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Podzolization, the dominant soil forming process in coniferous forests of southeast Alaska, appears to be associated with declining forest productivity. The following hypothesis was tested: Podzolization limits the supply of nutrients available for tree growth, but windthrow-caused soil disturbance counteracts the effect of podzolization and promotes sustained productivity. In three *Tsuga heterophylla-Picea sitchensis* stands in southeast Alaska, I used stand reconstruction methods to identify and date soil surfaces disturbed 50 to 500 years-ago by uprooted trees. With this soil chronosequence, I studied the rate of soil development and associated changes in soil carbon and nutrient dynamics, soil biology, and stand productivity. Mean illuvial horizon thickness was 1.5 cm in 150-yr-old soils and C, N, and P accumulated rapidly in the upper soil horizons. From 0-350 years, soil C (O horizon included) accumulated at 0.1-0.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$. Decomposition of cellulose declined with illuvial horizon development ($r = - 0.68$). Soil respiration, polysaccharidase enzyme activity, and the proportion of soil nitrogen available for mineralization all declined with soil age. Significant correlations existed between soil respiration and soil enzyme activity, including amylase, cellulase, xylanase, peroxidase, and phenol oxidase. Similar correlations were observed between total soil respiration and mineralizable-N, to a depth of 15 cm. Aboveground litterfall varied from 3.8 to 4.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (dry wt.), and aboveground net primary productivity varied from 4.9 to 9.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (dry wt.).

Soil Carbon and Nutrient Dynamics of Windthrow Chronosequences in Spruce-Hemlock Forests of Southeast Alaska

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INTRODUCTION

The Problem Context

In the highly productive western hemlock-Sitka spruce coastal rain forests of southeast Alaska, two processes interact to govern ecosystem structure and function: soil podzolization and the uprooting of trees. The observations of local researchers and managers suggest that soil productivity is enhanced where soils have been disturbed by the natural uprooting of trees. Similar productivity gains have been attributed to soil disturbance caused by ground-based timber harvesting. The link between productivity and soil disturbance is untested — it is based on anecdotal and fragmentary data — but if a relation does exist, one possible explanation is that soil disturbance reverses physical, chemical, and biological changes wrought by podzolization, the dominant soil forming process in southeast Alaska.

As the native forests of the region are harvested and replaced with managed stands, it is likely that windthrow and the associated soil disturbance will decrease. In addition, current silvicultural guidelines seek to minimize soil disturbance associated with timber harvesting. If the continued productivity of the region's soils is truly disturbance-dependent, these trends could lead to reduced forest productivity.

This study is part of a larger investigation of the relations among soil development, soil disturbance, and forest productivity in southeast Alaska. In this study, I have examined some of the changes in soil chemistry and biology that accompany podzolization, with particular emphasis on the cycling of carbon, nitrogen, and phosphorus.

Podzolization

Podzolization is a soil forming process characterized by removal and transport of Fe and Al sesquioxides and organic matter from upper soil horizons and subsequent deposition of this material in lower horizons. With time, the upper (eluvial) soil horizon becomes bleached and is recognized as an E horizon. The lower (illuvial) horizon becomes dark brown or red-brown, forming a spodic B horizon. The spodic horizon is diagnostic for the Spodosol soil order, presence of an E horizon is not (Soil Survey Staff 1975). Spodosols are common forest soils in southeast Alaska; Histosols prevail in poorly-drained areas and Entisols are found on recent alluvial and glacial deposits (Stevens 1965, Harris and Johnson 1983, Bowers 1987, Alexander *et al.* 1989)

Podzolization can change soils significantly within a single generation of trees. In northern Sweden, podzolization was observed in sandy lake bed soils drained 100 years previously (Jenny 1941). Crocker and Major (1955), Ugolini (1968), and Bormann and Sidle (1990) report spodic horizons formed in glacial deposits less than 250 years-old in Glacier Bay, Alaska.

