974, Harmon *et al*. 1986, Lemon 1945, McCullough 1948, Sharpe 1956, Thompson 1980).

Of the autotrophs growing upon logs, trees are perhaps the most impressive due to their size and the curiously shaped, stilt-like roots that develop when growing upon this substrate (Kozlowski and Cooley 1961). Numerous tree species of North America grow on rotting wood. In the southeastern United States, *Acer rubrum*, *Pinus caribaea*, *Pinus palustris*, *Pinus rigida*, *Pinus rigida* var. *serotina* and *Quercus nigra* grow on rotten wood although only *P. caribaea* reaches maturity according to Lemon (1945). *A. rubrum*, *Populus heterophylla*, *Populus deltoides*, *Quercus layrata* and *Taxodium distichum* seedlings grow on stumps and floating logs in a North Carolina swamp (Dennis and Bateson (1974). None of these species appears to reach maturity on logs in this setting, however. *Picea rubens* grows on stumps and logs in the southern Appalachian Mountains (Korstain 1937) as does Betula lutea and Betula lenta (Stupka 1964). In New England and New York, Abies balsamea, Picea glauca and P. rubens seedlings are often found on logs (Westveld 1931). In the virgin forests of the Adirondack Mountains of New York, Pinus strobus, P. rubens and Tsuga canadensis grow on logs (Knechtel 1903). Betula alleghaniensis roots on stumps in northern Wisconsin (Kozlowski and Cooley 1961). Rotten wood is a good seedbed for establishment of Picea mariana seedlings in Minnesota (LeBarron 1950). Picea engelmannii and Abies lasiocarpa grow on logs in Colorado (McCullough 1948) and in British Columbia (Griffith 1931, Smith 1955, Smith and Clark 1960). P. engelmanii is often rooted on rotting logs thoughout the northern Rocky Mountain region (Lowdermilk 1925).

In northwestern North America logs supporting tree growth or "nurse-logs" are prominent. Picea sitchensis and Tsuga heterophylla are frequently found growing on rotten wood in the coastal Picea sitchensis-Tsuga heterophylla zone from Oregon to Alaska (Minore 1972, Hines 1971, Kirk 1966, McKee et. al 1982, Taylor 1935). In the Cascade Mountains, T. heterophylla commonly grows on logs (Christy and Mack 1984, Fogel et al. 1973, Franklin et al. 1981, Maser and Trappe 1984, Stewart 1986, Thornburgh 1969, Triska and Cromack 1980).

Although trees frequently grow on logs and stumps, their importance is difficult to judge since few quanitative studies of their contribution to stand regeneration have been made. Since logs cover <25% of the forest floor in most ecosystems (Harmon et al.

1986) it is logical to assume that they are of minor role importance in terms of canopy replacement. While this may be true for many ecosystems, logs are an important seedbed in others. Picea-Tsuga forests of the north Pacific Coast are an outstanding example of the latter with 94 to 98% of the tree seedlings occurring on logs and stumps (McKee et al. 1982) that cover 6-11% of the forest floor (Graham and Cromack 1982). Within the Pacific Northwest, rotten wood may be an important seedbed within other forests types. Christy and Mack (1984) observed that 98% of the T. heterophylla seedlings growing in an old-growth Pseudotsuga-Tsuga stand occured on logs that covered 6% of the forest floor. Rotten wood is also an important seedbed in subalpine Picea-Abies forests of British Columbia with 75% of the seedlings growing on rotten wood that covered 9% of the forest floor (Smith 1955).

Investigations of the tree-log interaction or the nurse-log phenomenon within the Picea-Tsuga forests of coastal Washington and Oregon are reported in this thesis. It is in these wet, cool environments where the tree regeneration on logs appears most important. The proportion of tree seedlings on logs is so high as to suggest the possibility that tree recruitment may be seedbed (substrate) limited.

Factors producing the strong association between tree seedlings and rotten wood are examined in Chapter II. Numerous hypotheses have been offered to explain this phenomenon including: competitive exclusion from the forest floor (Sharpe 1956), soil pathogens (McKee et al. 1982), standing water (Graham and Cromack 1982), essential nutrient deficiencies in the soil (Quaye 1982), seedling burial by litter on the forest floor (Christy and Mack 1984), as well as allelopathy, predation of seeds and seedlings and amensalistic interactions. Field experiments testing the most likely hypotheses were conducted at Cascade Head Experimental Forest, Oregon and Hoh River, Olympic National Park, Washington.

Before seedlings can establish themselves on logs, seeds must fall on these surfaces and be retained until germination. Field investigations of log surface characteristics influencing seed retention at Cascade Head are reported in Chapter III. The potential limitation of log seedbeds on tree recruitment is examined with a model that incorporates the effects of seedbed coverage, seed retention, seedling survival and seed rain.

Trees growing on logs within Picea-Tsuga forests are often rooted in litter upon log surfaces (Minore 1972). Wood decays slowly in these forests (Graham and Cromack 1982, Grier 1978) and therefore these litter mats typically form a seedbed faster than the underlying wood. A field experiment examining the effect of litter biomass on establishment and growth of P. sitchensis and T. heterophylla seedlings is reported in Chapter IV.

Successional changes are initiated as soon as logs fall to the forest floor. This succession is complex because a number of processes interact over the sere and because logs are added to the forest floor in many decay states. While development of stilt-rooted trees is well described (Kozlowski and Cooley 1961, Lemon 1945, Sharpe 1956), successional development of entire log surfaces is not. Understanding this succession is important in assessing the long-term role of logs as seedbeds and determining whether canopy recruitment of *Picea*-*Tsuga* forests is seedbed limited. The general aspects of succession on logs are explored in Chapter V by examining changes in bark, bryophytes, humus and trees over a chronosequence of *P*. *sitchensis*, *Pseudotsuga* *menziesii* and *T*. *heterophylla* logs.

II. LOGS AS SITES OF TREE REGENERATION IN *PICEA-TSUGA* FORESTS

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ABSTRACT

Logs are the major seedbed for tree recruitment in many old-growth *Picea sitchensis-Tsuga heterophylla* forests. Field experiments were conducted at Cascade Head, Oregon and Hoh River, Washington to investigate whether pathogens, predation, competition or flooding caused this close association. Reciprocal transplants of soil and log blocks indicated log blocks had higher seedling survival than soils regardless of position, thus differences in substrate quality and not position were associated with the causal factor. Standing water did not occur at the Hoh River site; watertables reached the surface occasionally at the Cascade Head site, but not during the growing season. Thus, standing water was ruled out as a causal agent for the seedling-log association at both sites. Comparisons of caged and uncaged seedspots revealed predation effects were minor and of equal intensity on soils and logs. Sterilization of soils in the field with methylbromide and in the laboratory with steam pasteurization failed

to consistently increase seedling survival above controls; soil pathogens were thus also eliminated as an important factor. Clearing ground-layer vegetation from soil plots significantly increased the survival rate of planted and natural conifer seedlings above that of uncleared soils. Moss and herb layers were luxuriant at both experimental sites and taller than one-year-old Picea and Tsuga seedlings indicating the potential for competition to reduce seedling survival on soils. The possibility that mosses were preventing seeds from reaching the soil and killing seedlings via an amensalistic interaction was tested by measuring seed penetration rates through moss mats. These data indicate that given the moss biomass observed in the field and the time between seedfall and germination that <1% of the seedlings are killed by amensalistic interactions. Competition with herbs and mosses on the forest floor therefore appears responsible for the disproportionate number of tree seedlings found on logs. Competition with other vegetation growing on logs was also tested using field experiments and indicate seedling recruitment is also very low on old logs with thick moss mats. Apparently logs recently added to or disturbed on the forest floor represent sites where competitive effects are low enough to allow tree seedling recruitment within many Picea-Tsuga forests.

INTRODUCTION

When a tree dies, it enters the detrital food web and becomes the habitat for many species of decomposers. In some forests, dead trees also become a habitat for plants and when tree seedlings are established on the surface, a "nurse-log" develops. Nurse-logs are found in many forests throughout North America (Dennis and Batson 1974, Griffith 1931, Knechtel 1903, Korstain 1937, Kozlowski and Cooley 1961, Lemon 1945, McCullough 1948, Smith 1955, Smith and Clark 1960, Taylor 1935, Westveld 1931), but perhaps reach their zenith in the *Picea sitchensis* Zone of the Pacific Northwest (Franklin and Dyrness 1973). Nurse-logs and stilt-rooted trees (formed when logs or stumps completely decompose from beneath established trees) are conspicuous components of these forests (Franklin *et al*. 1980, Hines 1971, Kirk 1966, McKee *et al*. 1982, Minore 1972, Sharpe 1956). McKee *et al*. (1982) estimated 88%-97% of the tree seedlings grew on logs in alluvial *Picea sitchensis*-*Tsuga heterophylla* forests in the South Fork of the Hoh drainage of Olympic National Park. The abundance of seedlings growing upon logs is even more remarkable because only 6%-11% of the ground surface in these forests was covered by logs (Graham and Cromack 1982). The nurse-logs are well developed within this area is due, in part, to the relatively moist climate which reduces moisture stress of seedlings growing on logs. Another contributing factor is slow wood decay rates in the region (Sollins

1982, Graham and Cromack 1982); logs persist for centuries and form a long-term substrate for tree growth.

Many hypotheses have been proposed to explain the proponderance of tree seedlings growing upon logs in Picea-Tsuga forests. Sharp (1956) felt that the thick, continuous layer of bryophytes and herbs found in these forests excluded tree seedlings from the forest floor. Conversely, tree seedlings grew on logs because seedlings were subject to less moss and herb competition. McKee et al. (1982) hypothesized that soil pathogens or excessively long periods of standing water might exclude seedlings from the soil. The importance of standing water was also emphasized by Graham and Cromack (1982) who felt logs would offer protection from inundation. Minore (1972) hypothesized that, under the deep shade cast by a canopy, seedling root systems would be smaller than those of open grown seedlings; rotting logs might have improved nutrient availability with their deep accumulations of litter and duff. In contrast, Krajina (1969, p. 122) thought the soil was too rich in nutrients for Tsuga and that rotting wood presented one of the few sites sufficiently infertile to support the growth of this species. Quaye (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. Christy and Mack (1984) hypothesized that first-year seedlings in Pseudotsuga menziesii-Tsuga heterophylla forests were excluded from soils by litter accumulations. Logs were envisioned to slough much of the litterfall and therefore were safe-sites in terms of litter burial.

Other hypotheses can be proposed for the close link between tree seedlings and logs in Picea-Tsuga forests. A higher rate of seed or seedling predation on the forest floor might cause logs to have an abundance of seedlings. Leslie (1982) found 18.8-43.8% of the diet of Roosevelt elk is composed of Tsuga and seedlings growing on logs might escape this heavy browing pressure. Allelochemicals released by ground-vegetation might also restrict seedlings to logs. DeMoral and Cates (1971) stated many species occurring in the Pacific Northwest region were potentially allelopathic. Toxins formed during organic matter decomposition could also be released within the soil. The abundance of mycorrhizal fungi in logs has been noted in many coniferous forests (Harvey et al. 1979, Kropp 1982) and perhaps mycorrhizal fungi in the soil are less active than in logs causing lower survival of tree seedlings on soils.

This study was initiated to identify the major factors deterring establishment of tree seedlings on the forest floor in Picea-Tsuga forests in Washington and Oregon. Given the many possible explanations for the strong relationship between tree seedlings and logs in Picea-Tsuga forests, I thought it best to proceed from general to specific hypotheses (Figure II-1). Eleven experiments were conducted during two years and each has been numbered for easy identification. The most general hypothesis was that logs differed from soils in terms of some characteristic that was unique to the substrate. However, logs are above the soil; so an alternative hypothesis was that substrate position might cause differences in

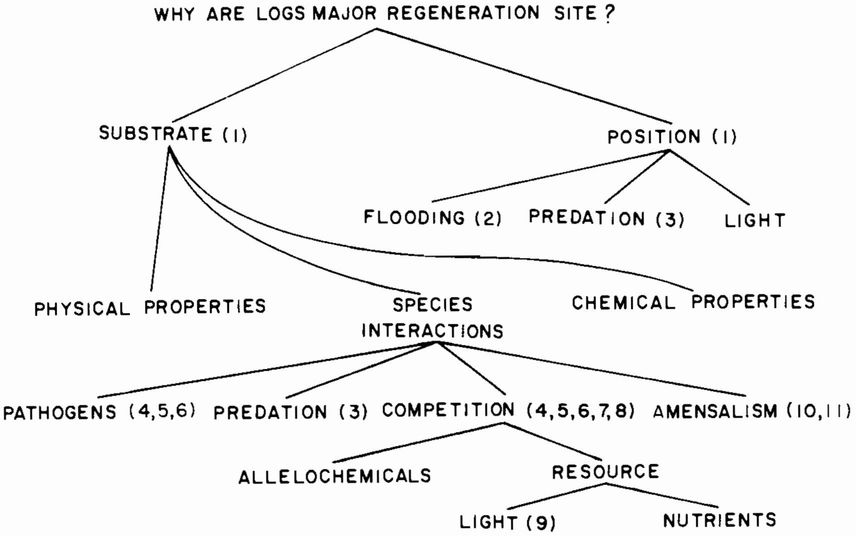

Figure II-1. Flowchart of hypotheses explored during the study of tree seedling establishment on log substrates in Picea-Tsuga forests. The numbers next to each hypothesis indicate the relevant experiments.

seedling survival. Within each general hypothesis a number of subhypotheses was arranged. For example, position effects could be caused by differences in flooding regime, light, or exposure to predation. On the other hand, characteristics of substrate quality might include chemical or physical properties or species interactions such as amensalism, competition, pathogens or predation. Experiments were then designed to test the most likely of these subhypotheses.

STUDY AREAS

Hoh River

The Hoh River experimental site is located in within Olympic National Park, Washington (47^{o} 50' N latitude and 123^{o} 53 W longitude). The climate is extremely wet and mild. Annual average precipitation is 320 cm at the Hoh River Ranger Station, which is 4 km northeast of the experimental plot. Mean, maximum and minimum temperatures of 10^{o} C, 36^{o} C and -11^{o} C, respectively were recorded between July 1981 to July 1982 on a thermograph within the experimental area.

Within Olympic National Park, Picea-Tsuga dominated forests occur on older river terraces in the Quinault, Queets, Hoh, and Bogachiel River Valleys (Franklin and Dryness 1973). The outstanding features of these forests include: 1) a very tall, open canopy layer which often exceeds 80 m in height 2), dominance of very large Picea and

Tsuga, 3) large, above-ground biomass (640-810 t/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 phenomena, such as stilt-rooted trees and a luxurious cover of bryophytes and herbs on the forest floor as well as an abundance of epiphytic bryophytes.

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

The 0.5 ha experimental plot at the Hoh River site was located at an elevation of 150 m on an upper terrace (equivalent to Fonda's (1974) level 4) within a mature Picea-Tsuga forest. This area was selected because it was representative of forests in the area where tree seedlings appeared to be restricted to logs. Charcoal found near the site indicate the stand originated after fire over 300 years ago. Tree basal area was 65.7 m^2/ha and this was composed of 51% Tsuga, 38% Picea and 11% Pseudotsuga. Total tree density was 346 trees/ha <1 cm diameter at breast height (dbh) of which 62% were Picea and 37%

were *Tsuga*. Herb, bryophyte and shrub cover were estimated to be 49%, 52% and 14%, respectively. Coverage of seedbeds within the plot was estimated along 550 m of line transect systematically distributed throughout the experimental plot. Logs covered 9% and undisturbed soil covered 82% of the forest floor. Soil disturbed by rootthrow covered 8% of the plot, but bare soil covered only 0.8% of the plot.

Cascade Head

The second experimental site was located within the Cascade Head Experimental Forest near Otis in Lincoln County, Oregon (45° 03' N latitude and 123° 59' W longitude). The climate at this site is also wet and mild. Mean annual precipitation at the Experimental Forest Headquarters, which is 13.5 km to the northwest of the experimental plot, is 232 cm. Mean, maximum and minimum temperatures of 10° C, 21° C and -7° C were recorded between October 1981 and October 1982 within the experimental plot. The forests at Cascade Head are also dominated by *Picea* and *Tsuga* and developed after a catastrophic crown fire in the 1840's (Morris 1934). Unlike the alluvial forest at Hoh River, Cascade Head forests grow on extremely dissected topography adjacent to the Pacific Ocean. The soils of the area are unclassified, but have been described by Franklin *et al*. (1968) as strongly acid, of silt loam to silty clay loam texture, moderately well drained, with a high CEC and high in N and organic matter. Tree roots rarely penetrate below 1 m in most soils at Cascade Head and shallow root systems are very common.

The 0.5 ha experimental plot at Cascade Head is located near a ridge-top on a west-facing and slightly convex surface. This area was selected because it represented areas at Cascade Head where tree seedlings were restricted to logs. The plot is on a upper slope with a gradient of 20% at 400 m elevation. It lies approximately 0.6 km from the ocean. Tree density (trees >1 cm dbh) was 226/ha of which 79% were *Tsuga* and the remainder *Picea*. Total basal area was 104 m^2/ha of which 83% was *Tsuga*. Bryophyte, herb and shrub cover was 43%, 58% and 22%, respectively. Seedbed coverage was estimated by the same methods used at the Hoh River site. Logs, undisturbed soil and soil disturbed by rootthrow covered 6%, 87% and 7% of the forest floor, respectively. No bare soil was encountered when the transects were originally sampled; however, a severe windstorm during the fall of 1981 uprooted some trees and exposed soil.

METHODS

Experiment 1: Substrate Versus Position

Logs and soils differ in two basic ways--position and substrate. The position effect attributes differences in seedling survival to the fact logs are usually located above the soil surface. Substrate effects account for higher survival on logs because of inherent differences in factors such as bulk density, nutrient content and vegetative cover. Experiment 1 was devised to examine the degree position and substrate effects accounted for seedling abundance on logs.

At the Hoh River site reciprocal transplants of soil and logs tested substrate versus position effects. 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 upon logs. A completely randomized factoral design was used with two types of substrate, two levels of position, four species and five replicates for a total of 80 experimental units. Each experimental log was chosen randomly after a complete log inventory. The position of an experimental unit on a selected log was determined by randomly choosing a distance from one end. Soil treatments were selected by randomly choosing X and Y coordinates in the 50 by 100 m plot. The experimental units were circular plots of soil or log 45 cm in diameter and 15 cm thick. Each plot was removed intact by sliding a 45 cm diameter plywood piece under it before moving. Soil and log pieces left in their original position were removed as the tranplanted pieces but then returned in order to control for handling effects. To reduce the consumption of seeds and seedlings by small animals, a wire screen collar (12 mm mesh) was placed around the plot below the soil surface and a cone, also made of wire, was placed over each plot . During November 1981, 100 seeds were scattered on the surface of each experimental plot. One of the following four species was placed in each plot: Picea, Pseudotsuga, Tsuga and Thuja plicata. The number of live and dead seedlings was counted at each plot on June 28, 1982 and on March 25, 1983. The dependent variable for the analysis of variance tests was the percentage of seeds which germinated and survived at a given date. The angular transformation was used on these data before analysis of variance was performed. In these and all subsequent experiments the results were considered significant if $0.01 < p < 0.05$ and highly significant if $0.01 < p$.

At Cascade Head, the reciprocal transplant approach was not used. However, pieces of logs were placed at the ground level to compare with plots of soil which had been left at the ground level. The later plots were removed and replaced as at Hoh river to control for handling effects. The characteristics of the experimental units, the method of randomly selecting the position of treatments and placement of seeds was similar to the Hoh River site. However, the seeds were placed in the field during January 1982. The statistical design was also a completely randomized factoral, but with two substrates, four species and five replicates of each for a total of 40 experimental units. The number of live and dead seedlings was counted in the plots on July 1, 1982 and on January 29, 1983.

Experiment 2: Flooding

Watertable depth was monitored by using wells similar Minore's (1969). Each well was a 10 cm diameter PVC pipe which had been placed 1 m or more into the ground after the soil was removed with a posthole digger. The minimum depth (i.e., when the watertable was closest to the soil surface) was estimated by placing ground styrofoam inside the well. As the watertable rose and fell, pieces of styrofoam adhered to a 2.54 cm diameter PVC pipe resting inside the larger pipe. The maximum depth (i.e., when the watertable was farthest from the soil surface) was estimated by placing a screw-top test tube inside the well. Each test tube was filled with enough water to make its top float even with the water surface inside the well. The test tube was tied to a string, which in turn was attached to a spool that played out string as the water level dropped. Three wells were monitored at the Hoh River site, while four wells were monitored at the Cascade Head site. The wells were placed systematically throughout the experimental plots. The maximum and minimum watertable depths were measured at biweekly to monthly levels from the summer of 1981 to the summer of 1982.

Experiment 3: Predation

Predation of seeds and seedlings by vertebrates was examined at both sites in experiment 3. Unprotected plots, similar in size and shape to those of experiment 1, were compared to protected plots. Because the mesh size was 12 mm, insects were able to enter the protected plots. At the Cascade Head site protected and unprotected soil plots were compared, while 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 statistical design was a completely randomized factoral with two levels of protection, four levels of species and five replicates of each. At the Hoh River site, the statistical design was also a completely randomized factoral, but there were two levels of protection, two substrates, four species and five replicates of each. The number of seedlings surviving was counted on June 28, 1982 and March 25, 1983 at Hoh River and on July 1, 1982 and January 29, 1983 at Cascade Head.

Experiment 4: Soil Pathogens versus Competition

The first field experiment on soil pathogens versus competition was conducted at both Cascade Head and Hoh River by comparing seedling survival on sterilized-cleared, unsterilized-cleared and unsterilized-uncleared plots. A complete, randomized factoral design was used, with three levels of sterilization-clearing treatment, four species and five replicates for a total of 60 plots. During March 1982 at each site, soil of 20, randomly selected 45 cm diameter plots was removed intact to a depth of 15 cm at each site and placed into plastic bags. After sealing the bags, methyl bromide was injected into each soil block two seperate times over 24 hours at a rate of 6 g methyl bromide/kg of dry soil. Methyl bromide is most effective when soils are at least 5°C and wetted to field capacity. Both conditions prevailed during the sterilization process. After fumigation the plastic was removed and the blocks were aired 24 hours. The soil blocks were then replaced in their original positions and protected from predation by a wire cloth collar and cone. Before the seeds were scattered upon the soil surface in March, the surface vegetation, which had been killed by the fumigation procedure, 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. Because of the very rapid rate of vegetation regrowth and colonization, the plots were periodically cleared of vegetation. During July 1983 a modified version of this experiment was performed at Cascade Head by comparing the number of natural *Tsuga* seedlings found in cleared plots to that of adjacent, uncleared plots. The statistical design of this modification was a randomized complete blocks with two levels of clearing treatment and 12 blocks.

