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Effects of Bark Fragmentation on Plant Succession on Conifer Logs in the *Picea-Tsuga* Forests of Olympic National Park, Washington

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ABSTRACT.—Plant succession on *Picea* (spruce), *Pseudotsuga* (Douglas fir) and *Tsuga* (hemlock) logs in the Hoh Rain Forest, Washington, was examined using the chronosequence method. Bark fragmentation patterns differed among these species; *Picea* and *Tsuga* logs lost their bark in 60 years and *Pseudotsuga* in 190 years. Bark of logs of all species was 85–90% covered by bryophytes within 11–19 years after tree fall. Live and dead bryophytes reached steady-state masses on bark of 324 and 684 g/m² within 91 and 150 years, respectively. Humus mass on bark of logs of all three species increased slowly the first decade and rapidly after 20 years; a steady-state humus mass of 4400 g/m² was predicted after 190 years. Tree density on bark peaked at 140/m² at 15–25 years and then thinned at a rate of 8%/yr. Bark fragmentation influenced succession by removing plants and reinitiated the sere. Modeling indicates differences in succession patterns among species of logs were caused by differences in bark fragmentation patterns. Although logs are a major seedbed in *Picea-Tsuga* forests, self-thinning, bark fragmentation and toppling of trees greatly reduced long-term survival on logs.

INTRODUCTION

Rotting logs, snags and stumps are often seedbeds for trees in temperate forests (Harmon *et al.*, 1986) especially in the Pacific Northwest (Christy and Mack, 1984; McKee *et al.*, 1982; Minore, 1972; Sharpe, 1956; Taylor, 1935). Rotting wood is more important in the Pacific Northwest because it covers more of the forest floor there (6–25%) than in other regions (1.6–4%) (Harmon *et al.*, 1986) and because seedling density is greater on rotten wood than on the forest floor (Christy and Mack, 1984; McKee *et al.*, 1982).

Nurse-logs (logs with trees and seedlings growing upon them) and stilt-rooted trees (formed where the underlying log decomposes) are conspicuous components of *Picea sitchensis-Tsuga heterophylla* forests of the Pacific Northwest (Franklin and Dyrness, 1973). Although most tree seedlings in *Picea-Tsuga* forests grow on rotten wood, the importance of these seedlings in replacing canopy trees is unclear. Seedling survival is initially low on the forest floor because of severe competition with mosses and herbs (Harmon, 1986) but the survival rate may increase once seedlings are established. In contrast, seedling survival on rotten wood is initially high but may decrease with age because of competition among seedlings and fragmentation of the wood substrate.

Few studies have been done on nurse-log succession despite its relevance to canopy recruitment. In a Colorado *Picea engelmannii-Abies lasiocarpa* forest, McCullough (1948) found that lichens colonize logs first and are subsequently followed by bryophyte, herb and shrub dominated stages. He also determined that tree seedlings grow as well on slightly decayed logs as on those that were thoroughly decayed; their establishment appears independent of other taxa. In *Picea-Tsuga* forests of Olympic National Park, Sharpe (1956) found that after tree fall, epiphytic bryophytes and vascular plants are replaced by bryophytes, herbs and shrubs that also grow on the forest floor. Lichens are relatively unimportant during the sere in these forests. Tree seedlings establish once bryophytes cover the log and competition then increases rapidly as seedling density and size increase. Sharpe (1956) hypothesized that seedling growth is very slow until roots reach the mineral soil.

Many other factors, however, influence plant succession and tree development on logs (Harmon *et al.*, 1986). As logs decay, bark is sloughed which in turn removes plants and reinitiates the sere. Rooting in mineral soil enhances tree stability as well as nutrient availability; large trees rooted solely in rotten wood or surface humus deposits are very prone to toppling. Initially, bryophyte colonization of logs increases seed retention, but as mats increase in depth, seedling establishment is reduced (Harmon, 1986). Finally, litter deposits on logs permit tree establishment even on undecayed logs (Harmon, 1987).

In this study, successional processes on nurse-logs were examined in *Picea-Tsuga* forests of Olympic National Park, Washington. A chronosequence of logs of *Picea sitchensis* (Bong.) Carr. (Sitka spruce), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) was examined to determine how bryophyte mass (live and dead), humus mass and tree density varied over the course of nurse-log development. To assess the impact of bark fragmentation on succession, the development of bryophyte mass (live and dead), humus mass and tree density on stable pieces of bark was compared to development on the entire log surface (*i.e.*, bark and wood surfaces combined). Finally, succession on the three species of logs was modeled and compared to determine potential differences caused by bark fragmentation patterns.