Podzolization may cause nutrients to accumulate in forms less available to trees. Podzolization is accompanied by the buildup of thick mor humus surface horizons. Organic matter that accumulates in illuvial horizons may contain significant pools of nutrient elements (N, P, etc.) in forms resistant to normal mineralization and uptake processes, leading to declines in forest productivity (Bormann and Sidle 1990). Dense spodic horizons may resist root and hyphal penetration, limiting access to nutrients contained in those horizons.

Highly-developed spodic horizons are less permeable to water than are juvenile soils. The decreased permeability of illuvial horizons increases the water saturation of overlying soil, possibly reducing rates of organic matter decomposition. The permeability of surface soils has been observed to increase following windthrow (Denny and Goodlett 1956).

In few regions has soil development been studied so extensively as in the northern part of southeast Alaska. Glacial recession and shoreline uplift have created soil surface chronosequences that have captured the attention of several generations of ecologists and pedologists.

Chandler (1942) examined soils along a glacial-recession chronosequence in the Mendenhall Valley near Juneau and identified soil surfaces 15-, 90-, 250-, and ca. 1000-years-old. The oldest site was 0.5 km from the Heintzleman Ridge site used in the current study. He did not observe eluvial (E) or illuvial (Bh or Bs) horizons in the 250-yr-old profile; they were present, however, in the oldest (1000-yr-old) profile, which had 5-10 cm of A2 (E) and 15-20 cm of B (Bh and Bs). He estimated that 500-1000 yr were required to form a mature and stable podzol (Spodosol).

Crocker and Dickson (1957) found only weak evidence of podzolization in soils developing on Mendenhall Glacier recessional moraines and concluded that, in this region, 'typical podzols' were not the end product of soil development on recessional moraines. In contrast, Stevens (1963) described a profile of a soil surface on a moraine exposed for 500-1000 yr (also near the Mendenhall Glacier) which had accumulated an 18-cm organic layer, a 5-cm A2 (E) horizon, and a 7-cm spodic horizon.

At Glacier Bay, roughly 90 km NW of Juneau, Ugolini (1968) found soils developed incipient B horizons by 55 yr, traces of eluvial horizons by 150 yr, and distinct but shallow eluvial horizons by 250 yr. However, Ugolini and Mann (1979) did not observe spodic horizons in soils on a 400-yr-old uplifted beach terrace near Lituya Bay, Alaska, approximately 180 km NW of Juneau.

From these accounts, it appears that soil development rates vary widely within this region. This is consistent with the findings of Messer (1988) in south-central Norway. She attributed variations in rates of soil development to local variations in climate and vegetation. It is likely that these factors are responsible also for the variable rate of podzolization observed in southeast Alaska.

Paludification and the Muskeg Climax Hypothesis

The prevalence of peatlands, known locally as 'muskegs', in southeast Alaska has fostered a long-running unresolved controversy over the regional climax vegetation. Zach (1950) suggested that muskegs, not mixed age hemlock-cedar forests, are the true climax on flat-to-moderately sloping sites below the alpine zone in southeast Alaska. Discussing post-glacial succession, Lawrence (1958) described a stage of "forest deterioration and muskeg development" following the spruce-hemlock forest stage. In contrast, Stephens *et*

al. (1970) concluded that the area covered by muskegs has decreased greatly since the Pleistocene deglaciation and that muskeg is not the climax vegetation type.

Several mechanisms have been proposed for paludification, the conversion of forest or other mesic plant communities to muskegs. Lake infilling and impermeable parent material, such as compacted glacial till and water-deposited glacial silt, were cited by Stephens *et al.* (1970). Zach (1950) blamed the abundant rainfall and the accumulation of water-retaining organic material, which is promoted by favorable conditions for plant growth coupled with cool temperatures that hinder decomposition. Lawrence (1958) speculated that patches of *Sphagnum* become established during the spruce-hemlock stage of succession, and as the patches grow the soils become water-saturated and the forest declines, eventually becoming a muskeg. Noble *et al.* (1984) attributed paludification to *Sphagnum* invasion 175-600 years after glacial recession. Their conclusions are questionable because *Sphagnum* was absent from surrounding stands of similar age (191 yr) and the water table was rising in the study area, making it equally likely that *Sphagnum* invasion was a *response* to changing soil moisture, not the *cause.*

