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The influence of litter and humus accumulations and canopy openness on *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. seedlings growing on logs

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The influence of litter and humus accumulations on the surface of logs and canopy openness upon growth and survival of *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. seedlings was tested experimentally at Cascade Head Experimental Forest, near Otis, Oregon. This was done by adding litter and humus to the surface of freshly fallen logs. Survival rates of both species increased asymptotically as litter accumulations on logs increased. Mean maximum survival was 58% for *Picea* and 34% for *Tsuga*. *Picea* seedling survival peaked when tree canopy cover ranged from 70 to 80% with lower survival at either higher or lower values. *Tsuga* survival was highest under closed canopies. Seedling growth increased as litter–humus accumulation and canopy openness increased.

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Les effets de l'accumulation de la litière et de l'humus à la surface des troncs, ainsi que de l'ouverture du couvert foliacé sur la croissance et la survie des semis de *Picea sitchensis* (Bong.) Carr. et de *Tsuga heterophylla* (Raf.) Sarg. ont été déterminés expérimentalement à la Cascade Head Experimental Forest, près de Otis en Oregon, en ajoutant de la litière et de l'humus à la surface de troncs d'arbres nouvellement renversés. Le taux de survie des deux espèces a augmenté de façon asymptotique à mesure qu'augmentaient les accumulations de litière sur les troncs. La survie maximale moyenne a été de 58% pour *Picea* et de 34% pour *Tsuga*. La survie des semis de *Picea* a culminé lorsque le couvert foliacé atteignait 70–80% et elle a été moindre lorsque le degré du couvert était moindre ou plus élevé. La survie du *Tsuga* fut maximale sous un couvert fermé. La croissance des semis a augmenté à mesure que l'accumulation de la litière et de l'humus augmentait et que le couvert devenait plus ouvert.

[Traduit par la revue]

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, logs, stumps, and large woody fragments cover from 6 to 14% of the forest floor (Harmon 1986) but account for as much as 98% of the tree regeneration (McKee *et al.* 1982). Logs are an important seedbed in many *Picea–Tsuga* forests because a luxuriant moss and herb layer out-competes young tree seedlings on the forest floor (Harmon 1986). Logs are a good seedbed only during stages when moss mats growing on them are not sufficiently thick to exclude tree seedlings.

Tree seedlings growing on logs often root in fine litter and humus (derived from needles, dead mosses, twigs, etc.) that have accumulated on the log surface (Minore 1972). Wood decays slowly in *Picea–Tsuga* forests (Grier 1978; Graham and Cromack 1982) and surficial litter–humus accumulations form seedbeds on logs faster than wood decays. Furthermore, by the time wood decay provides a suitable rooting medium, a layer of live and dead mosses thick enough to exclude tree seedlings may develop on log surfaces (Harmon 1986). In addition to serving as a rooting medium, moss- and litter-covered surfaces are more likely to retain seeds than bare wood- or bark-covered surfaces (Harmon 1986).

These factors indicate that litter–humus- and moss-covered logs are important seedbeds in *Picea–Tsuga* forests. The effect of varying moss depth on seedling survival is reported elsewhere (Harmon 1986). This study assesses the effect that litter–humus accumulations on logs and canopy openness have upon tree seedling growth and survival. The basic hypothesis was that tree seedlings in *Picea–Tsuga* forests can establish on the surficial litter and humus deposits that cover logs without sending roots into the log. Heavy litter accumulations on the forest floor are often viewed as detrimental to conifer seedling survival (Moore 1926; LeBarron 1948; Place 1955; Smith 1955; Davis and Hart 1961) because they are prone to drying and prevent seedling root systems from quickly reaching mineral soil. However, on logs, especially those that are fairly undecayed, litter and humus accumulations may form the only rooting media. If tree seedlings survive on these deposits, then colonization of logs by tree seedlings may be controlled more by surface characteristics than wood decay. In order to broaden the scope of inference, the litter–humus and seedling survival relationship was examined under a range of canopy conditions.

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 coasts of Oregon, Washington, British Columbia, and south central Alaska. The climate at the study site 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, whereas June through August are relatively rain free (16 cm). Forests at Neskowin Crest are dominated by *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. (Greene 1982), originating after a catastrophic fire that occurred during the 1840s (Morris 1934). Diameter at breast height and height of trees in these stands are 75–100 cm and <60 m, respectively (Greene 1982).