STUDY AREA

The Hoh Rain Forest is on alluvial terraces in a glacial valley on the west 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 in the study area is 150 m. The strongly acid soils are of the Queets and Hoh Series, with silt-loam to fine-sand texture (Fonda, 1974; McCreary, 1975). Successional development of these alluvial forests is described by Fonda (1974) and McKee *et al.* (1982). Vegetation on the lowest and youngest forested terraces is dominated by *Alnus rubra* Bong. (red alder). As succession proceeds, this species is replaced by *Acer macrophyllum* Pursh-*Picea sitchensis* (bigleaf maple-Sitka spruce) forest. Invasion of western hemlock and decline of bigleaf maple then leads to a Sitka spruce-western hemlock forest. The climax community described by Fonda (1974) is dominated by western hemlock. Sitka spruce persists even on the oldest terraces, however, suggesting that a mixture of western hemlock and Sitka spruce is climax. Douglas fir occurs in low numbers on all terrace levels, especially in the transition zone between terraces (McKee *et al.*, 1982).

METHODS

Successional patterns were examined by sampling 30 Sitka spruce, 22 Douglas fir and 28 western hemlock logs. Only logs in alluvial forests dominated by Sitka spruce and western hemlock on the main stem of the Hoh River were sampled. Logs were selected to represent each species in all successional stages and ranged from freshly fallen to extremely decayed.

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). Comparison of fall scars and tree ages indicated that the largest tree on the log often started growing within 2 years of log fall. Fragmentation of bark, which removes seedlings, is the largest source of error when tree age is used to estimate log age. Therefore, only trees growing on areas with bark remaining were aged. The species and decay class of each log (see Fogel *et al.*, 1973; Triska and Cromack, 1980; Sollins, 1982) were recorded. The degree of canopy opening over the log was visually estimated and the species in the canopy were also noted.

Four contiguous 5-m-long quadrats were established on each log at an end selected by

coin toss. Quadrat width equaled log diameter. The upper half of the log in each 5-m quadrat was stratified into surface types, which were subsampled for plant cover and depth as well as stem density. The surface types were classified according to whether they were bark, sapwood or heartwood surfaces and whether they were primarily bare or covered by bryophytes or by litter. In some cases, the underlying log had completely decomposed and the surface type was classified as bryophytes covering tree roots. The areal extent of each surface type in each quadrat was calculated by electronic digitizer from a map sketched in the field.

Each surface type in each 5-m quadrat was characterized in detail. Cover of bare wood and bark, bryophytes, litter and humus was visually estimated to the nearest percent. The minimum and maximum depths of living and dead bryophytes, litter and humus were measured to the nearest millimeter and the mean depth calculated. Sampling of bryophyte layers on several logs indicated that depths were normally distributed. Cover and mean depth were used to calculate the volume of these four classes of materials. The densities of live and dead bryophytes and humus were determined from 75, 17-cm² circular sample cores for which depth was recorded and oven-dry weight (55 C, 48 h) determined. Mass of live and dead bryophytes and humus was estimated by multiplying volume (cm³/m²) by densities of 0.0064, 0.0201 and 1.0689 g/cm³, respectively.

Tree, sapling and seedling densities were determined for each surface unit present. Seedlings were stems <20 mm diameter at ground height (dgh); saplings were stems >20 mm dgh but <1.6 m tall; and trees were stems >1.6 m tall. Two methods were used to estimate seedling density. When seedling density was high and the area covered by the surface type was large, density was estimated by counting stems in three 0.1-m² quadrats systematically placed to sample the top and both sides of the logs. If seedling density was low or the area of the surface unit was small, a total count of the seedlings was made. An entire count was made for saplings growing on each surface type. Diameter of trees at breast height (to the nearest cm) and the surface type in which they were rooted were recorded. The location of live and dead trees was also recorded on the maps of surface types prepared for each quadrat. Dead trees were classified as standing or else down with their root system torn from the log.

Cover of bryophytes, bare bark, bare wood and litter, mass of live and dead bryophytes and humus and tree density were calculated for each quadrat by weighting each surface type by its areal extent. These means were calculated in two ways: (1) for surfaces underlain by bark and (2) for the entire log surface including both bark and wood. Calculations for the bark surfaces were used to provide data for successional development on surfaces of known age. For the purposes of the analyses presented in this study, density of seedlings, saplings and trees were added to give total woody stem density. The overall mean for a log was calculated from the weighted mean of the five quadrats.

Nonlinear regressions (SAS procedure NLIN, SAS Institute, 1979) were used to model the changes in bark cover, bryophyte cover and mass, humus mass and tree density. These models were then used to predict how bark fragmentation patterns would affect successional development of nurse-logs. Changes in bark cover were modeled by adding a lag-time coefficient to the negative exponential decay curve, so that an early period with no losses was included (Harmon *et al.*, 1986). For bryophyte cover and mass, a negative exponential model with a steady-state level was fitted to the data. In the case of bryophyte cover, only bark surfaces <20 years were used to fit the equations. For humus mass, a sigmoidal pattern of increase to a steady-state level was used to reflect the slow rate of accumulation early in succession. I made the ecologically-reasonable assumption that bryophyte and humus mass would reach a steady state because neither would increase forever. To calculate the rate