Experiment 5: Soil Pathogens versus Competition

The second field experiment on pathogens was conducted at Hoh River and utilized a split-plot of a complete randomized blocks 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 X 70 cm plot was divided into three treatments: 1) a control with no clearing or sterilization 2) an unsterilized area with had the surface vegetation removed and 3) a sterilized area with the surface vegetation removed. The sterilization procedure followed the methods described in experiment 4 except that fumigation was conducted 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 choosen half. These seeds had been stratified for two months at $1^{o}C$ and had germinated when they were planted on July 19, 1982. The radical of the seedlings was inserted into the litter layer and then the seedlings were watered every three days during the first two weeks of the experiment. Each block was protected from predation by covering it with a wire cloth cage with a 6 mm mesh size. The number of seedlings was monitored periodically throughout the remainder of 1982 and 1983. The number of naturally established *Tsuga* seedlings was also counted on these plots in July 1983.

Experiment 6: Soil Pathogens and Shading

In experiment 6 the effects of sterilization and shading on seedlings were investigated using a growth chamber. The statistical design of this experiment was a completely randomized factoral 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 and screened and then placed into 10 X 10 X 10 cm plastic pots. One half of the pots were randomly selected and sterilized by means of steam pasteurization twice for 1 hour during a 24 hour period. Screens constructed of 1 mm mesh nylon netting supported by wire were used to test the effect of shading. One layer of the netting removed 50% of the light, while two layers removed 75% of the light. This gave three photosynthetically active radiation (PAR) levels of 50, 25 and 12.5 microeinsteins m^{-2} s^{-1}. These values correspond to 2.5, 1.2 and 0.6 % of full sunlight on a clear day, respectively (Cambell 1977, p. 47). Screens were placed over both sterilized and unsterilized pots. Twenty Picea seeds were planted in each of the pots. All the pots were then randomly arranged in a growth chamber set at a 12 hour daylength, 20°C day temperature and a 10°C night temperature. The soil was watered every other day to keep it very moist. The number of living and dead seedlings was counted periodically until 90 days after planting. At the end of 90 days the seedlings were harvested to measure the length of the shoots and roots and to count the number of needles over 1 mm in length. The latter three variables were analyzed on a mean per pot basis.

Experiment 7 Competition with Mosses

The importance of mosses in excluding tree seedlings from the soil was also explored using a growth chamber in experiment 7. The statistical design of this experiment was a completely randomized factoral with six levels of moss depth, two seedling species and two replicates. Soil from the Hoh River site was collected, screened, mixed and placed into plastic pots as in experiment 6. A total of 24 pots were prepared. Moss was added to pots so that biomasses of 0, 1, 2, 3, 4, 5 g, dry wt. (which corresponded to 0, 100, 200, 300, 400 and 500 g dry wt/m^2) were replicated four times. The mosses were collected from the Hoh River site and consisted of *Hylocomium splendens* and *Rhytidiadelphus loreus*. Twenty seeds of *Picea* were planted in each of 12 randomly choosen pots and 20 seeds of *Tsuga* were planted in each of the remaining pots. The pots were randomly arranged within the growth chamber and the growth conditions were 12 hour day length, a day temperature of 20°C and a night temperature of 10°C. After 30 days germination rate was determined and at 90 days the number of survivors and the number of needles exceeding 1 mm in length were counted; and root and stem length were measured.

Experiment 8: 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 then pieces of these were transplanted to experimental units. Each experimental unit was a wooden box 60 cm in length and 35 cm in width that was nailed to a recently fallen log. The bottom of the box was formed by the log itself. Each box was divided into quarters, one of four moss depths (1.4 cm, 3.7 cm, 7.8 cm, 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 this experiment were conducted. In the first trial, a split-plot of a complete randomized block design was used with 8 blocks, four moss depths and two seedling species. Fifty seeds of *Tsuga* and fifty seeds of *Picea* were scattered on one-half of each of the moss treatments during March 1982. The number of seedlings was counted in July 1982. In a second trial of this experiment, the seedlings surviving the first trial were removed and replaced by *Picea* seeds on July 19, 1982. These seeds had been stratified at $1^{\circ}C$ for 2 months and were germinating when planted. A total of 40 seeds were planted on each moss depth. The statistical design of trial 2 was a randomized complete blocks design with 8 blocks and 4 moss depth treatments. The numbers of *Picea* seedlings surviving were counted periodically throughout 1982 and 1983. In the third trial of this experiment the number of natural *Tsuga* seedlings that had established within the boxes by July 1983 was counted. This trial also utilized a randomized complete blocks design with 8 blocks and four moss depth treatments.

Experiment 9: Light Extinction in Mosses

Mosses derive their mineral nutrition from precipition and dust and not from soil (Tamm 1953). Therefore, their major competitive influence upon tree seedlings should be on light levels. The shading ability of moss was measured by adding known quantities of moss to pots with a clear plastic bottom and determining the fraction of photosynthetically active radiation (PAR) passing through mosses in an air dry and wet condition. PAR was measured with a model Li-185A Licor light meter using a quantum sensor. Three dominant forest floor moss species at Hoh River, *Hylocomium splendens*, *Rhytidiadelphus loreus* and *Eurhynchium oreganum* were used. Beer's law was used to model light extinction as a function of moss biomass. The parameters of this model were estimated by using a semilogarthmic regression with the Y-intercept assumed to be 1.0.

Experiment 10: Ammensalism

The mechanisms whereby mosses effect tree seedling establishment depend, in part, upon the rate seeds penetrate moss mats. If a seed completely penetrates a deep moss mat and germinates, roots are in contact with the soil, but leaves are shaded. On the other hand, if the seed germinates before fully penetrating, the roots are in a nutrient-poor media which is prone to drying. Mortality caused by insufficiency of nutrients and water would be because of an amensalistic interaction between the mosses and seedlings.

An experiment was conducted at Cascade Head to measure the effect of seed species and moss biomass on seed penetration rate through a mat of *R. loreus*. A split-plot of a complete randomized block design with three blocks was used; five moss biomass levels were the main plot effect, while two seed species *Picea* and *Thuja*, were the subplot treatments. Each experimental unit was a 35 X 80 cm wooden box 15 cm deep with the top and the bottom covered with with 12 mm wire mesh. The box was mounted on four wooden legs suspending it above the soil. Each box was divided with wooden separators into ten 15 X 15 cm compartments. Weighed quanities of *R. loreus* were added to each compartment at rates of 126, 250, 400, 600 and 790 g dry wt/m^2. The moss was loosely packed to mimic natural conditions. After the moss had been added, 50 seeds of *Picea* or *Thuja* were added to each container. The seeds of *Picea* were dewinged and also painted orange to increase their visibility. After 81 days the moss were harvested, oven dried and examined to recover the seeds that had not penetrated the moss mat.

Experiment 11: Ammensalism

The effect of moss species, moss biomass and time on seed penetration rate was explored in experiment 11. The overall design was a split-split-plot of a complete randomized block design with 3 blocks, 5 moss biomass treatments and 2 species of moss, R. loreus and H. splendens, within each biomass treatment. Fifty P. sitchensis seeds were added 6 separate times so that penetration times of 0, 21, 42, 63, 84 and 105 days were established. The seeds added at each time were a different color so the effect of time on penetration rate could be determined. At the end of the experiment the moss was harvested, oven dried and then examined for seeds as in experiment 13.

Seed Characteristics

The seeds used in these experiments were tested for viability by stratification at 1°C for 30 days and germination on paper blotters in petri dishes using 12 hour daylength and a day temperature of 30°C and a night temperature of 20°C. The percentage of germinated seeds after 30 days based on 200 seeds was 99%, 99%, 88% and 89% for Picea, Pseudotsuga, Thuja and Tsuga, respectively.

RESULTS

Experiment 1: Substrate versus Position

Seedling survivorship at Hoh River was generally higher on logs than soils in June 1982 (Table II-1). However, these differences were

Table II-1--The establishment of _Picea sitchensis_, _Pseudotsuga menziesii_, _Thuja picata_ and _Tsuga heterophylla_ seedlings at the Hoh River site in experiment 1. The log left on log and the soil left on ground treatments represent controls while the soil placed on the log and the log placed on soil represent reciprocal transplants used to test position effect.

Treatment	Seedling Species			
Date	_P. sitchensis_	_P. menziesii_	_T. plicata_	_T. heterophylla_
Log left on log				
6/26/82	4.7 (3.41)[A]	0 (0)	5.2 (1.63)	1.4 (0.51)
3/25/83	4.2 (3.23)	0 (0)	3.0 (1.31)	1.8 (0.81)
Log Placed on ground				
6/28/82	3.2 (1.72)	0 (0)	13.2 (3.44)	1.6 (0.81)
3/25/83	2.8 (1.39)	0 (0)	10.6 (3.56)	2.4 (1.47)
Soil left on ground				
6/28/82	0.4 (0.24)	5.2 (4.95)	3.4(1.54)	0.8 (0.49)
3/25/83	0 (0)	0 (0)	0 (0)	0 (0)
Soil Placed on Log				
6/28/82	2.0 (1.31)	0 (0)	5.0 (1.05)	1.4 (0.60)
3/25/83	0.4 (0.24)	0 (0)	0.6 (0.40)	0 (0)

[A] The values are the number of seedling counted/plot (X (SE), N = 5). Each plot was planted with 100 seeds.

not significant. There were highly significant differences among the four tree species at this time. Survival rates were low for all species during this early phase of establishment with a maximum value of 13% for Thuja growing logs placed at ground level. Pseudotsuga had the lowest survival with only the soil left at ground level having any survivors at all.

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 analysis. At this date there was significantly higher survival 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 dependent and, as at Hoh River, took a long period to develope. The initial sample in July 1982 at Cascade Head did not reveal significant differences in seedling survival were caused by substrates, species or their interactions (Table II-2). The mean seedling survival rate for all species and substrates at this time 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, whereas all species were able to survive and establish on the log surfaces placed at ground level.

Table II-2—The establishment of *Picea sitchensis*, *Pseudotsuga menziesii*, *Thuja plicata* and *Tsuga heterophylla* seedlings at the Cascade Head site on protected and unprotected soils and logs placed at the ground surface (experiments 1 and 3).

Treatment Date	Species *P. sitchensis*	*P. menziesii*	*T. plicata*	*T. heterophylla*
Soil left at ground and protected				
7/1/82	1.8 (0.49)[A]	0.2 (0.20)	3.0 (1.84)	3.4 (2.23)
1/29/83	0 (0)	0 (0)	0.6 (0.60)	1.2 (0.97)
Log placed on ground				
7/1/82	1.6 (1.13)	0.6 (0.40)	4.4 (2.23)	4.6 (1.81)
1/29/83	1.0 (1.00)	0.6 (0.24)	2.2 (1.11)	3.2 (1.02)
Soil left at ground and unprotected				
7/1/82	4.2 (2.85)	0 (0)	2.0 (2.00)	2.2 (1.15)
1/29/83	1.6 (1.03)	0 (0)	1.0 (1.00)	0 (0)

[A] The values are the mean number of seedlings/plot (SE). N = 5. Each plot was planted with 100 seeds.

Experiment 2: Flooding

Flooding did not appear to be important in excluding seedlings from the forest floor at either site. The watertable did not rise into the wells at the Hoh River site in 1982 or 1983; therefore it probably lay at least 1 m below the surface during this time. The soils at the Hoh River site were very gravelly at a depth of 0.3 to 1 m and appeared to drain quickly. Examination of the experimental site and adjacent area failed to reveal any water accumulating on the soil surface. In contrast to Hoh River, the watertable at Cascade Head was often high during fall, winter and early spring (Figure II-2). Although the watertable rose to the surface during winter in 1982 and 1983, it was not near the surface when seeds germinated in May through July. Moreover, even when the watertable was high, it quickly dropped to the maximum depth within a day.

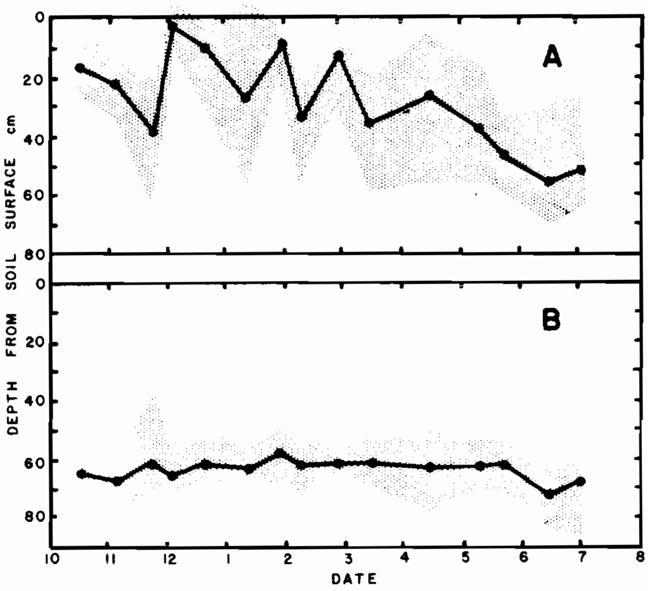

Figure II-2. Watertable level at Cascade Head from October 15, 1981 to July 1, 1982. The heavy line indicates the mean depth and the shaded area indicates the range (N = 4). A. Minimum watertable depth 8. Maximum watertable depth.

Experiment 3: Predation

The results of the predation experiment indicate a significant predation effect on seedling survival early during the growing season, but that substrate differences mask these patterns later in the year. On June 1982 at Hoh River, there were significantly more seedlings on protected soil and log plots than on unprotected plots (Tables II-1 and II-3). However, these differences were not large. For example, protected soil plots had an average survival rate of 2.45%, whereas the unprotected soil plots had a survival rate of 0.45%. Differences in survival rates between species and substrates were not significant at this time, nor were any of the interactions significant. By March 1983 significantly more seedlings grew on logs than soils at the Hoh River site. No significant effects could be attributed to species, protection treatment or any of the interactions. The mean survival rate was 1.95% for log surfaces and 0.03% for soil surfaces. The fact the substrate-predation interaction was not significant may indicate that predation was not selectively heavier on soils than on logs.

At Cascade Head during July 1982, there were no significant differences between species or unprotected versus unprotected soils in terms of seedling survival (Table II-2). As in the other experiments, survival was low on all the treatments with a mean survival rate on soils of 2.1%. None of the main effects (i.e., species or protection) or the interaction term were significant as of January 1983 (Table II-2), when the mean survival rate on soils was 0.55%.

Table II-3—The establishment of _Picea sitchensis_, _Pseudotsuga menziesii_, _Thuja plicata_ and _Tsuga heterophylla_ at the Hoh River site on logs and soils unprotected from predation (Experiment 3). These results were compared to protected logs and soils (Table II-1) to assess predation effects on seedling survival.

Treatment	Seedling Species			
Date	_P. sitchensis_	_P. menziesii_	_T. plicata_	_T. heterophylla_
Unprotected Logs				
6/26/82	0.40 (0.27)[A]	0.40 (0.45)	4.6 (4.32)	1.6 (1.30)
3/25/83	0.40 (0.27)	0.20 (0.22)	4.0 (4.47)	1.2 (1.34)
Unprotected Soils				
6/26/82	0.40 (0.27)	0 (0)	0.40 (0.27)	0.8 (0.89)
3/25/83	0 (0)	0 (0)	0.20 (0.43)	0 (0)

[A] The values are the number of seedlings counted/splot x (standard error), N = S. Each plot was planted with 100 seeds.

Experiment 4 Soil Pathogens versus Competition

If pathogens were killing seedlings growing on soil, then seedling survival should be higher on sterilized soil than unsterilized soil. Under field conditions sterilization kills vegetation, which, in turn, releases nutrients unless it is removed. However, because there could be a increase in seedling survival associated with vegetation clearing, it was necessary to compare the effect 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 equivilent effects. In contrast, competition would be indicated if the sterilized + cleared and the cleared plots were equal and had greater survival rates than the control.

Pathogens were potentially important at the Hoh River site, because the sterilization + clearing increased survival, especially of *Picea*, over the other two treatments. A significant interaction between species and soil treatments occurred in the June 1982 Hoh River data (Figure II-3). 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 the control for *Picea* and *Thuja* but not for *Pseudotsuga*, which had no living seedlings on this treatment. By March 1983 there was also a highly significant interaction between species and soil treatments.

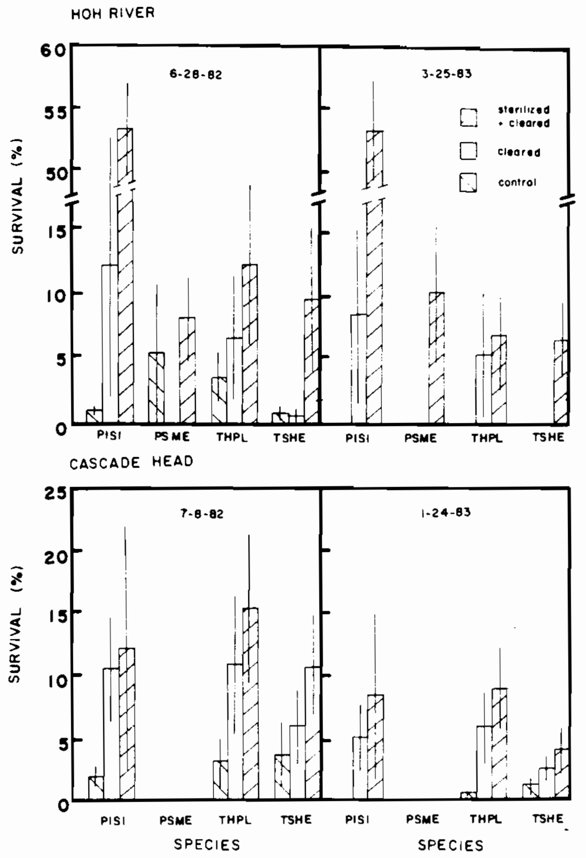

Figure II-3. Results at two sampling dates for the competition versus pathogen experiment (number 4) conducted at the Hoh River and Cascade Head Sites. Each point represents the mean of 5 observations and vertical lines are standard errors. The species codes are: Pisi (*Picea sitchensis*), Psme (*Pseudotsuga menziesii*), Thpl (*Thuja plicata*) and Tshe (*Tsuga heterophylla*).

None of the species had survived on the control plots at the March sampling. Survival on cleared soils at this date was 8.4, 5.4 and 0.2% for Picea ,Thuja and Tsuga, respectively. Survival on the sterilized + cleared plots was similar to the June 28 values for all four species. Although this experiment indicates the potential presence of pathogens,the results were influenced by two factors that made them equivocal. First, the seeds on sterilized plots were applied two to three months later than the other two treatments and that may have influenced germination and survival. Further, the seeds on sterilized soils germinated later than on other treatments and this may have allowed more individuals to escape the drought that occurred in May and June, 1982.

In contrast to the Hoh River results, the cleared and sterilized + cleared plots were very similar at Cascade Head. The results at both sampling times at Cascade Head indicate competition and not pathogens was responsible for the exclusion of seedlings from the soil. On July 1982 highly significant differences in seedling survival were associated with species and soil treatments (Figure II-3). The main species distinction was that Pseudotsuga failed to survival on any treatment. 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 the controls but slightly lower than the sterilized + cleared treatments.

Vegetation clearing also significantly increased the survival rate of naturally established Tsuga seedlings at Cascade Head. In cleared plots the mean seedling density was 146 ± 2.6 seedlings/m^2, whereas on the control plots the density was 14 ± 0.98 seedlings/m^2. As with the planted seed, competition was implicated as an important factor excluding seedlings from the forest floor at Cascade Head.

Experiment 5: Soil Pathogens and Competition

The second set of field experiments conducted to investigate competition and soil pathogens at Hoh River circumvented the failings of experiment 4. Effects due to seed movement or season of planting were eliminated by hand planting germinated seeds on the same day. However, only two species, Picea and Pseudotsuga, were used.

Seedling survival on cleared plots exceeded that on sterilized + cleared and on control treatments almost from the first and these differences became even more pronounced with time (Figure II-4). Initially Pseudotsuga survival was higher than that of Picea for all treatments, but after 250 days the situation was reversed. At 370 days there were highly significant differences in survival associated with sterilization-clearing treatments; and Picea had significantly higher survival than Pseudotsuga on all

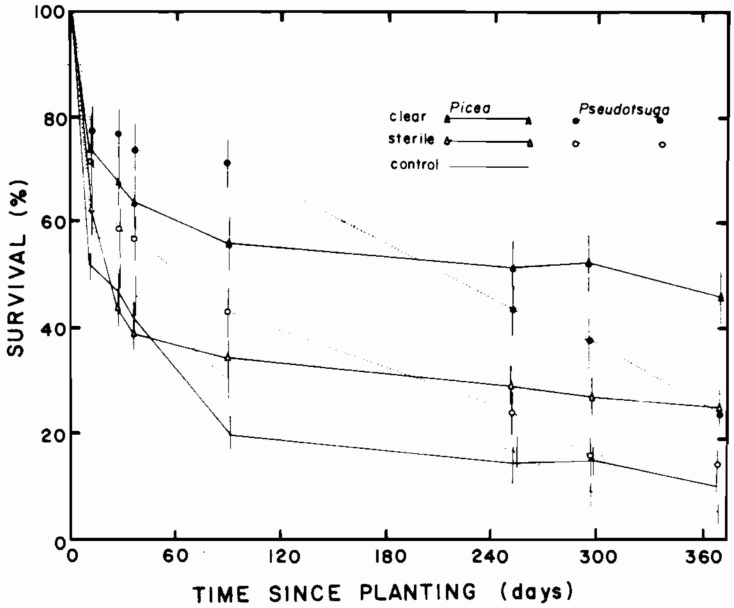

Figure II-4. Survival of <u>Picea</u> <u>sitchensis</u> and <u>Pseudotsuga</u> <u>menziesii</u> seedlings as a function of time on sterilized and cleared, cleared and control plots (experiment 5). Each point is a mean and vertical lines indicate standard errors (N = 10).

treatments. No significant effects were attributed to species-treatment interactions. For Picea the mean survival at this time was 10% for the controls, 46% for cleared plots and 25% for the sterilized + cleared plots. At the same time Pseudotsuga survival was 5%, 23% and 14% on the control, cleared and sterilized + cleared plots, respectively. The lower survival rate of the sterilized + cleared plots relative to the cleared-only plots is difficult to explain but developed early in the experiment. Explanations could include a reduction of mycorrhizal activity or a modification of the soil caused by sterilization.