Methods

The overall design of the experiment was a split-plot of a randomized complete blocks design, with eight naturally fallen logs as the block effects, five litter biomass treatments as the main plot effect, and two seedling species as the subplot effect. One 36 × 70 cm wooden tray 10 cm deep was nailed onto each of eight freshly fallen *Picea* or *Tsuga*

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

	Treatment				
	1	2	3	4	5
Litter	0.7	1.1	1.5	1.5	1.5
Humus	0	0.5	2.0	3.9	7.8
Total	0.7	1.6	3.5	5.4	9.3

TABLE 2. Regression equations used to predict seedling biomass from total stem length

Species and components	B_0	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	1.30	0.82	32

NOTE: The equation form is $Y = B_0X^{B_1}$ where X is the stem length (mm), B_0 and B_1 are regression constants, and Y is the component mass (mg). B_0 values are corrected for bias using the correction factor of Baskerville (1972).

logs. Logs varied in diameter from 60 to 150 cm and were at least 30 m long. Logs were selected to represent a range of canopy conditions. Tray position on each log was assigned randomly along the length of the log that met the canopy openness class. 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 five equal segments (470 cm^2) and a range of litter and humus layers (Table 1) were randomly assigned within each tray. The range of litter and humus accumulations exceeded the 0–5 kg/m^2 reported for a chronosequence of nurse logs from *Picea–Tsuga* forests in Washington (Harmon 1986). However, four of the treatments were at levels observed in nature. Litter and humus were obtained from the base of *Picea* and *Tsuga* trees. Litter and humus derived from mosses were not examined in this study, but it is likely the humus derived from mosses is generally similar to that derived from needle litter. Each layer was mixed separately and large fragments of wood and bark were removed. When added to the trays, litter was placed on top of the humus layer. In March 1982, a randomly selected half of each litter–humus treatment received 50 *Picea* seeds and the other half received an equal number of *Tsuga* seeds. When added to trays, seeds were scattered on the surface. The initial seed density was 1000 seeds/m^2 and 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 growth analysis. Roots of harvested seedlings were washed in an aqueous solution of sodium tripolyphosphate to remove adhering humus and then separated from the aboveground parts. Roots, stems, and needles were oven-dried for 24 h at 55°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 2). This procedure was necessary because the biomass of the seedlings could not be measured directly in 1982 without destructive sampling. Seedling stem length 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 fish-eye (180°) photograph was taken of the canopy above each log. The photographs were then digitized to measure the degree of canopy openness and provide a relative measure of the amount of diffuse light available to seedlings.

Survivorship data were transformed using arcsine p before the split-plot analysis of variance on the effect of litter–humus accumulation on survival was performed. Two regression models were used to determine the relationship between the number of survivors and litter–humus amount. In the first, the natural logarithm of X_1, the amount of litter–humus (kg/m^2), was regressed against Y, the mean percentage of survivors. The second regression model was a rectangular hyperbola:

$$[1] \quad Y = \frac{B_0X_1}{B_1 + X_1}$$

where Y is the mean percentage of survivors, X_1 is the amount of litter and humus (kg/m^2), B_0 is the maximum percentage surviving, and B_1 is the amount of litter and humus 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 of each species was also analyzed using multiple regression with canopy openness, amount of litter and humus, and combinations of these two terms as independent variables. The proportion of open sky, amount of litter and humus, their squares, and an interaction term using the square of open sky and litter biomass were used as independent variables in a stepwise regression analysis of seedling biomass. Use of the complex interaction term was appropriate since seedling biomass was linearly related to litter biomass and curvilinearly related to canopy openness. For these two analyses, each combination of litter–humus accumulation and canopy openness was considered an observation. Combinations without survivors were excluded (for *Picea*, $N = 39$; for *Tsuga*, $N = 37$). Unless noted elsewhere, all statistical tests were deemed significant or highly significant when $0.01 < p < 0.05$ or $p < 0.01$, respectively.

Results

Survival

Mortality was highest during the first 50 days (Fig. 1). At that time, there were no significant differences among the litter treatments, although there were highly significant differences between species. *Picea* survived better than *Tsuga* (59% vs. 39%). After 90 days of growth, the numbers of survivors declined where litter and humus accumulations were <3.45 kg/m^2, but remained relatively constant where accumulations exceeded this amount.

