Retention of needles and seeds on logs in *Picea sitchensis* – *Tsuga heterophylla* forests of coastal Oregon and Washington

MARK E. HARMON

Department of Forest Science, Oregon State University, Corvallis, OR 97331, U.S.A.

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Logs are a major seedbed in *Picea sitchensis* – *Tsuga heterophylla* forests; therefore, 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 on them, but rotten wood, sound wood, and bark of *Tsuga heterophylla*, *Picea sitchensis*, and *Pseudotsuga menziesii* retained few (0–8%). Examination of logs mapped in five *Picea sitchensis* – *Tsuga heterophylla* stands in Oregon and Washington indicated a mean projected log cover of 9.9%. Thin (<5 cm) and thick (>5 cm) moss mats were the most abundant log surfaces and covered 59 and 25% of the logs, respectively. Analysis of data on seedbed coverage, retentive characteristics, and seedbed-specific seedling survival indicated approximately 1% of a seed cohort would survive the 1st year on log surfaces.

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Les troncs d'arbres abattus constituent un germoir important dans les forêts de *Picea sitchensis* – *Tsuga heterophylla*; donc, l'interception et la rétention des graines sur ces surfaces peuvent restreindre le recrutement d'arbres. La capacité qu'ont les surfaces des rondins dans les forêts de *Picea*–*Tsuga*, à retenir les aiguilles et les graines a été étudiée à la Forêt Expérimentale de Cascade Head, en Orégon. Les surfaces couvertes de mousse et de détritus ont retenu plusieurs (48–98%) des graines et des aiguilles qu'on y avait placées, mais le bois pourri, le bois sain et l'écorce des *Tsuga heterophylla, Picea sitchensis* et *Pseudotsuga menziesii* n'en ont retenu que peu (0–8%). L'examen des troncs relevés dans cinq bouquets de *Picea sitchensis* – *Tsuga heterophylla* en Orégon et au Washington a indiqué une moyenne projetée de couvert de rondins de 9,9%. Des tapis de mousse minces (<5 cm) et épais (>5 cm) étaient les surfaces les plus abondantes et couvraient 59 et 25% des rondins respectivement. L'analyse des données sur l'étendue de la couche, les caractéristiques de rétention et la survie des semis suivant le type de couche a indiqué qu'environ 1% d'une cohorte de graines pourrait survivre pendant la 1e année sur la surface des rondins.

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Introduction

Forest floors can be viewed as a mosaic of microsites with differing rates of tree seedling recruitment, growth, and survival (Harper 1977). Common forest-floor microsites include pits and mounds (Beatty 1984), rotten wood (Harmon *et al.* 1986), and light gaps (Runkle 1981). In addition, there are variations in soil depth (Bratton 1976) and litter depth (Knapp and Smith 1982). Rotting logs are an important microsite in many *Picea*–*Tsuga* forests and are often a major site of tree regeneration (Harmon and Franklin 1989; McKee *et al.* 1982; Minore 1972). Rotting logs in mature and old-growth *Picea*–*Tsuga* forest represent a microsite or safe-site (*sensu* Harper 1977, p. 123), where the competitive effects of bryophytes and herbs are temporally reduced to the point that tree seedlings can establish successfully (Harmon and Franklin 1989).

Density of tree seedlings varies greatly among logs in mature and old-growth *Picea*–*Tsuga* forests and depends partially on the type of surface covering logs (Harmon 1988). Survival and growth of *Picea* and *Tsuga* seedlings on litter-covered surfaces increases with litter depth (Harmon 1987). In contrast, survival on moss-covered surfaces increases with depth until 5 cm and then decreases because taller mosses shade tree seedlings (Harmon and Franklin 1989). Survival on moss- and litter-covered surface types is a function of the light environment, with highest survival under partial canopy shading. Seedling density is lower on bare wood-covered surfaces and bare bark-covered surfaces than on moss- and litter-covered surfaces (Harmon 1988). One possible explanation for this pattern is that seed retention is lower on bare wood-covered surfaces and bare bark-covered surfaces than on moss- and litter-covered surfaces.