Few Picea seedlings were able to overtop the moss or the herb layers growing in the experimental plots, whereas Pseudotsuga overtopped the moss on a few plots but was always below the herb layer. The mean heights (SE, N = 10) of mosses and herbs was 5.7 cm (0.41) and 12.1 cm (0.87), respectively. Herb and moss cover on the control plots also indicated potentially severe competition with 63.5 ± 6.95% for the former layer and 95.0 ± 2.68% for the latter. In summary, the cover and height of the vegetation on the soil as well as the 10-fold increases in planted seedling survival associated with vegetation clearing indicated competition and not pathogens excluded seedlings from the soil at Hoh River.

Clearing of vegetation also significantly increased the success of unplanted Tsuga seedlings on soil. Tsuga density was lowest in the control plots (197 ± 62 seedlings/m^2, x ± SE), higher in cleared plots (855± 179 seedling/m^2) and highest in the sterilized + cleared plots (1010± 200 seedlings/m^2).

Experiment 6: Soil Pathogens and Shading

At the end of 90 days, there was significantly higher survival of Picea in growth chambers on the unsterilized and unshaded treatments than the other treatments (Figure II-5). Lack of a significant shading-sterilization interaction indicated pathogens did not selectively kill seedlings weakened by shading. The differences in sterilization treatments reflected lower rates of emergence on sterilized soils during the first month of the experiment. Significantly more seeds germinated and emerged on the unsterilized soils (94%) than on the sterilized soil (62%). The steam pasteurized soil had a very hard and massive structure, making radicle penetration of the soil surface difficult and this could have reduced successful germination and emergence. Damping-off symptoms were noted on only one seedling out of 360 during this experiment, indicating these pathogens were not an important form of mortality. The high rate of survival on unshaded and unsterilized Hoh River soils also indicates that soil pathogens were of minor importance under the conditions examined. The shading treatments provided a dramatic contrast. The

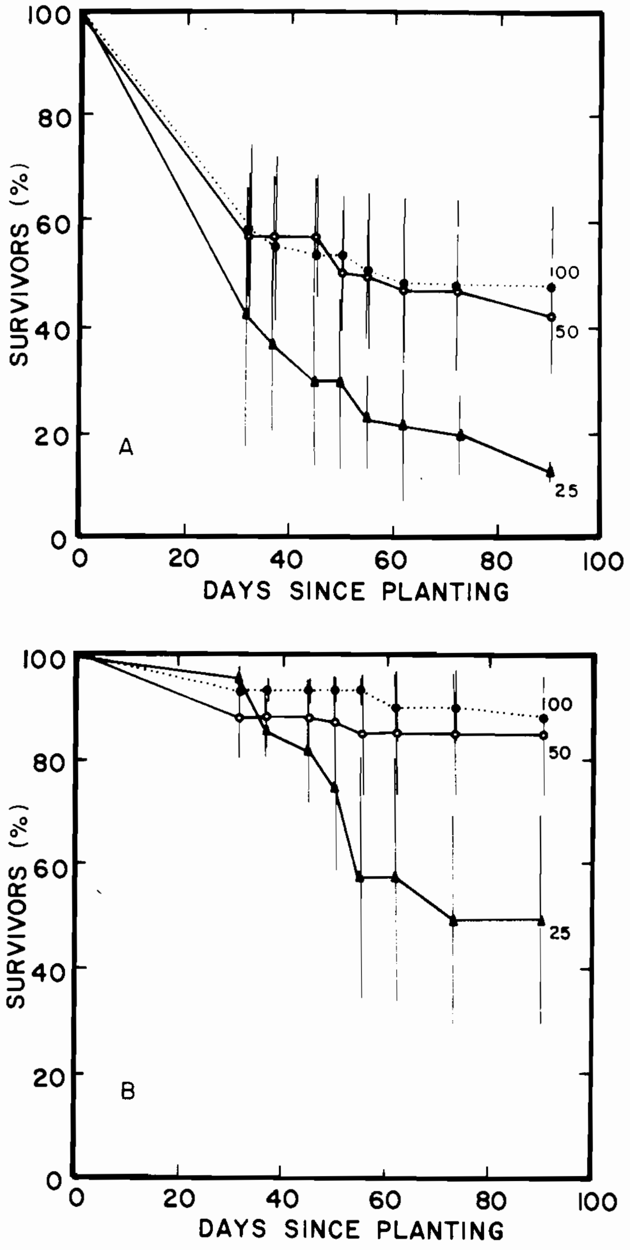

Figure II-5. Changes in Picea sitchensis survival over time on (A) sterilized and (B) unsterilized soils (control) that have been shaded (experiment 6). The amount of photosynthetically active radiation (PAR) was 50 microeinsteins m^{-2} s^{-1} and the shade treatments allowed 100, 50 and 25% of this value to reach the seedlings. Each point represents a mean and vertical lines indicate the standard errors (N=3).

100% and 50% light treatments were very similar; for example, on unsterilized soils there was a mean survival rate of 88% under full light and 85% under 50% full light. Reducing the light to 25% of full level reduced survival at 90 days to 13% on sterilized soils and 50% on the unsterilized soils.

The sterilization and shading treatments also had highly significant effects on the form of <u>Picea</u> seedlings (Table II-4). Seedlings growing in sterilized soils had significantly shorter root systems than those growing in unsterilized soils, probably reflecting the unfavorable changes in soil structure caused by the steam pasteurization. Root length also declined significantly with increasing shade. As with root length, the number of needles/seedling was negatively influenced by pasteurization at least when light was not limiting. There was a highly significant interaction effect of shading and sterilization on the mean number of needles <1 mm long. At 25% of full light, the number of needles/seedling was very similar for sterilized and unsterilized soils. However, as shading decreased the differences between sterilized and unsterilized soils increased. Unlike root length and needle number, hypocotyl length was not influenced significantly by shading or the interaction between sterilization and shading. However, hypocotyl lengths were significantly longer for the unsterilized (35 mm) than for the sterilized soil (29 mm), reflecting the negative effects of pasteurization.

Table II-4—Effect of steam pasteurization of Hoh River soils and shading upon the morphology of *Picea sitchensis* seedlings in experiment 6.

Light Level Microeinsteins $m^{-2}5^{-1}$	Root Length[A] mm	Shoot Length mm	Needles number/plant
	Unsterilized Soils		
50	42 (4.0)[B]	35 (0.6)	7.6 (0.79)
25	25 (0.9)	36 (1.3)	3.4 (0.66)
12	18 (1.1)	36 (0.5)	0.9 (0.49)
	Sterilized Soils		
50	28 (4.1)	27 (0.7)	3.9 (0.90)
25	11 (0.6)	31 (2.8)	2.0 (0.40)
12	5 (0.9)	28 (3.2)	1.3 (0.51)

[A] Based on mean value for each pot at the end of 90 days of growth.

[B] Mean (standard error), N = 3.

Experiment 7: Competition with Mosses

Increasing moss biomass decreased the survival and growth of Picea and Tsuga seedlings in the growth chamber. Germination was not significantly effected by moss biomass or seedling species and averaged 73.5%. At 90 days, survival decreased significantly as a linear function of moss biomass (Figure II-6). Analysis of covariance indicated there was no significant difference for the two species in terms of survival with respect to moss biomass.

Increasing moss biomass also decreased root growth and needle formation of both species. Mean root length declined significantly as moss biomass increased (Figure II-7). Analysis of covariance indicated that the regression equations for the two species did not differ significantly. The number of needles/plant also declined as a significant function of moss biomass (Figure II-8).

Experiment 8: Competition on Logs

All three trials of this experiment concerning competition on logs at Hoh River indicated that moss excluded tree seedlings from logs with deep mats. In the first trial of experiment 8, both Picea and Tsuga readily established where moss was <3.7 cm deep, but had poor survival where moss exceeded this depth. Differences in survival between moss depths and species were highly significant. Picea had higher survival than Tsuga at all moss depths. The mean survival rate

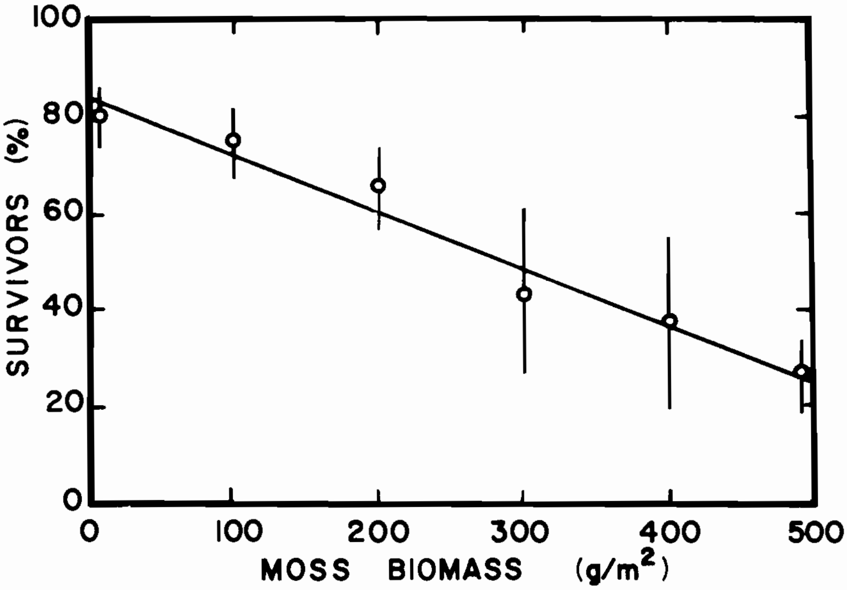

Figure II-6. Decrease in Picea sitchensis and Tsuga heterophylla seedling survival 90 days after planting as a function of moss biomass (experiment 9). These seedlings were grown in Hoh River soil under growth chamber conditions described in the text. Each point is the mean and the vertical lines indicate standard errors (N = 4). The regression equation is $Y = 83.6 - 0.115 X$, where Y is the percentage of seedlings surviving at 90 days and X is the moss biomass in g dry wt/m^2.

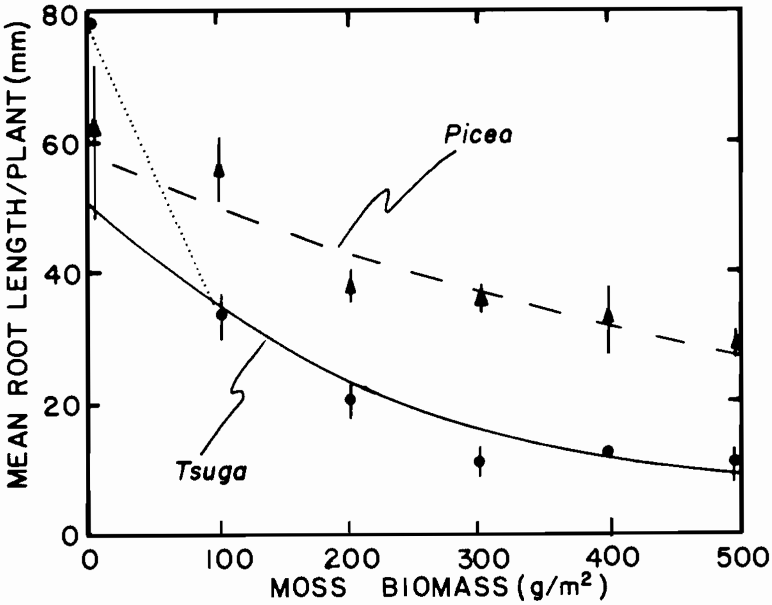

Figure II-7. Mean root length per seedling decreases in response to increasing moss biomass (experiment 9). Seedlings of Picea sitchensis and Tsuga heterophylla were grown 90 days inside a growth chamber on Hoh River soils. Each point is a mean and the vertical lines represent the range (N = 12). The regression equations for Picea and Tsuga are Y = 58 exp[-0.0015X] (r^2=0.92) and Y = 49 exp[-0.0036] (r^2=0.79), respectively. Y is the mean root length/seedling (mm) and X is moss biomass (g/m^2).

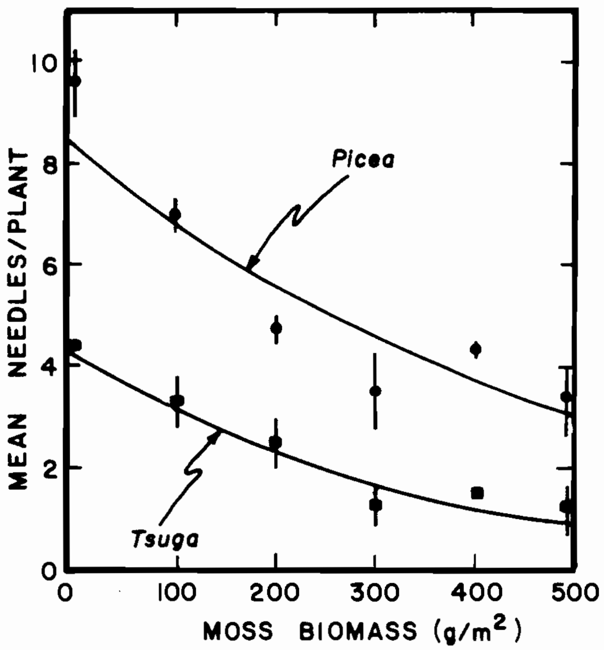

Figure II-8. Mean number of needles per seedling decreases with increasing moss biomass (experiment 9). Seedlings of <u>Picea sitchensis</u> and <u>Tsuga heterophylla</u> were grown 90 days in a growth chamber on the Hoh river soils. Each point represents the mean and the vertical lines indicate the range (N = 12). The regression equations for <u>Picea</u> and <u>Tsuga</u> are $Y = 8.2 \exp[-0.002X]$ ($r^2=0.74$) and $Y = 4.3 \exp[-0.003X]$ ($r^2=0.75$). Y is the number of needles/plant and X is moss biomass (g/m^2).

for Picea species was 9% at 1.4 cm, 13% at 3.7 cm and 1% for both 7.8 cm, and 11.0 cm moss depths. In contrast, Tsuga did not survive at the two deepest moss depths. At the 1.4 cm moss depth the survival rate of this species was 6% and at the 3 cm depth it was 7%.

In the second trial of experiment 8, germinating seeds of Picea were planted and watered for the first few weeks. Although these procedures increased survival, the response was similar to the first trial with a highly significant difference due to moss depth (Figure II-9). At the end of the trial (370 days), survival was highest for the 3.7 cm moss depth and lowest for the 7.8cm and 11.0 cm depths.

The third trial examined the effect of moss depth on unplanted Tsuga establishment and revealed patterns similar to planted seeds with maximum density at the 3.7 cm depth (Figure II-9). Moss depth effects on density of natural Tsuga seedlings were highly significant. Density where moss depth was <3.5 cm was an order of magnitude higher than where moss exceeded this depth. As with planted seeds, this trial indicated deep moss layers could exclude seedlings from logs as well as the forest floor.

Experiment 9: Light Extinction in Mosses

Transmission of photosyntheticaly active radiation (PAR) through the artifical moss mats closely followed Beer's law (Figure II-10). Analysis of covariance indicated there were no significant differences

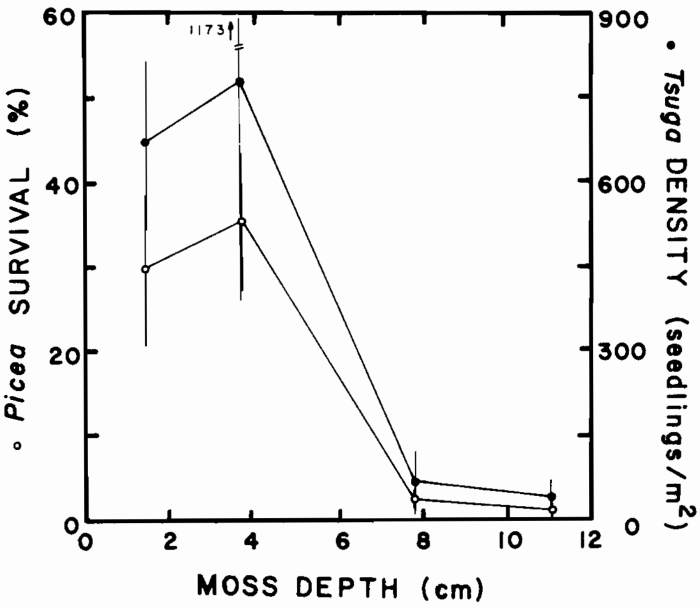

Figure II-9. Survival of planted Picea sitchensis after 370 days and density of natural Tsuga heterophylla seedlings in midsummer (7-30-83) as a function of moss depth on logs (N = 8) (experiment 10). The standard errors are indicated by vertical lines.

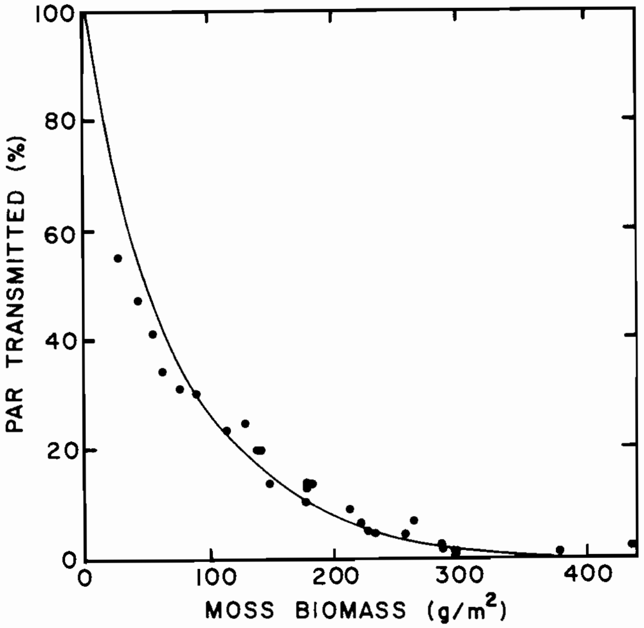

Figure II-10. Reduction of photosynthetically active radiation (PAR) through three species of mosses: Hylocomium splendens, Rhytidiadelphns loreus and Eurhynchium oreganum. The regression equation describing the relationship is Y = 100 exp[-0.013X], where Y is the percent of PAR transmitted and X is moss biomass in g/m^2. (r^2 = 0.93, N = 24) in terms of light extinction for mosses in a wet versus an air dry condition; thus moss shading was independent of hydration. Analysis of covariance also indicted no significant differences in PAR transmission among the three moss species. All the observations were used to calculate a single light extinction equation:

$$Y = e^{-0.013X} \qquad r^2 = 0.93,\ N = 24$$

where Y is the fraction of PAR transmitted and X is the moss biomass in g dry wt/m^2. This equation predicts one-half of the PAR would be transmitted through the moss mat of 53 g/m^2. When biomass reaches 230 g/m^2, only 5% of the PAR is predicted to be transmitted through the moss mat. Sampling of moss biomass on the forest floor near the Hoh River gave a mean value of 220 g/m^2 (N = 20) (Harmon, unpublished data) This means that 5.6% of the PAR reaching the top of the moss layer would reach the soil layer. Seedlings receive more light because their cotyledons are embedded within the moss layer and are not at the soil layer. Assuming the cotyledons are embedded halfway into the moss mat and that moss biomass is distributed evenly with height, light would be reduced to approximately 25% of the level reaching the top of the moss mat.

Experiment 10: Ammenalism

Although mosses temporally suspended seeds above the soil, the measured rates of penetration were rapid enough for most seeds to penetrate mats <400 g/m^2 within three months (Figure II-11). At 21

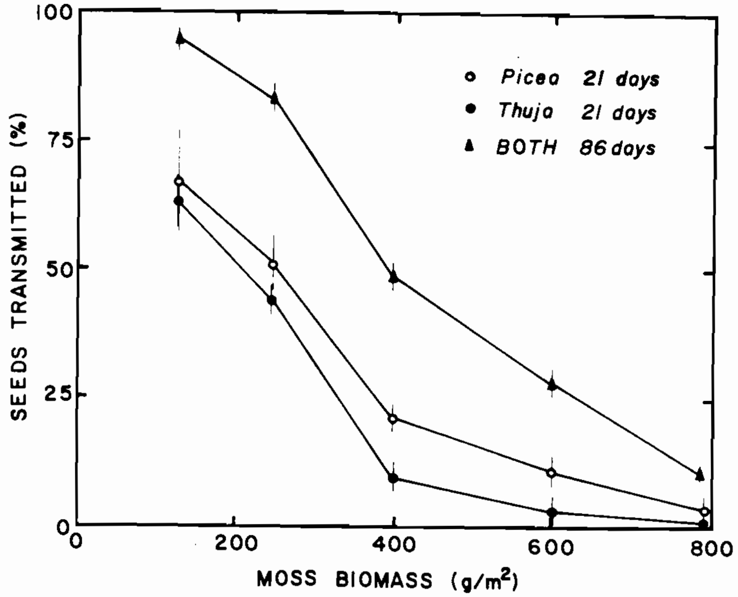

Figure II-11. Proportion of <u>Picea sitchensis</u> and <u>Thuja plicata</u> seeds moving through <u>Rhytidiadelphus loreus</u> mats as a function of time and moss biomass (experiment 10). The points represent means and the vertical lines are standard errors.

days the proportion of seeds transmitted through mats of R. loreus was significantly effected by moss biomass and species of seed. The proportion of seeds transmitted was a function of the logarithm of moss biomass. Dewinged Picea seeds penetrated moss mats faster than Thuja seeds. At 86 days, a larger proportion of the seed penetrated a given biomass than was the case at 21 days. There was a highly significant effect due to moss biomass, although there was no difference between seed species. This indicates that over the long-term the density of seeds (i.e., mass/volume) has little effect on penetration rate.