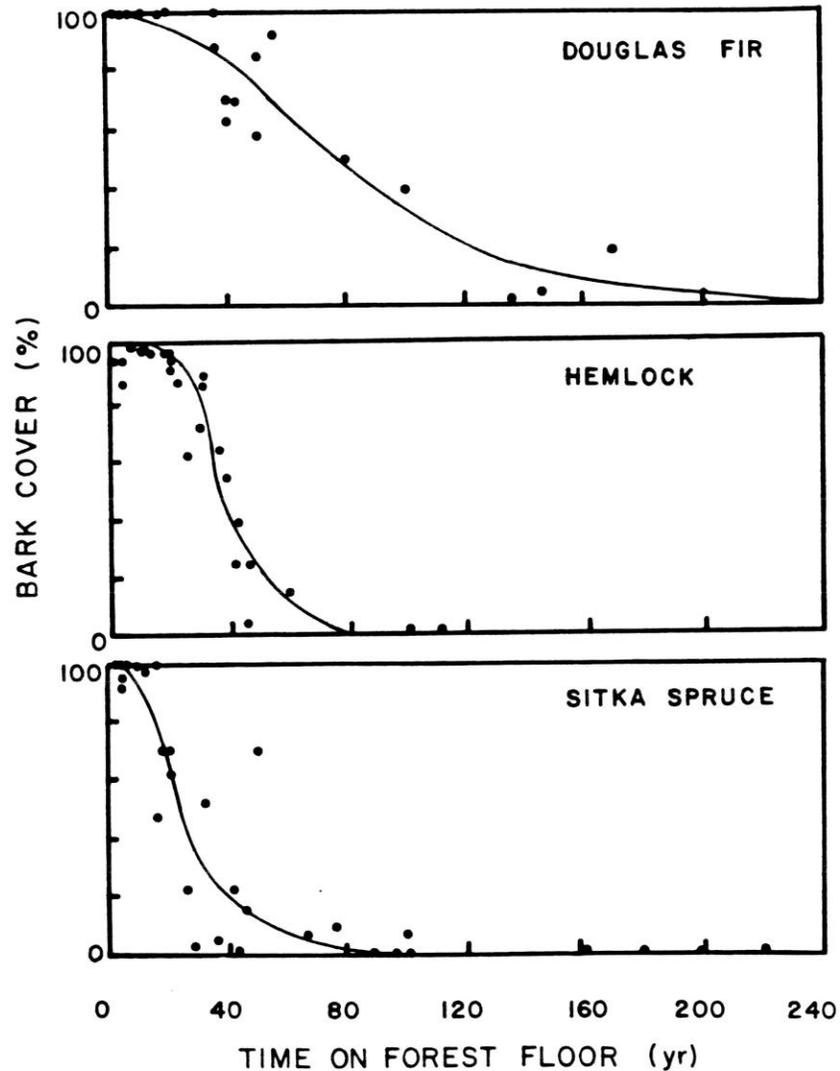


FIG. 1.—Percent bark cover of Sitka spruce, Douglas fir and western hemlock logs as a function of time on the forest floor. Regression equations are from Table 1. Points represent the mean of five samples per log

trees thinned on logs, I assumed density of the main cohort recruited onto bark surfaces peaked at 15 years and that a constant proportion of the population died each year. The former assumption was based on examination of the data. This relation was modeled with a negative exponential equation. Depending on the equation form, the time required to reach 5 or 95% of the steady-state value was computed from the estimated rate-constants. These values were chosen because exponential equations are asymptotic and the steady-

TABLE 1.—Nonlinear regression coefficients of bark fragmentation and predicted time of 95% loss ($t_{0.95}$) for Douglas fir, Sitka spruce and western hemlock logs

Species	B_1 (/year) ^a	B_2	$t_{0.95}$ (year)	R^2	n
Douglas fir	0.022	3.30	190	0.91	22
Sitka spruce	0.073	3.33	57	0.85	30
Western hemlock	0.098	25.78	63	0.93	28

^a 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 time in years

state value is never actually reached. All the nonlinear regression equations reported here were highly significant ($P < 0.01$).

Bark fragmentation patterns may explain successional differences among species of logs. Model simulations were used to explore the hypothetical impact of this process on bryophyte mass and tree density. The regression coefficients for bark loss, live bryophyte mass and tree density (Tables 1, 3) were used as parameters for a difference equation model. The bark loss equations were used to predict the area of wood exposed on a time step of two years. The live bryophyte mass and tree density regressions were used to predict how bark and newly exposed wood surfaces would develop. The succession on bark and wood was assumed to be similar for this modeling exercise. Simulations were run for all three species of log and for a stable-surface. The latter situation is unnatural, but served as a reference point to assess the impact of fragmentation.

RESULTS

Bark.—Bark remained a stable surface for up to 10, 20 and 30 years for Sitka spruce, western hemlock and Douglas fir, respectively (Fig. 1). In the case of Sitka spruce and western hemlock, some bark was removed when the tree fell. After a period of little fragmentation, the bark of each species fragmented at different rates (Table 1); western hemlock was fastest and Douglas fir slowest. When both fragmentation rate and lag-time coefficient were considered, 5% bark was remaining after 57 years on Sitka spruce logs, 63 years on western hemlock logs and 190 years on Douglas fir logs.

