Cellulose decomposition in southeast Alaskan forests: effects of pit and mound microrelief and burial depth

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In southeast Alaska, where wildfires are rare, uprooting is the predominant disturbance influencing stand development in *Tsuga heterophylla* (Raf.) Sarg. – *Picea sitchensis* (Bong.) Carr. forests. We compared 1-year decomposition of confined cellulose filter paper placed in the organic horizon and at the organic–mineral interface on both tree-throw mounds and adjacent pits. Decomposition rates were not significantly different between pits and mounds, but filter papers within the organic layer lost 33.7% of their original dry mass, and packs within the mineral layer lost 14.5% of their mass. This effect was highly significant ($p < 0.01$). We concluded that the greater organic accumulations observed in pits are largely due to litter redistribution.

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Dans le sud-est de l'Alaska où les feux de forêt sont rares, le chablis est la principale perturbation qui influence le développement des peuplements de *Tsuga heterophylla* (Raf.) Sarg. – *Picea sitchensis* (Bong.) Carr. Nous avons comparé la décomposition de papier filtre de cellulose confiné qui avait été placé pendant 1 an dans l'horizon organique et à la limite des horizons organique et minéral sur les monticules créés par le renversement des arbres et dans les dépressions adjacentes. Les taux de décomposition sur les monticules et dans les dépressions n'étaient pas significativement différents mais les papiers filtres avaient perdu 33,7% de leur poids sec dans l'horizon organique et 14,5% dans l'horizon minéral. Cette différence était très significative ($p < 0{,}01$). L'accumulation plus importante de matière organique dans les dépressions serait en grande partie due à la redistribution de la litière.

[Traduit par la revue]

Introduction

Uprooting of forest trees and the attendant pit and mound microrelief are common in temperate forests of North America and Europe (Stephens 1956; Troedsson and Lyford 1973; Stone 1975; Beke and McKeague 1984; Schaetzl *et al.* 1989*a*, 1989*b*). In southeast Alaska, where wildfires are rare, uprooting is the predominant disturbance influencing forest stand development (Harris and Farr 1974; Deal 1987). In eastern North America, tree-throw mounds are favored microsites for tree establishment (Lutz 1940; Denny and Goodlett 1956; Lyford and MacLean 1966; Schaetzl *et al.* 1989); similar patterns are observed in southeast Alaska. For example, 3-year height growth of planted seedlings is greatest on mounds and least on rotten wood (Shaw *et al.* 1987). In three mature stands with a wide range of site indexes, a strong positive relation exists between the degree of uprooting disturbance and site index; and the basal area per hectare of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is four times greater on mounds as opposed to pit or undisturbed microsites (B.T. Bormann, unpubished data on file, Forestry Sciences Laboratory, Juneau, Alaska). Pits tend to be wetter; they have thicker, more sapric organic horizons, and they can develop hydrophilic plant assemblages, often including skunk-cabbage (*Lysichitum americanum* Hult. & St. John) (Bowers 1987).

We hypothesized that decomposition is more rapid on mounds than in pits because mounds are presumably warmer and better drained. To test this hypothesis, we compared decomposition (proportion of mass lost) of confined cellulose filter paper placed in the organic horizon and at the organic–mineral interface on both tree-throw mounds and adjacent pits.

In an early use of confined substrates in a field decomposition study, Falconer *et al.* (1933) measured mass losses from forest-floor samples confined in galvanized iron wire baskets. Bocock and Gilbert (1957) further refined the method by enclosing litter in nylon hairnets; the flexible, large mesh (1 cm) freely admitted the soil mesofauna and allowed better incorporation of the sample with the surrounding litter. The mesh bag itself may influence decomposition rates by excluding larger soil animals (Bocock and Gilbert 1957), increasing substrate moisture (Lousier and Parkinson 1976), or reducing colonization by fungal vegetative structures (St. John 1980).

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The use of cellulose filter paper as a model substrate (Witkamp and van der Drift 1961; Clymo 1965) offers several advantages over native litter in field decomposition studies: the use of standardized material simplifies comparisons of decomposition rates between ecosystems by eliminating variation resulting from litter quality; filter paper is easily obtained and processed; and its decomposition is not complicated by leaching, resistant cuticles, or inhibitory compounds (Rosswall *et al.* 1975; Berg *et al.* 1975). On the other hand, filter paper cellulose may decompose more rapidly than the lignocellulose complexes found in native litter (Ljungdahl and Eriksson 1985), and decomposition of filter paper cellulose may depend on nutrients and simpler carbon sources imported from the surrounding soil (St. John 1980). Although filter paper packs may not yield reliable estimates of actual litter cellulose decomposition, they do allow useful comparisons of relative rates between treatments or sites.