Experiment 11: Ammenalism

In experiment 10 seed penetration was examined at two points in time and extrapolation to times >90 days was not possible. Experiment 11 was designed primarily to examine seed penetration as a function of time. As with experiment 10, the majority of seeds had penetrated mats of <400 g/m^2 within three months (Figure II-12). Penetration of dewinged Picea seed was significantly affected by moss biomass, time and the interaction between time and moss biomass. There were no significant effects due to moss species. The proportion of Picea seeds penetrating moss mats increased with decreasing moss biomass and increasing time. In the case where moss biomass was 175 g/m^2, 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 upon the mat. After 23 days 95% of the seeds had penetrated

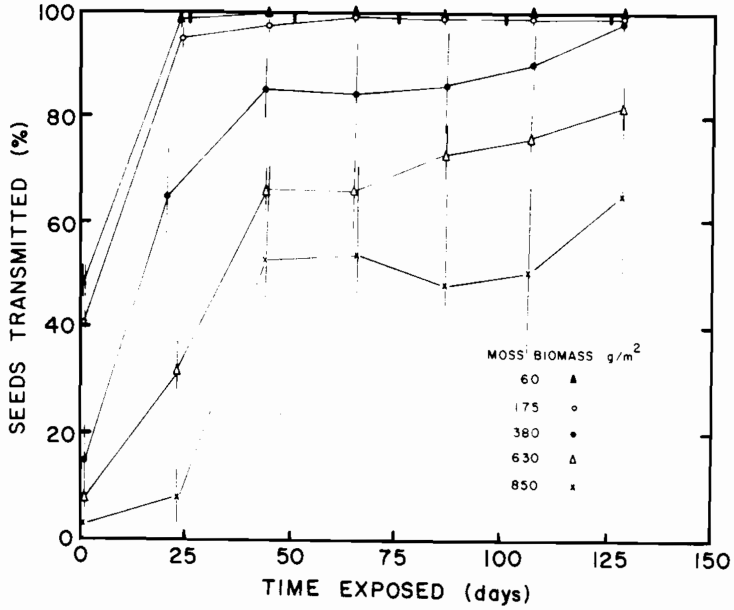

Figure II-12. Penetration of Picea sitchensis seeds through Rhytidiadelphus loreus and Hylocomium splendens mats in experiment 13 as a function of moss biomass and time. In most situations within Picea-Tsuga forests, moss biomass is less than 380 g/m^2. Each point represents a mean and the vertical lines are standard errors (N = 6).

and by 65 days almost all (99%) of the seeds had penetrated the mats. When the moss biomass was 380 g/m^2, only 128 days were required to have 98% of the seeds to penetrate the moss mat. These results indicate that most natural moss mats in Picea-Tsuga forests would not be deep enought to prevent seeds from reaching the soil.

DISCUSSION

Factors Excluding Tree Seedlings From the Forest Floor

The substrate versus position experiments conducted at Hoh River and Cascade Head indicated substrate and/or species-substrate interactions were responsible for differences in seedling establishment. Position effects were of minor importance. The differences between logs and soils would have been even more dramatic if moss depth and cover on logs had been controlled. First, the absence of moss or litter from some experimental log surfaces probably drastically reduced seed retention (Harmon 1986). Secondly, some experimental logs had deep moss mats which subsequent experiments showed exclude seedlings. Lack of a position effect indicated flooding was probably not important in determining the close link between tree regeneration and logs on the study sites. The slow development of the seedling-log relationship indicates that causal factors do not kill seedlings within the first month of growth. This makes pathogenic and allelochemical mechanisms of doubtful importance in determining the pattern.

Flooding appears to have the least support of all the hypotheses tested. Wells indicated that flooding and saturated soils were absent when the seedlings were germinating or growing during the summer. Moreover, the lack of any position effect in experiment 1 indicates a lack of flooding or standing water effects at the study sites. However, there are probably some areas within the Picea-Tsuga forest type where flooding is important. For example, Minore and Smith (1971) found that Picea and Tsuga were both absent from soils having a mean watertable less than 5 cm from the surface. Sites with standing water during winter often have Carex obnupta and Scirpus microcarpus growing on them (Minore 1968). This cover type did not occur in the experimental plots. It therefore seems unlikely that standing water could be restricting tree seedlings to logs within most of this forest type.

Predation has the potential to remove a large fraction of tree seeds and seedlings (Gashwiler 1967, Lawrence and Rediske 1962, Place 1955, Raduanyi 1966) but a very small portion of the seedlings were eaten by vertebrate predators in the present study. The abundance of ground cover at the two experimental sites may have reduced predation effects by making seeds harder to find. Moreover, in light of the ability of the Picea-Tsuga forests to produce seeds it is unlikely that seed predation is very important in the long-run. For example, during good seed years a range of 5 to 35 million seeds/ha may be produced (Ruth and Burntsen 1955). Even with very high predation rates (e.g., 90%) recruitment during these years would greatly exceed the number required to maintain stand density.

Damping-off fungi also have a large potential to influence conifer seedling populations. Fungi can kill as many as 20-38% of seedlings <1 month old (Duncan 1954, Lawrence and Rediske 1962, Place 1955). 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 indicate pathogens were not a primary factor in the close link between rotting wood and seedlings. Furthermore, although shading may increase the susceptibility of conifer seedlings to damping-off fungi (Smith 1951, Taber and Cooke 1975, Vaartaja 1962) these effects were not seen in experiment 6.

Although both laboratory and field studies indicate that seedling survival decreases with increasing moss biomass, observed rates of seed penetration indicate ammensalism is not involved in the relationship. Deep moss mats, other than Sphagnum, are considered poor seedbeds because they dry rapidly and prevent contact between the seedling and soil (Johnston 1971, LeBarron 1948, Place 1955,Smith 1951). At the moss biomass levels observed in this study it seemed possible that some seedlings could be killed by amensalistic interactions. Calculations taking into account the penetration rate and time between seed-fall and germination show otherwise. In

Picea-Tsuga forests 90% of seeds fall between October and February (Ruth and Berntsen 1955). Germination times range from March to June for this forest type. Assuming that the Ruth-Berntsen (1955) pattern of seed fall is typical, the fraction of seeds penetrating a moss mat of 175 g/m^2 can be calculated. With June germination virtually all seeds reach the soil before germination. On the other hand, if germination occurred in March, then 99% of the seeds reach the soil before germination. Even if a moss mat had 380 g/m^2 of biomass, it would allow 91% of the seeds to penetrate by the March germination date. Although these are hypothetical examples, they indicate few seeds will germinate within the moss mat and die because of an amensalistic interaction.

The evidence from experiments 4 and 5 indicate competition excludes tree seedlings from the forest floor. In experiment 1 the factor responsible is shown to be transferable and related to substrate quality but not position. Clearing of surface vegetation improved survival of planted and natural seedlings dramatically at both experimental sites. Deep mosses mats were also associated with low seedling survival on logs in experiment 8 adding weight to the competition hypothesis, for there is no reason why competition would occur on soils and not on logs. Shading by screens and mosses in a growth chamber (experiments 6 and 7) both reduced seedling survival and growth. Furthermore, the mosses at the study sites occur at biomass values large enough to dramatically reduce available light. Herbs also compete with tree seedlings by reducing light and absorbing nutrients and water. Finally, height relationships of seedlings and potential competitors indicated that the latter overtop the former in most cases. For example, the mean hypocotyl length of 100 natural Tsuga seedlings at the Hoh River site was 14 mm. In contrast, the mean heights of the moss and herb layers at this site are 44 and 39 mm, respectively (Harmon, unpublished).

Seedlings could be excluded from sites occupied by allelopathic inhibition. Aqueous extracts of Tsuga canadensis litter were allelopathic to T. canadensis seedlings (Ward and McCormic 1982). T. heterophylla could have similar effects on its seedlings. However, the fact that seedlings germinate and survive on cleared plots indicates T. heterophylla allelopathy is not critical. Moreover, 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 non-vascular plants (Fisher 1979) although the mosses found in the present study have yet to be implicated. Germination was not affected by moss biomass (experiment 9) which indicates allelopathy must affect the later stages of seedling survival. It also appears that if a allelopathic mechanism is involved the toxin is not stored in litter because clearing alone increases survival. . Moreover, the toxin must be very potent because it operates under conditions of very high and constant precipitation.

The evidence for competition is very strong. The abundance of precipitation, which makes the allelopathy 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 have been noted in many other North American forests (Duncan 1954, LeBarron 1948, Place 1955, Smith 1951). Because mosses derive their nutrition from precipitation, dust and rainsplash (Tamm 1953) their main competitive effect is light removal. The present study centered on mosses but in some _Picea_-_Tsuga_ stands, such as Cascade Head, herbs are probably also major conifer-seedlings competitors. The importance of herb competition in reducing conifer seedling survival has been observed in other forests (Maguire and Forman 1983, Shirley 1945). Another form of competition excluding seedlings from the forest floor might be root competition with canopy trees (Korstian and Coile 1938, Toumey and Keinholz 1931). However, low densities of seedlings on soil at the experimental sites is probably not due to tree root competition because experiments 1-5 involved trenching tree roots to a depth of at least 15 cm and seedlings still survived poorly on uncleared surfaces. In summary, indirect resource competition with mosses and herbs offers a simple, yet adequate explanation of the close linkage between seedlings and rotting wood in many _Picea_-_Tsuga_ forest.

Substrate Limited Recruitment of Seedlings

The close linkage between conifer seedlings and rotten wood in the *Picea*-*Tsuga* type indicates tree recruitment may be, in fact, limited by seedbed availability. Given the high degree of competition on the forest floor and old log surfaces it appears that freshly fallen logs are one of the few sites where tree recruitment occurs. Colonization of the log by bryophytes initially increases recruitment (Chapter III) but this competition-free "window" closes once the moss layer exceeds 5 cm depth. Further recruitment occurs on older logs when the surfaces are disturbed by bark sloughing and bole fragmentation. Disturbance of the soil surface would also reduce competitive effects and allow seedling recruitment. One of the few places seedlings are consistently observed growing on soil is on tip-up mounds and soil pits associated with windthrown trees. However, these sites are areally less extensive than logs and therefore are even more limited in terms of tree recruitment.

Widescale disturbances such as forest fires and logging would remove competition effects reducing the importance of rotten wood as a seedbed. Disturbed stands should therefore have higher tree densities than old-growth stands, all other factors being equal. The deeper shade cast by a dense canopy of young trees would suppress the development of a luxuriant moss and herb layer at least until canopy openings develop (Alaback 1982).

The hypothosis that tree recruitment in old-growth Picea-Tsuga forests is seedbed limited is worth testing. Modeling first-year survivorship of Tsuga seedlings in a Picea-Tsuga forest indicate seedling survival is very low on soils (0.02%) (Chapter III). However, given the heavy seedrain 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 "safesites" where mortality agents is reduced, then long-term survival could 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 1986). The long-term recruitment of canopy trees from soils may therefore be larger than suggested by the proportion of seedlings on the two seedbeds. Clearly a resolution of whether tree recruitment is seedbed-limited within Picea-Tsuga forests will require a longer term perspective of seedling demography on soils and logs within these forests.

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III. LOG RETENTION OF NEEDLES AND SEEDS IN *PICEA*-*TSUGA* FORESTS

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ABSTRACT

Because logs are a major seedbed in *Picea sitchensis*-*Tsuga heterophylla* forests, the interception and retention of seeds on these surfaces is a potential limitation on tree recruitment. The ability of log surfaces within *Picea*-*Tsuga* forests to retain needles and seeds was studied at Cascade Head Experimental Forest, Oregon. Moss- and litter-covered surfaces retained many (48-98%) of the seeds and needles placed upon them, while rotten wood, sound wood and bark of *Tsuga heterophylla*, *Picea sitchensis* and *Pseudotsuga menziesii* retained few of them (0-8%). Crevices and holes were the only microsites retaining seeds or needles on bark and wood surfaces. Experiments using artificially constructed holes and crevices indicated the fraction of seeds retained in these microsites increased as their depth and angle from the vertical increased and as width decreased. Examination of logs mapped in 5 *Picea sitchensis*-*Tsuga*

heterophylla stands in Oregon and Washington indicated a mean projected log cover of 9.9%. Thin (<5cm) and thick (>5cm) moss mats were the most abundant type of log surface and covered 59% and 25% of the log surfaces, respectively. Theoretical analysis of data on seedbed coverage, retentive characteristics and seedbed-specific seedling survival indicated that 1.3% of a seed cohort would survive the first year on log surfaces and 0.02-0.18% would survive on undisturbed forest floor.

INTRODUCTION

The *Picea-sitchensis-Tsuga heterophylla* forests, growing along the cool, very moist coastal zone of the Pacific Northwest, are notable for their high productivity (Fujimori 1971), luxuriance of understory and epiphytic growth and large tree size (Franklin and Dyrness 1973). Another notable feature, and the subject of this chapter, is the importance of coarse woody debris as a seedbed within these forests. Rotting logs are often the primary sites where tree regeneration is abundant (McKee *et al*. 1982, Minore 1972). Up to 98% of the tree seedlings have been reported to occur on this seedbed (McKee *et al*. 1982). The close linkage between coarse woody debris and tree seedlings is often associated with a heavy bryophyte and herb cover on the forest floor. Rotting wood represents a safe-site (sensu Harper 1977, p. 123) where the competitive effects of bryophytes and herbs is reduced to the point tree seedlings can establish successfully (Chapter II).

Poor seedling recruitment on undisturbed forest floor and relatively low log cover within stands suggests forest regeneration may be substrate limited within many *Picea-Tsuga* forests. For example, in one stand on the Olympic Peninsula only 6 to 11% of the forest floor was covered by logs but 88 to 98% of the seedlings occurred on log seedbeds (Graham and Cromack 1982, McKee *et al*. 1982). The substrate available for seedling recruitment is restricted even further by low rates of seedling establishment on old logs with thick moss coverings (Chapter II).

The ability of log surfaces to retain seeds and leaf litter is another aspect of seedling recruitment in *Picea*-*Tsuga* forests. It is mainly that fraction of seeds that fall and stay on logs until germination that provide tree recruitment. Thus, it is necessary to understand the factors involved in the process of seed retention on logs as well as the areal extent of various seedbeds within *Picea*-*Tsuga* forests to determine whether tree recruitment is substrate limited. It is also important to understand how log surfaces retain needle litter because this material forms a nutrient-rich rooting medium for seedlings that are growing upon wood (Chapter III, Minore 1972).

The following study was initiated to answer these questions concerning seed and needle retention, to determine the extent of various seedbeds in the *Picea*-*Tsuga* type and to examine some the implications of these results on forest structure. Four experiments examined the ability of log surfaces to retain seeds and needles. During the course of these experiments, it became apparent holes and cracks were crucial in retaining seeds on wood and bark surfaces. Two experiments, using artificialy constructed holes and cracks, were therefore conducted to examine retention in these microsites. Finally, the areal extent of logs and surface types was examined in five *Picea*-*Tsuga* forests and the theoretical implications of seed retention examined.

METHODS

Study Area

The following experiments were conducted at the Cascade Head Experimental Forest near Otis, Oregon. This forest is located within the coastal *Picea sitchensis* Zone of Oregon and Washington (Franklin and Dyrness 1973). Most stands at Cascade Head are dominated by mixtures of *P. sitchensis* and *T. heterophylla* , although *Pseudotsuga menziesii* is locally abundant. *Alnus rubra* communities are another important type found within the Experimental Forest and the site of one set of experiments. However, most experiments were conducted within *Picea sitchensis-Tsuga heterophylla* stands. The climate at this location is cool and very moist with a mean annual temperature of 10^{o}C and mean annual precipitation of 250 cm. The heaviest precipition occurs during December and January, while June -August are relatively rain-free (16 cm).

Seeds on Natural Surfaces

Seed retention qualities of natural surfaces, including wood, litter, bark and moss, were explored in two experiments. In the first experiment, seven surfaces were used: 1) a moss mat 5 cm thick composed of *Eurhynchium oreganum*, 2) a combination of *Picea* and *Tsuga* litter 2 cm thick, 3) rotten *Tsuga* wood, 4) sound *Picea* wood lacking bark cover, 5) bare Pseudotsuga bark, 6) bare Picea bark and 7) bare Tsuga bark. The overall design was a split-plot of a complete randomized block with five blocks that were located within the same stand. Within each block, seven surface treatments were randomly located along a 10 m transect, and within each surface type retention of three species of seed--Picea sitchensis, Pseudotsuga menziesii and Thuja plicata--was tested. To create the surfaces log slabs were mounted on a 30 X 60 cm wooden platform which elevated the slab 5 cm above the forest floor. The log slabs were cut from 40-50 cm diameter logs and had a semicircular cross-section varying in thickness from 8 cm in the center to 1 cm at the edges. Moss- and litter-covered surfaces were created by adding material to the slab surfaces. Bark surfaces used in this experiment were wire brushed to remove moss and litter. One hundred seeds of each species were added to a randomly selected portion of each surface by scattering the seeds from a height of 20 cm. Seeds were exposed between 27 January and 26 February 1982. Surfaces were protected from small mammals and birds by a 12 mm wire mesh 10-15 cm above the surface.

Seeds retained on bark and wood surfaces were determined after 31 days of exposure. Moss and litter surfaces were collected, oven dried and sorted to find the remaining seeds. Arcsine angular transformation was applied to the data before a split-plot of a complete randomized block analysis of variance was calculated. Examination of the log surfaces at the completion of this experiment revealed that many of the Pseudotsuga seeds had been partially eaten, therefore this seed species was excluded from the analysis. In this, and all the following statistical calculations, results were considered significant and highly significant when $0.01<p<0.05$ and $p<0.01$, respectively.

In the second seed retention experiment Picea seeds were used to test differences among three types of moss coverings in addition to wood, bark and litter surfaces. The statistical design was randomized complete blocks with three blocks each of which was located in a different stand. The same mounted, screened log slabs used in the first experiment were used. The surfaces tested were 1) a very thin layer (0.2 cm) of Hypnum circinale which corresponds to a very early period in log surface succession; 2) cushions of Dicranum fuscescens and Rhizominium personii which ranged in thickness from 2 to 4 cm which corresponds to logs that have lain on the forest floor for 10 to 40 years; 3) a 5 cm thick layer of feather mosses E. oreganum and Rhytidiadelphus loreus which is typical of log surfaces >30 years; 4),5) and 6) bare bark of Picea, Pseudotsuga and Tsuga; 7) rotten Tsuga wood; and 8) a litter-covered surface. Two hundred orange-painted Picea seeds were scattered on each surface on 19 December 1982 from a height of 20 cm. The bark and wood surfaces were examined for seeds after 86 days and the moss and litter surfaces were collected at this time. The harvested material was oven dried, screened and sorted to find the seeds. Raw data were tranformed using the arcsine angular method before a randomized blocks analysis of variance was calculated.

Needles on Natural Surfaces

In the first needle retention experiment, the differences in retention of three species of conifer needles-- *P. sitchensis*, *P menziesii* and *T. heterophylla*-- were tested on six natural logs surfaces. The statistical design was a split-plot with complete randomized blocks. All three blocks were located within the same stand. Log surface type was the main plot treatment, while needle species was the sub-plot treatment. The surfaces were the same as those used in the first seed experiment except that sound wood was not used. The surfaces were randomly located along a 10 m transect within each block. The needles were collected from freshly fallen branches, oven-dried and spray painted orange. Each of the six log surfaces within each block was divided into thirds, and each third received 100 needles of a randomly selected species. The needles were scattered on 12 March, 1982 from a height of 20 cm. The subsequent addition needles from litterfall was not restricted. The number of needles retained on the bark and rotten wood surfaces was counted 28, 54, 88, 132, and 238 days after the experiment was started. The number of needles remaining on moss and litter surfaces was estimated by counting the number of needles that had fallen off these platforms and that lay on the surrounding forest floor. The raw precentage data were tranformed before analysis using the angular arcsine method.

In the second needle retention experiment, P. sitchensis and P. menziesii needles were used to test the retentive characteristics of the eight surfaces used in the second seed retention experiment. The primary purpose was to explore the differences in needle retention associated with moss succession on logs. The statistical design was a split-plot of complete randomized blocks with three blocks, each of which was located in a different Picea-Tsuga stand. Log surface was the main plot treatment and the needle species was the sub-plot treatment. Each of the eight log surfaces was divided in half and recieved 100 painted needles, the species being randomly selected. The number of needles on each surface was determined as previously described 21, 42 and 65 days after placement on 19 December 1982. The raw data were transformed using the arcsine angular method before analysis of variance.

Retention of Seeds in Holes

During the course of the experiments using natural surfaces, it became apparent that holes created by insects were crucial in retaining seeds on rotten wood surfaces. An experiment was designed to explore three major variables influencing seed retention within holes: 1) diameter, 2) depth and 3) orientation with respect to the vertical. It was hypothesized that retention would decrease as hole diameter increased, as hole depth decreased and as the angle from the vertical increased. A split-split plot with a randomized complete block design was used to test the effect of these three variables on seed retention in holes. Hole angle was the main-plot treatment, hole depth was the sub-plot treatment and hole diameter was the sub-sub-plot treatment. There were 4 blocks and each was located in a separate stand. Three blocks were within Picea-Tsuga and the fourth within A. rubra forest. Within each block, 4 slopes from the vertical were assigned at random: 0, 33, 66 and 100%. Because materials were limited and only one experimental unit was available for each block, the slope treatments were assigned to different time periods.

The basic experimental unit used to test these hypotheses was a 8 X 50 cm strip of 6 mm thick masonite in which holes were drilled. Hole diameters were 6, 13, 19 and 25 mm; 20 holes each of the two smallest diameters were placed on a single masonite strip, while the two largest each had 20 holes on their own strip. The hole thickness was varied by stacking one to four of the strips, and this gave depths of 6, 13, 19 and 25 mm. Twelve strips, giving 4 diameters for each of 4 thickness were mounted on a 150 X 50 cm masonite sheet which formed the bottom of the holes. This sheet was in turn nailed to a wooden frame for support. The entire surface was protected from the larger seed predators by a cage of 12 mm wire mesh.

The experiment ran from 19 December 1982 to 15 March 1983. To measure seed retention, a single, orange painted Picea seed was placed in the bottom of each hole and exposed for 21 to 23 days. The holes were then examined for the presence of seeds. After the examination, the seeds were removed, the holes filled with fresh seed and the slope changed so that at the end of 86 days each angle had been represented once at each block. In the analysis of the results, a split-split plot analysis of variance using arcsine transformed proportions was performed.

Retention of Seeds in Crevices

Cracks and crevices are also important sites of seed retention on bark and wood surfaces, so the influence of width, depth and angle of cracks upon seed retention was tested. As with holes, it was hypothesized that seed retention should decrease as crack width increases, as crack depth decreases and as angle from the vertical increases. The statistical design was a split-split plot of a randomized complete block design, with 3 blocks each of which was located within a different *Picea*-*Tsuga* stand. Crack slope was the main plot treatment, crack depth was the subplot treatment and crack width was the sub-sub-plot treatment. Four slopes, 0, 33, 66, 100% were assigned over time because only one complete set of depth and width treatments was available for each site. The dimensions of the widths and depths were 6 mm, 13 mm, 19 mm and 25 mm. These were cut along the long axis of 5 X 10 X 30 cm boards using a table saw. On each board one of the 16 combinations of 4 widths and 4 depths was cut. The boards were then mounted inside 5 X 30 X170 cm boxes which were covered with a cage of 12 mm wire mesh. Two boxes were required to mount all 16 of the width and depth treatments. Seed retention was measured by placing 20 orange painted Picea seeds in each crack and counting the number remaining after 21 days of exposure. Once the seeds were counted, they were removed, the slope was changed and fresh seeds were added to start the next trial. This experiment was conducted from 29 January to 11 April and November 9 to 30 of 1983. The data were converted using the arcsine transformation of proportions before the split-split plot analysis of variance was preformed.