Bryophytes.—Bryophytes rapidly covered bark surfaces on all three species of log. Bryophyte cover of approximately 90% was reached on Sitka spruce and western hemlock bark in 11 and 13 years, respectively (Table 2). Bryophyte cover on Douglas fir bark developed more slowly and reached a maximum of 85% in 19 years. The lower maximum of biomass cover on Douglas fir reflected higher litter cover and not more bare bark.

TABLE 2.—Nonlinear regression coefficients for bryophyte cover on bark of Douglas fir, Sitka spruce and western hemlock logs <20 years old and predicted time to reach 95% of steady-state ($t_{0.95}$)

Species	B_1 (%) ^a	B_2 (/year)	$t_{0.95}$ (year)	R^2	n
Douglas fir	85	0.156	19	0.59	7
Sitka spruce	91	0.281	11	0.67	12
Western hemlock	90	0.227	13	0.80	12

^a The regression equation is of the form $Y = B_1[1 - \exp(-B_2 t)]$, where Y is the percent of bark covered by bryophytes, B_1 is the bryophyte cover at steady-state, B_2 is the bryophyte increase-rate constant and t is time in years

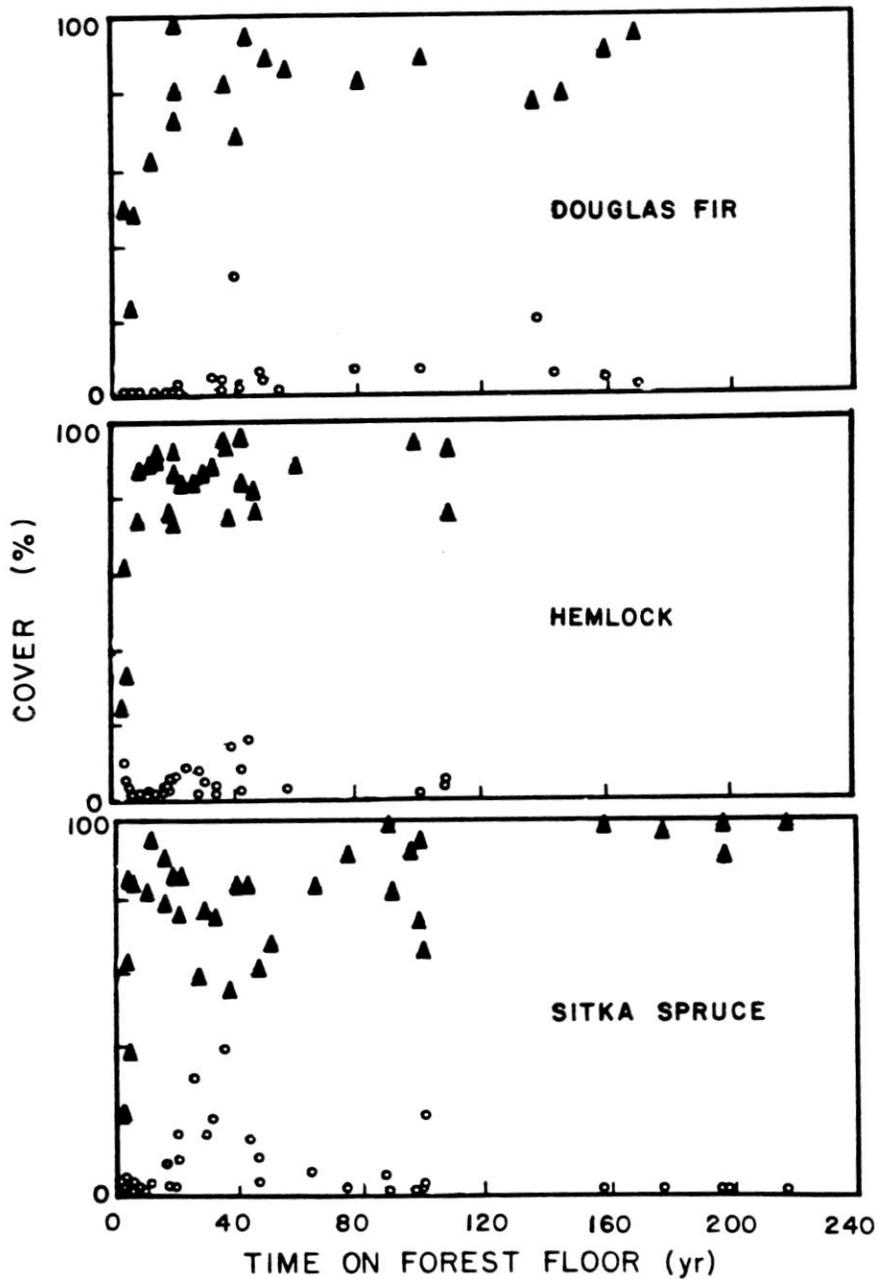


FIG. 2.—Cover of bryophytes and bare wood on Sitka spruce, Douglas fir and western hemlock logs as a function of time on the forest floor. Points represent the mean of five samples per log. ▲, bryophytes; ○, bare wood