This study was conducted to test if seed retention varied among the surface types covering logs. Christy and Mack (1984) hypothesized that logs are favorable microsites for *Tsuga* seedlings because they slough litter. However, the factors that favor seed retention are likely to favor litter retention. Therefore, I also tested whether needle litter retention was effected by log surface type to examine the Christy and Mack (1984) hypothesis. In addition to measuring retention, the areal extent of logs and log surface types was determined in five *Picea*–*Tsuga* stands to explore the theoretical implications of retention on seedling recruitment in mature and old-growth forests.

Methods

Study area

Experiments were conducted in three mature *Picea sitchensis* – *Tsuga heterophylla* stands at the Cascade Head Experimental Forest near Otis, Oregon. This forest is located in the coastal *Picea sitchensis* Zone of Oregon and Washington that is noted for high productivity (Fujimori 1971), luxuriant understory and epiphytic growth, and large tree size (Franklin and Dyrness 1973). Most stands at Cascade Head are dominated by mixtures of *P. sitchensis* and *T. heterophylla* that originated after a catastrophic fire during the 1840's (Morris 1934). Diameter at breast height (dbh), height of trees, and stem density in these stands are 75–100 cm, 45 m, and 230–540 trees/ha (>5 cm dbh), respectively (Harcombe 1986; Greene

TABLE 1. Percentage retention and range of *Picea sitchensis* seeds and *Picea sitchensis* and *Pseudotsuga menziesii* needles on eight kinds of log surfaces

Log surface	*Picea* seeds			*Picea* needles			*Pseudotsuga* needles		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
Hypnum circinale	52.0	28.6	5.5−78.5	94.0	1.87	91−95	93.7	4.14	87−98
Dicranum−Rhizomnium	48.3	17.39	20.0−64.5	92.7	0.41	95−96	91.0	3.74	85−95
Eurhynchium−Rhytidiadelphus	71.7	20.36	38.5−90.0	99.3	0.82	98−100	97.7	1.08	96−99
Litter	58.9	28.92	12.0−88.0	93.0	4.42	86−98	83.3	7.36	80−95
Picea bark	0.2	0.21	0−0.5	4.7	2.48	1−8	3.3	2.86	1−8
Pseudotsuga bark	0.5	0	0.5−0.5	3.7	1.47	2−6	8.3	0.41	8−9
Tsuga bark	0	—	—	0.3	0.41	0−1	1.3	1.08	1−3
Rotten *Tsuga* wood[a]	0.5	0.62	0−1.5	7.7	3.19	3−12	8.3	2.27	6−12

[a]Decay class III.

1982). The climate is cool and very moist, with a mean annual temperature of 10°C and mean annual precipitation of 250 cm. The heaviest precipitation occurs during December and January, and June−August are relatively rain free (16 cm).

Seed retention

In the seed-retention experiment, *Picea* seeds were used to test differences among three types of moss coverings in addition to those of wood, bark, and litter surfaces. The experimental design was complete randomized blocks with three blocks each located in a stand selected to represent typical mature *Picea−Tsuga* forests in the area. The surfaces tested were (*i*) a very thin layer (0.2 cm) of *Hypnum circinale* that corresponds to a very early period in log-surface succession; (*ii*) cushions of *Dicranum fuscescens* and *Rhizomnium* sp., ranging in thickness from 2 to 4 cm, which corresponds to logs on the forest floor for 10−40 years; (*iii*) a 5 cm thick layer of feather mosses *E. oreganum* and *Rhytidiadelphus loreus* that is typical of log surfaces >30 years old; (*iv*), (*v*), and (*vi*) bare bark of *Picea*, *Pseudotsuga*, and *Tsuga*; (*vii*) rotten *Tsuga* wood; and (*viii*) a litter-covered surface. To create the surfaces, log slabs were mounted on a 30 × 60 cm wooden platform that elevated the slab 5 cm above the forest floor. Slabs were cut from 40−50 cm diameter logs and had a semicircular cross section that varied 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. Surfaces were protected from small mammals and birds by a 12-mm wire mesh 10−15 cm above the surface.