Seedbed Abundance

To determine the extent of seedbeds within the Picea-Tsuga type, data from five reference stand maps was used (unpublished maps on file at Research Work Unit 1251, Forest Sciences Laboratory, Corvallis, Oregon). Stands were located in the Cascade Head Experimental Forest, Oregon (1 stand), the Quinault Research Natural Area, Washington (2 stands) and the South Fork of the Hoh River in Olympic National Park, Washington (2 stands). Each map covered 1 to 2 ha and included data on the location, length, end diameters, species and decay class of logs. These data were used to calculate total log cover and cover by species and decay class. Four logs of each species and decay class were sampled at Hoh River and Cascade Head Experimental Forest to determine the extent of bare bark, rotten wood, thin moss (<5 cm), thick moss (>5 cm), and litter cover. The cover of each surface type was occularly estimated for five 2 m segments on the upper half of each log. It was not always possible to find decay class IV and V logs >10 m long, so as many of these logs as were needed to give 40, 2 m long plots were sampled. The cover of each seedbed type was then calculated from the log cover and surface type coverage data.

RESULTS

Seeds on Natural Surfaces

No seeds were observed on *Tsuga* bark, rotten *Tsuga* wood or sound wood surfaces, whereas litter- and moss-covered surfaces retained many seeds (Table III-1). *Picea* and *Pseudotsuga* bark retained some *Thuja* seeds after 31 days, but in proportions far below moss and litter. The interaction between seed species and surface was highly significant. Litter and moss covered logs retained similar quanities of *Thuja* seed, whereas litter retained twice as many *Picea* seeds as moss did. However, since unpainted *Picea* seeds were harder to see than the *Thuja* seeds this may be a methodological artifact .

Results of the second seed rentention experiment were similar to the first: moss and litter surfaces retained seeds better than rotten wood or the three bark types (Table III-2). Block and log surface effects were highly significant . Seed retention was similar for all moss treatments, although the *Eurhynchium*-*Rhytidiadelphus* mats retained more seeds (72%) than the other two moss surfaces (48-52%). Of the three bare bark surfaces, *Pseudotsuga* retained the largest

Table III-1. Percentage of Sitka spruce (*Picea sitchensis*) and western red cedar (*Thuja plicata*) seeds retained upon different log surfaces after 31 days of exposure.

Species of Seed	LOG SURFACE TYPE						
	Moss	Litter	*Picea* Bark	*Pseudotsuga* Bark	*Tsuga* Bark	Rotten Wood	Sound Wood
Picea sitchensis	21.8 (14.74)[1]	43.6 (19.20)	0(0)	0(0)	0(0)	0(0)	0(0)
Thuja plicta	69.6 (10.26)	71.6 (6.98)	0.4 (0.89)	1.4 (1.95)	0(0)	0(0)	0(0)

1/ mean (standard deviation), N = 5.

Table III-2. Retention of *Picea sitchensis* seeds and *Picea sitchensis* and *Pseudotsuga menziesii* needles retained on eight kinds of log surfaces. Seeds were exposed 86 days and each observation was based on 200 seeds. Needles were exposed for 65 days and each observation was based on 100 needles.

Log Surface	*Picea* Seeds	*Picea* needles	*Pseudotsuga* needles
Hypnum circinale mat 0.2 cm thick	52.0(28.60)[1]	94.0(1.87)	93.7(4.14)
Dicranum-*Rhizomnium* mat 2-3 cm thick	48.3(17.39)	92.7(0.41)	91.0(3.74)
Eurhynchium-*Rhytidiadelphus* mat 5 cm thick	71.7(20.36)	99.3(0.82)	97.7(1.08)
Picea-*Tsuga* litter 3 cm thick	58.9(28.92)	93.0(4.42)	83.3(7.36)
Picea bark	0.2(0.21)	4.7(2.48)	3.3(2.86)
Pseudotsuga bark	0.5(0)	3.7(1.47)	8.3(0.41)
Tsuga bark	0(0)	0.3(0.41)	1.3(1.08)
Rotten *Tsuga* wood[2]	0.5(0.62)	7.7(3.19)	8.3(2.27)

---

1. mean (standard deviation), N = 3.

2. The log was decay class III.

fraction of seeds (0.5%), which was probably a result of deeper crevices found on this surface. The only seeds retained on rotten wood were those in insect galleries and cracks. In summary, the second seed retention experiment confirmed that moss and litter retain seeds better than other surfaces and that moss succession will produce a minor increase in seed retentive qualities. It is probably during the transition from a moss-free to a moss-covered surface that the major increase in retentive ability occurs.

Needles on Natural Surfaces

In the first needle retention experiment, needles of all three species were rapidly lost from wood and bark surfaces (Figure III-1) and many were relatively free of needles in as little as 30 days. After 238 days all the bark and wood surfaces were quite similar and retained only a few of the original needles (0-10%). In contrast, Eurhynchium and litter covered surfaces retained the most needles (97-98%). There was a significant needle species and log surface interaction at 238 days. However, this interaction was caused by a single Tsuga bark surface that retained 57% of the Pseudotsuga needles; this surface was partially protected by an overhanging fern. When this observation was removed from the analysis, surface type was highly significant.

In the second needle experiment, needles were lost from the bark and wood surfaces faster than in the first experiment. This was

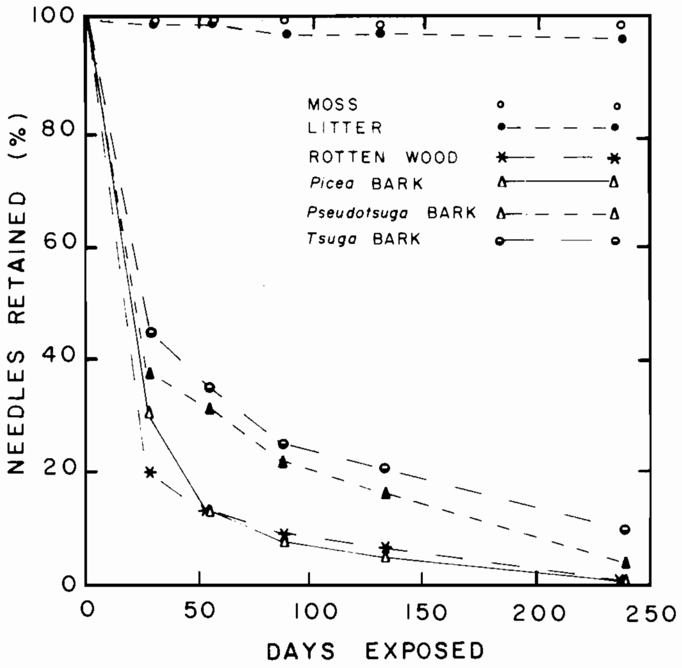

Figure III-1. Percentage of needles retained on wood-, bark-, moss- and litter-covered log surfaces as a function of time.

probably caused by greater precipitation during the winter experiment. The dichotomy between moss- and litter-covered surfaces and those of bark and wood was quite apparent (Table III-2). The significant interaction between needle species and log surface type, appears to be caused by random fluctuations rather than by any biological mechanism. In contrast, differences among surface types was highly significant and paralleled earlier findings. It therefore seems reasonable to ignore the interaction and interpret the main effects. Of the moss surfaces, Eurhynchium-Rhytidiadelpus mats retained the highest proportion of needles (98.5%), while the other two moss surfaces kept a slightly lower fraction (92.8%). Because the differences among moss surfaces were small, the major increase in needle retention probably occurs as logs are colonized. Needle retention on litter-covered surfaces averaged 88%, slightly less than moss surfaces, but much higher than wood or bark surfaces. Rotten Tsuga wood retained more needles than bark surfaces (8 versus 5%) because needles were trapped in cracks and insect galleries.

Seed Retention in Holes and Cracks

Crevices, and holes were the primary microsites which retained seeds on rotten wood and bark surfaces. Retention on these surfaces depends not only on the total area covered by holes and cracks, but also their diameter, depth and orientation.

Diameter X depth interaction, diameter and depth effects were highly significant in the artificial hole experiment. There were also significant effects due to blocks, slope and the diameter X slope interaction. The probability that a seed would remain in a hole increased as hole diameter decreased and hole depth increased (Figure III-2). This general pattern was influenced by the diameter X depth interaction. In the case of shallow holes (<6 mm) there was only a minor response to hole diameter; small diameter holes were as likely to lose seeds as large diameter holes. In contrast, retention increased as diameter decreased for holes deeper than 6 mm. The increase in seed retention as slope from the horizontal increases was probably due to protection offered by the upper side of the hole which reduced the impact from rain drops. It was originally hypothesized that increasing the slope would decrease the vertical distance needed to leave a hole and thus decrease seed retention. However, these effects were apparently offset by increased protection.

Overall seed retention patterns for artificial cracks was similar to those for holes. There were highly significant effects due to crack depth, width, the width X slope interaction and the width X depth interaction. As with holes, seed retention increased as crack width decreased and as crack depth increased (Figure III-3). However, shallow cracks (6 and 13 mm) exhibited less change as a function of width than did deeper cracks; this result suggests a depth below which the width effect is very small. The width X slope interaction was attributable to the fact that at 0% slope there was little increase in

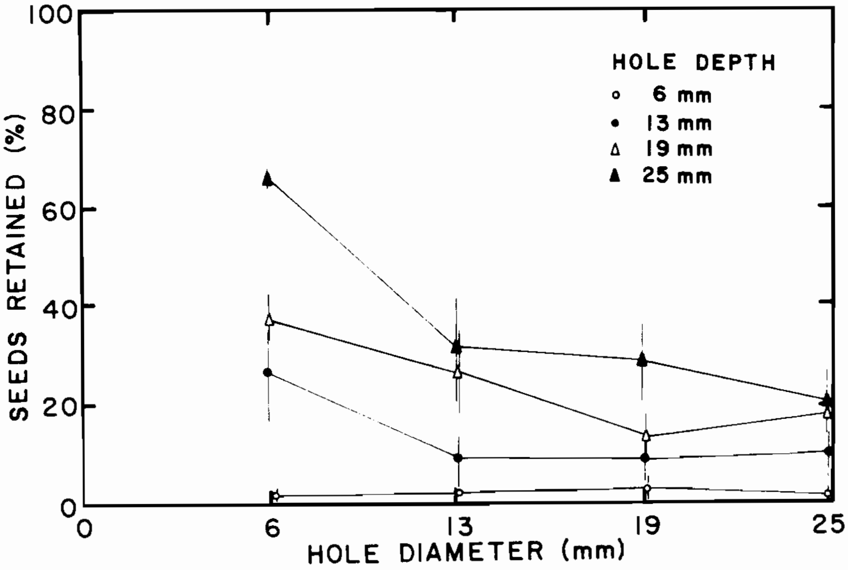

Figure III-2. Probability of <u>Picea</u> seed retention in relation to hole diameter and depth. The slope was equal to zero. Each point represents the mean proportion retained at 21 days and the vertical lines are standard errors (N = 4).

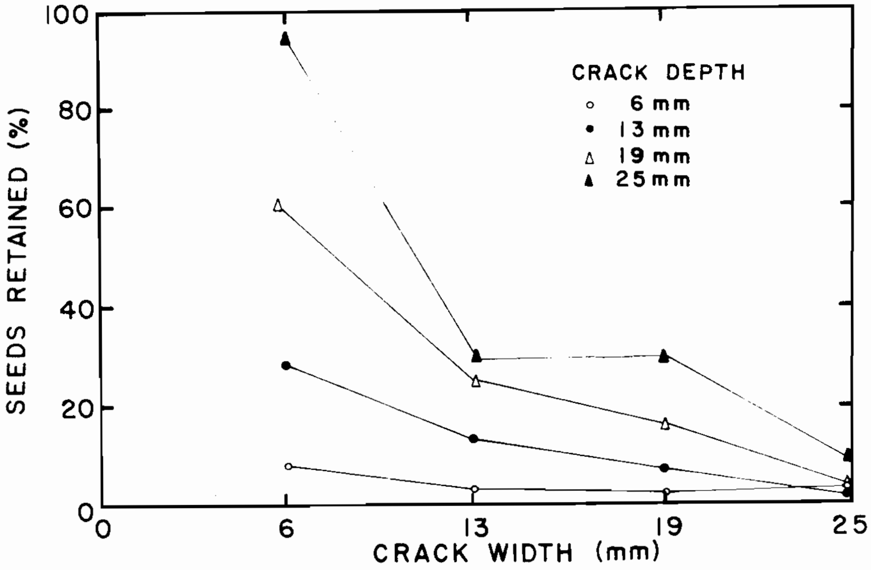

Figure III-3. Probability of Picea seed retention in relation to width and depth of cracks with a slope of 66%. Each point represents the mean proportion retained at 21 days.

retention as depth increased, but as slope increased the effect of depth increased. In summary, relationships between retention and depth, width and slope of cracks appear generally similar to those for holes, although holes apparently retained more seeds than cracks.

Seedbed Abundance

Total projected log cover in the five *Picea* -*Tsuga* stands averaged 9.9% and ranged from 6.1 to 14.3% (Table III-3). *Tsuga* logs were more common than *Picea* with mean total projected covers of 7.6 and 2.3%, respectively. On average, 23% of the logs were *Picea*. However, the proportion that was *Picea* ranged from 2 to 55%, reflecting stand composition. Class III logs (i.e., those in intermediate stages of decay) were the most common decay class in all stands with a mean projected cover of 5.1%. Class I (i.e., freshly fallen) and V logs (i.e., those in very advanced decay state) were the least abundant with mean projected cover of 0.45 and 0.44%, respectively. The observed distribution of decay classes matches that expected for a population of logs in steady-state (Harmon et al. 1986).

There were major differences among decay classes in terms of surface type (Table III-4). Bark was the major surface type for class I *Picea* and *Tsuga* logs with a mean cover of 70.4 and 80.8%, respectively. The proportion of bare bark decreased markedly as logs age. Class II logs had a mean of 19.5% bare bark cover, while class III logs had 0.5% bare bark cover . The major surface type for class

Table III-3. Projected log cover by species and decay class for 5 *Picea sitchensis*-*Tsuga heterophylla* stands in Oregon and Washington

Species	*Picea sitchensis*					*Tsuga heterophylla*					
Decay Class	I	II	III	IV	V	I	II	III	IV	V	TOTAL COVER%
Mean Cover%	0.05	0.48	1.28	0.48	0.04	0.4	1.34	3.86	1.59	0.41	9.93
Standard Error (N = 5)	0.06	0.33	0.65	0.18	0.04	0.22	0.21	1.20	0.28	0.17	1.59

Table III-4. Mean proportional cover of seedbed types for *Picea sitchensis* and *Tsuga heterophylla* logs for each of 5 decay classes.

Species		*Picea sitchensis*					*Tsuga heterophylla*					
Decay Class		I	II	III	IV	V	I	II	III	IV	V	TOTAL COVER%
Surface Type												
Bare Bark	X	70.4[1]	16.3	0.1	0	0	80.8	72.8	0.7	0.1	0	0.78[2]
	SE	9.7	5.7	0.1	0	0	3.3	6.1	0.4	0.2	0	
Wood	X	0.5	4.9	10.1	3.6	1.6	0	0	2.5	3.6	1.4	0.33
	SE	0.5	2.7	3.4	1.2	1.0	0	0	1.2	1.5	0.8	
Litter	X	16.7	4.9	10.4	13.3	26.6	2.3	8.3	1.2	2.8	0.5	0.45
	SE	6.0	2.5	5.6	6.6	11.8	1.1	3.4	0.6	1.0	0.2	
Thin Moss	X	12.4	73.9	72.8	34.2	14.1	16.9	68.9	58.4	41.4	18.0	5.44
Mats	SE	5.5	7.2	9.1	9.5	5.9	3.0	5.8	13.4	9.4	7.6	
Thick Moss	X	0	0	6.6	48.9	57.6	0	0	37.0	52.1	80.0	2.93
Mats	SE	0	0	6.6	11.7	13.5	0	0	13.9	10.6	7.7	
	N	8	8	8	10	11	8	8	11	13	17	

1/ Proportion of log covered by surface

2/ This is the product of decay class specific surface cover and the proportion of ground surface covered by the decay classes summed over all decay classes.

II and III logs were thin moss mats (<5 cm), which covered a range of 69 to 74% of each of these decay classes. Deep moss mats (>5 cm), began to appear in decay class III, and increased in both decay classes IV and V for both species of log.

Summing the product of log cover and surface type proportions for each decay class over all decay classes yielded the total cover of each surface type (Table III-4). Thin moss mats comprised the majority of the log seedbeds (54.8%) and covered an average of 5.4% of the stand area. Thick moss mats were the second-most abundant log-related seedbed and covered 29.2% of the logs and 2.9% of the average Picea-Tsuga stand. The other seedbed types each covered less than 1% of the stand area and only litter, because of its high seed retention, would be an important site for tree seedling recruitment. Assuming logs covered by thin moss mats and litter are the only sites of seedling recruitment, 5.9% is the average surface area for tree seedling recruitment.

DISCUSSION

Seed and needle retention varies considerably by log decay class and seedbed type. Moss- and litter-covered surfaces have similar retentive qualities, but because of their greater extent, moss-covered surfaces are more important. Logs retain more seeds and litter as they age, primarily because of increases in moss cover and not moss thickness. Retention of needles on logs by mosses helps build an organic soil and this increases the survival and growth of tree seedlings (Chapter IV). As logs age, mosses increase in thickness until young tree seedlings are excluded by competition (Chapter II). Therefore, class IV and V logs recruit few seedlings in spite of high seed retention and a greater degree of wood decay.

One way to envision the combined effects of seed retention and competition is to model the fate of a cohort of seeds during their the first year (Figure III-4). The results of this study and of Chapter II were used to calculate the proportion of seeds surviving the pathways illustrated in Figure III-4. Assuming that seedfall is proportional to seedbed cover, 90% of the seeds will land on the undisturbed forest floor, while the remaining 10% will land on log seedbeds. Of those landing on logs, most will be on either thin (55%) or thick (30%) moss mats. A much smaller fraction will land on bark (8%), wood (3%) and litter (5%) seedbeds. Very few seeds (<1%) will be retained upon the bark and wood seedbeds. In contrast, one-half or more of the seeds landing upon litter or moss will be retained. First year survival of seedlings growing on moss mats is a function of moss thickness; Mean first-year survival rate was 40% for mats <5 cm thick and was 4% for mats >5 cm thick (Chapter II). First-year survival on litter seedbeds is an increasing function of litter depth (Chapter IV). However, since litter depths were not sampled in the present study it was assumed that 25% of the seedlings would survive the first year on the average litter seedbed. Survival rates on natural bark and wood seedbeds have not been measured, so a very liberal value of

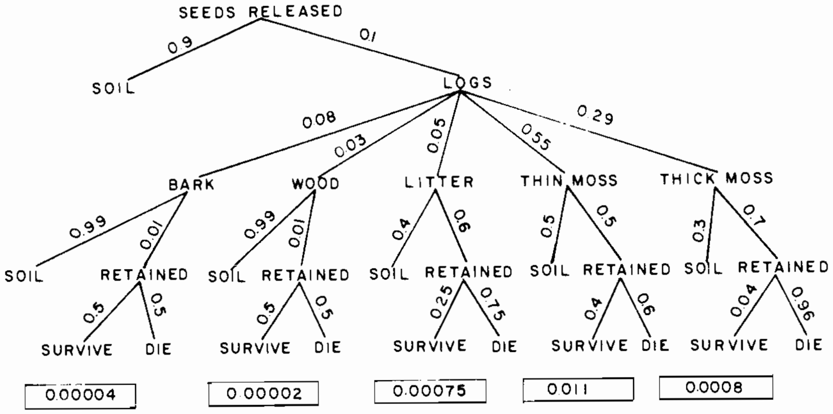

Figure III-4. Theoretical survival of seedlings within a typical <u>Picea sitchensis</u>-<u>Tsuga heterophylla</u> forest by seedbed type. The data on first-year survival on moss mats and litter are from Chapters II and IV, respectively. The numbers in boxes represent the proportion of the original cohort surviving upon each seedbed.

50% was assumed. By multiplying probabilities along the chain of events described from seed release to the end of the first year, one can calculate the probability a seed (or the proportion of the intial cohort) will survive the first year on a given seedbed. Approximately 1.3% of the original cohort would survive on all the log seedbeds but most of the seedlings (87%) would occur on thin moss seedbeds (i.e., 1.1% of the original cohort). Given the overall survival rate on logs, it is also possible to calculate a theoretical first-year survival rate on soil by knowing the proportion of seedlings growing on forest floor versus logs. For example, to get the 98:2 log to soil seedling ratio reported by McKee _et_ _al_. (1982), the first year survival rate on soil would be as low as 0.02%. This is an order of magnitude lower than the rate on soil found at Cascade Head, but similar to that of Hoh River (Chapter II). The rates of seed retention, survival probabilities, and seedbed distribution vary from stand to stand as well as from year to year. Moreover, the effects of predation and variations in light were not considered in this analysis. The values presented here are therefore only theoretical. Nonetheless, they probably do reflect the order of magnitude of survival to be expected in a _Picea_-_Tsuga_ stand and indicate the very high rate of mortality occuring in the first year of a cohort's existence.

Although the total proportion of seedlings surviving the first year is indeed small, the actual number of seedlings recruited can be very large because of the abundance of seed rain within the

Picea-Tsuga type. Ruth and Berntsen (1955) reported a range of 6.7×10^6 to 3.5×10^7 sound seeds/ha falling in forests of coastal Oregon during a good seed year. Assuming that 1.3% of this crop survives on logs and that logs are the sole suitable seedbed, a recruitment of rate of 9×10^4 to 4.6×10^5 seedlings/ha would occur in a good seed year. Therefore, in spite of the very low overall survival rate and low availability of suitable seedbeds, the actual amount of recruitment could be very large and since most of these seedlings are restricted to a limited area, the amount of competition among seedlings in later years would be very high. Also, in spite of the very low rates of survival calculated for undisturbed forest floor, the number of seedlings growing on undisturbed forest floor can be large after a good seed-year and could range from 1.2 to 6.3×10^3 seedlings/ha. This density would be more than adequate to replace the stand if survival rates improved markedly the second year. However, if the survival rates do not improve the second year, then seedling recruitment on forest floor would be very low to non-existent at the end of the second year (0.24-1.26 seedlings/ha).