TABLE 3.—Nonlinear regression coefficients for live and dead bryophyte mass for bark surfaces and predicted time to reach 95% of steady-state ($t_{0.95}$)^a

Type	B ₁ (g/m ²)	B ₂ (/year)	t _{0.95} (year)	R ²	n
Live	324	0.033	91	0.68	57
Dead	684	0.020	150	0.49	57

^a The regression model is of the form $Y = B_1[1 - \exp(-B_2t)]$, where Y is the bryophyte mass (g/m²), B₁ is the bryophyte mass at steady-state, B₂ is the bryophyte mass increase-rate constant and t is time in years

After the initial colonization, bryophyte cover remained high on Douglas fir and western hemlock logs but declined on Sitka spruce logs from 15–35 years as bark sloughed (Fig. 2). In the case of western hemlock, bare wood surfaces were created on logs 20–50 years old. For Douglas fir, bare wood surfaces were exposed on logs 40–150 years old.

Although total bryophyte cover remained high, a succession of species occurred (Harmon, 1986). Early dominants included *Dicranum* spp. (Hedw.) and *Hypnum circinale* Hook. After the first decade, *Hypnum circinale* and several species of liverworts were the primary cover. By the end of the second decade, mixtures of *Rhizomnium* spp. (Broth.) Koponen and *Dicranum* dominated, but feather mosses *Eurhynchium oregonum* (Sull.) Jaeg., *Hylocomium splendens* (Hedw.) B.S.G. and *Rhytidiadelphus loreus* (Hedw.) Warnst were also common. On surfaces >50 years old, feather mosses formed most of the cover with occasional patches of *Sphagnum girgensohnii* Russow. The sere on rotten wood surfaces appeared similar to that on bark except that feather mosses colonized wood from adjacent patches of bark.

Live bryophyte mass on bark of all three species of log increased more slowly than cover; 91 years appeared necessary to reach 95% of the steady state value of 324 g/m² (Table 3). Dead bryophyte mass on bark accumulated more slowly than live mass with 95% of the steady state of 684 g/m² reached in 150 years (Table 3).

Live bryophyte accumulation on all log surfaces (bark and wood) was non-linear (Fig. 3). For example, live mass on Sitka spruce exhibited a plateau from 20 years to 80 years. This plateau may have been caused by bark fragmentation. In the case of Douglas fir, bark fragmentation may have caused a small decrease in live bryophyte mass between 100 and 140 years. Live bryophyte biomass on western hemlock logs appeared to increase steadily during succession. The trend in dead bryophyte mass was similar to live bryophyte mass.

Humus accumulation.—Humus accumulations on bark were low for the first 10 years and then increased. The maximum value and the rate of increase were difficult to estimate because too few old bark surfaces were sampled. The equation describing the accumulation of humus mass was:

$$Y = 4400[1 - \exp(-0.02t)]^{2.3}$$

where Y is the humus mass (g/m²) and t is time in years ($R^2 = 0.69$, $n = 57$). This equation indicated a steady state mass of 4400 g/m² was reached in 190 years.

Accumulation patterns of humus mass on log surfaces were strongly affected by bark stability. On Sitka spruce logs, bark sloughed just when humus was rapidly accumulating; consequently, little humus accumulated until fragmentation ceased. On Douglas fir logs, humus accumulation occurred until 40 years, when bark fragmentation prevented further accumulation until 140 years. Humus accumulation on western hemlock logs appeared to increase steadily.

Trees.—Many woody species grew on logs, including: *Acer circinatum* Pursh, *A. macro-*