We compared decomposition on mounds and pits in two stands, one with a northeast aspect and another with a southwest aspect. The short growing season and cool summer temperatures led us to believe that decomposition in the southwest-facing stand would be considerably greater than in the northeast-facing stand. Because litter decomposition is more rapid near the surface than at the organic–mineral interface (Clymo 1965; Binkley 1984), we also expected mass loss of filter papers to be more rapid near the surface.

Site descriptions

The Heintzleman Ridge site (58°22′N, 134°34′W), 15 km northwest of Juneau, Alaska, lies on a nearly level, glacial–marine till bench deposited about 9000 years ago. It is about 75 m above sea level and has a southwest aspect. Precipitation, evenly distributed throughout the year, averages 1368 mm · year^{-1} at an official collection station less than 1.5 km away. Average annual temperature is 4.4°C, ranging from a monthly mean of −5.5°C in January to 12.7°C in July, with a mean frost-free period of 131 days. The Sitka spruce – western hemlock stand developed after a catastrophic windthrow around 160 years ago that left abundant pit and mound microrelief. Spruce site index is 24 m, 50-year basis (Farr 1984).

A contrasting site was selected near Eagle River (58°31′N, 134°48′W), about 40 km northwest of Juneau, Alaska. This site lies on a northeast-facing, glacially scoured hillside having a slope of 10–20°. The soils, developed on glacial till, were shallower on this site and appeared colder (spring snowmelt occurred later). This site is 60 m above sea level. No precipitation or temperature data are available. The forest, consisting of mostly western hemlock with scattered Sitka spruce, originated after a large windthrow about 115 years ago. Spruce site index is 26 m, 50-year basis (Farr 1984).

The sites had similar microrelief, forest floors, and soils. At Heintzleman Ridge, about 60% of the plot had pit and mound microrelief greater than 0.5 m. We did not determine the extent of pit and mound microrelief at Eagle River, but it appeared to affect slightly less than half of the plot. Windthrow mounds were 0.5–1.5 m high and covered 3–6 m^2; pit areas ranged from 1 to 2 m^2. Average depths of the organic horizons were 7 cm on mounds and 11 cm in pits. Organic horizons comprised mostly fibric material, but a few pits contained up to 20 cm of hemic material. The soils were well-drained gravelly silt loams. Developed soils were Humic Cryorthods; younger windthrow-disturbed soils were Ochrepts.

Methods

Filter paper packs

Five cellulose filter papers (ca. 1.85 g ovendried, VWR quantitative grade 74, 7 cm diameter) were weighed and sewed into 9 × 9 cm, nylon mesh (1 mm) packs. We assigned each pack a unique number and recorded the air-dried mass of the enclosed filter paper; the ovendried mass was estimated by subsampling each box of filter papers.

TABLE 1. Analysis of variance of 1-year loss of cellulose mass

Source of variation*	df	SS	MS	*F*	*p*
Site	1	0.035	0.035	0.91	0.35
Error A	18	0.699	0.039	2.41	0.01
Position	1	0.029	0.029	0.78	0.39
Site × position	1	0.012	0.012	0.32	0.58
Error B	18	0.656	0.036	2.27	0.02
Depth	1	0.739	0.739	45.96	<0.01
Site × depth	1	0.012	0.012	0.73	0.40
Position × depth	1	<0.001	<0.001	<0.01	0.94
Site × position × depth	1	<0.001	<0.001	0.01	0.91
Error C	36	0.579	0.016		
Total	79	2.760			

NOTE: Each *F* has as its denominator the following error MS. Each observation is the mean of three packs in one treatment combination.

*Site, Heintzleman Ridge vs. Eagle River; error A, pit–mound pair within site; position, pit vs. mound; error B, pair × position within site; depth, Oi–Oe interface vs. organic–mineral interface; error C, residual error.

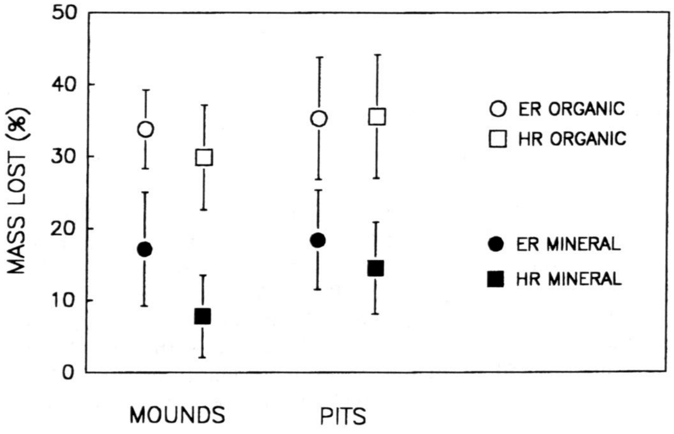

FIG. 1. One-year mass loss of filter papers placed at the Oi–Oe (organic) and O–mineral (mineral) interfaces on mound and pit microsites at the Eagle River (ER) and Heintzleman Ridge (HR) sites. Error bars represent 95% confidence intervals. For each point, $n = 30$.

