

Amount, position, and age of coarse wood influence litter decomposition in postfire *Pinus contorta* stands

Alysa J. Remsburg and Monica G. Turner

Abstract: Spatial variation in vegetation and coarse wood is a major source of forest heterogeneity, yet little is known about how this affects ecosystem processes. In 15-year-old postfire lodgepole pine (*Pinus contorta* var. *latifolia* Englem.) stands in Yellowstone National Park, Wyoming, we investigated how the decomposition rate varies with the position of coarse wood and other dominant structures within and among stands. Tongue depressors (TD) (made of birch (*Betula* sp.)) and litterbags containing herbaceous litter (HL) and needle litter (NL) were deployed for 2 years within 3 burned stands and among 17 burned stands (each 0.25 ha). Within stands, the decomposition rate varied among six microsite treatments (above and below legacy wood, below logs on the ground and elevated logs, below saplings, and on open soil). Two-year mean mass loss from all litter types was least under elevated logs (HL 34.0%, NL 8.6%, TD 3.5%) and greatest under legacy wood (HL 55%, NL 33%, TD 12%). The moisture level was consistently lowest under elevated logs and highest beneath logs on the ground. Among forest stands, 2-year mass losses from HL and TD were negatively related to the amount of elevated wood. The influence of coarse wood on litter decomposition at two spatial scales suggests that coarse-wood accumulation creates long-term spatial heterogeneity in carbon and nutrient cycles.

Résumé : La variation spatiale dans la végétation et les débris ligneux grossiers est une source majeure d'hétérogénéité de la forêt. Malgré cela, on connaît peu de choses sur la façon dont cela affecte les processus de l'écosystème. Dans les peuplements de pin tordu (*Pinus contorta* var. *latifolia* Englem.) issus de feux et âgés de 15 ans dans le parc national de Yellowstone, au Wyoming, nous avons étudié comment la décomposition varie dans et entre les peuplements selon la position des débris ligneux grossiers et des autres structures dominantes. Des abaisse-langues (*Betula* sp.) (AL) et des sacs à litière contenant de la litière herbacée (LH) ou des aiguilles (LA) ont été déployés pendant deux ans dans 3 peuplements brûlés et parmi 17 peuplements brûlés (0,25 ha chacun). Dans les peuplements, la décomposition variait entre six microsites (sur le dessus et sous les débris ligneux provenant du peuplement précédent, sous les billes au sol et les billes surélevées, sous les gaules et sur le sol à découvert). La perte moyenne de masse après deux ans était la plus faible sous les billes surélevées (LH 34,0 %, LA 8,6 %, AL 3,5 %) et la plus forte (LH 55 %, LA 33 %, AL 12 %) sous les billes provenant du peuplement précédent. L'humidité était aussi toujours la plus faible sous les billes surélevées et la plus élevée sous les billes au sol. Parmi les peuplements forestiers, la perte de masse de LH et AL après deux ans était négativement reliée à la quantité de billes surélevées. L'influence des débris ligneux grossiers sur la décomposition de la litière à deux échelles spatiales indique que l'accumulation de débris ligneux grossiers engendre à long terme une hétérogénéité spatiale dans le recyclage du carbone et des nutriments.

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Introduction

Discerning patterns and causes of spatial variation in energy flow and nutrient dynamics has emerged as a critical challenge for ecosystem and landscape ecologists (Turner and Carpenter 1999; Chapin et al. 2002; Lovett et al. 2005; Turner 2005). Understanding the controls on carbon cycling, notably decomposition, is fundamental to improving predic-

tive models. As fire suppression and climate change may alter disturbance regimes (Clark 1990; Baker 1995; Easterling and Apps 2005), understanding the effects of disturbance on ecosystem functions at multiple scales becomes increasingly important (e.g., Walters and Korman 1999). Decomposition is particularly critical for nitrogen cycling in disturbed systems (e.g., Vitousek and Melillo 1979) and in areas limited by nitrogen, such as lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests (Fahey and Knight 1986). We investigated variation of fine-litter decay with structural heterogeneity both within and among lodgepole pine (*Pinus contorta* var. *latifolia* Englem.) stands regenerating in Yellowstone National Park following extensive fires in 1988.

Structural heterogeneity across postfire landscapes is a conspicuous long-term ecological consequence of fires. Understanding ecosystem effects of fallen coarse wood is critical for decisions on postdisturbance management practices

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such as salvage logging. Coarse wood produced by the 1988 fires in Yellowstone National Park will be an important structural feature of the system for decades (Wei et al. 1997; Tinker and Knight 2000). Its distribution is highly variable at multiple scales, resulting in a range of environmental conditions that potentially influence decomposition. Across the postfire landscape, density of fallen coarse wood ranges from <100 to >1600 stems/ha (H.D. Lyons and W.H. Romme, personal communication, 2005). In many places fallen trees have piled >1 m high since the 1988 fires. Legacy coarse wood from prefire disturbances also contributes to within-stand structure (Tinker and Knight 2000). The water-holding capacity of wood at different decay stages (Boddy 1983; Harmon and Sexton 1995; Wang et al. 2002) and the position of fallen logs relative to the ground (Fahey 1983; Erickson et al. 1985; Edmonds et al. 1986; Rice et al. 1997) influence wood decomposition. Microclimate conditions and protection by these large structures likely alter nutrient cycling and the ecology of soil- and surface-dwelling organisms (Edmonds et al. 1986; Harmon et al. 1986; Harmon and Sexton 1995; Spies 1998), although their influence on litter decomposition remains unknown.

Climatic controls on regional decay rates have been well characterized (e.g., Meentemeyer 1978; Long-Term Intersite Decomposition Experiment Team 1995; Gholz et al. 2000; Trofymow et al. 2002), but the influence of microclimate is less clear. Within forest stands, canopy shading can alter microbial activity at fine scales (Ward et al. 1991; Zhang and Zak 1998; Barg and Edmonds 1999; Menezes et al. 2001). Some research has suggested decomposer-community specialization for the most prevalent types of litter (Anderson and Ultsch 1987; Hunt et al. 1988; Gholz et al. 2000). This proposed "home-field advantage" could result in faster needle decay at locations where more litter of this type accumulates (presumably under its trees of origin). Considerable research has shown that individual plants affect soil processes via the quantity and quality of accumulated litter (e.g., Burke et al. 1989; Hobbie 1992; Mummey et al. 2002; Epron et al. 2004), but fewer authors have focused on the microclimatic effects of within-stand physical structures on decomposers on the soil beneath (Busse 1994; Marra and Edmonds 1998; Spears et al. 2003; Spears and Lajtha 2004).