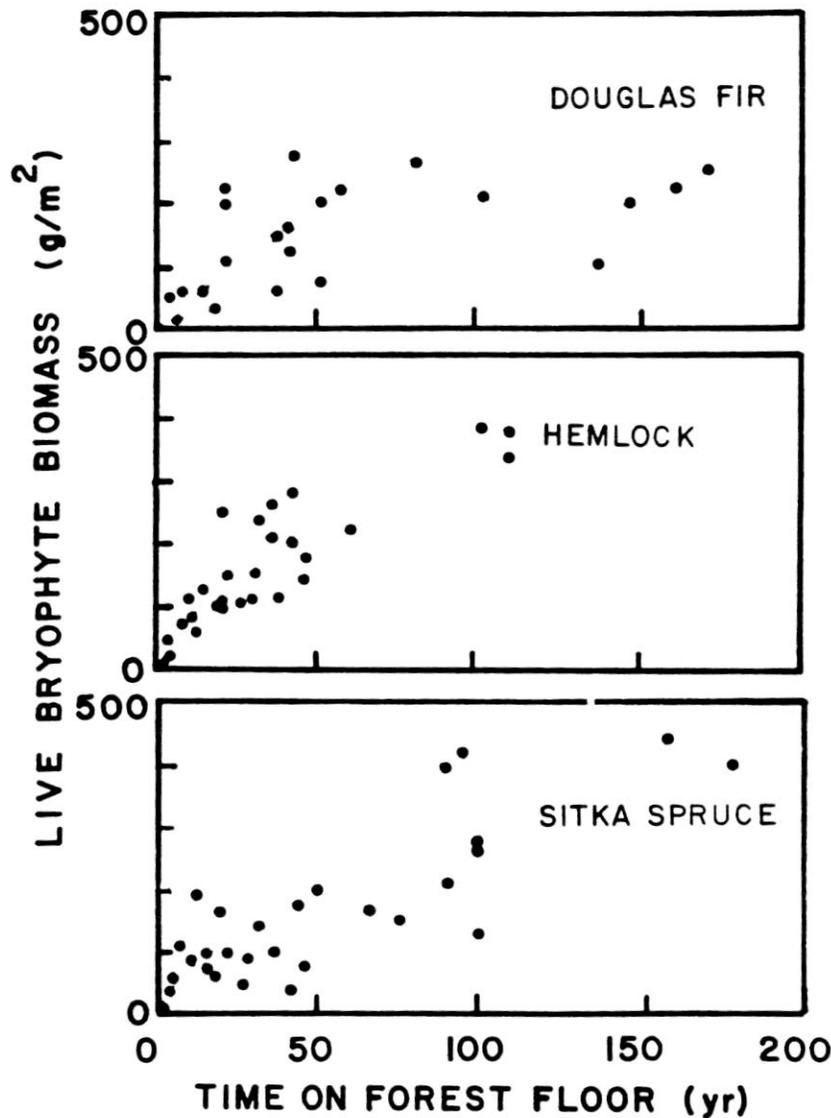


FIG. 3.—Increase in live bryophyte biomass on Sitka spruce, Douglas fir and western hemlock logs as a function of time on the forest floor. Points represent the mean of five samples per log

phyllum Pursh, *Alnus rubra* Bong., *Gaultheria shallon* Pursh, *Menziesia ferruginea* Smith, *Picea sitchensis*, *Pseudotsuga menziesii*, *Rhamnus purshiana* D.C., *Rubus spectabilis* Pursh, *Sambucus racemosa* L., *Thuja plicata* Donn., *Tsuga heterophylla*, *Vaccinium alaskense* Howell and *V. parvifolium* Smith. The following analysis considers only Sitka spruce and western hemlock because they composed the majority (i.e., 99%) of individuals.

Tree seedlings began growing on bark surfaces within 2 years after logs fell. Total tree