At 500 days, survivorship of both species increased with amounts of litter and humus and approached a maximum value of 55% for *Picea* and 34% for *Tsuga* (Fig. 2). For this period, there were highly significant effects due to blocks, litter biomass, and species. The regression of survival on the logarithm of litter–humus amounts for *Picea* was highly significant, but was not for *Tsuga* ($0.10 > p > 0.05$) (Table 3). The rectangular hyperbola regression was also highly significant for *Picea* but not for *Tsuga*. 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).

The highly significant differences among blocks appear related to canopy openness (Fig. 3). Stepwise multiple regression analysis using the proportion of open sky (X_1), X_1^2, the amounts of litter and humus (X_2 in kg/m^2), and ln X_2 as independent variables was used to test the combined effect of canopy openness and amounts of litter and humus on survival (Y). The ln X_2 term was used because it was significant when litter–humus amount was examined separately. This analysis

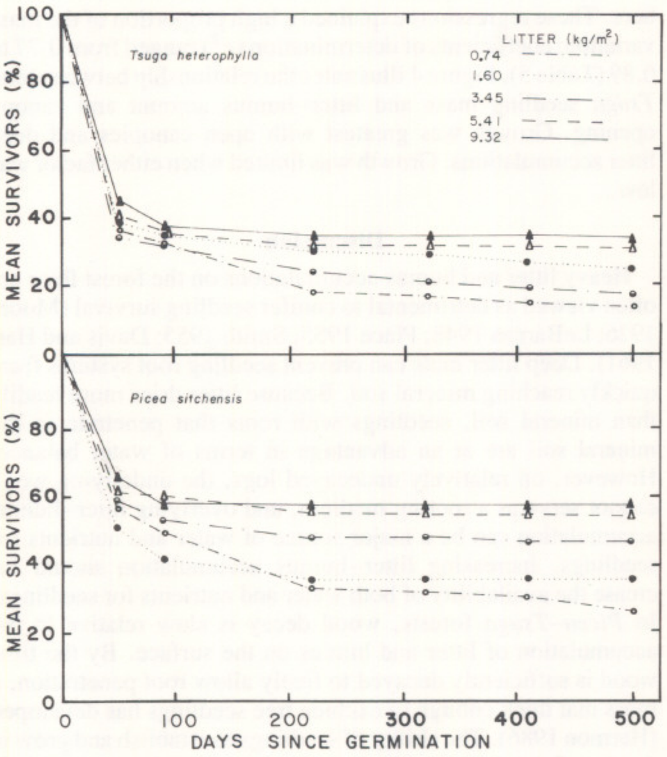

FIG. 1. Mean survivorship of *Picea sitchensis* and *Tsuga heterophylla* seedlings on logs as a function of time since germination and litter biomass on logs.

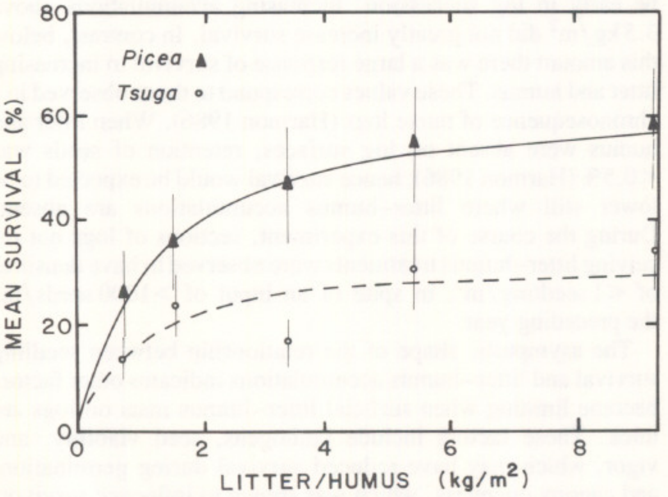

FIG. 2. Mean survivorship of *Picea sitchensis* and *Tsuga heterophylla* seedlings at 500 days after germination as a function of litter biomass placed on a log. The regression equations predicting the survival response to litter biomass are from Table 3. The solid line represents the regression for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

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

$$[2] \quad Y = -35.7 + 520\,X_1 - 795X_1^2 + 13 \ln X_2 \qquad r^2 = 0.52, N = 39$$

$$[3] \quad Y = 26.8 - 64X_1^2 + 8 \ln X_2 \qquad r^2 = 0.40, N = 37$$

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.