Yellowstone National Park contains numerous forest stands with similar structural elements (primarily *P. contorta* stacked logs, legacy logs, and *P. contorta* saplings), making it an ideal natural laboratory for investigating stand-level structural effects on decomposition. We tested how the microclimates and substrates resulting from structural heterogeneity influence rates of fine-litter decay and nutrient release over 2 years. The objectives of our study were (i) to investigate the role of coarse-wood position and age on fine-litter decay within forest stands, and (ii) to evaluate how differences in the abundance of different coarse-wood types among forest stands affect fine-litter decay. Based on moisture limitations in the *P. contorta* system (Fahey 1983), we hypothesized that litter decomposition under some types of fallen logs is faster than on open soil exposed to extreme temperatures and desiccation. In particular, we expected moisture conditions under highly decayed wood to cause faster litter decay than at other microsites (Boddy 1983; Wang et al. 2002). Less-decayed logs in contact with the

ground may decay faster than elevated logs (Fahey 1983; Erickson et al. 1985; Edmonds et al. 1986; Rice et al. 1997; Wei et al. 1997), but we thought that consistently cooler conditions and blockage of precipitation would result in slower litter decay beneath logs on the ground than beneath elevated logs. We expected that lateral water flow and moderate sunlight would moderate litter-decomposition rates beneath elevated logs. Among burned forest stands, we also expected decay rates to be highest across those with an abundance of highly decayed wood or logs elevated above the ground.

Methods

Study area

Yellowstone National Park, situated on a high forested plateau, encompasses 9000 km² in northwestern Wyoming. Stand-replacing fires in 1988 burned about 25%–30% of this area (Knight and Wallace 1989; Harmon and Sexton 1995), including our study plots. The Yellowstone plateau generally has moist springs and dry summers, with annual average (non-snow) precipitation of 61.9 cm (9/1978–9/2005 Old Faithful Normals; Western Regional Climate Center 2005). Average total snowfall is 541.8 cm, with average depth of 33.0 cm. Average monthly maximum temperature is 9.6 °C (–2.0 °C in January and 23.6 °C in July) and average monthly minimum temperature is 7.4 °C (–17.8 °C in January and 3.9 °C in July). We worked in southern and central areas of Yellowstone National Park that are composed entirely of *P. contorta* var. *latifolia* forests. Infertile rhyolitic soils, classified in the Cryochrept or Cryumbrept families, dominate this area (Trettin 1986). We selected three 0.25-ha study plots in which to replicate our microsite treatments. All three plots had moderate coarse-wood abundance and sandy loams with low clay content (2%–7%), but soil chemistry and aboveground net primary productivity varied (Table 1). To test whether patterns observed at the microsite treatments scale up to broader effects, we selected 17 additional 0.25-ha stands with a range of percent cover of fallen wood (11%–28%) from areas that burned in 1988. Three stands in mature forest (approximately 250 years old) were also included for comparison. All 23 sites for within-stand and among-stands studies had elevations between 2200 and 2500 m, slope less than 10°, and a northerly aspect (site locations are given in Remsburg 2005).

Within-stand litter decomposition

We deployed mesh litterbags and birch (*Betula* sp.) tongue depressors (TDs) in August 2002 at six microsite treatments representing the most prominent forest-floor microsites in this postfire landscape: (1) below logs elevated 1–10 cm off the ground (elevated log), (2) below logs where they contacted the ground (contact log), (3) below the canopy of *P. contorta* var. *latifolia* saplings 1.5–2.5 m tall, (4) on open mineral soil devoid of aboveground vegetation, (5) below highly decayed wood contacting the ground (below legacy log), and (6) on top of highly decayed wood (above legacy log). Elevated and contact logs were killed in the 1988 fires, and had no bark but sound wood (decay class II; Harmon et al. 1986), whereas the highly decayed wood treatments consisted of legacy logs from previous disturbances (decay class

Table 1. Biotic and abiotic characteristics of three 0.25-ha study plots.

	Biscuit Basin	Lewis Canyon	Riddle Lake
Sapling density (stems·ha ⁻¹)	18 100	11 333	7 000
Elevation (m)	2 228	2 377	2 437
Aboveground net primary productivity (Mg·ha ⁻¹ ·year ⁻¹)			
Pinus contorta var. latifolia ^a	11.5	6.6	2.2
Herbaceous ^a	0.47	1.22	1.24
Basal area of fallen coarse wood (m ² ·ha ⁻¹) ^b	20.1	18.2	17.9
Soil properties ^c			
pH	5.8 (0.01)	5.2 (0.02)	5.4 (0.02)
K content (kg·ha ⁻¹) ^d	424.2 (50.7)	358.2 (23.4)	442.7 (31.3)
Ca content (kg·ha ⁻¹) ^d	1 411.2 (29.2)	644.5 (29.4)	1 137.9 (32.7)
P content (kg·ha ⁻¹) ^e	24.0 (2.1)	9.8 (0.7)	18.0 (1.2)
Mg content (kg·ha ⁻¹) ^d	237.8 (7.6)	106.9 (7.5)	173.5 (10.3)
Total N (%) ^f	0.07 (0.01)	0.07 (0.01)	0.07 (0.04)
C:N ratio	44.2 (7.7)	57.1 (6.8)	120.5 (67.7)
Organic matter (%) ^g	2.8 (0.1)	4.2 (0.1)	3.9 (0.1)

Note: Soil and vegetation were sampled in 2002. Values are given as the mean ($n = 5$) with standard error (in parentheses) of soil properties.

^aFor measurement methods see Turner et al. (2004).

^bMeasured by the planar intersect method (Brown 1971).

^cSoils were sampled to 15 cm depth. All soil properties were tested at the Soil and Plant Analysis Laboratory, Madison, Wisconsin.

^dMeasured by atomic absorption after extraction with H₂SO₄ (Schulte et al. 1987).

^eMeasured by Truog method (Schulte et al. 1987).

^fA micro-Kjeldahl procedure was used for total N determination (Jackson 1958).

^gDetermined by dry combustion using the Tekmar-Dohrman 183 TOC Boat Sampler DC-190 (Tekmar-Dohrman, Mason, Ohio).

V; Harmon et al. 1986). For all treatments we selected logs >20 cm in diameter and maintained them in their original positions relative to the ground. This required the use of peaveys to lift and gently replace logs contacting the ground. Treatments were replicated 20 times across each study plot, with five replicates in each of four quadrants to ensure spatial coverage and at least 2 m separating replicates. We nailed pairs of litterbags to the ground side by side so that mass remaining could be recorded after 1 and 2 years of decay, summing to 720 litterbags for the microsite experiment.