Two hundred orange-painted, dewinged *Picea* seeds were scattered on each surface from a height of 20 cm on 19 December 1982. A preliminary experiment indicated that the presence of wings on seeds had little effect on seed retention (Harmon 1986). The bark and wood surfaces were examined for seeds after 86 days, when the moss and litter surfaces were collected. The harvested material was oven-dried, sifted, and sorted to find the seeds. In this and the needle experiment, the arc sine angular transformation was applied to the data before analysis of variance.

Needle retention

In the needle-retention experiment, *P. sitchensis* and *Pseudotsuga menziesii* needles were used to test the retentive characteristics of the eight surfaces used in the seed-retention experiment. The experimental design was a split plot of complete randomized blocks, with three blocks each located in a different *Picea−Tsuga* stand. Log surface was the main-plot treatment, and the species of needle was the subplot treatment. Each of the eight log surfaces was divided in half and received 100 needles painted orange, with species randomly selected. The number of needles on each surface was determined as described for seeds 21, 42, and 65 days after placement on 19 December 1982.

Seedbed abundance

To determine the extent of logs in the *Picea−Tsuga* type, maps from five "reference" stands were used (unpublished maps on file at Research Work Unit 1251, Forestry Sciences Laboratory, Corvallis, OR). Stands were 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 1−2 ha and included data on the location, length, end diameters, species, and decay class of logs. Five decay classes, based on the presence of twigs, branches, bark, tree seedlings, moss cover, and depth of wood decay, were used to indicate the relative state of decomposition, with class I being the least decayed and class V being the most decayed (Graham and Cromack 1982). Mapped logs were >15 cm in diameter and >1 m in length. 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 estimated for five 2-m segments on the upper half of each log. Decay class IV and V logs >10 m long could not always be located, 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

Seed retention

Moss and litter surfaces retained seeds better than rotten wood or the three bark types (Table 1). Log surface effects on seed retention were highly significant ($p < 0.01$) (Table 2). 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 fraction of seeds (0.5%); this was probably a result of deeper crevices on this surface. The only seeds retained on rotten wood were those in insect galleries and cracks.

Needle retention

Needles were lost from the bark and rotten wood surfaces faster than litter- or moss-covered surfaces (Fig. 1). At 86 days, there was a significant interaction between needle species and log surface type, but this result could not be attributed to any biological mechanism (Table 3). In contrast, differences among surface types were highly significant ($p < 0.01$). Therefore, ignoring the interaction and interpreting the main effects seems reasonable (Table 1). Of the moss surfaces, *Eurhynchium−Rhytidiadelphus* mats retained the highest proportion of needles (97.7−99.3%); the other two moss surfaces kept a slightly lower fraction (91.0−94.0%). Because the differences among moss surfaces were small, the major

TABLE 4. Projected log cover by species and decay class for five *Picea sitchensis* – *Tsuga heterophylla* stands in Oregon and Washington

	Picea sitchensis					*Tsuga heterophylla*					
	I	II	III	IV	V	I	II	III	IV	V	Total
Mean cover (%)	0.05	0.48	1.28	0.48	0.04	0.40	1.34	3.86	1.59	0.41	9.93
Standard error	0.06	0.33	0.65	0.18	0.04	0.22	0.21	1.20	0.28	0.17	1.59

NOTE: $n = 5$.

TABLE 5. Mean percent cover of seedbed types for *Picea sitchensis* and *Tsuga heterophylla* logs for each of five decay classes

	Picea sitchensis					*Tsuga heterophylla*					Total cover (%)[a]
	I	II	III	IV	V	I	II	III	IV	V	
Surface type											
Bare bark	70.4	16.3	0.1	0	0	80.8	22.8	0.7	0.1	0	0.78
	(9.7)	(5.7)	(0.1)	(0)	(0)	(3.3)	(6.1)	(0.4)	(0.2)	(0)	
Wood	0.5	4.9	10.1	3.6	1.6	0	0	2.5	3.6	1.4	0.33
	(0.5)	(2.7)	(3.4)	(1.2)	(1.0)	(0)	(0)	(1.2)	(1.5)	(0.8)	
Litter	16.7	4.9	10.4	13.3	26.6	2.3	8.3	1.2	2.8	0.5	0.45
	(6.0)	(2.5)	(5.6)	(6.6)	(11.8)	(1.1)	(3.4)	(0.6)	(1.0)	(0.2)	
Thin moss	12.4	73.9	72.8	34.2	14.1	16.9	68.9	58.4	41.4	18.0	5.44
	(5.5)	(7.2)	(9.1)	(9.5)	(5.9)	(3.0)	(5.8)	(13.4)	(9.4)	(7.6)	
Thick moss	0	0	6.6	48.9	57.6	0	0	37.0	52.1	80.0	2.93
	(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	

NOTE: Standard error is given in parentheses below each mean value.
[a]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.