In summary, it remains to be shown that tree recruitment in Picea-Tsuga forests is in fact seedbed limited because little is known about long-term survival on logs and the forest floor. There is little doubt, however, that a large proportion of seedlings occur on log-related seedbeds and that these seedbeds differ considerably in terms of their extent, retentive qualities and survival characteristics. Because of the heavy seed rain in Picea-Tsuga forests, adequate recruitment of one-year-old seedlings could occur even on forest floors. Further studies on seedling survival after the first-year, especially on soils, would be quite revealing since continued low survival on soils would strongly indicate that tree recruitment in old-growth Picea-Tsuga forests is substrate limited.

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IV. THE INFLUENCE OF LITTER ACCUMULATIONS AND CANOPY OPENNESS ON PICEA SITCHENSIS AND TSUGA HETEROPHYLLA SEEDLINGS GROWING ON LOGS

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ABSTRACT

The influence of litter and humus accumulations, on the surface of logs and canopy openness upon growth and survival of *Picea sitchensis* and *Tsuga heterophylla* seedlings was tested experimentally at Cascade Head Experimental Forest in Oregon. Survival rates of both species increased asymtotically as litter accumulations on logs increased. Mean maximum survival was 62% for *P. sitchensis* and 34% for *T. heterophylla*. Seedling survival peaked when tree canopy cover ranged from 70-80% with lower survival at either high or lower values. Seedling growth increased as a synergistic function of litter accumulation and canopy openness with the greatest growth occurring when organic mats were deep and the tree canopy was open.

INTRODUCTION

Logs are a major site of tree regeneration in the moist, temperate *Picea sitchensis*-*Tsuga heterophylla* forests of the Pacific Northwest. In these forests, rotten wood covers from 6 to 14% of the forest floor (Chapter III) but may account for as much as 98% of the tree regeneration (McKee *et al*. 1982) indicating that logs are more favorable for seedling establishment than other seedbeds. The close association between logs and tree seedlings is caused, in part, by a luxuriant moss and herb layer that are out-competes young tree seedlings on the forest floor (Chapter II). Even rotten wood is a good seedbed during stages when moss mats sufficient to exclude tree seedlings are absent.

Tree seedlings growing on logs often root in litter which has accumulated upon the log surface (Minore 1972). Wood decays slowly in these forests (Graham and Cromack 1983, Grier 1978), and surficial litter accumulations will form a seedbed faster than wood decay. Furthermore, a thick layer of competing mosses can develop on log surfaces before wood decay provides a suitable rooting medium. Since the bulk of this litter is derived from decaying needles and bryophytes, it is a better nutrient source than rotten wood alone (Minore 1972). Another consideration is the superior ability of moss- and litter-covered surfaces to retain seeds (Chapter III). Seeds falling on rotten wood or bark surfaces are more likely to be blown or washed off than those falling on organic mats. All these factors indicate that litter deposits on logs are important seedbeds in *Picea-Tsuga* forests. This study was initiated to assess the effect litter biomass and canopy openness have upon tree seedling growth and survival.

STUDY AREA

The experiments were conducted within the Neskowin Crest Research Natural Area at Cascade Head Experimental Forest near Otis, Oregon. The forest lies within the *Picea sitchensis* Zone (Franklin and Dyrness 1973) which occurs along the coastal Oregon and Washington. The climate is cool and very moist with a mean annual temperature of 10°C and 250 cm of annual precipitation (Greene 1982). The heaviest precipitation occurs during the winter, while June through August are relatively rain-free (16 cm). Forests at Neskowin Crest are dominated by *Picea sitchensis* and *Tsuga heterophylla* (Greene 1982), originating after a catastrophic fire which occured during the 1840's (Morris 1934). The elevation of the experimental site is 400 m.

METHODS

The overall design of the experiment was a split-plot of a randomized complete blocks design, with eight logs as the block effects, five litter biomass treatments as the main plot effect and two seedling species as the sub-plot effect. One 36 X 70 cm wooden tray 10 cm deep was nailed onto each of eight freshly fallen Picea or Tsuga logs. Logs varied in diameter from 60-150 cm and were located beneath a wide range of canopy conditions. The log formed the tray bottom and the top was covered by a wire screen cage of 12 mm mesh to reduce seed predation. Each box was divided into 5 equal segments with wooden dividers to give an area of 470 cm^2 per litter biomass treatment. Litter and humus were added so that each of the treatments (Table IV-1), which ranged from a light litter covering (0.74 kg/m^2) to a deep layer of litter and humus (9.32 kg/m^2), was represented once in each tray. Biomass treatment was randomly assigned within each tray. Litter and humus were obtained from the base of two Picea and two Tsuga trees. Each layer was throughly mixed and large fragments of wood and bark were removed. During March 1982, 50 Picea seeds and 50 Tsuga seeds were scattered on the surface of a randomly selected half of each biomass treatment. This gave an initial seed density of 1,000 $seeds/m^2$, which represents a good seed-year for both species.

Seedlings were counted at 100 day intervals from germination in June 1982 until October 1983. Seedlings from natural seeding in 1983 were removed to reduce competition effects with the planted 1982 seedlings. Seedlings were harvested in October 1983 for biomass analysis. Root systems of harvested seedlings were washed in an aqueous.solution of sodium tripolyphosphate to remove adhering soil litter and then separated from the above ground parts. Needles were removed from the stems by oven drying the tops and hand picking the

Table IV-1. Dry weight (kg/m^2) of litter and humus added to trays in litter biomass experiment.

	Treatment				
	1	2	3	4	5
Litter	0.74	1.11	1.49	1.49	1.49
Humus	0	0.49	1.96	3.91	7.83
Total	0.74	1.60	3.45	5.41	9.32

foliage. Roots, stems and needles were oven dried for 24 hours at 55^{o} C. Seedlings of both species were selected over a range of sizes to develop a double logarithmically transformed regression equation that would predict biomass from total stem length (Table IV-2). This was necessary, because the biomass of the seedlings could not be measured directly in 1982. The stem length of each seedling in 1982 was therefore used to predict root, stem and needle biomass at the end of the first growing season.

Seedling survival and growth appeared to vary with canopy closure. To test for these effects, a high contrast, black and white fisheye (180°) photograph was taken of the canopy above each log. These photographs were then digitized to measure the degree of canopy opening. This provided a relative measure of the amount of diffuse light that reached seedlings.

Survivorship data were altered by using the arcsine transform of proportions before the split-plot analysis of variance on the effect of litter biomass on survival was preformed. Two types of transformations were used to fit the relationship between the number of survivors and litter biomass. In the first, the natural logarithm of X_1, the amount of litter (kg/m^2) was regressed against, Y, the mean percentage of survivors. The second regression model was a rectangular hyperbola:

$$Y = \frac{B_o \quad X_1}{B_1 + X_1} \qquad (1)$$

where Y is the mean percentage of survivors, X_1 is litter biomass (kg/m^2), B_o is the maximum percentage surviving and B_1 is the

Table IV-2. Regression equations used to predict seedling biomass from total stem length. The equation form is $Y = B_0X^{B1}$ where X is the stem length (mm), B_0 and B_1 are regression constants and Y is the component mass (mg).

Species Component	B_0 1/	B_1	r^2	N
Picea sitchensis				
Needles	0.009	2.03	0.87	34
Stem	0.005	2.01	0.89	34
Roots	0.008	1.90	0.66	34
Tsuga heterophylla				
Needles	0.037	1.58	0.94	32
Stem	0.025	1.53	0.94	32
Roots	0.057	1.304	0.82	32

1/ Corrected for bias using correction factor of Baskerville (1972).

litter biomass where survival equals half the maximum value. The constants B_0 and B_1 were calculated from a double reciprocal transformation of X_1 and Y (Lehninger 1975, p. 198). Survival and growth of each species and litter treatment was also analyzed using multiple regression with canopy openness, litter biomass and combinations of these two terms as independent variables. Unless noted elsewhere, all statistical tests were deemed significant or highly significant when $0.01<p<0.05$ or <0.01, respectively.

RESULTS

Survival

Mortality was highest during the first 50 days of growth (Figure IV-1). At that time there were no significant differences among the litter treatments, although there was a highly significant effect due to species and a significant effect due to blocks. Picea survived better than Tsuga (59% versus 39%). The block effect was due to very low survival in the tray located under the most open canopy. After 90 days of growth, the numbers of survivors declined on the three thinnest organic layers (i.e., 0.74, 1.60 and 3.45 kg/m^2), but remained constant on the two deepest layers. At the end of 200 days the final ranking of the litter layers had developed, although mortality continued on the thinnest layers.

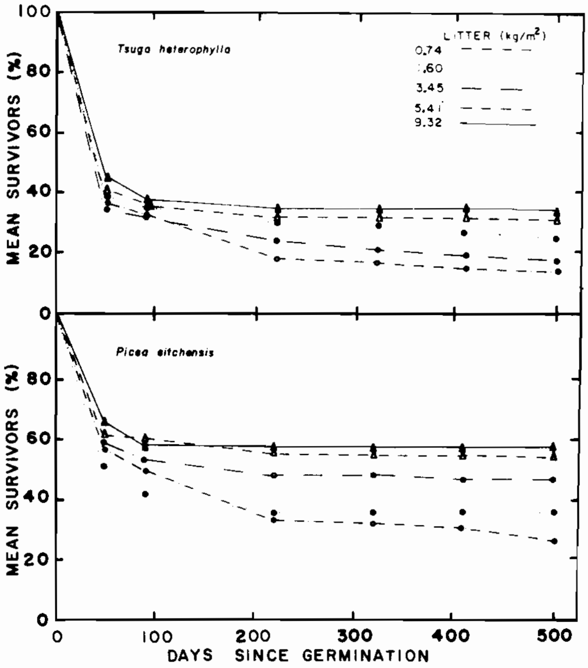

Figure IV-1. Mean survivorship of A) _Picea_ _sitchensis_ and B) _Tsuga_ _heterophylla_ seedlings on logs as a function of time since germination and litter biomass upon logs.

At 500 days, survivorship of both species increased with litter biomass and appeared to asymtotically approach a maximum value of 62% for Picea and 34% for Tsuga (Figure IV-2). For this period there were highly significant effects due to blocks, litter biomass and species. As at 50 days, Picea had more survivors than Tsuga for all litter treatments. The regression of survival on the logarithm of litter biomass for Picea was highly significant, but not for Tsuga ($0.10>p>0.05$) (Table IV-3). The poorer fit of the Tsuga regression was due to a lower than expected survival at the intermediate litter biomass value (3.4 kg/m^2). When this point was excluded the regression became highly significant and the coefficient of determination (r^2) increased to 0.94. The rectangular hyperbola regression was also highly significant for Picea but not for Tsuga. Exclusion of the single intermediate organic biomass data point for Tsuga gave a highly significant relationship with a higher value of B_1 (1.4) than the non-significant regression.

The highly significant effect due to blocks appears to be related to the degree of canopy openness (Figure IV-3). Stepwise multiple regression analysis using the proportion of open sky (X_1), $X_1{}^2$, the litter biomass (X_2 in kg/m^2) and $\ln X_2$ as independent variables was used to test the combined effect of canopy openness and litter biomass on survival. The $\ln X_2$ term was used because it was significant when litter biomass effects were examined alone. This

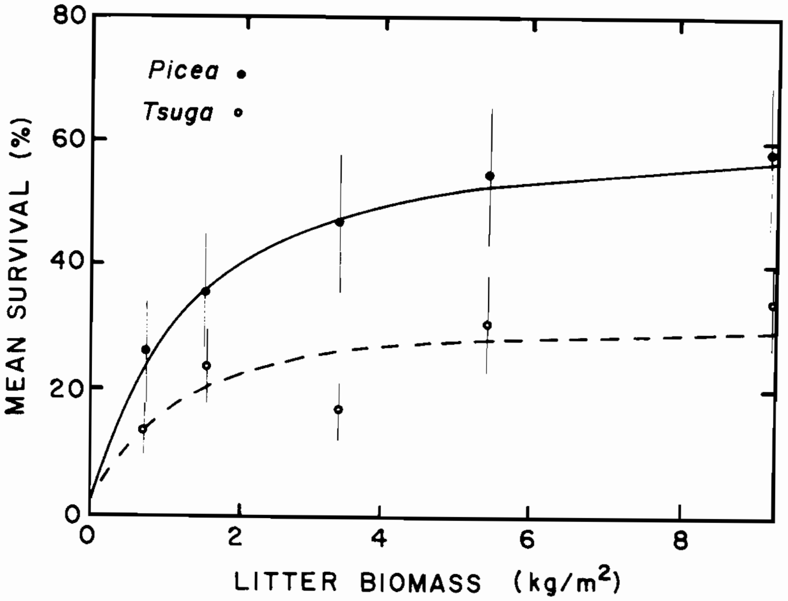

Figure IV-2. Mean survivorship of Picea sitchensis and Tsuga heterophylla seedlings at 500 days after germination as a function of litter biomass placed upon a log. The regression equations predicting the survival response to litter biomass are from Table IV-3. The solid line represents the regression for P. sitchensis, and the dashed line represents the regression for T. heterophylla. Standard errors are indicated with vertical lines (N=8).

Table IV-3. Regression equations for predicting survival (%) of two-year-old *Picea sitchensis* and *Tsuga heterophylla* seedlings from litter biomass (kg/m^2). Two regression models, double logarithmic and rectangular hyperbola, were used.

Species	B_0	B_1	r^2[1]	N
		logarithmic		
Picea sitchensis	30.6	13.2	0.99^{**}	5
Tsuga heterophylla	16.8	7.2	0.69^{ns}	5
		rectangular hyperbola		
Picea sitchensis	63	1.08	0.99^{**}	5
Tsuga heterophylla	42	0.96	0.69^{ns}	5

[1] ns not significant; ** $p<0.01$

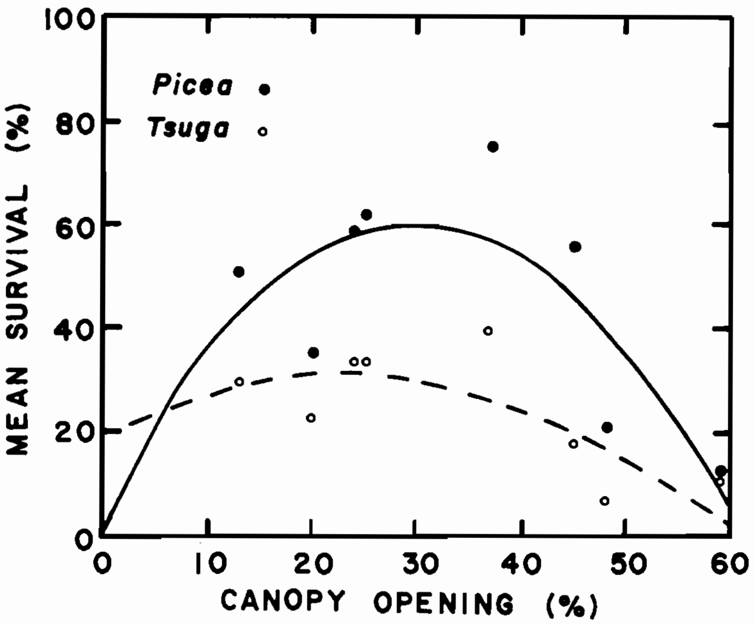

Figure IV-3. Mean survivorship of <u>Picea sitchensis</u> and <u>Tsuga heterophylla</u> seedlings 500 days after germination as a function of canopy opening. Data points represent the mean for litter biomass treatments (N=5).

analysis indicated the following equations were highly significant for Picea and Tsuga, respectively:

$$Y = -35.7 + 520\ X_1 - 795X_1{}^2 + 13.1nX_2 \quad r^2 = 0.52 \quad N = 39 \quad (2)$$

$$Y = 26.8 - 64X_1{}^2 + 8.1nX_2 \quad r^2 = 0.40 \qquad N = 37 \quad (3)$$

These equations predicted maximum survival of P. sitchensis with 33% open sky and reduced survival with either more open or closed canopies. Tsuga survived best under closed canopies and mortality increased as the canopy opened. The multiple regressions also indicated that Picea had greater survival than Tsuga for all combinations of canopy openness and litter depth except where canopies were <5% open.

Growth Rates

The proportion of open sky (X_1), $X_1{}^2$, litter biomass (X_2 in kg/m^2), $X_2{}^2$, and the interaction term, $X_2X_1^2$, were used as independent variables in a stepwise regression analysis of seedling biomass. Use of the complex interaction term seemed appropriate as a visual analysis of the data revealed that seedling biomass was linearly related to litter biomass, and curvilinearly related to canopy openness. Moreover, low values of either variable were associated with low seedling biomass, a further indication of an interaction (Figure IV-4).

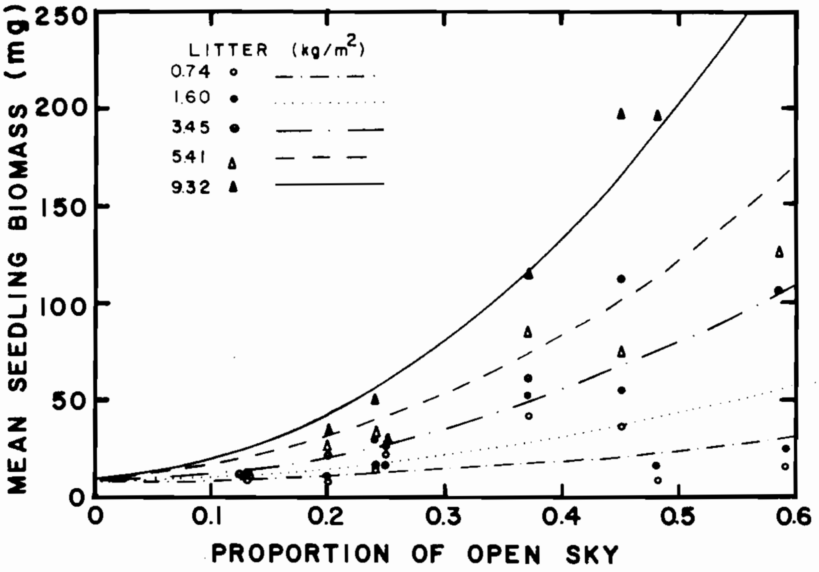

Figure IV-4. Predicted versus observed values of <u>Tsuga heterophylla</u> seedling biomass (mg) after 500 days of growth as a function of portion of open sky (X_1) and litter biomass (X_2). The curves were plotted from the regression in Table IV-5.

The biomass of *Picea* needles and roots at the end of one growing season did not vary significantly as a function of any of the independent variables. *Picea* stems and total biomass as well as *Tsuga* needle, stem, root and total biomass were significantly related to the interaction term but not to the other terms. The general form of these equations is:

$$Y = B_0 + B_1 \; X_2 \, X_1^{\;2} \qquad (4)$$

where Y is biomass (mg), X_1 is the portion of open sky, X_2 is the litter biomass (kg/m^2) and B_0 and B_1 are regression constants. However, this independent variable accounted for a very small portion of the biomass variance and had low predictive value (e.g., the maximum r^2 of the six was 0.16). *Picea* seedlings were significantly larger than *Tsuga* in terms of mean needle, stem, root and total biomass at the end of a single growing season. (Table IV-4).

At the end of the second growing season (500 days), seedling biomass increased synergistically with increasing litter biomass and canopy openness. The relationships between needles, stem, root and total seedling biomass of both species and the interaction of canopy openness and litter biomass described in equation 4 were highly significant. Other terms were added in later interations of the stepwise procedure, but they were usually not significant or added in

Table IV-4. Predicted mean biomass (mg) for one-year-old *Picea sitchensis* and *Tsuga heterophylla* seedlings.

Components[1]	*Picea*			*Tsuga*		
	X	SE	N	X	SE	N
	mg			mg		
Needles	4.7	0.16	39	3.8	0.18	37
Stem	2.5	0.08	39	2.6	0.10	37
Roots	2.9	0.09	39	2.6	0.10	37
Total	10.1	0.33	39	8.5	0.37	37

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[1] These values were predicted from stem measurements and equations in Table IV-2.

a consistant order. Addition of the main effects added 0.01-0.07 to the coefficient of determination. Therefore only regressions of the form of equation 4 are reported here. These regressions explained a high proportion of the biomass variation; coefficients of determination (r^2) ranged from 0.77 to 0.89 (Table IV-5). Figure IV-4 illustrates the relationship between total *Tsuga* seedling biomass and litter biomass and canopy opening. Growth was greatest with open canopies and deep litter accumulations. Growth was limited when either factor was low. The response of growth to litter biomass appeared linear, whereas the response to canopy openness was curvilinear; hence as canopy openness increased it became more effective in promoting growth.

DISCUSSION

Heavy litter accumulations are often viewed as detrimental to conifer seedling survival (Davis and Hart 1961, LeBarron 1948, Moore 1926, Place 1955 and Smith 1955). Deep litter mats can prevent seedling root systems from quickly reaching mineral soil. Since litter dries more readily than mineral soil, seedlings with roots that penetrate to the mineral soil are at an advantage in terms of water balance. However, on logs sound underlying wood can not serve as a rooting medium and overlying litter is, therefore, the major source of water and nutrients for seedlings. Increasing litter accumulation will increase the availability of both water and nutrients for

Table IV-5. Regression equations to predict *Picea sitchensis* and *Tsuga heterophylla* biomass after 2 growing seasons from the interaction of litter biomass and canopy opening. The general form of the regression equation is $Y = B_0 + B_1 X_2 X_1^2$ where Y is the mean biomass (mg), X_2 is the litter biomass per plot (kg/m^2), X_1 is the proportion of the canopy that is open and B_0 and B_1 are regression constants.

Species component	B_0	B_1	r^2	N
Picea sitchensis				
needles	8.25	33.83	0.84	39
stem	3.30	25.37	0.77	39
roots	2.18	28.19	0.78	39
total	13.3	87.40	0.84	39
Tsuga heterophylla				
needles	5.89	34.30	0.80	37
stem	1.77	28.19	0.89	37
roots	2.52	19.27	0.78	37
total	10.18	81.77	0.87	37

seedlings in this case. Abundant precipitation, heavy cloud cover and low temperatures also may allow seedlings to survive and grow on these organic mats within the Picea sitchensis Zone. In drier regions, even thick organic mats may dry and reduce seedling survival.

Seedling survival should increase with litter biomass because water and nutrient storage would increase. However, seedling root systems can only explore a limited volume of litter. Increasing the volume of litter above this point should not increase survival and other factors should become limiting. The shape of the relationship between seedling survival and litter biomass indicates that factors other than water and nutrient relationships do become limiting when organic mats are thick. The response of seedling survival to canopy cover is complex with reduced survival due to shading under closed canopies and drying under open canopies.