Three dataloggers with six probes each for temperature (HOBO sensor TMC6-HA, accuracy ±0.5–1.7 °C, Onset Computer Corp., Bourne, Mass.) and moisture (Watermark sensor model 6450, Spectrum Technologies, Inc., Plainfield, Ill.) were placed at each of the treatments across the three plots to record litter moisture every 2 h from August 2003 to August 2004 and litter temperature every 2 h from August 2004 to August 2005. Regional weather for both years of recording was consistent with 110-year averages (Wyoming Climate Division 2; National Climate Data Center 2006). Although June and July of 2003 had the least precipitation since 1996, our moisture records did not begin until August 2003, when precipitation did not differ from the long-term average. One set of dataloggers and one temperature probe failed, however, so we present all data obtained from two plots rather than three. Temperature data at the second site (Biscuit Basin) were only available for four of the treatments (probes above and below legacy logs failed midseason).

Although confining litter in mesh bags to track mass loss may lead to underestimation of actual rates of decomposition, in most decomposition studies it is assumed that this method reflects general trends in unconfined litter (Wieder and Lang 1982). Litterbags contained 5 g each of (air-dried)

needle and herbaceous litter collected near the study plots during July 2002. We collected senescing needles from 13- to 14-year-old *P. contorta* var. *latifolia* saplings. Herbaceous litter (HL) was composed of an even mixture (by mass) of fireweed (*Epilobium angustifolium* L.), Geyer's sedge (*Carex geyeri* Boott), and western pearly everlasting (*Anaphalis margaritacea* (L.) Benth.). Selected species represent three of the more common herbaceous species in the burned forest, and mixed litter types allow for potential interactive effects of naturally mixed leaf litter (Blair et al. 1990; Palm and Rowland 1997; Kaneko and Salamanca 1999). Needle litter (NL) and HL in each 19.5 × 20 cm litterbag were kept separate by a seam sewn down the center. Use of 1.5 mm mesh fiberglass screening prevented measurable litter loss but allowed entry of microarthropods (primarily Acari and Collembola; Ward et al. 1991), which may influence litter decay rates (Santos and Whitford 1981; Douce and Crossley 1982; Seastedt 1984; Heneghan et al. 1998). To test treatment effects on a uniform woody substrate, we also placed TDs (15.2 cm × 1.8 cm × 0.2 cm) adjacent to each litterbag. We chose litter with a range of lignin concentrations (2%–30%) for this comparative study because litter types may vary in their level of sensitivity to microclimate or substrate changes (Taylor et al. 1991; Hyvonen and Agren 2001). Because of numerous broken or missing TDs after the second year of decay at Lewis Canyon, data on mass loss from TDs are presented from only two of the three study plots. TDs found broken were not used for analysis, but unfortunately, often appeared to be the most decayed.

The change in oven-dried litter biomass represents the decay rate for the field incubation period. "Traveler" bags for each of the plots were nailed to treatment positions as other

litterbags, but not left in the field. These 24 bags were weighed immediately to estimate the average mass losses caused by fragmentation and leakage during the transport and handling of litterbags (Blair 1988). Following field incubation of experimental litterbags, remaining litter mass (dried to a constant mass at 55 °C) was corrected for mineral-soil contamination by calculating mean ash-free dry mass (AFDM) for each treatment and site. To estimate the fraction of the litterbag that was actually litter (Fli), we used the following equation (Blair 1988):

$$[1] \quad \text{Fli} = (\text{SaAFDM} - \text{S1AFDM}) / (\text{LiAFDM} - \text{S1AFDM})$$

where SaAFDM is the percentage of AFDM in the entire litterbag sample; S1AFDM is the average percentage of AFDM in soil at the site; and LiAFDM is the initial percentage of AFDM in the litter substrate.

We also corrected the final masses of litterbags under legacy logs by estimating the mean mass of fine wood particles that entered empty litterbags during field incubation.

To test for density differences beneath logs, we estimated soil bulk densities for each treatment by removing and weighing 74 dried soil cores of known volume (1178 cm³). Cores included both litter and soil to a depth of 15 cm. Prior to litterbag placement and again after 2 years of decay at the six treatments and across the three plots, 48 samples of both NL and HL were analyzed for carbon and nitrogen contents with a CHN dry-combustion analyzer (LECO, St. Joseph, Mich.) at Colorado State University, and for lignin and ash with acid-detergent fiber methods (Rowland and Roberts 1994) at the Soil and Plant Analysis Laboratory in Marshfield, Wisconsin.

Among-stand litter decomposition

We estimated stand-level decomposition rates for the three litter types using 40 litterbags and TDs placed randomly in 2003 across each of the 17 burned and 3 mature stands ($n = 680$). At burned stands, random placement often meant that litterbags were positioned beneath different types of coarse wood. In both 2004 and 2005, 20 litterbags were removed from each stand. We estimated percent cover of fallen logs at these stands in 2004 by recording the proportion of three 50 m long transects intercepted by logs (to the nearest 1%). Transects could be situated parallel to each other because logs fell randomly in all compass directions (H.D. Lyons and W.H. Romme, personal communication, 2002). Wood was categorized as either legacy or post-1988 log, and as contacting the ground or elevated 1–10 cm or >10 cm off the ground. We also estimated sapling density within a 2 m wide belt along the three 50 m long transects (300 m² sampling area per site) and percent cover of 15 ground-cover categories in 0.25-m² circular quadrats around each litterbag. Cover categories, recorded by a single observer to the nearest 5% if >10% or to the nearest 1% if <10%, were as follows: elevated post-1988 log, post-1988 contact log, legacy log, *P. contorta* var. *latifolia* sapling or seedling, graminoid, forb or shrub, open soil, needle litter, duff, fine wood (diameter <7.5 cm), moss or lichen, scat, charcoal, rock, and other; however, only six of these categories (all post-1988 coarse wood, legacy wood, saplings, graminoids, fine wood, and open soil) were selected a priori for data analysis to re-

duce covariance among parameters. We focused on these six cover categories, based on their hypothesized influence on litter quality or microclimate.