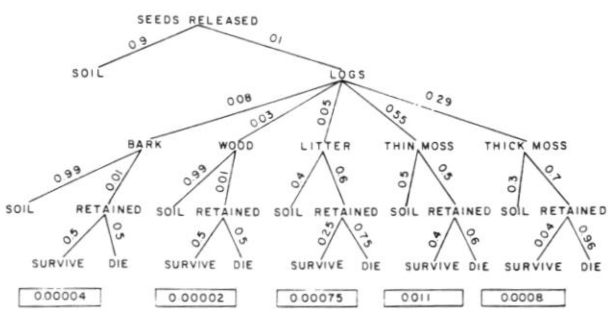

FIG. 2. Theoretical survival of seedlings by seedbed type in a typical *Picea sitchensis* – *Tsuga heterophylla* forest. The data on 1st-year survival on moss mats and litter are from Harmon (1987) and Harmon and Franklin (1989). The numbers in boxes represent the proportion of the original cohort surviving on each seedbed.

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 mature to old-growth *Picea–Tsuga* stand and indicate the very high mortality occurring in the 1st year of a cohort's existence.

Although the total proportion of seedlings predicted to survive the 1st year is indeed small, the actual number of seedlings recruited can be very large because of the abundance of seed rain in *Picea–Tsuga* forests (Ruth and Berntsen 1955). Therefore, despite the low survival rate and low availability of suitable seedbeds, the actual amount of recruitment could be large, and because most of these seedlings are restricted to a limited area, the amount of competition among seedlings in later years would be very high (Harmon 1988).

In summary, a large proportion of seedlings occur on log-related seedbeds in mature and old-growth *Picea–Tsuga* forests, and these seedbeds differ considerably in their extent, retentive qualities, and survival characteristics. Because of the heavy seed rain in *Picea–Tsuga* forests, adequate recruitment of 1-year-old seedlings could occur even on surfaces with very low retention or survival. Further studies on seedling survival after the 1st year, especially on soils, would be quite revealing because continued low survival on soils would strongly indicate that tree recruitment in old-growth *Picea–Tsuga* forests is substrate limited.

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TABLE 2. Analysis of variance of seed-retention experiment

Source of variation	df	Sum of squares	Mean squares	F-ratio	p
Blocks	2	1 991.2	995.6	6.916	<0.01
Surface type	7	14 074.4	2 010.6	13.97	<0.001
Error	14	2 015.2	143.9		
Total	23	18 080.9			

NOTE: Experimental design was randomized complete blocks.

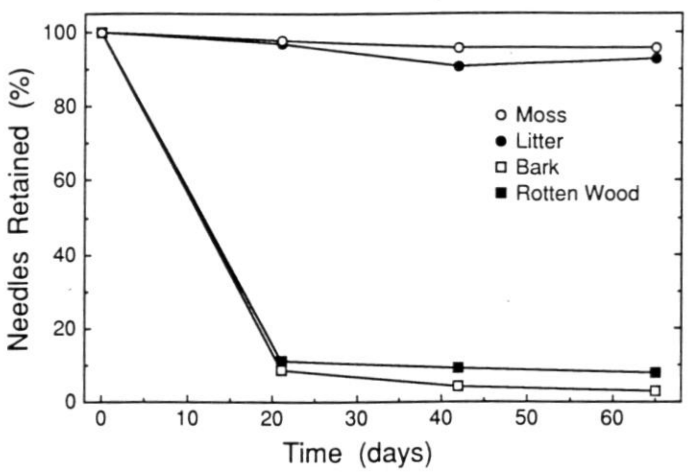

FIG. 1. Percentage of *Picea sitchensis* needles retained on rotten wood-, bark-, moss-, and litter-covered log surfaces as a function of time. Values for moss- and bark-covered surfaces are means of the three moss treatments and the three bark treatments shown in Table 1.