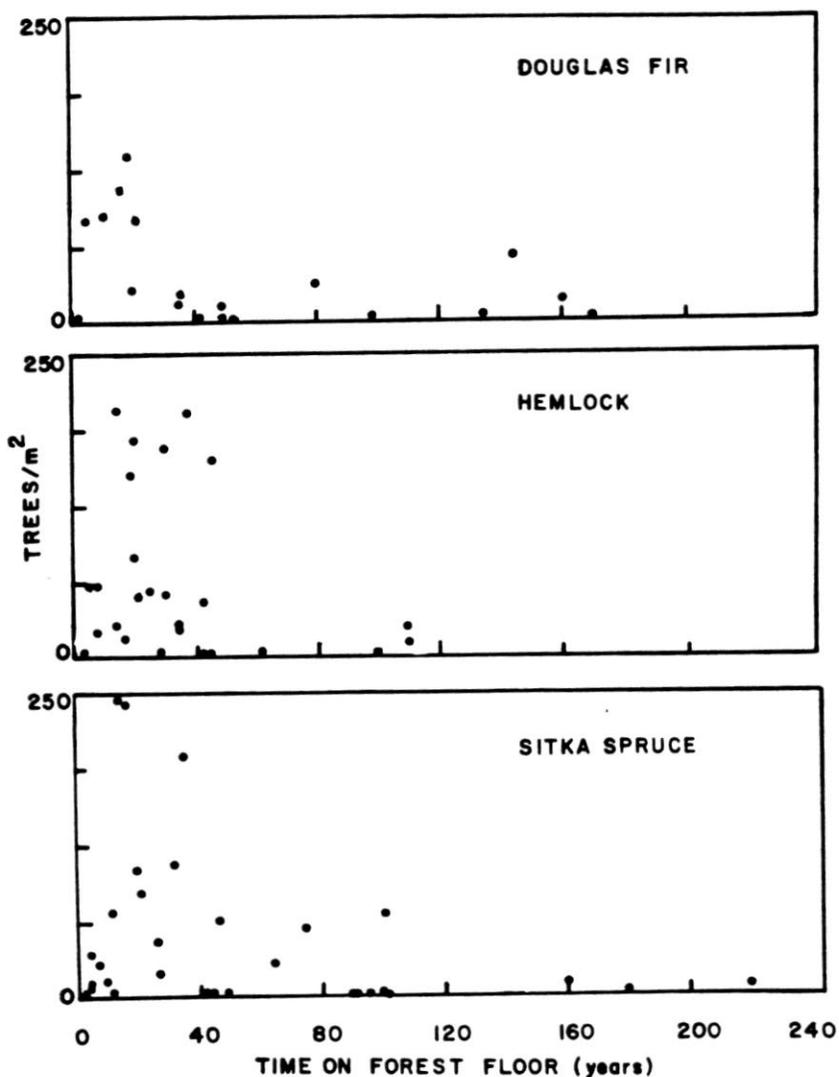


FIG. 4.—Total tree density (all sizes) on Sitka spruce, Douglas fir and western hemlock logs as a function of time on the forest floor. Points represent the mean of five samples per log

density on bark reached a mean maximum of 150 trees/m² at 15–25 years, but the range was quite high (14–422 trees/m²). Peak density may have been related to canopy closure; the highest values occurred when canopy cover was about 25%. Polynomial regression indicated seedling density on bark was significantly influenced by bryophyte mass ($P < 0.01$) and was highest when total bryophyte mass was between 50 and 350 g/m². Tree density on wood of Sitka spruce and western hemlock logs reached a maximum of 150–250/m² at 15–40 years. On Douglas fir logs, wood surfaces supported a maximum of 75–100 trees/m² at 80–150 years. The pattern of tree density on entire log surfaces was highly

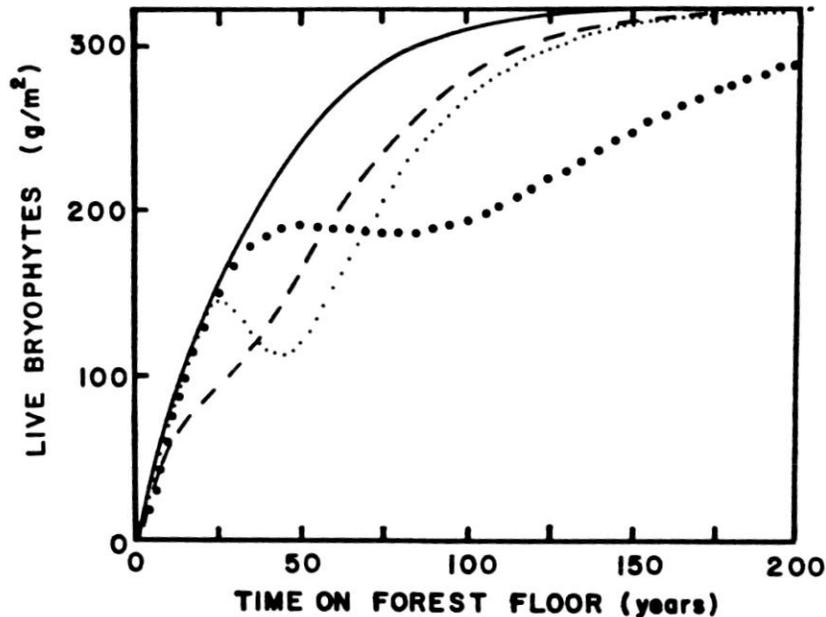


FIG. 5.—Changes in live bryophyte mass on stable surfaces (—), Sitka spruce (---), Douglas fir (●●●●) and western hemlock (·····) logs predicted by model simulations

variable, but was highest when logs had been on the forest floor for 15 to 50 years (Fig. 4).

Tree density on all species of log rapidly decreased on bark surfaces 15–45 years old. The tree-thinning rate on bark was calculated with a negative exponential equation for all species of logs > 15 years old. Peak density of 140 trees/m² and a thinning-rate-constant of 0.08/year were calculated ($R^2 = 0.75$, $n = 36$). The asymptotic 95% confidence intervals for these parameters were 0.03–0.12/year and 108–173 trees/m², respectively. This approximated a mortality or thinning rate of 8%/year 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 about 1 tree/m², suggesting a low mortality rate.

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 (73% of the 173 dead trees observed had exposed root systems).

Model simulation.—Without fragmentation, the model predicted live bryophyte mass increased to a steady state in approximately 90 years (Fig. 5). The departure of each species from this stable-surface curve depended on bark fragmentation patterns. Bryophyte accumulation rate on Sitka spruce was predicted to be lower than the stable-surface. On Douglas fir logs, bryophyte mass was predicted to plateau between 50–90 years. Rapid bark fragmentation on western hemlock logs is predicted to cause a decrease in bryophyte mass between 25 to 50 years.