TABLE 3. Regression equations for predicting survival (%) of 2-year-old *Picea sitchensis* and *Tsuga heterophylla* seedlings from amounts of litter and humus (kg/m²)

Species	B_0	B_1	r^2	N
Logarithmic model				
Picea sitchensis	30.6	13.2	0.99**	5
Tsuga heterophylla	16.8	7.2	0.69ns	5
Rectangular hyperbola model				
Picea sitchensis	63	1.08	0.99**	5
Tsuga heterophylla	42	0.96	0.69ns	5

NOTE: ns, not significant; **, $p < 0.01$.

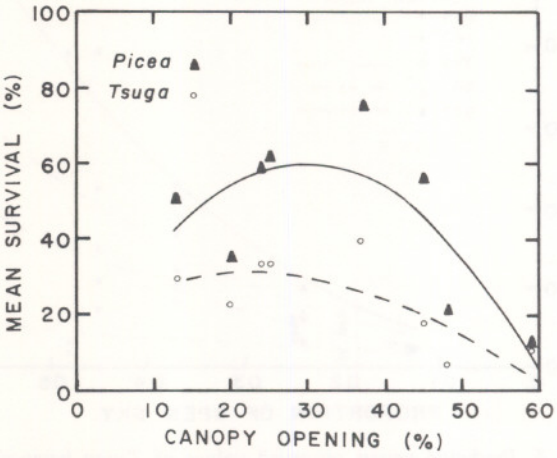

FIG. 3. Mean survivorship of *Picea sitchensis* and *Tsuga heterophylla* seedlings 500 days after germination as a function of canopy opening. Data points represent the mean for litter biomass treatments ($N = 5$). The solid line represents the regression for *P. sitchensis*, and the broken line represents the regression for *T. heterophylla*.

Seedling mass

The mass 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 mass as well as *Tsuga* needle, stem, root, and total mass were significantly related to the interaction term but not to the other terms. The general form of these equations is

$$[4] \quad Y = B_0 + B_1X_2X_1^2$$

where Y is mass (mg), X_1 is the portion of open sky, X_2 is the amount of litter and humus (kg/m²), and B_0 and B_1 are regression constants. However, the independent variable accounted for a very small portion of the mass variance and had low predictive value (e.g., the maximum r^2 of the six regressions was 0.16). *Picea* seedlings were significantly larger than *Tsuga* in terms of mean needle, stem, root, and total mass at the end of a single growing season (Table 4).

At the end of the second growing season (500 days), seedling mass increased with the amount of litter and humus and canopy

TABLE 4. Predicted mean biomass (mg) for 1-year-old *Picea sitchensis* and *Tsuga heterophylla* seedlings

	Picea			*Tsuga*			
Components[a]	$\bar{X}$	SE	*N*	$\bar{X}$	SE	*N*	p^b
Needles	4.7	0.2	39	3.8	0.2	37	<0.01
Stem	2.5	0.1	39	2.2	0.1	37	<0.01
Roots	2.9	0.1	39	2.6	0.1	37	<0.01
Total	10.1	0.3	39	8.5	0.4	37	<0.01

[a] These values were predicted from stem measurements and equations in Table 2.

[b] Significance level of one-tailed *t*-test.

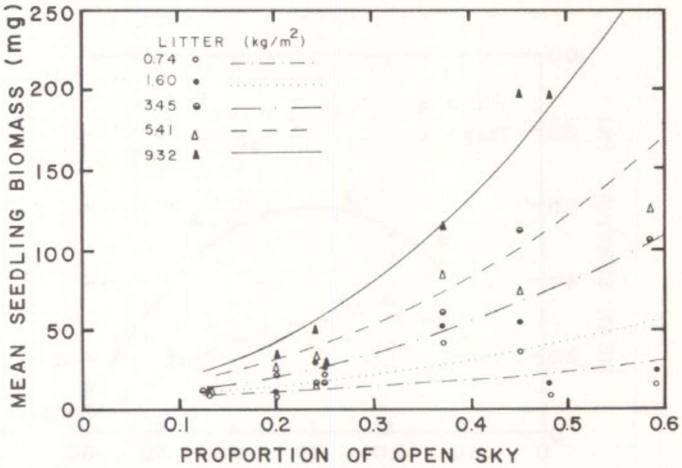

FIG. 4. Predicted versus observed values of *Tsuga heterophylla* seedling biomass (mg) after 500 days of growth as a function of portion of open sky (X_1) and litter biomass (X_2). The curves were plotted from the regression in Table 5.