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. Rotten *Tsuga* wood retained more needles than bark surfaces (8 vs. 5%) because needles were trapped in cracks and insect galleries.

Seedbed abundance

Total projected log cover in five *Picea*–*Tsuga* stands averaged 9.9% and ranged from 6.1 to 14.3% (Table 4). Major differences in surface type were evident among decay classes (Table 5). Bark was the major surface type for class I *Picea* and *Tsuga* logs, with a mean cover of 70 and 81%, respectively. The major surface type for class II and III logs was thin moss mats (<5 cm), which covered a range of 68.9 to 73.9% 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.

Thin moss mats comprised the majority of the log seedbeds (54.8%) and covered an average of 5.4% of the stand area (Table 5). 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. Assuming logs covered by thin moss mats and litter were the only sites of seedling recruitment, 5.9% was the average surface area for tree-seedling recruitment.

Discussion

The similar response of seeds and needles to log surface types indicates that a basic assumption of the Christy and

TABLE 3. Analysis of variance of needle-retention experiment

Source of variation	df	Sum of squares	Mean squares	F-ratio	p
Blocks	2	166.0	83.0	2.96	ns
Surface type (A)	7	53 200.9	7 600.1	271.2	<0.001
$Error_A$	14	392.4	28.0		
$Total_A$	23	53 759.3			
Needle species (B)	1	0.6	0.6	0.05	ns
A × B	7	268.2	38.3	3.00	<0.05
$Error_B$	16	204.0	12.7		
$Total_B$	24	472.8			
Total	47	54 232.1			

NOTE: Experimental design was split-plot, randomized complete blocks.

Mack (1984) hypothesis is incorrect. Logs are predicted to retain more seeds and litter as they age, primarily because of increases in moss cover. Moss cover reached a maximum within 10–15 years on a log chronosequence within a *Picea*–*Tsuga* forest (Harmon 1988), and retention would be predicted to reach a maximum during the same period. This is also the period of maximum seedling density on logs (Harmon 1988).

Retention of needles on logs by mosses helps build an organic soil, and this increases the survival and growth of tree seedlings (Harmon 1987). As logs age, mosses increase in thickness until young tree seedlings are excluded by competition (Harmon and Franklin 1989). Therefore, class IV and V logs would be expected to recruit few seedlings, in spite of high seed retention and greater degree of wood decay than class I–III logs. This prediction matches the pattern of tree density on a nurse-log chronosequence from the *Picea*–*Tsuga* forests of Olympic National Park (Harmon 1988).

One way to envision the effects of seed retention on seedling recruitment at the stand level is to model the fate of a cohort of seeds during their 1st year (Fig. 2). The results of this study, along with those of Harmon (1987) and Harmon and Franklin (1989), were used to calculate the proportion of seeds surviving the pathways illustrated in Fig. 2. Of the seeds landing on logs, most will be on either thin (55%) or thick (30%) moss mats. Very few seeds (<1%) will be retained on the bark and wood seedbeds. In contrast, one-half or more of the seeds landing on litter or moss will be retained. First-year survival of seedlings growing on moss mats is a function of moss thickness; mean 1st-year survival rates were 40% for mats <5 cm thick and 4% for mats >5 cm thick (Harmon and Franklin 1989). First-year survival on litter seedbeds is an increasing function of litter depth (Harmon 1987). Because litter depths were not sampled in the study, the assumption used was that 25% of the seedlings would survive the 1st year on the average litter seedbed. Survival rates on natural bark and wood seedbeds have not been measured, so a very liberal value of 50% was assumed.

By multiplying probabilities along the chain of events described from seed release to the end of the 1st year, the probability that a seed (or the proportion of the initial cohort) will survive the 1st year on a given seedbed can be calculated. About 1.3% of the original cohort would survive on all the log seedbeds, but most of the seedlings would occur on thin moss seedbeds. The actual rates of seed retention, survival probabilities, and seedbed distribution differ from stand to stand as

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