Data analysis

Annual decay constants (k) were calculated from percent mass remaining using Olson's (1963) single negative exponential decay model: percent remaining = e^{-kt} , where t is time in years. Two-way analysis of variance (ANOVA) blocked by the three plots was used to test treatment and plot effects on litter mass loss, soil bulk density, lignin, and nitrogen litter components within stands after 1 and 2 years. Arcsine square root transformations normalized TD mass loss data (Zar 1999) but were unnecessary for other variables to meet parametric assumptions. Tukey's honest significant differences (HSD) test was used to compare treatment means. Because first-year (2003) litterbags were removed from the field over a span of 6 weeks (for a complementary study on microarthropods; unpublished data), we performed a linear regression to test for a measurable effect of the number of incubation days on mass remaining (none observed; $p > 0.8$). We also assessed relationships between 2-year mass-loss rates and final litter lignin and nitrogen contents using multiple linear regressions.

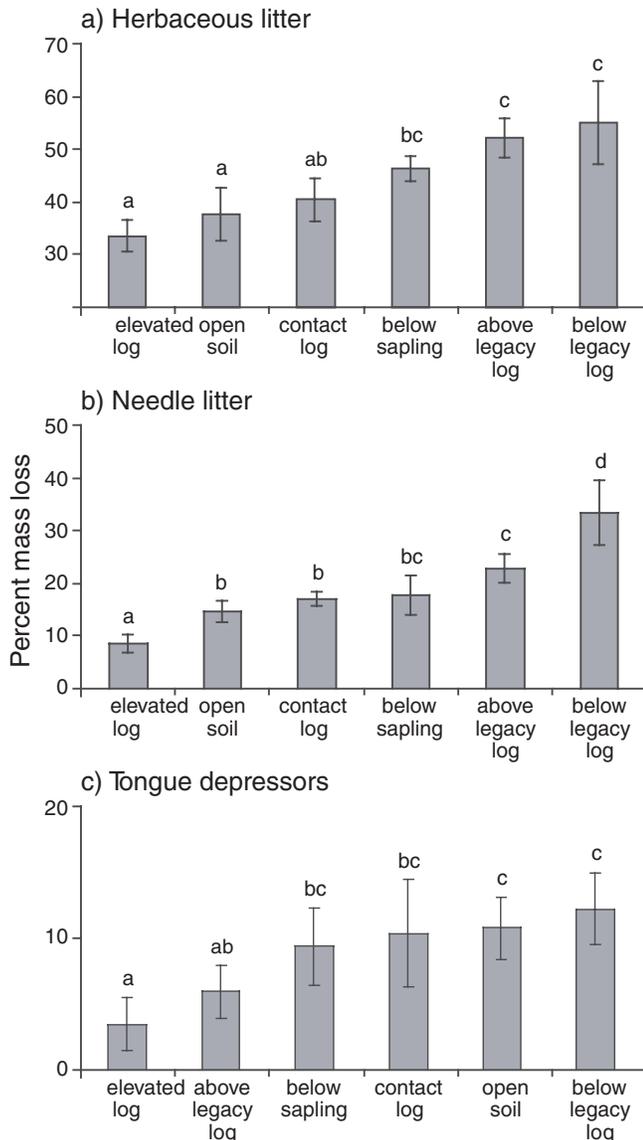
Mean mass loss values were compared between burned and mature stands using Welch's two-sample t test (Davenport and Webster 1975). To investigate the role of coarse-wood abundance among forest stands, we regressed mean stand-decomposition rate for each litter type against percent cover of each coarse wood type (following natural log transformations) in the 17 burned stands. Relationships among the six stand-level percent-cover parameters (following arcsine square root transformations) and decay rates were investigated using multiple linear regression. Stepwise selection, comparing second-order criterion Akaike's Information Criterion (AIC_c) values, suggested the best regression models (Burnham and Anderson 2002). AIC_c has a bias-correction term for small sample sizes. The level of empirical support for a model, i , is indicated by Δ_i , the difference between the AIC_c value for model i and the smallest AIC_c value for the candidate models. Based on Burnham and Anderson's (2002) rules of thumb, we only included models with $\Delta_i < 5$ as candidate models. The relative strength of evidence for the candidate models can be compared using Akaike weights, w_i , the log-likelihood of model i divided by the sum of log-likelihoods for all candidate models. For each litter type we present candidate models that together explain at least 60% of w_i . All analyses were performed with R 2.1.1. software (2003, R Development Core Team) using the `lm`, `Anova` (type III), and `step` commands. Null hypotheses were rejected when $p < 0.05$.

Results

Within-stand litter decomposition

First- and second-year annual decay constants (mean with standard error (SE) in parentheses) were 0.53 (0.02) and 0.31 (0.01) for HL, 0.16 (0.01) and 0.11 (0.006) for NL, and 0.03 (0.004) and 0.03 (0.005) for TD, respectively. We report mass losses from only the litterbags removed after 2 years; unless otherwise noted, results were qualitatively

Fig. 1. Percent mass loss (mean \pm 2 SE) from litter among microsite treatments after 2 years. Including replicates across three study plots, $n = 353$ for the herbaceous litter mixture (a), $n = 342$ for needle litter (b), and $n = 167$ for tongue depressors (c). Different letters above the bars indicate significant treatment differences ($p < 0.05$) by Tukey's HSD test. Note the different ordering of treatments among the three panels.



similar after 1 year (values are given in Remsburg 2005). Decomposition of HL was slowest under elevated logs, under contact logs, and on open soil, and fastest under legacy logs, above legacy logs, and under saplings (Fig. 1a). Mass loss from both NL and TDs was least (<10%) under elevated logs and greatest (NL 33%; TD 12%) below legacy logs (Figs. 1b and 1c). Mass loss from all three litter types varied with microsite treatment and the interaction between treatment and plot (Table 2). Differences in mass loss among the three study plots were not significant; the treatment \times plot interaction term constituted less of the variance than the treatment term.

There was a moisture deficit beneath elevated logs at both plots throughout the year (except at Biscuit Basin in the

spring; Fig. 2). Probes on open soil, under saplings, and above legacy logs also detected less moisture than probes under contact and legacy logs, especially during the fall. At both plots during the growing season, temperature was lowest and least variable (Fig. 3) beneath contact logs and legacy logs (SE = 0.08 and 0.07 °C, respectively, at Lewis Canyon; 0.12 °C for contact logs at Biscuit Basin), but not under elevated logs. Variability in temperature beneath elevated logs at Lewis Canyon and Biscuit Basin (SE = 0.13 and 0.17 °C, respectively) was more similar to that on open soil (SE = 0.14 and 0.19 °C, respectively) and under saplings (SE = 0.16 and 0.20 °C, respectively). In winter, litter beneath legacy logs appeared to be warmer than that beneath contact logs or at other treatments (Fig. 3).