At each site, we selected 10 pit–mound pairs with mounds of similar size, soil development, forest-floor accumulation, and extent of decay in the uprooted bole. After determining the ages of trees growing on mounds and examining scars and release patterns in residual trees, we concluded that the tree falls occurred 50 to 160 years ago. Mounds and pits from the same tree fall were paired to reduce the effects of within-site environmental variation. An extra pit–mound pair was selected at Heintzleman Ridge for early destructive sampling. Packs were installed on 4 September (Eagle River) and 5 September (Heintzleman Ridge) 1985. We installed the packs in the center of the pits and on the mound sides facing the pit. Mound placements varied: upturned roots and continued soil deposition occupied many mound crests, so we placed the packs at the uppermost undisturbed point available on each mound. At each position, three packs were buried at the interface of the Oi (fibric) and Oe (hemic) horizons, and three packs were buried at the interface of the organic and mineral horizons; all packs were placed parallel to the forest-floor surface. Openings in the forest floor were made with a sharp knife to minimize disruption of the surrounding soil. At the Heintzleman Ridge site only, we measured the thickness of the pit and mound organic layers.

TABLE 2. Field studies of cellulose filter paper decomposition

Location	Vegetation	Depth	Time	Loss	k	Reference
Vancouver Is., Canada	*Thuja plicata – Picea sitchensis*	Oi–Oe interface	0.17	0.069	0.428	Binkley 1984
		Oe–Oa interface		0.028	0.170	
		Oa–mineral interface		0.031	0.189	
	Tsuga heterophylla – Pseudotsuga menziesii	Oi–Oe interface		0.109	0.691	
		Oe–Oa interface		0.106	0.671	
		Oa–mineral interface		0.091	0.571	
	Tsuga mertensiana – Abies amabilis	Oi–Oe interface		0.338	2.470	
		Oe–Oa interface		0.250	1.723	
		Oa–mineral interface		0.166	1.087	
North England, United Kingdom	*Sphagnum* bog	Surface (0–10 cm)	0.98	0.177	0.199	Clymo 1965
		Water table (6–18 cm)		0.070	0.074	
		Deep (75 cm)		0.030	0.031	
Interior Alaska, United States	*Populus tremuloides*	Base of Oe (6.2 cm)	1.06	0.904	2.213	Fox and Van Cleve 1983
	Betula papyrifera	Base of Oe (6.5 cm)		0.886	2.051	
	Picea glauca	Base of Oe (7.0 cm)		0.603	0.872	
	Picea glauca	Base of Oe (13.4 cm)		0.537	0.727	
	Picea mariana	Base of Oe (12.3 cm)		0.412	0.501	
	Picea mariana	Base of Oe (12.5 cm)		0.204	0.215	
Oregon Cascades, United States	*Tsuga mertensiana*	Base of Oe	1.17	0.670	0.950	Waring *et al.* 1987
Southeast Alaska, United States	*Tsuga heterophylla – Picea sitchensis*	Oi–Oe interface	1.04	0.337	0.396	Current study
		O–mineral interface		0.145	0.151	

NOTE: Time is the duration of experiment, in years; loss is the proportion of mass lost; k is the annual decay constant, from eq. 1.

We collected packs from the extra pit–mound pair on 29 April 1986 (235 days in place). The filter papers appeared unchanged, so we removed only 5 of the 12 packs present. All remaining packs were retrieved on 18 September 1986 (379 days in place). Packs were stored frozen until processed. The papers were cleaned and then dried for 24 h at 105°C. Papers in contact with mineral soil were ignited at 550°C for 6 h, and the ash mass was subtracted from the final dry mass to correct for mineral contamination.

Data analysis

Decomposition rate was calculated as the proportion of the original dry mass lost from a pack during 1 year. We calculated mean values for the three packs at each placement and tested the resulting 80 means for site, position, and layer main effects and interactions with a split–split plot analysis of variance (ANOVA).

Rate comparisons

We compared mass loss data from several filter paper decomposition studies to losses observed in the current study. Because the study durations ranged from 2 to 14 months, direct comparisons of the proportions of mass lost were inappropriate; annual decay constants provided a better means of comparison. Accordingly, we fitted the mass losses to the single-exponential decay model (Jenny *et al.* 1949; Olson 1963):

$$[1] \quad X_t = X_0 \, e^{-kt}$$

where X_t = final dry mass, X_0 = initial dry mass, k = annual decay constant, and t = time in years. This single-exponential model adequately describes mass losses during the decomposition of single-component substrates (Minderman 1968; Wieder and Lang 1982).