Soil development, particularly podzolization, may play a role in paludification according to Ugolini and Mann (1979), who argued that the development of a relatively impermeable placic soil horizon impedes drainage of the overlying soil and forest floor, leading to paludification after 500-1000 years of soil development. Klinger *et al.* (1990) discounted this mechanism, even though their soil profiles showed strong podzolization (including an ironpan) of the soil underlying the muskegs they studied.

Several site factors or mechanisms may resist or reverse paludification. Zach (1950) stated that muskegs are absent only from sufficiently steep slopes with good drainage or from high-elevation sites above the range of peat-forming vegetation. Lawrence (1958) suggested that windthrow-caused soil disturbance prevents paludification of level soil surfaces by improving drainage into the substrate. Stephens *et al.* (1970) asserted that many timber stands exist on flat or gentle slopes on old, well-drained surfaces with no evidence of paludification. They said these sites have experienced 'no major disturbance since Pleistocene ice recession', but it is unclear whether they considered windthrow a major disturbance, since most observers fail to recognize evidence of past windthrow disturbance.

Windthrow

The toppling of trees and the associated soil disturbance have inspired a significant body of jargon: windthrow, tree-throw, uprooting, blowdown, arbroturbation, tree falls, mound and pit microrelief, pit and mound microrelief, cradle-knoll microrelief, and hillocks. The Soil Conservation Service prefers 'cradle-knoll microrelief' for describing the irregular soil surfaces created when trees are uprooted (Soil Conservation Service 1981).

Stephens (1956) studied tree uprooting, listing and classifying the causal factors. He noted that uprooting is rarely the result of a single factor; combinations of mechanical factors (e.g., wind, ice, snow, soil saturation) and physiological factors (e.g., damage from pathogens, insects, or fire, senescence) contribute to uprooting. This suggests that the terms 'windthrow' and 'blowdown' are not always precise or correct, and that the term 'uprooting' is more appropriate, because it does not imply causality.

Tree size, species, and condition partly determine the degree of soil disturbance following uprooting. The largest trees are more likely to be uprooted (Brewer and Merritt 1978). Mueller and Cline (1959) found that the volume and surface area of soil disturbed by uprooting increased with tree size. The tree size was of much greater importance than any soil effects on mound size. Denny and Goodlett (1956) found the mounds produced in a second-growth forest were half the size of mounds dating from the original forest. Putz (1983) found pit volume, pit and mound area, and pit depth all increased with tree diameter in a tropical rain forest. Live trees produce larger tree throw mounds than dead trees, diameters being equal (Lyford and MacLean 1966). Mound morphology depends on tree rooting habits: hardwoods, white pines, and hemlocks in eastern North America are deep rooted and form deep pits with large mineral mounds; in contrast, fir and spruce, with plate-like root systems, form shallow pits and small mounds (Veneman *et al.* 1984, Lyford and MacLean 1966). In well-drained, deep soils, however, Sitka spruce is known to root deeply (Fraser and Gardiner 1967). More windthrown trees are found on soils with poor drainage than on well-drained soils (Mueller and Cline 1959).

Tree uprooting has been reported widely in the northeastern USA, Canada, and Sweden. Stephens (1956) examined stands extensively in the USA east of the continental divide and in the Canadian Maritime Provinces and found evidence of windthrow uprooting throughout the region. He asserted that uprooting is not an isolated, accidental event,

but a normal forest process: "The microrelief of mounds and pits was observed to be as much a characteristic of the forest as the trees." More than 90% of forested land in Appalachian region of Canada is affected by mound and pit microrelief, except in forests established on old-fields (Beke and McKeague 1984).