Lignin and nitrogen concentrations increased through time at all treatments and litter types. Initial lignin contents were 3% (HL) and 28% (NL), initial nitrogen contents were 1.2% (HL) and 1% (NL), and initial carbon contents were 43% (HL) and 50% (NL). After 2 years of incubation at the six microsite treatments, lignin and nitrogen contents had increased (470%–830% (HL) and 150%–180% (NL) of initial lignin, 130%–230% (HL) and 110%–140% (NL) of initial nitrogen), while carbon content had decreased (80%–100% (HL) and 70%–100% (NL) of initial carbon). Decay rates of both types of leaf litter were positively related to nitrogen and lignin remaining in litter after 2 years (except for lignin in HL; Table 3). The percentage of lignin remaining in HL was greater under legacy logs and contact logs than at other treatments ($n = 48$, ANOVA, $F = 5.90$, $p < 0.001$; Fig. 4), whereas differences in NL lignin concentration among treatments were similar ($n = 48$, $F = 2.33$, $p = 0.07$; mean across all treatments = 49%, SE = 0.01%). The percentage of nitrogen remaining did not vary significantly among treatments for either litter type (HL cumulative mean = 2.0%, SE = 0.04%; NL cumulative mean = 1.3%, SE = 0.02%), although NL had slightly less nitrogen under elevated logs (mean = 1.1%) than at the open-soil treatment (mean = 1.4%; $n = 48$, $F = 2.33$, $p = 0.06$).

Soil bulk density to 15 cm depth varied by plot (Biscuit Basin: mean = 0.34 g/cm³, SE = 0.006 g/cm³; Riddle Lake: mean = 0.25 g/cm³, SE = 0.008 g/cm³; Lewis Canyon: mean = 0.25 g/cm³, SE = 0.006 g/cm³). There was a small plot \times treatment interaction effect, with bulk density lower for the sapling treatment only at the Riddle Lake plot. Soil bulk density was not correlated with litter decay rate.

Among-stand litter decomposition

For the 17 burned stands, ranges of mean percent cover around litterbags were 0%–18% saplings, 6%–48% graminoids, 4%–28% forbs or shrubs, 1%–37% open soil, 3%–28% fine wood, 3%–13% legacy wood, 1%–5% contact logs, and 3%–16% elevated logs. The strongest Pearson's product-moment correlations were observed for elevated logs with contact logs ($r = 0.52$), open soil ($r = -0.41$), and fine wood ($r = 0.35$). Correlations for contact and legacy logs with other cover categories were weaker ($r < 0.30$).

Percent cover of coarse wood in mature stands was much lower than in burned stands: 1%–2% legacy wood, 4% elevated logs, and 2%–3% contact logs, with more of the cover represented by forbs and shrubs (range 18%–49%). For all litter types, mean proportions of mass loss at the three ma-

Table 2. ANOVA results for mean mass loss after 2 years among six microsite treatments and three study plots.

Variable	Sum of squares	df	F	p > F	Adjusted R ²
Herbaceous litter		17, 335	8.2	<0.001	0.26
Intercept	5.53	1	196.5	<0.001	
Treatment	2.56	5	18.2	<0.001	
Plot	0.01	2	0.2	0.8	
Treatment × plot	1.78	10	6.3	<0.001	
Residuals	9.43	335			
Needle litter		17, 324	20	<0.001	0.46
Intercept	0.77	1	72.4	<0.001	
Treatment	2.34	5	44.2	<0.001	
Plot	0.06	2	2.9	0.06	
Treatment × plot	1.41	10	13.3	<0.001	
Residuals	3.43	324			
Tongue depressors		11, 155	6.2	<0.001	0.26
Intercept	0.09	1	22.6	<0.001	
Treatment	0.09	5	4.5	0.001	
Plot	0.01	1	2.1	0.14	
Treatment × plot	0.05	5	2.4	0.04	
Residuals	0.65	155			

Note: Too few tongue depressors were retrieved from the Lewis Canyon plot to make comparisons with this plot meaningful. Data from the other two study plots are presented.

Fig. 2. Hourly water availability averaged by month (August 2003 – July 2004), illustrating microsite treatment differences. The six moisture probes were within 1 m of each other at the Lewis Canyon study plot (a) and Biscuit Basin study plots (b).

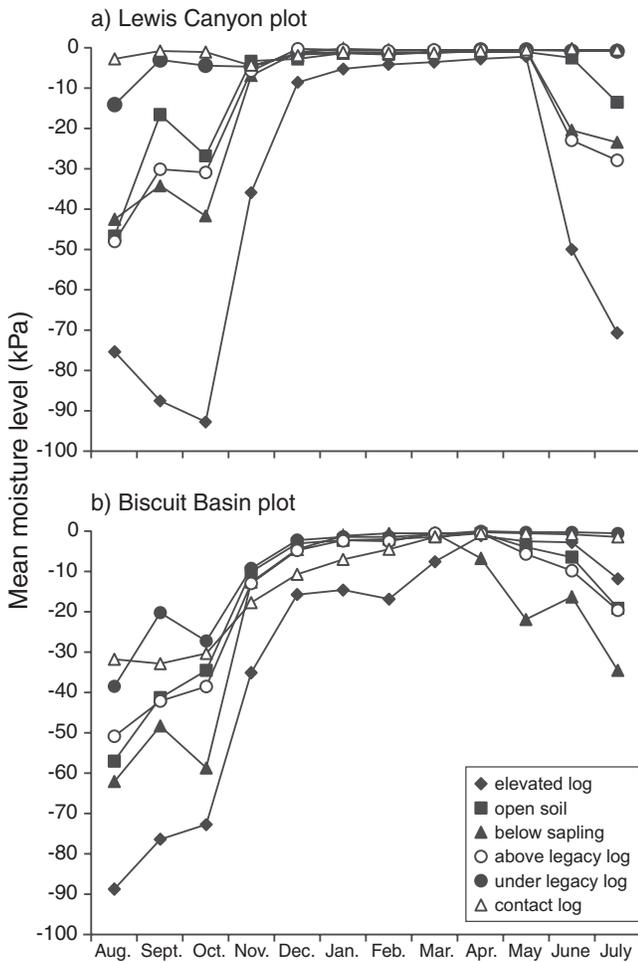
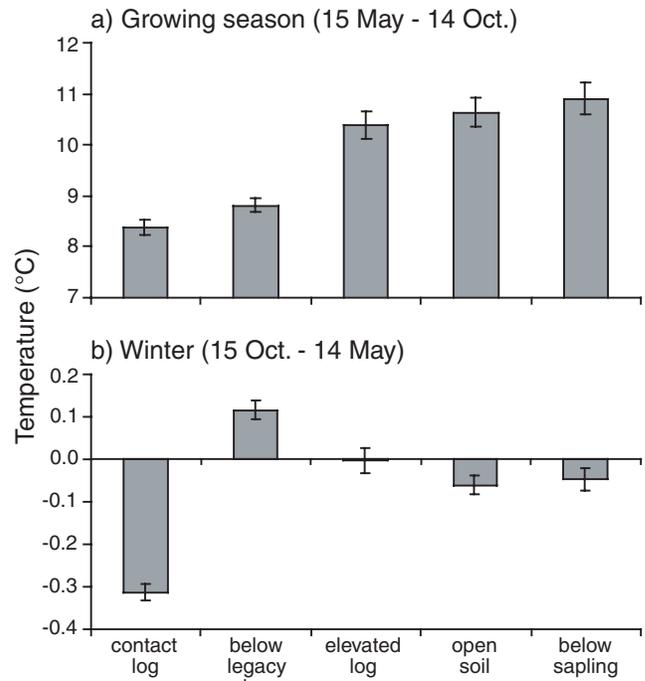