Competition should have increased mortality rates if these experiments had continued. Competition-caused mortality should occur earliest on the thickest organic mats under moderately open canopies, because these sites had the highest survival rate and a moderate growth rate. The interaction of canopy openness and litter biomass controls seedling growth and this indicates that both factors can limit seedling growth. These limitations, especially those imposed by litter, are likely to increase as seedlings grow.

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V. PLANT SUCCESSION ON LOGS AT HOH RIVER, OLYMPIC NATIONAL PARK, WASHINGTON

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ABSTRACT

The general features of plant succession on *Picea*, *Pseudotsuga* and *Tsuga* logs in the alluvial forests of Hoh River, Washington were examined using the chronosequence method. Bark fragmentation patterns differed markedly among species; *Picea* and *Tsuga* lost most of their bark in 60 years and *Pseudotsuga* in 190 years. Bark was 85-90% covered by bryophytes within 11-19 years of tree fall. Live and dead bryophyte biomass reached steady-state levels on bark of 325 and 685 g/m^2 within 90 and 150 years, respectively. Humus biomass on bark increased very slowly the first decade and rapidly after 20 years; a steady-state biomass of 4400 g/m^2 is predicted after 150 years. Tree density on bark peaked at $140/m^2$ at 15-25 years and then thinned at a rate of 8%/yr. Wood surfaces appear similar to bark surfaces in general temporal trends of bryophyte and humus biomass and tree density . Bark sloughing strongly influenced successional development by removing plants and by reinitating the sere on a small

scale. Modeling results suggest that many of the differences among log species could be due to bark fragmentation patterns. Although logs are a major site of seedling establishment in Picea-Tsuga forests, the combined effects of high competitive stress, bark fragmentation and toppling greatly reduces long-term survival of trees on this seedbed.

INTRODUCTION

In northern temperate forests, rotten wood is often a seedbed for trees (Baldwin 1927a, 1927b, Christy and Mack 1984, Dennis and Bateson 1974, Dimbly 1953, Fogel _et al_. 1973, Griffith 1931, Jones 1945, Knetchtel 1903, Korstain 1937, Kozlowski and Cooley 1961, Lemon 1945, Lowdermilk 1925, McCullough 1948, Smith 1955, Smith and Clark 1960, Thornburgh 1969, Westveld 1931). It is in the Pacific Northwest, however, and the _Picea sitchensis_ Zone in particular, where rotting logs, snags and stumps appear to be most important as a seedbed for trees (Franklin and Dyrness 1973, Hinds 1971, Kirk 1966, McKee _et al_. 1982, Minore 1972, Sharpe 1956, Taylor 1935).

"Nurse-logs", logs with trees and seedlings growing upon them, and stilt-rooted trees, formed when the underlying log decomposes, are conspicuous components of _Picea sitchensis_-_Tsuga heterophylla_ forests of the _Picea sitchensis_ Zone (Franklin and Dyrness 1973). Rotting wood covers more of the forest in the Pacific Northwest (6-25%) than in many other regions (1.6-4%) (Harmon _et al_. 1986). Moreover, tree seedlings in the Pacific Northwest region can be >100 times more concentrated on rotten wood than on the forest floors (Christy and Mack 1984, McKee _et al_. 1982). In some _Picea_-_Tsuga_ forests, tree seedlings are nearly excluded from the forest floor by competing bryophytes and herbs (Chapter II). Rotten wood represents a site where this competition is initially absent and tree seedlings can become established. However, development of bryophyte and herb layers on logs eventually restricts recruitment on these sites as well.

Although most of the tree seedlings in Picea-Tsuga forests occur on rotten wood, their importance for canopy tree replacement is not clear. Seedling survival is initially low on the forest floors, but may increase once a seedling is established. In contrast, seedling survival on rotten wood is initially very high, but may decrease with age because of competition among seedlings. Furthermore, rotten wood is subject to fragmentation and this could reduce seedling survival. A better understanding of nurse-log development would help to resolve the role of rotten wood seedbeds in canopy tree replacement.

Few studies have been conducted on successional development of nurse-logs despite their relevance to canopy recruitment. McCullough (1948) examined plant succession on logs within a Colorado Picea engelmannii-Abies lasiocarpa forest. As succession proceeded, larger and more complex species grew on logs, although they did not necessarily exclude plants of previous stages. Succession was slower on xeric than mesic or hydric sites, but the seres were similar. Tree seedlings could grow on slightly as well as throughly decayed logs and their establishment appeared independent of other taxa.

General facets of nurse-log development in Picea-Tsuga forests of Olympic National Park were described by Sharpe (1956). After tree fall, many epiphytes die and are replaced by species that also grow on the forest floor. Tree seedlings establish once bryophytes cover the log and competition then increases rapidly as seedling density and size increases. Sharpe (1956) hypothesized that seedling growth was very slow until roots reached the mineral soil and individuals with these roots would be at a competitive advantage relative to seedlings with roots only on the log. Sharpe therefore emphasized competition as a major determinant of nurse-log development.

There are, however, many other factors that influence plant succession and tree development on logs (Harmon et al. 1986). As logs decay, bark is sloughed and this in turn removes plants and reintiates the sere. Mineral soil rooting enhances tree stability as well as expanding the nutrient capital available to trees; large trees rooted solely in rotten wood or the surficial humus deposits are very prone to rootthrow. Initally bryophyte colonization of logs increases seed retention, but as mats increase in depth seedling establishment is reduced (Chapters II and III). Finally, litter deposits on logs permit tree establishment even on undecayed logs (Chapter IV).

This study assesses the importance of successional processes in establishment of trees on logs within Picea-Tsuga forests of Olympic National Park. A chronosequence of logs of three species were used to examine how bryophyte biomass (live and dead), humus biomass and tree density varies over the course of nurse-log development and how bark fragmentation influences succession.

STUDY AREA

The Hoh River study area is located on alluvial terraces within a glacial valley on the western side of the Olympic Mountains in Olympic

National Park, Washington (47° 50' N latitude and 123° 53' W longitude). The climate is extremely wet and mild with mean annual precipitation of 349 cm and a mean annual temperature of 9° C. Elevation within the study area is 150 m. Soils are of the Queets and Hoh Series, are strongly acid and silt-loam to fine sand in texture (McCreary 1975, Fonda 1974). Successional development of these alluvial forests is described by Fonda (1974) and McKee et al. (1982). Vegetation on the lowest forested terraces are dominated by Alnus rubra, which soon gives way to Acer macrophyllum-Picea sitchensis forest. Tsuga heterophylla invasion and decline of Acer then leads to a Picea-Tsuga forest. The climax community described by Fonda (1974) is dominated by Tsuga. However, Picea persists even on the oldest terraces suggesting a mixture of Tsuga and Picea is climax.

METHODS

Successional patterns were examined by sampling Picea, Pseudotsuga and Tsuga logs of varying age on the floor of conifer dominated alluvial forests. The age of each log was determined by aging fall scars on adjacent trees or the largest tree growing on the log (Harmon et al. 1986). A comparison of fall scars and tree ages indicated that the largest tree often started growing within 2 years of log fall. Fragmentation, which removes seedlings, is the largest source of error when tree age is used to estimate log age. Therefore, only trees growing on stable log surfaces (i.e., areas with bark) were aged. The species and decay class of each log (a modified version of Fogel _et al_. 1973, Triska and Cromack 1980, Sollins 1982) was recorded. The degree of canopy opening over the log was ocularly estimated and the species in the canopy were also noted.

Logs were sampled by first mapping surface types of the logs and then subsampling the surface types for plant cover, tree density and other variables of interest. One end of each log was randomly selected, and then four 5 m sections for a total distance of 20 m were marked off from that point. Most plants grew on the upper half of log surfaces; therefore only this part was mapped to estimate the area of each of ten surface types. The types corresponded to areas underlain by bark, sapwood and heartwood. These areas were in turn sudivided into bare, bryophyte and litter covered surfaces for a total of nine surface types. Each surface had to be >50% covered with bryophytes or litter in order to be classified in that map type. The tenth type corresponded to bryophyte covered surfaces underlain by tree roots.

Detailed characterization of each surface type within each 5 m section were made. Cover of bare wood and bark, bryophytes, litter, and humus was visually estimated. The minimum and maximum depth of living and dead bryophytes, litter, and humus was measured to the nearest mm and averaged to approximate the mean depth. Sampling of bryophyte layers on a number of logs indicated depths were normally distributed. Cover and depth were used to calculate the volume of these materials. Biomass of live and dead bryophytes and humus was estimated by multipling volume (ml/m^2) by densities of 0.0064, 0.0201 and 1.0689 g/ml, respectively. These densities were determined from 75, 17 cm^2 circular sample cores for which depth was recorded and oven dry weight (55^oC, 48 hr) determined.

Trees and shrubs density by size class was determined for each map unit present. Seedlings were trees or shrubs <20 mm diameter at ground height (dgh). Two methods were used to estimate seedling density by 2 mm size classes. When seedling density was high and the area covered by the mapping type was large, density was estimated by counting stems in 3, 0.1 m^2 quadrats placed to sample the top and both sides of the logs. If seedling density was low or the area of the mapping unit was small, a total inventory of the seedlings was made. Saplings were trees >20 mm dgh but <1.6 m tall; shrubs exceeding the seedling size class were sampled as saplings. All saplings growing on each surface type were tallied by 2 mm diameter classes. Trees were stems >1.6 tall; the diameter (to the nearest cm) and the surface type in which they were originally rooted was recorded. The location of live and dead trees was also recorded on the surfaces maps. Dead trees were classified as to whether standing dead or down with their root system torn from the log.

Regression equations were used to calculate biomass from stem diameters. For seedlings and saplings, complete individuals of the two most common species, Picea sitchensis and Tsuga heterophylla were harvested from logs near the Hoh River Ranger Station. The plant was separated into leaves, stems and roots and oven dried at 55^oC for

48 hr. Dry weight and dgh were used to develop double logarithmic regressions (Table V-1). Equations were corrected for bias using Baskerville's (1972) method. Tree biomass was estimated using the regressions of Gholz et al (1979).

Nonlinear regressions (SAS procedure NLIN, SAS Institute 1979) were used to model the changes in bark cover, bryophyte cover and biomass, humus biomass and tree density. These models were then used to predict how bark fragmentation patterns would affect successional development of nurse-logs. A modification of the negative exponential decay curve, which incorporated a early period with no losses, was used to model bark cover changes. This modification was appropriate because the bark of all three species did not begin to fall off until a period of decay had occurred. In the case of bryophyte cover and biomass, it was assumed that a negative exponential model with a steady-state level would mimic the data. For humus biomass, a sigmoidal pattern of increase with a steady-state level was used in order to reflect the slow rate of accumulation early in succession. The assumption that bryophyte and humus biomass would reach a steady-state was ecologically reasonable (i.e., neither would be expected to increase forever) and simplified modelling efforts. To calculate the rate trees thinned on logs, it was assumed that the density of the main cohort recruited onto bark surfaces would peak at 15 years and that a constant proportion of the population would die each year. This relationship was modelled with a negative exponential equation. All the nonlinear regression equations reported here were highly significant (0.01>p).

Table V-1. Regression equations used to predict seedling biomass (g) from stem diameter at ground height (mm). The equation form is $Y=B_0X^{B_1}$, where X is stem diameter, Y is the component biomass and B_0 and B_1 are regression constants.

Species component	B_0	B_1	r^2	N
Picea sitchensis[2]				
needles	0.073	2.29	0.97	34
stem	0.040	2.75	0.98	34
roots	0.034	2.42	0.96	34
Tsuga heterophylla[3]				
needles	0.49	2.35	0.95	32
stem	0.26	2.93	0.98	32
roots	0.21	2.58	0.97	32

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1. Corrected for bias using Baskerville's (1972) method.

2. Range of diameters 0.4-17.8 mm.

3. Range of diameters 0.4 mm-16.9 mm

RESULTS

Bark

Bark fragmentation from upper surfaces of all log species did not occur until decay proceeded (Figure V-1). Bark remained a stable surface for 10, 20 and 40 years for Picea, Tsuga and Pseudotsuga, respectively. The bark of each species fragmented at different rates (Table V-2); Tsuga was fastest and Pseudotsuga slowest. When both fragmentation rate and lag-time were considered, Picea logs lost bark fastest with 5% remaining after 57 years. The long lag-time and slow fragmentation rate of Pseudotsuga bark made it a fairly stable surface with 5% still remaining after 190 years. Tsuga logs had 5% bark cover in 63 years, which was quite similar to Picea. However, the overall dynamics of the two species differed in that bark on Tsuga logs was stable twice as long as Picea.

Bryophytes

Byophytes rapidly covered bark surfaces of all three log species (Figure V-2). Bryophyte cover of 90% was reached on Picea and Tsuga bark in 11 and 13 years, respectively (Table V-3). Bryophyte cover development on Pseudotsuga bark was slower and reached a maximum of 85% in 19 years. The lower maximum for Pseudotsuga reflects higher litter cover and not more bare bark.

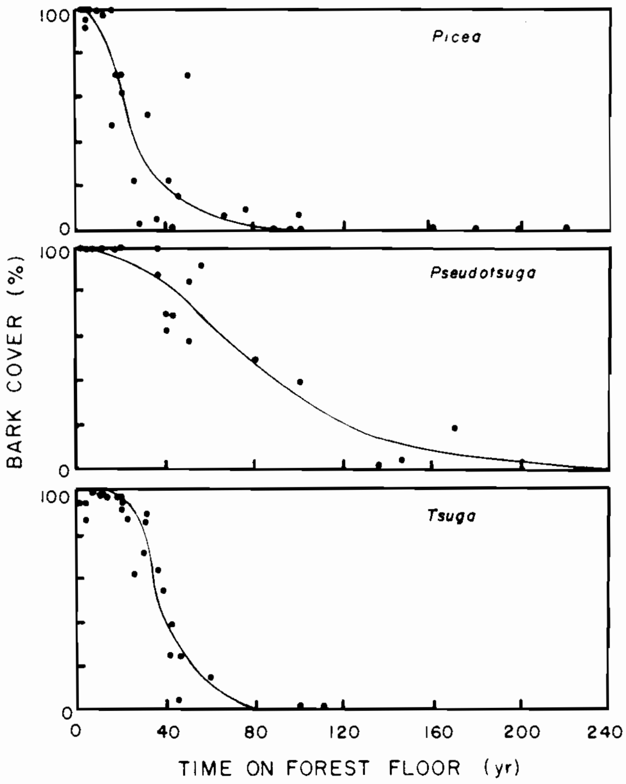

Figure V-1. Bark cover of <u>Picea sitchensis</u>, <u>Pseudotsuga menziesii</u> and <u>Tsuga heterophylla</u> logs as a function of time on forest floor. Regression equations from Table V-2.

Table V-2. Nonlinear regression coefficients of bark fragmentation and predicted time of 95% loss ($t_{0.95}$) for *Picea sitchensis*, *Pseudotsuga menziesii* and *Tsuga heterophylla* logs.

Species	B_1 (yr^{-1})[1]	B_2	$t_{0.95}$ (yr)	R^2	N
Picea sitchensis	0.073	3.33	57	0.85	30
Pseudotsuga menziesii	0.022	3.30	190	0.91	22
Tsuga heterophylla	0.098	25.78	63	0.93	28

1/ The regression equation is of the form $Y = 1-(1-\exp[-B_1 t])^{B_2}$ where Y is the fraction of the log covered by bark, B_1 is the bark fragmentation rate constant, B_2 is the lag-time coefficient and t is in yr.

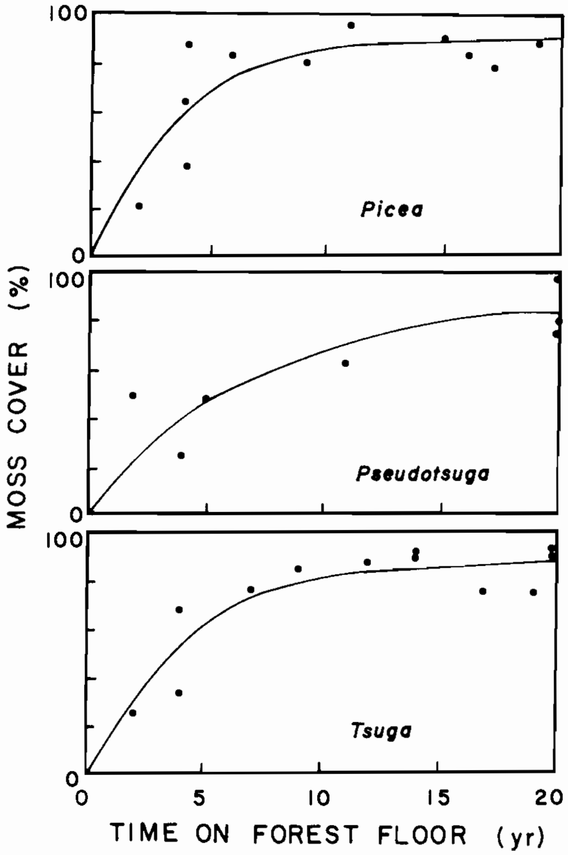

Figure V-2. Increase of bryophyte cover on bark of Picea sitchensis, Pseudotsuga menziesii and Tsuga heterophylla logs <20 years old. Regressions from Table V-3.

Table V-3. Nonlinear regression coefficients for bryophyte cover, live and dead bryophyte biomass, humus biomass and tree density as a function of bark surface age.

Species	B1	B_2 (yr^{-1})	B_3	Model[1]	$t_{0.95}$ (yr)	R^2	N
Bryophyte Cover (%)							
<u>Picea</u>	91	0.281	--	1	11	0.67	12
<u>Pseudotsuga</u>	85	0.156	--	1	19	0.59	7
<u>Tsuga</u>	90	0.227	--	1	13	0.80	12
Live Bryophyte Biomass (g/m^2)							
All	324	0.03	--	1	91	0.68	57
Dead Bryophyte Biomass (g/m^2)							
All	684	0.02	--	1	150	0.49	57
Humus Biomass							
All	4400	0.02	2.3	2	190	0.69	57
Tree Density (number/m^2)[2]							
All	140	0.08	--	3	40	0.75	36

<u>1</u>/ The three regression models were:

1) $Y = B_1(1-\exp[-B_2t])$ with t in years and B_1 in % or g/m^2

2) $Y = B_1(1-\exp[-B_2t])^{B_3}$ with t in years, B_1 is in g/m^2 and B_3 is dimensionless

3) $Y = B_1\exp[-B_2t]$ with t in years and B_1 is in number/m^2

<u>2</u>/ Applies to bark surfaces >15 yr old.

After the initial colonization, bryophyte cover remained high on *Pseudotsuga* and *Tsuga* logs, but it temporally declined on *Picea* logs from 15-35 years as bark sloughed (Figure V-3). Increase in bare wood cover is a more sensitive indicator of bark loss than reduction in moss cover. The temporary increase in bare wood cover suggests moss cover declined temporally for all three species of log. In the case of *Picea* and *Tsuga*, bare wood covered up to 40% of logs 20-50 years old. Bare wood covered 2-18% of the *Pseudotsuga* logs 50-150 years old. Temporary decreases in bryophyte cover could also be caused by shading from trees which thick carpet logs 20-50 years after log fall but the significant negative correlation between bryophyte cover and tree leaf biomass that would be expected was not found.

Although total bryophyte cover remained high, a succession of bryophyte species occurred. Early dominants included epiphytes such as *Dicranum* spp. and *Hypnum circinale*. After the first decade *Hypnum circinale* and a number of Hepaticae were the primary cover. By the end of the second decade, mixtures of *Rhizomnium personii* and *Dicranum* spp. dominate, but many of the "climax" feather mosses are also present. On surfaces >50 years old the feather mosses, *Hylocomium splendens* and *Rhytidiadelphus loreus* form the bulk of the cover with occasional patches of *Eurhynchium oreganum* and *Sphagnum girgensohnii*. The sere on rotten wood surfaces appears similar to that on bark except that feather mosses often colonize wood from adjacent patches of bark.

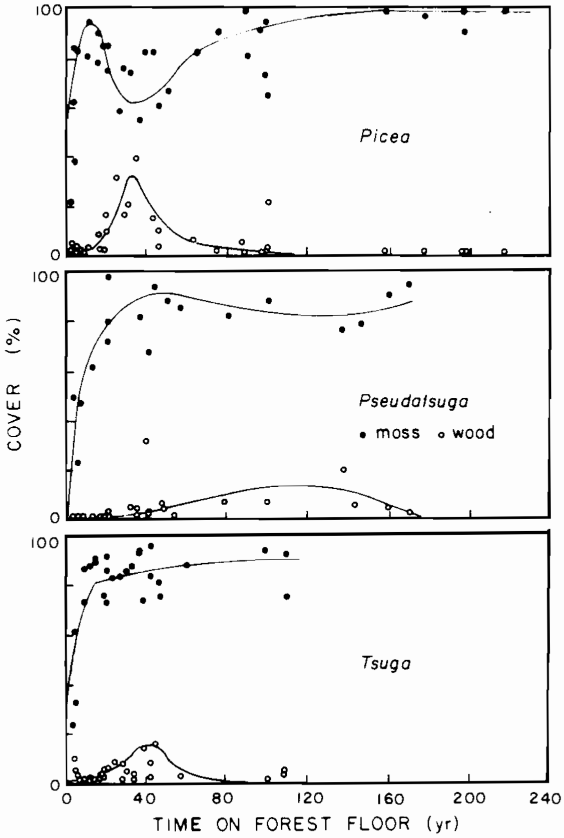

Figure V-3. Bryophyte cover on Picea sitchensis, Pseudotsuga menziesii and Tsuga heterophylla logs as a function of time on forest floor. Curve fitted by eye.

Live bryophyte biomass on bark increased slower than cover; 90 years appeared necessary to reach 95% of the steady-state value of 325 g/m^2 (Table V-3). Unfortunately, the data were insufficient to detect species differences. The steady-state on Picea bark was apparently lower and reached more rapidly than on Pseudotsuga bark (Figure V-4). Dead bryophyte biomass on bark accumulated slower than live biomass with a steady-state of 684 g/m^2 reached in 150 years (Table V-3).