Uprooting has been studied in tropical forests of Panama (Putz 1983) and Costa Rica (Vitousek and Denslow 1986). Pit and mound microrelief is not common in the tropical rain forests of Panama: only 0.09% of the ground was in pits or mounds and the average disturbance involved only 16 m^2 of soil (Putz 1983).

Wind-caused uprooting is the primary cause of stand replacement in southeast Alaska, an area where fire and insect outbreaks are unimportant (Harris 1989). Uprooting may involve single trees or small groups of trees; extensive uprooting may occur during fall and winter gales (Harris 1989). One quarter of the southeast Alaskan tree mortality reported by Hutchison and LaBau (1975) was attributed to windthrow.

Clearly, uprooting is common in many forested regions. Within these forests, much of the soil surface is disturbed. Holmes (1893) found almost half the surface of a Minnesota forest in pits or mounds. Stephens (1956) discovered evidence of four uprooting events, with an average return frequency of 160 years (my calculation), covering 14% of the forest floor with pit and mound surfaces. In some Pennsylvanian forests, most surface horizons (upper 1 m) were disturbed in the last 300-500 years. Auger holes revealed that much of the supposed intermound area was old eroded mounds and filled-in pits (Denny and Goodlett 1956). Lyford and MacLean (1966) found 500 mounds and 600 pits per acre; 35% of the stand area was in mounds, 10% in pits. Uprooting-related disturbance was present in 19% of the samples taken by Armson and Fessenden (1973); they estimated that up to 35% of the soil surface was disturbed by uprooting. Troedsson and Lyford (1973) noted recent uprooting in some Swedish forests; pit and mound microrelief covered approximately one-third of the site.

Microrelief becomes less distinct with age (Troedsson and Lyford 1973, Denny and Goodlett 1956). Stephens (1956) observed that horizons in his oldest mounds (450-550 yrs-old) had returned nearly to normal, obscuring the effects of the uprooting disturbance. Lutz (1940) could identify mounds with estimated ages of 300 years. Pit-mound microrelief may last only 5-10 years in Panamanian tropical rain forests, because pits refill

rapidly with mineral soil (ca. 8.1 $cm \cdot yr^{-1}$), especially during rainy periods when high intensity rainfall washes over exposed, mounded soil (Putz 1983).

Man's activities affect mound disappearance rates. Clearcutting appeared to hasten microrelief reduction in Pennsylvania (Denny and Goodlett 1956). Conversion of forest to farmland in Massachusetts destroyed microrelief, but it returned upon reestablishment of forests on old-fields (Veneman *et al.* 1984). Lack of pit and mound microrelief in eastern North American and European forests suggests agricultural leveling, according to some (Troedsson and Lyford 1973, Stone 1975).

Lutz's (1940) experience suggests that mounds are favored sites for tree germination and establishment. Denny and Goodlett (1956) reported that trees did not grow in the bottom of pits and were rare on mound crests; most trees grew at mound ends. Lyford and MacLean (1966) examined tree distributions in natural stands and plantations and found mounds had more and larger trees, intermediate sites (neither pit nor mound) had fewer trees, and pits had the fewest trees — 0-4% of site totals. Small feeder roots were found mostly in the forest floor, in mounds, and in areas where soil was well-mixed by tree throw. Deal (1987) found 60% of Sitka spruce regeneration on mineral mounds.

Pits are poor sites for small plants because of standing water, ice sheets and needles, frost heaving, and smothering litter deposits (Lyford and MacLean 1966, Stone 1975). But growth on mounds is risky: as mounds collapse with age, most seedlings established on mounds are destroyed (Beatty and Stone 1986).

Uprooting creates mineral soil seedbeds and gaps in the forest canopy, which are favored or required by some tree species (Denny and Goodlett 1956, Lyford and MacLean 1966, Armson and Fessenden 1973). This may allow certain early-seral species to persist in long-established forests. For example, white pine may owe its existence in one area of northern Pennsylvania to uprooting (Denny and Goodlett 1956). The presence of Sitka spruce in old-growth western hemlock-Sitka spruce forests of southeast Alaska depends on windthrow openings (Harris 1989).