Fig. 3. Temperatures (°C; mean ± 2 SE) among microsites at the Lewis Canyon plot. Temperatures at the Biscuit Basin plot were similar, but are not presented because datalogger probes failed at two treatments. Dataloggers at the third plot failed to operate for the full year. Hourly data were averaged by season for 2004–2005. Note the different y-axis scales for growing-season (a) and winter temperatures (b).



ture stands were similar to mean values for the 17 burned stands after 2 years of decay (Fig. 5). Mean mass loss at burned stands was greater from NL ($t = 3.5$, $df = 5.9$, $p = 0.01$) and TDs ($t = 4.4$, $df = 7.8$, $p = 0.002$) only after 1 year of decay.

Table 3. Results of multiple linear regression analyses relating 2-year litter-decomposition rates to final nitrogen and lignin contents ($n = 48$).

Response	Predictor variable	Parameter estimate	Partial R^2	p
Herbaceous litter decay	Nitrogen content	0.28	0.36	<0.001
	Lignin content	-0.49	0.10	0.08
Needle litter decay	Lignin content	1.07	0.38	0.003
	Nitrogen content	0.20	0.10	0.01

Note: The adjusted overall model R^2 values were 0.43 for herbaceous litter and 0.44 for needle litter.

Fig. 4. Percentage of lignin (mean \pm 2 SE) in remaining herbaceous litter after 2 years at different microsite treatments. Including replicates across three study plots, $n = 48$ for each litter type. Different letters above the bars indicate significant treatment differences ($p < 0.05$) by Tukey's HSD test.

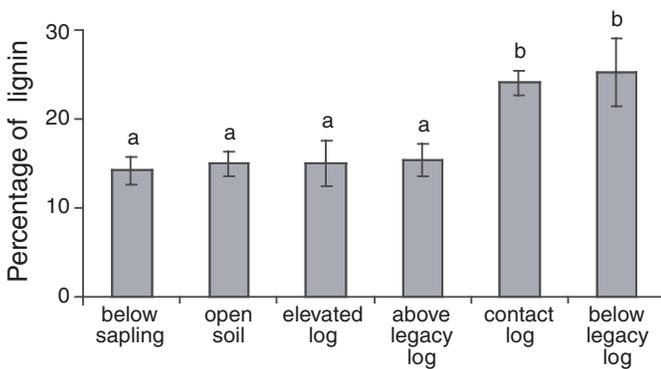
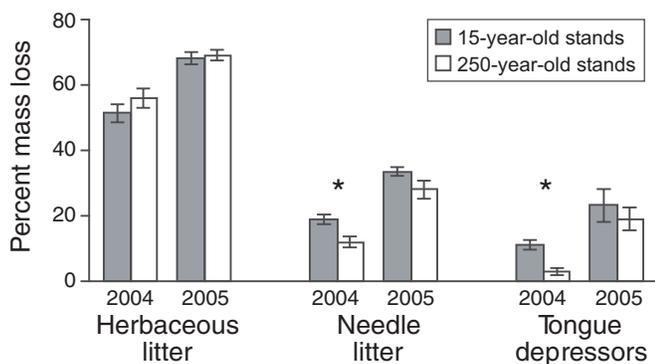


Fig. 5. Percent litter mass loss among 0.25-ha stands, comparing stands that burned in 1988 (15-year-old stands; $n = 17$) with mature stands (aged approximately 250 years; $n = 3$). Values are given as the mean \pm 2 SE for three litter types after 1 and 2 years (2004 and 2005) of litterbag incubation at the stands. An asterisk indicates a significant difference between stand ages for the same litter types.



Among stands burned in 1988, we found negative relationships between decomposition and percent cover of elevated logs for most litter types (Fig. 6), but linear regressions between decomposition rate and total cover of coarse wood were generally not significant ($p = 0.05$). Furthermore, linear relationships were stronger when we used logs elevated at least 10 cm above the ground as the predictive variable rather than all elevated logs. After the first year of field incubation, only TD decay rates were negatively correlated with elevated logs (adjusted $R^2 = 0.39$, $n = 17$, $p = 0.004$;

Fig. 6. Stand-level mean percent mass loss for tongue depressors after 1 year (a), tongue depressors after 2 years (b), herbaceous litter after 2 years (c), and needle litter after 2 years (d), plotted as a function of log-transformed elevated log abundance (percent cover). Across each of the 17 burned stands, elevated logs were only counted if they were at least 10 cm above the ground at the transect. Note the different y-axis scales.