Model simulations predict that bark fragmentation will extend the period of tree recruitment (Fig. 6). Sitka spruce was predicted to have a lower peak tree-density than the stable-surface. This is due to the exposure of fresh wood surfaces with low tree densities

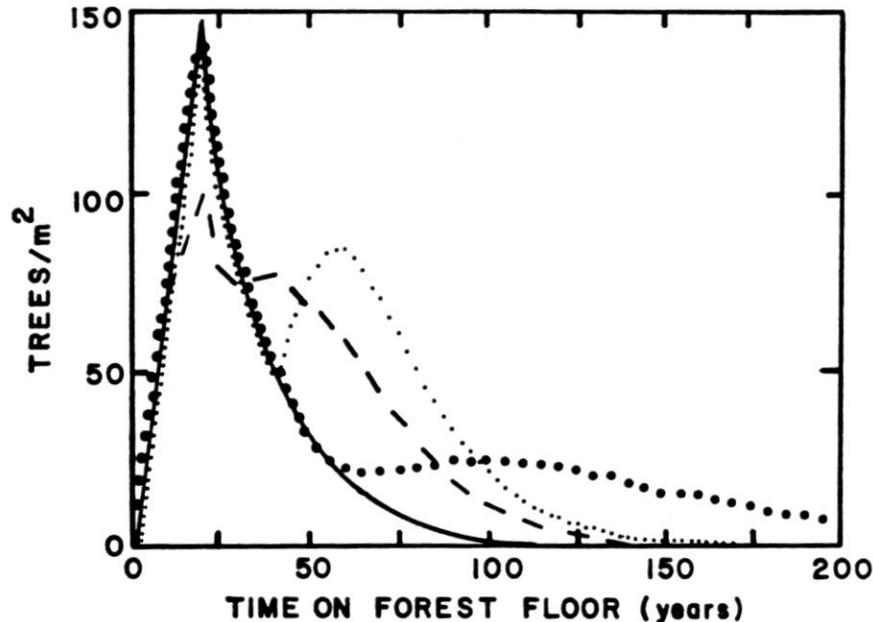


FIG. 6.—Changes in tree density (all sizes) on stable surfaces (—), Sitka spruce (---), Douglas fir (●●●●) and western hemlock (·····) logs predicted by model simulations

when the peak in tree density on bark is occurring. Tree density on Sitka spruce and Douglas fir logs was predicted to remain higher than on the stable-surface because the period of recruitment is extended by bark fragmentation. As with bryophyte mass, fragmentation of western hemlock bark made the tree-density curve complex. During the first 40 years of succession, western hemlock was predicted to be similar to the stable-surface curve. However, between 40–60 years, the rapid exposure of bare wood is predicted to cause a secondary peak in tree density.

DISCUSSION

The nurse-log sere is initially dominated by vascular and bryophytic epiphytes that are unable to tolerate forest floor conditions (Sharpe, 1956). Although eventually replaced by bryophytes, herbs and shrubs tolerant of these conditions, epiphytes may speed tree colonization of logs by retaining seeds and forming organic soil as they decay. The largest and fastest growing tree seedlings on logs often root in masses of dying and decaying epiphytes.

Bryophytes also perform several functions during the sere. Small species, such as *Hypnum circinale*, rapidly cover the log within the first decade, increasing retention of seeds and needle litter on logs (Harmon, 1986). As intermediate-sized bryophytes colonize the log and a humus layer accumulates, establishment rate of trees increases (Harmon, 1987). These intermediate-sized bryophytes (e.g., *Dicranum* and *Rhizomnium*) are eventually replaced by the feather mosses (*Hylocomium splendens*, *Rhytidiadelphus loreus* and *Eurhynchium oregonum*), which are sufficiently tall and dense to prevent establishment of tree seedlings (Harmon, 1986).

Light probably influences the rate and nature of succession on logs. The degree of canopy

openness influences the rate tree seedlings establish on litter-covered logs and bryophyte-covered logs (Harmon, 1986; Harmon, 1987). Under deep shade, few tree seedlings survive on logs, but bryophytes may continue to grow and eventually exclude tree seedlings.

Bark fragmentation was a major factor in seedling and sapling mortality, although other thinning agents may be more important in terms of cumulative mortality. The actual number of trees killed by bark fragmentation cannot be measured directly using the chronosequence data. However, the tree-thinning and bark-cover regressions can be used to calculate the cumulative mortality due to self-thinning and bark fragmentation expected over the sere. These calculations indicated 7, 22 and 40% of the initial cohort of trees were removed by bark fragmentation on Douglas fir, western hemlock and Sitka spruce, respectively. Bark fragmentation was of minor importance for Douglas fir because it does not begin until a major fraction of the self-thinning has occurred.

This study indicated that the long-term survival rate of trees on logs was quite low. On logs with stable surfaces, high density was followed by rapid thinning. Bark fragmentation also killed a large proportion of trees, especially on Sitka spruce logs. Unless trees surviving competition and fragmentation sent roots into the mineral soil, they were prone to toppling from logs. Finally, longer-term studies are required in order to test the exact influence of these processes in controlling nurse-log succession and the relative contribution of nurse-logs to canopy replacement in Sitka spruce-western hemlock forests.

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