Live bryophyte biomass accumulation on all log surfaces (bark and wood) was complex for Picea and Pseudotsuga (Figure V-5). In the case of Picea, live biomass rapidly increased to 150 g/m^2 by 25 years and then remained constant until 70 years when biomass again rapidly increased to a steady-state of 300 g/m^2. Bryophyte biomass steadily increased on Pseudotsuga logs to 250 g/m^2 by 80 years, then decreased slightly by 135 years and finally increased back by 170 years. The plateau in biomass accumulation on Picea logs and the decrease on Pseudotsuga logs was probably caused by bark sloughing. No clear trend was obvious for Tsuga, but a major decrease in moss biomass was expected when bark fragmentation was high. Although the rate of bryophyte biomass increase could not be estimated for wood surfaces, the live biomass on wood surfaces >60 years old was quite similar to the steady-state predicted for bark (344 versus 324 g/m^2). The overall trend in dead bryophyte biomass was similar to live bryophyte biomass.

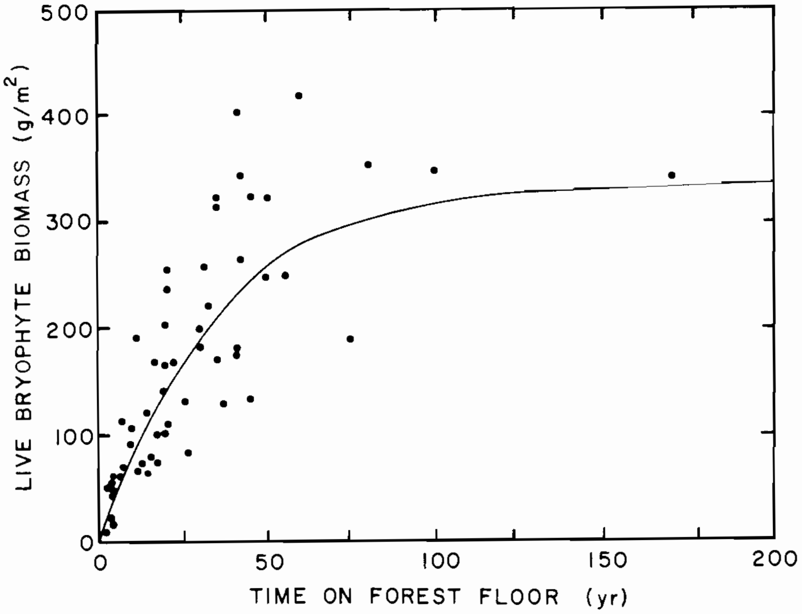

Figure V-4. Increase of live bryophyte biomass on bark of logs as a function of time on forest floor. Regression equation from Table V-3.

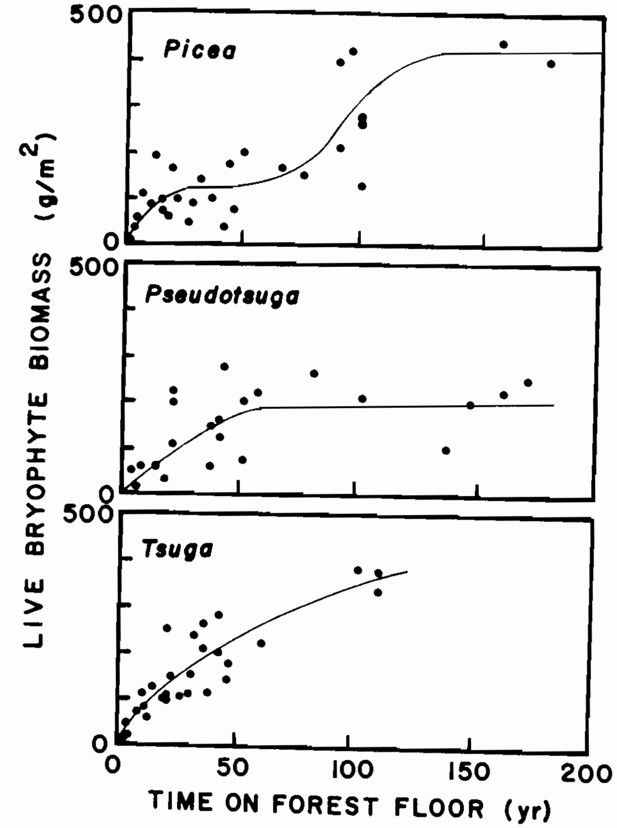

Figure V-5. Increase live bryophyte biomass on _Picea sitchensis_, _Pseudotsuga menziesii_ and _Tsuga heterophylla_ logs as a function of time on forest floor. Curves fitted by eye.

Humus Accumulation

Humus accumulation patterns on bark of all three species was apparently sigmoidal (Figure V-6). Humus accumulations were low for the first 10 years and then rapidly increased. If the assumption that a steady-state is eventually reached is valid, this level must be reached after 100 years. The maximum value and the rate of increase were difficult to estimate because insufficient numbers of old bark surfaces were sampled. A steady-state biomass of 4420 g/m^2 was calculated to be reached in 190 years (Table V-3). If this general pattern also occurred on wood surfaces it is unlikely that most of the wood surfaces were old enough to approximate the steady-state. However, two logs with wood surfaces which probably exceeded 150 years had humus biomass of 3500-6100 g/m^2 and this value brackets the value predicted for bark.

Humus biomass accumulation patterns on all log surfaces was strongly affected by bark stability. In the case of Picea, bark sloughed just when humus was rapidly accumulating on this surface;consequently little humus accumulated until sloughing ceased. On Pseudotsuga logs humus accumulation occurred and paralleled the bark accumulation curve until 40 years when bark sloughing prevented further accumulation until 140 years. Humus accumulation on Tsuga logs did not decrease as for Picea and Pseudotsugae and bark sloughing effects were obscurred.

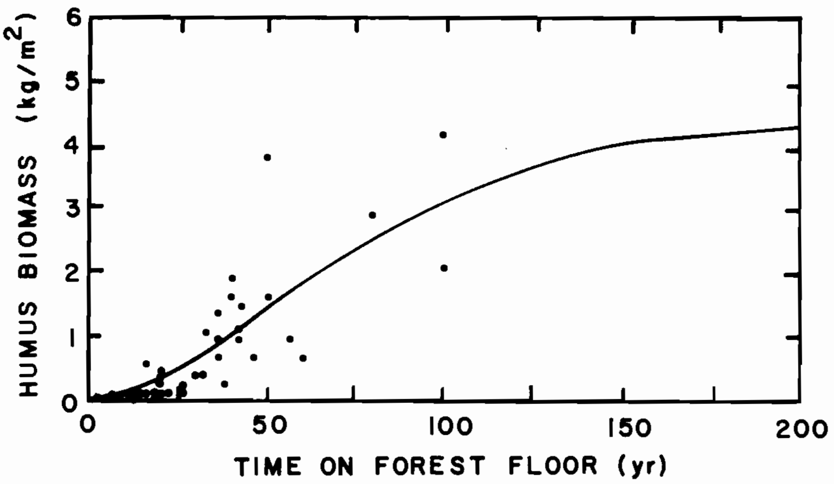

Figure V-6. Increase in humus biomass on bark surfaces of logs as a function of time on forest floor. Regression equation from Table V-3.

Trees

A large number of woody species were observed growing on logs including: *Acer circinatum*, *A. macrophyllum*, *Alnus rubra*, *Gaultheria shallon*, *Menziesia ferruginea*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Rhamnus purshiana*, *Rubus spectabilis*, *Sambucus racemosa*, *Thuja plicata*, *Tsuga heterophylla*, *Vaccinium alaskensae* and *V. parvifolium*. The following analysis considers only *P. sitchensis* and *T. heterophylla* since they comprised the majority of individuals.

Tree seedlings began growing on bark surfaces within two years after logs fell to the forest floor. Total tree density on bark reached a maximum of 150 trees/m^2 at 15-25 years but variability was quite high (14-422 trees/m^2). Peak density may have been related to canopy closure; the highest values occurred when canopy cover was 25%. Seedling density on bark was significantly influenced by bryophyte biomass ($P<0.01$) and lowest when total biomass was <50 g/m^2 or >350 g/m^2. Tree density on wood of *Picea* and *Tsuga* logs reached a maximum of 150-250/m^2 at 15-40 years. On *Pseudotsuga* logs, wood surfaces supported a maximum of 75-100/m^2 seedlings at 80-150 years.

Tree density rapidly decreased on bark surfaces 15-45 years old (Figure V-7). The tree thinning rate on bark was calculated for logs >15 years old with a negative exponential equation. This model is based on the assumption that a constant proportion of the population dies each year. Seedlings were not included for logs >35 years old

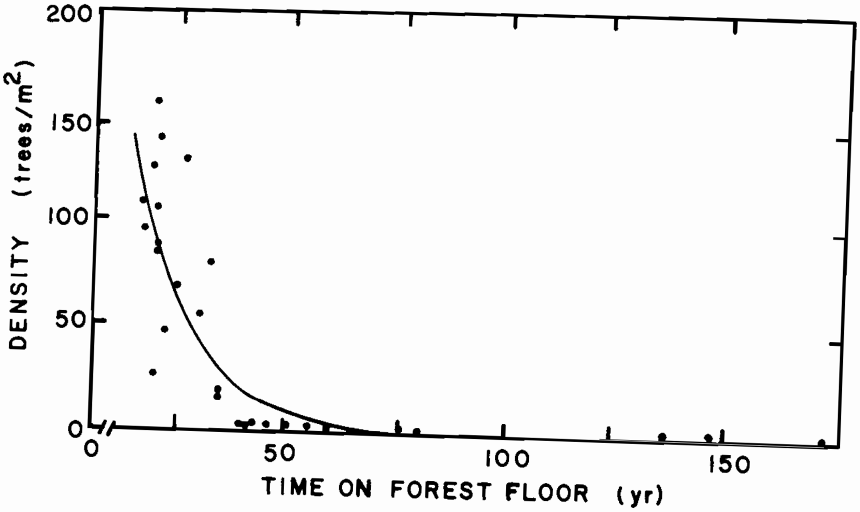

Figure V-7. Reduction in tree density on bark surfaces of logs >15 years old. Regression from Table V-3.

because they were not part of the original seedling "cohort". Peak density of 140 trees/m^2 and a thinning rate-constant of 0.08/yr were calculated. The asymtotic 95% confidence intervals for these parameters were 0.03-0.12 yr^{-1} and 108-173 trees/m^2, respectively. This approximated a mortality or thinning rate of 8%/yr and indicated that 5% of the "initial" cohort remained 40 years after the peak . On bark surfaces >45 years old, tree density remained constant at approximately 1 tree/m^2 suggesting a low mortality rate.

The overall pattern of tree density on logs varied by species bark loss patterns (Figure V-8). In the case of Picea, bark fragmentation reduced the peak in tree density and increased the period of tree recruitment. On Pseudotsuga, tree density closely followed bark surfaces for the first 40 years, but then increased from 60-160 years when wood surfaces were exposed. The effect of Tsuga bark sloughing on tree density was similar to Picea with a reduction in peak density and an increased period of recruitment.

Although many seedlings and saplings probably died on logs from competitive stress, a large proportion of trees (>1.6 m tall) died by toppling off logs. Of the 173 dead trees observed, 27% were standing indicating death due competitive interactions. The remaining 126 trees had exposed root systems indicating they had toppled off logs before dying.

Bark fragmentation was another major form of seedling and sapling mortality, although competition appeared to be a more important thinning agent on all three log species. Calculations based on tree

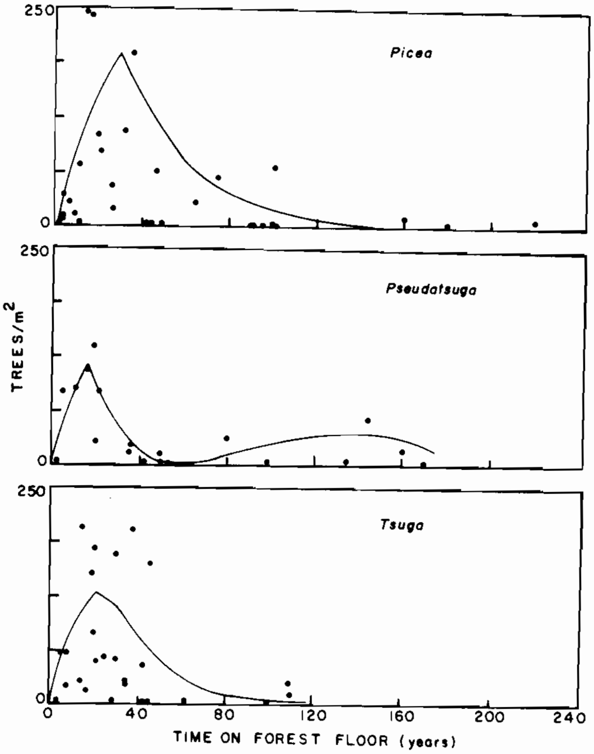

Figure V-8. Tree density on Picea sitchensis, Pseudotsuga menziesii and Tsuga heterophylla logs as a function of time on forest floor. Curves fit by eye.

thinning and bark cover regressions indicated 7, 22 and 40% of the initial "cohort" of trees was removed by bark sloughing on Pseudotsuga, Tsuga and Picea, respectively. Bark sloughing was of minor importance for Pseudotsuga and Tsuga because it does not begin until a major fraction of the competitive thinning has occurred.

DISCUSSION

A log on the forest floor is subject to a complex plant succession. General features of such a sere have been identified for a cool, moist environment. The sere begins with the death of epiphytes unable to tolerate forest floor conditions. Temperate rainforest epiphytes which succumb early in the sere include lichens, bryophytes (Sharpe 1956) and two vascular plants, Sellaginella oreganum and Polypodium glycyrhiza. These epiphytes can speed the colonization of trees by retaining seed and forming a organic soil as they decay. The largest and fastest growing tree seedlings often grow on dying and decaying epiphytes. Living trees vary considerably in epiphyte cover; as fresh logs, trees with heavy epiphyte cover speed development of the sere.

The bryophytes which replace the epiphytes play several roles during the sere. Species of small stature, such as Hypnum circinale, rapidly cover the log within the first decade. This increases retention of seeds and needle litter on logs (Chapter III). As intermediate sized bryophytes colonize the log and a humus layer accumulates, establishment rate of trees increases (Chapter IV). These intermediate sized bryophytes (e.g., *Dicranum*, *Rhizomnium*) are eventually replaced by the feather mosses (*Hylocomium splendens*, *Rhytidiadelphus loreus* and *Eurhynchium oreganum*) which are sufficiently tall and dense to prevent establishment of tree seedlings.

Bark fragmentation is an important factor influencing succession on logs and may underlie many of the differences among log species. On one hand, bark fragmentation retards succession by removing plants and humus. However, bark fragmentation reduces competition by thinning trees, ultimately increasing growth and speeding succession to tree dominance. Bark fragmentation may increase the probability a log will support a tree by removing thick bryophyte mats. Wood, particularly the sapwood of *Pseudotsuga*, was also prone to fragmentation, but this process occurs on a smaller scale than bark loss and may not create patches sufficiently large to reinitiate the sere.

The light environment probably influences the rate and nature of succession. The degree of canopy openness influenced the establishment rate of tree seedlings on bryophyte and litter covered logs (Chapter IV). Under deep shade, few seedlings on logs survive to become trees. However, bryophyte continue to grow deeper and eventually exclude tree seedlings. The dominant plant on logs in these cases would be shade-tolerant shrubs, such as *V. parvifolium*.

Some differences in successional development amoung log species were probably related to the light environment of the logs. Tsuga boles, for example, are more likely to fall in denser forests than those of Picea or Pseudotsuga. When log age and canopy openness are similar, successional development for Tsuga and Picea appeared similar.

Bark fragmentation patterns may explain successional differences among log species. The theoretical impact of this process on byrophyte biomass and tree density is illustrated in Figures V-9 and V-10. These two variables represent the two basic patterns of change over time. The regression coefficents for bark loss, live bryophyte biomass and tree density (Tables V-2 and V-3) were used to derive these curves by assuming similar succession on bark and wood. Without fragmentation, live bryophyte biomass monotonically increases to a steady-state in 90 years. The departure of each species from this "stable surface" curve depends upon bark fragmentation patterns. Picea departs after 10 years, and exhibits a lower rate of bryophyte accumulation until 50 years when bare wood surfaces are no longer being created. Pseudotsuga differs from Picea: departure from the stable-surface curve starts later causes bryophyte biomass to plateau between 50-90 years. Fragmentation is so rapid on Tsuga logs that bryophyte biomass temporally decreases.

Bark fragmentation extends the period of tree recruitment. Picea has a lower peak tree density than the stable-surface because wood surfaces with low tree densities are being created when the bark peak

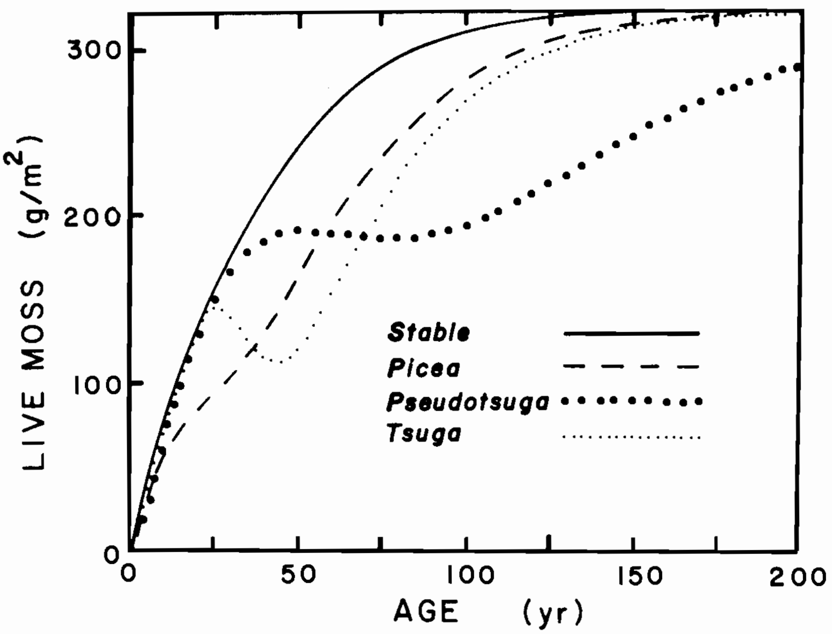

Figure V-9. Predicted changes in live bryophyte biomass on stable bark, Picea sitchensis, Pseudotsuga menziesii and Tsuga heterophylla logs as a function of time on forest floor.

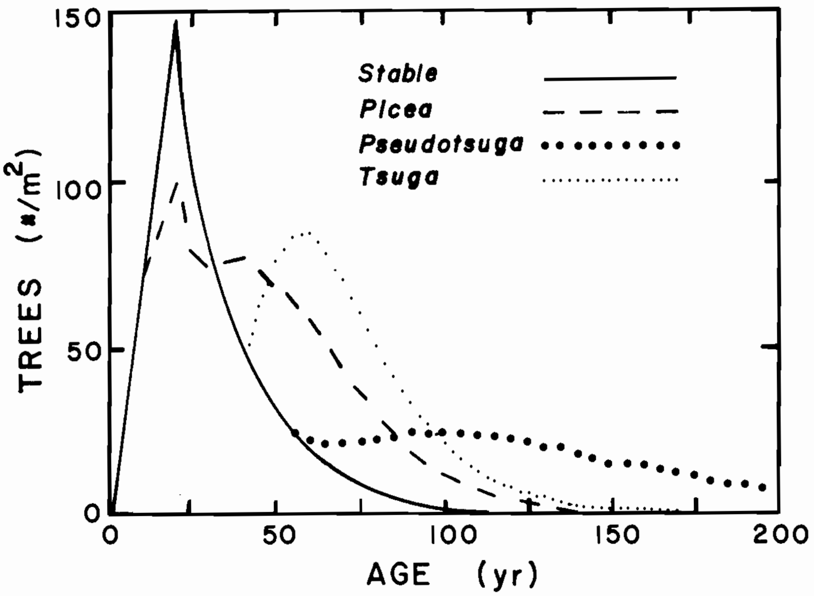

Figure V-10. Predicted changes in tree density on stable bark, <u>Picea sitchensis</u>, <u>Pseudotsuga menziesii</u> and <u>Tsuga heterophylla</u> logs as a function of time on forest floor.

is occurring. There is also a secondary peak in tree density as wood surfaces exposed decades before reach peak density. Tree density remains higher than the stable-surface because the period of recruitment is extended by fragmentation. Pseudotsuga generally follows the stable-surface curve until 50 years, but there is a minor secondary peak in density at 100 years. As with bryophyte biomass, fragmentation of Tsuga bark makes the tree density curve complex. Up until 40 years Tsuga follows the stable-surface curve closely. Between 40-60 years there is a secondary peak in tree biomass caused by the rapid exposure of bare wood.

This study indicates that while tree densities are often high on logs, the overall survival rate is probably quite low. On logs with stable surfaces, high density leads to competition and rapid thinning. Bark fragmentation also kills a large proportion of trees especially on Picea logs. Moreover, unless trees surviving competition and fragmentation send roots into the mineral soil they are prone to toppling. Finally, it may be misleading to assume the contribution of a seedbed is equal to fraction of seedlings growing upon it. This study suggests long-term survival rates on logs and the forest floor may be more similar than originally supposed.

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VI. SUMMARY

1. Logs are a very important seedbed for conifer seedlings within the *Picea sitchensis-Tsuga heterophylla* forests of coastal Washington and Oregon.

2. Field experiments conducted at Hoh River, Washington and Cascade Head, Oregon indicated that conifer regeneration was excluded from the forest floor by competition from mosses and herbs.

3. Experiments conducted at Hoh River showed deep bryophyte mats on old, stable log surfaces also prevented tree seedling establishment. Relatively young logs, with moss mats of thin to moderate thickness, offer the best competition-free site for tree establishment.

4. Field experiments at Cascade Head indicated retention of seeds was very high (48-98%) for moss- and litter-covered log surfaces. In contrast, retention was low (0-8%) on bare bark and wood surfaces except when deep, narrow cracks or holes are present.

5. Logs covered an average of 9.9% of the forest floor in five *Picea-Tsuga* forests. Litter- and moss-covered surfaces, which are most likely to retain seeds, comprised 89% of the log surfaces. Deducting logs with thick moss mats suggested that 59% of the log surface area were likely sites for tree seedling recruitment.

6. Field experiments at Cascade Head revealed that *Picea-sitchensis* and *Tsuga heterophylla* can establish and grow quickly when rooted in the litter on log surfaces. This enables trees to colonize logs even when the underlying log is not sufficiently decayed to allow root penetration.

7. A chronosequence of *Picea*, *Pseudotsuga* and *Tsuga* logs at Hoh River reveals that bark sloughing affected successional development of bryophyte cover and biomass, humus biomass and tree density.

8. Although tree establishment rates are considerably higher on logs than on the forest floor, collective effects of competition, bark fragmentation and toppling indicate that long-term survival rates of trees on logs are quite low.

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