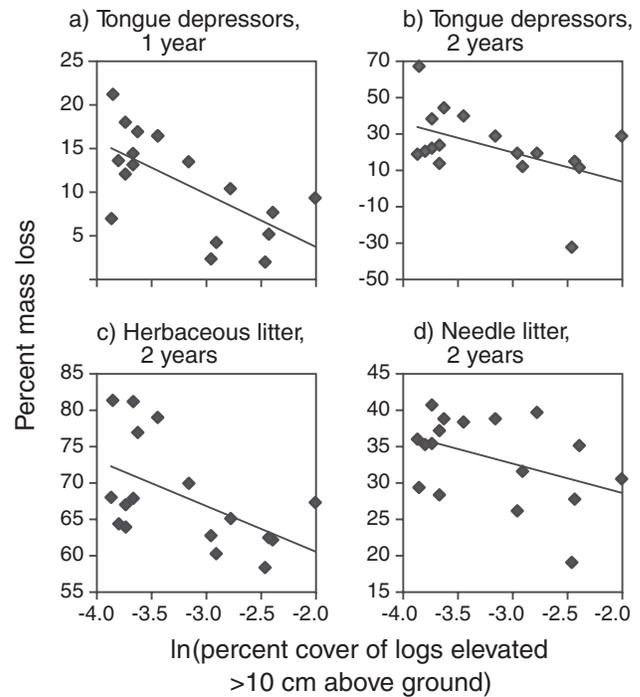


Fig. 6a). After 2 years, TD mass loss was again negatively related to elevated logs (adjusted $R^2 = 0.19$, $n = 17$, $p = 0.047$; Fig. 6b), as was HL decomposition (adjusted $R^2 = 0.24$, $n = 17$, $p = 0.027$; Fig. 6c). NL had a weak negative relationship with elevated logs (adjusted $R^2 = 0.12$, $n = 17$, $p = 0.092$; Fig. 6d).

Model selection identified which of the six cover categories best helped to explain 2-year litter decomposition rates among stands (Table 4). There were more candidate models with roughly equivalent support (seven models with $\Delta_i < 5$) for TDs than for other litter types (NL: five models with $\Delta_i < 5$; HL: five models with $\Delta_i < 5$). For all litter types, decay rates were negatively related to percent cover of fine woody debris in each of the candidate models. HL decomposition rates also correlated positively with percent graminoid cover, whereas NL- and TD-decomposition models included positive coefficients for percent open soil.

Table 4. The best multiple linear regression models (with coefficients) chosen by second-order criterion Akaike's Information Criterion (AIC_c) from six stand-level percent-cover categories (all post-1988 coarse wood (elevated + contact logs), legacy wood, saplings, graminoids, fine wood, and open soil) to predict mean 2-year mass loss across stands ($n = 17$).

Model	Δ_i^a	w_i^b	Residual SE	Adjusted R^2
Herbaceous litter				
Mass loss = $-(0.17)$ post-88 coarse wood + (0.42) graminoids – (0.40) fine wood + 0.690	0.61	0.03	0.78	
Needle litter				
Mass loss = $-(0.57)$ fine wood + 0.45	0	0.47	0.05	0.30
Mass loss = $-(0.57)$ fine wood + (0.16) open soil + 0.42	0.92	0.29	0.05	0.33
Birch (<i>Betula</i> sp.) tongue depressors				
Mass loss = $-(2.46)$ fine wood + 0.75	0	0.34	0.14	0.50
Mass loss = $-(2.31)$ fine wood + (0.45) new coarse wood + 0.86	1.32	0.18	0.14	0.52
Mass loss = $-(2.46)$ fine wood + (0.31) open soil + 0.67	2.03	0.12	0.14	0.50

^aDelta AIC (Δ_i) is the difference between the given model's AIC_c value and that of the model with the lowest AIC_c value.

^bAkaike weights (w_i) sum to 1 for the set of candidate models compared (models with $\Delta_i < 5$); larger values indicate a greater probability that the i th model is better than the other candidate models (Burnham and Anderson 2002).

Discussion

Microsite treatment effects were strong across the three plots, regardless of plot differences in productivity and other attributes (Table 1). Repetition of treatment effects in multiple locations substantially strengthens inferences that can be drawn from this study (Binkley and Menyailo 2005). Additionally, microsite treatment results were consistent for both 1- and 2-year mass losses. We expected that microclimates resulting from structural heterogeneity would have measurable effects on litter decomposition, including faster decay rates under highly decayed legacy wood. Our results support this wood-age hypothesis, but not our idea that elevated logs would also facilitate litter decay by moderating temperature and evaporation while allowing lateral moisture inputs.

All structural components moderated summer temperatures (Fig. 3), but moisture was notably less under elevated logs than at the other treatments (Fig. 2). Unlike elevated logs, those on the ground can transfer water directly to the underlying soil (Harmon and Sexton 1995) and have less exposed surface area for evaporation (Brackebush 1975). Graham's (1925) finding that higher sections of logs hold less water than lower sections suggests that some moisture in wood travels down the length of an elevated log. Logs on the ground could also have higher water-holding capacity if they decayed more quickly than elevated logs (Fahey 1983; Erickson et al. 1985; Edmonds et al. 1986; Rice et al. 1997; Wei et al. 1997), although we did not observe a difference in decay stages between elevated and contact logs. Decomposition in *P. contorta* forests continues through the winter (Fahey 1983; Edmonds et al. 1986), so snowfall interception and meltwater runoff around frozen logs may also affect litter mass loss. Our findings of lower decay rates where moisture levels remained lowest concur with Fahey's (1983) assertion that moisture limits decomposition in *P. contorta* forests.

Two separate — although not mutually exclusive — roles of moisture could explain its influence on decomposition: soluble carbon leaching and micro- or meso-faunal activity. Leaching can account for 30% of mass loss from decomposing *P. contorta* litter (Yavitt and Fahey 1986). A possible negative relationship between fungal growth and UV-B radiation could, however, obscure leaching effects at the open treatments (Gehrke et al. 1995; Duguay and Klironomos

2000; Hughes et al. 2003). Microbial activity is often positively correlated with areas of greater soil moisture (e.g., Zhang and Zak 1998; Barg and Edmonds 1999; Bengtson et al. 2005). Soil microbial respiration in Yellowstone National Park also correlates with soil moisture rather than soil temperature (Litton et al. 2003). Positive correlations among microarthropod density, litter moisture, and litter decomposition (A.J. Remsburg and M.G. Turner, unpublished data) support the hypothesis that microsites with higher moisture levels facilitate the activity of decomposer communities. Additionally, at the elevated-log treatments, K.L. Metzger and M.G. Turner (unpublished data) found a greater abundance of hydroxyl and cyclopropyl gram-negative bacteria guilds than other guilds, and high levels of extracellular enzymes associated with carbon and nitrogen acquisition.