TABLE 5. Regression equations to predict *Picea sitchensis* and *Tsuga heterophylla* biomass after two growing seasons from the interaction of litter biomass and canopy opening

Species and components	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

NOTE: The general form of the regression equation is $Y = B_0 + B_1X_2X_1^2$ where Y is the mean biomass (mg), X_2 is the litter biomass per plot (kg/m²), X_1 is the proportion of the canopy that is open, and B_0 and B_1 are regression constants.

openness (Fig. 4). The relationships between needles, stem, root, and total seedling mass of both species and the interaction of canopy openness and litter–humus amounts described in eq. 4 were highly significant. Other terms were added in later iterations of the stepwise procedure, but they were usually not significant or added in a consistent order. Addition of the main effects added 0.01–0.07 to the coefficient of determination. Therefore, only regressions of the form of eq. 4 are reported here. These regressions explained a high proportion of the mass variation; coefficients of determination (r^2) ranged from 0.77 to 0.89 (Table 5). Figure 4 illustrates the relationship between total *Tsuga* seedling mass and litter–humus amount and canopy opening. Growth was greatest with open canopies and deep litter accumulations. Growth was limited when either factor was low.

Discussion

Heavy litter and humus accumulations on the forest floor are often viewed as detrimental to conifer seedling survival (Moore 1926; LeBarron 1948; Place 1955; Smith 1955; Davis and Hart 1961). Deep litter mats can prevent seedling root systems from quickly reaching mineral soil. Because 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 relatively undecayed logs, the underlying wood cannot serve as a rooting medium, and overlying litter–humus accumulation can be a major source of water and nutrients for seedlings. Increasing litter–humus accumulation should increase the availability of both water and nutrients for seedlings. In *Picea–Tsuga* forests, wood decay is slow relative to the accumulation of litter and humus on the surface. By the time wood is sufficiently decayed to freely allow root penetration, a moss mat thick enough to exclude tree seedlings has developed (Harmon 1986). The ability of seedlings to establish and grow in these surficial deposits allows plant succession to proceed ahead of that predicted by wood decay alone.

The results of the experiment indicates the largest response of tree seedlings to increasing litter–humus accumulations would be early in log succession. Increasing accumulations above 3.5 kg/m² did not greatly increase survival. In contrast, below this amount there was a large response of survival to increasing litter and humus. These values correspond to those observed in a chronosequence of nurse logs (Harmon 1986). When litter and humus were absent on log surfaces, retention of seeds was <0.5% (Harmon 1986); hence survival would be expected to be lower still where litter–humus accumulations are absent. During the course of this experiment, sections of logs not receiving litter–humus treatments were observed to have densities of <1 seedling/m², in spite of an input of >1000 seeds/m² the preceding year.

The asymptotic shape of the relationship between seedling survival and litter–humus accumulations indicates other factors become limiting when surficial litter–humus mats on logs are thick. These factors include pathogens, seed viability, and vigor, which may have reduced survival during germination, and canopy openness, which was shown to influence survivorship. The response of seedling survival to canopy cover is complex, with reduced survival due to shading under closed canopies and excessive drying of the litter–humus mat under open canopies. As seedlings grow, competition will also likely limit survival. Mortality caused by competition should occur earliest where litter–humus accumulations on logs are thick and under moderately open canopies, because these sites had the highest survival rate and a moderate growth rate. Competitive thinning of tree seedlings begins approximately 20 years after log fall, when recruitment is at a maximum and litter and humus are accumulating at a high rate (Harmon 1986).

Abundant precipitation, heavy cloud cover, and low temperatures may allow seedlings to survive and grow on surficial mats of litter and humus that cover relatively undecayed logs within the *Picea sitchensis* Zone. Thus, tree colonization in these forests may proceed relatively independent of wood decay. In drier regions, even thick accumulations of litter and humus on logs may dry and tree colonization of logs would be strongly dependent on the degree of wood decay. The presence of thick litter and humus mats on logs in drier climates may decrease survival because the chance of roots reaching moist decayed wood should decrease with accumulation thickness.

In conclusion, this experiment demonstrated that in *Picea–Tsuga* forests, tree seedlings can establish and grow under a wide range of light conditions on litter and humus deposits that accumulate on logs. The system tested here was similar to the first 20 years of succession on sound logs. However, tree seedlings also colonize rotten wood from snag falls as well those from living trees. Further work is needed to examine the degree to which tree seedlings growing on logs derive nutrients and water from surficial litter and humus accumulations versus the underlying bark and wood.

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