Results and discussion

Decomposition rates were not significantly different ($p = 0.39$) between pits and mounds (Table 1, Fig. 1). We failed to confirm either the results of Beatty and Stone (1986), who stated that decomposition was slower in pits, or those of Dwyer and Merriam (1981), who found hardwood leaf litter to decompose 3.5 times faster in pits than on mounds (16-month basis). In the latter study, low soil moisture and high temperatures in summer were said to limit decomposition on mounds. In contrast, summers in southeast Alaska are cool and cloudy, with abundant precipitation, so strong pit–mound temperature or moisture gradients would be unlikely to develop. The pits used for this study were young and had highly permeable soils; older pits with less-permeable Bh horizons may develop the hydric character and reduced decomposition observed elsewhere.

The mean proportional mass loss at the Oi–Oe interface was roughly twice that at the organic–mineral interface (Fig. 1). Packs within the organic layer lost 33.7% of their original dry mass, and packs within the mineral layer lost 14.5% of their mass. This effect was highly significant ($p < 0.01$, Table 1). The declining decomposition with depth agrees with the results of Clymo (1965) and Binkley (1984) (Table 2) and may be attributed to cooler temperatures and more frequent water saturation at lower depths. Greater nutrient availability within the organic layer also might increase decomposition. Witkamp and van der Drift (1961) found that filter paper decomposition peaked during September and suggested that nitrogenous compounds leached from freshly fallen litter were partly responsible. Binkley (1984) found that N availability, as measured by ammonium and nitrate accumulation on ion-exchange resins, and filter paper decomposition rates generally were greater on clear-cut sites than in adjacent uncut forests. Waring *et al.* (1987) found greater N incorporation into decayed filter papers placed in areas of higher soil N availability.

Site and interaction effects were all nonsignificant (Table 1). Mass losses varied greatly within each treatment class: coefficients of variation at the organic–mineral interface (100 to 198%) were 1.5 to 3.0 times greater than those at the Oi–Oe interface (43 to 65%), a result of smaller mass losses in the former treatment and roughly equal treatment variances. Fox and Van Cleve (1983) reported within-stand coefficients of variation in the 10 to 80% range.

Table 2 summarizes several studies in which cellulose filter papers were used to estimate field decomposition rates. The annual decay constants for our sites are only slightly lower than those calculated from Binkley's data (1984) for a coastal, low-elevation site on Vancouver Island, British Columbia. Curiously, all but one of the Alaskan taiga stands (Fox and Van Cleve 1983) had greater annual decay constants than our stands. This finding may reflect the warmer summers in the Alaskan interior.

The filter papers that we retrieved early (29 April) had decomposed less than 2%, although the exponential model predicted that they should have been at least 23% (organic) and 9% (mineral) decomposed. This result suggests that most of the decomposition of litter in southeast Alaska occurs from May through September, in contrast with sites in the summer-dry climate of the Oregon Cascades, where 60% of the annual decomposition occurred under snowpack (Waring *et al.* 1987). Although based on a very small sample ($n = 5$), the appearance of such a significant lag in decomposition in our study suggests that the exponential model may be inappropriate for modeling the short-term (<1 year) course of decay in climates where decomposition rates vary widely during the year.

At the Heintzleman Ridge site, we found the mean organic horizon thickness to be significantly greater ($p < 0.01$) in the pits (11.2 cm, SD = 3.39 cm, $n = 10$) than on the mounds (6.7 cm, SD = 3.16 cm, $n = 10$). Because decomposition of filter paper apparently proceeds with similar rates on mounds and in pits, we concluded that the thicker organic horizons of young (50- to 160-year-old) pits primarily resulted from redistribution and accumulation of fallen litter, rather than from reduced decomposition in pits. In consequence, pits must be receiving a disproportionate share of the litter-fall nutrient return on these sites. Heterogeneous distributions of litter and nutrients have been observed in hardwood forests of North America (Orndorff and Lang 1981; Welbourn *et al.* 1981; Beatty and Stone 1986). Effective return of nutrients to the tree biomass would require that trees growing on mound microsites send feeder roots to exploit this nutrient pool. Root turnover is an unknown, but possibly important, contributor to the organic accumulation in these soils but we have no knowledge at present of root distribution and turnover patterns on mound and pit microsites.

A second consequence of litter redistribution affects the calculation of Jenny's *k* from forest-floor mass and litter-fall data. Assuming a homogeneous litter distribution in these stands would yield substantial underestimates for *k* in pit microsites.

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