Faster decay above and below legacy logs may be attributed to biotic controls, based on contrasts with treatments in similar microclimates. Faster decomposition of all litter types under legacy logs than under post-1988 contact logs (Fig. 1) could have resulted from greater microbial colonization or activity in these microsites. Mean moisture levels could help explain this difference, but legacy logs had only slightly higher moisture levels than contact logs during part of the year (Fig. 2). A complementary study (K.L. Metzger and M.G. Turner, unpublished data) confirmed that soil beneath legacy logs contained more bacteria from the monounsaturated and hydroxyl guilds. Higher decay rates above legacy wood than on open soil for NL and HL (Fig. 1) also suggest that decomposers present in legacy wood (probably fungal hyphae) contribute to decomposition of litter that falls onto legacy wood. Again, dataloggers did not indicate higher moisture levels above legacy logs than on open soil (Fig. 2).

Because NL did not decay faster under saplings (Fig. 1), our data did not support the home-field-advantage hypothesis (Gholz et al. 2000). The high decay rates for both leaf-litter types under legacy logs, where leaf input would be blocked for decades by the fallen logs, are also inconsistent with the hypothesis. However, the positive association between percent graminoid cover and mass loss from HL — but not the other litter types — (Table 4) could have resulted from the activity of microbial communities specializing in graminoid litter at these stands. Leachates from structures above the litter layer (Yavitt and Fahey 1986; Harmon and

Sexton 1995; Northup et al. 1998; Spears and Lajtha 2004; Hafner et al. 2005) or variations in litter input among treatments may have influenced nutrient turnover (e.g., Burke et al. 1989; Roy and Singh 1994; Epron et al. 2004), confounding the relationship between litter type and microsite community.

Aside from novel patterns related to coarse-wood microsites, decomposition of each litter type followed general trends reported in the literature. Leaf litter decay constants for Ross' avens, *Acomastylis rossii* (R. Br.) Greene in the alpine tundra of Colorado varied with moisture level in a range similar to our HL decay constants: from 0.33 in the driest habitat to 0.52 in moist habitat (O'Lear and Seastedt 1994). For *P. contorta* needles in southern Wyoming, Yavitt and Fahey (1986) found an annual decay constant of 0.14. At Canadian sites, *Pseudotsuga menziesii* (Mirb.) Franco needles had an annual decay constant of 0.13 (Moore et al. 1999), similar to our NL constants. And despite differences in wood chemistry between TDs and native woody litter, decay constants were similar to those for wood in other *P. contorta* forests (Fahey 1983; Busse 1994; Tinker and Knight 2001). For litter that lost more mass, percentages of lignin and nitrogen were higher in remaining litter, as has been demonstrated in many places (e.g., Schlesinger 1985; Berg 1986; Yavitt and Fahey 1986; Aber et al. 1990; Xu et al. 2004; Romero et al. 2005). Differences in lignin concentration corroborate our conclusion that decomposition varied among treatments. Increasing nitrogen concentrations, regardless of treatment, and mass losses generally below 50% suggest that our 2-year study included the decay phases with greatest nitrogen immobilization (McClaugherty et al. 1985; Aber et al. 1990).

Among stands, relatively small differences in mean mass loss between burned and mature stands (Fig. 5) may relate to similar soil moisture levels in mature and 13-year-old postfire *P. contorta* stands (Litton et al. 2003). In particular, the lack of difference in first-year HL decay rates suggests that enhanced leaching does not differ significantly between burned and mature stands. Interestingly, Litton et al. (2003) provided evidence of higher temperatures in burned stands than in mature stands, which could help explain the differences in NL and TD mass loss between burned and mature stands after 1 year. Greater accumulation of recalcitrant NL in the O horizon of mature stands could also negatively affect decomposition by separating litterbags from the biotic communities and nutrients in the mineral horizon.

Variations in the amount of coarse wood were greatest in burned stands. Negative correlations between stand decomposition rates and coverage of elevated wood suggest that relationships observed in the microsite experiment scaled up. An abundance of elevated wood could have reduced soil moisture at numerous microsites across these stands. Some of the precipitation may be channeled to locations in the stand where logs contact the ground (Graham 1925). Stronger negative correlations between decomposition rate and percent cover of the highest elevated wood, rather than logs raised just 1–10 cm off the ground, suggest that moisture may flow down the length of logs, especially at steeper angles. Negative correlations of decomposition rate with percent cover of fine wood, however, would have resulted not from moisture interference but perhaps from nitrogen limita-

tions of a soil community that receives mostly nutrient-poor litter (Aber et al. 1990; Bjornlund and Christensen 2005). Alternatively, the relationship with fine wood may result from the positive correlation between coarse wood and fine wood.

Our among-stands decomposition results suggest a legacy of predisturbance stand density on soil processes because stands with more fallen coarse wood generally resulted from higher prefire stand density. The snag fall rate also influences total coarse wood density and could thereby affect stand-level decomposition. More specifically, our results suggest that litter decomposition is sensitive to the rate at which coarse wood falls and comes into contact with the ground and to rates of wood decay. The negative influence of elevated coarse wood on litter decay appears to be neutralized when logs come into contact with the ground, and reverses to a positive influence on litter decay when the wood becomes more decayed (Fig. 1). Projecting the cumulative influence of coarse wood on stand-level decomposition rates poses an important challenge for future research.

The higher relative abundance of elevated logs resulted in slower decomposition at the stand level, which should increase litter accumulation, decrease nutrient inputs to the soil, and decrease CO₂ release to the atmosphere. Thus, coarse wood may have broad-scale effects on the spatial variation of nutrient cycling and soil biological activity. Microbes, microarthropods, and plants, for example, exhibit spatial variation that may be a response to a heterogeneous nutrient and water supply (e.g., Tousignant and Coderre 1992; Roy and Singh 1994; Herman et al. 1995; Aerts and Chapin 2000). An abundance of elevated logs could also increase the spatial heterogeneity of water available within stands by channeling water to particular locations and blocking it from others. Because of the persistence of coarse wood on the forest floor, these structures may have a lasting effect on the processes beneath. The abundant and persistent wood suspended above the ground is a structural component that distinguishes naturally disturbed areas from clearcuts (Wei et al. 1997) and areas cleared by salvage logging following disturbance (Lindenmayer et al. 2004). Where much coarse wood accumulates, piles tend to form, so large portions of the logs remain elevated for several decades (Tinker and Knight 2000). Although previously understudied, the position, age, and abundance of coarse wood can significantly influence litter decomposition and thus other ecosystem properties. Removal of coarse wood by salvage logging alters patterns of structural heterogeneity, which can have long-term ecosystem effects. Within-stand and among-stands structural heterogeneity, which is particularly evident following disturbances, warrants consideration by researchers implementing sampling designs and by modelers aiming to predict ecosystem processes at multiple scales.

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