The most obvious effect of uprooting on forest soils is the creation of pit and mound microrelief. This phenomenon has been described thoroughly by many workers, some of whom have presented elaborate classification schemes and terminology (Shaler 1891, Lutz and Griswold 1939, Stephens 1956, Beatty and Stone 1986, Johnson *et al.* 1987, Schaetzl *et al.* 1989b). Beatty and Stone (1986) emphasize the diversity of uprooting-

caused soil disturbances and contend that the type of disturbance determines the microsite type created.

Less obvious to the casual observer is the disruption or elimination of soil horizons as uprooting lifts and mixes soils. Soil on young mounds is unconsolidated and soil horizons in young mounds and pits are absent or irregular and discontinuous (Lutz 1940, Denny and Goodlett 1956, Lyford and MacLean 1966, Beke and McKeague 1984). Folding of horizons sometimes creates abnormally thick O and E horizons (Lutz and Griswold 1939, Veneman *et al.* 1984). As mounds age, their relief decreases and their soil horizons regain continuity and regularity (Lyford and MacLean 1966, Troedsson and Lyford 1973).

Soil mixing continues long after the tree has toppled. The elevated roots and adhering soil slowly disintegrate and collapse, partly filling the pit and sometimes burying the adjacent forest floor. The deposited soil is usually well-mixed, but it may develop strata when cemented chunks of soil are plucked up by roots (Lutz and Griswold 1939) or when collapsing mounds bury organic layers (Beke and McKeague 1984). Mixing destroys horizons and brings together forest floor material and weathered and unweathered soil (Denny and Goodlett 1956). In effect, the soils are rejuvenated: much of the evidence of soil forming processes is eliminated by mixing.

For nutrient cycling, this rejuvenation may be the most important effect of uprooting. Lutz (1940) suggested that mixing of soil horizons recycles eluviated materials:

> Disturbance of a forest soil, particularly a podzol, by windthrown trees enriches the surface soil in minerals that are valuable as sources of plant nutrients. The soil turbulence resulting from windthrow of trees to some extent counteracts the effects of podzolization. (p. 17)

Lutz (1940) goes on to suggest that decomposition of organic material accelerates with burial and mixing during uprooting. Armson and Fessenden (1973) suggested that windthrow disturbance of soil may reduce the intensity of podzolization, noting that the most intense podzolization is associated with heath vegetation, where windthrow is absent. In southeast Alaska, Sitka spruce site index was positively related to the proportion of windthrow-disturbed soil area within stands (B.T. Bormann, personal communication), suggesting a positive effect on site nutrient availability.

Windthrow, like wildfire, insects, and pathogens, is viewed by most foresters as something to be avoided. The short-term economic loss from large windthrow events can be substantial, especially if timber salvage is delayed or prevented. Windthrow effects may extend beyond the current rotation: pit and mound microrelief created by windthrow impedes vehicle operation in ground-based harvest systems (Beke and McKeague 1984). Most forest management organizations seek to prevent blowdown, and undertake aggressive salvage operations when it inevitably occurs. As native forests are harvested, windthrow frequency may increase slightly due to the creation of windthrow-prone leave strips and non-windfirm cutting unit boundaries. Once large tracts of native forest are converted to second-growth managed forest, significant decreases in windthrow are likely.

What might be the effects of eliminating windthrow? Armson and Fessenden (1973) suggested that where stand management reduces or eliminates windthrow, podzolization might be more intense than under natural stands. They also noted the success, in terms of improved tree growth, of silvicultural systems that include some form of soil disturbance. Similarly, Lutz (1940) suggests that logging disturbance could duplicate the favorable effects of windthrow. We need to determine if windthrow is essential for maintaining the productivity of the western hemlock-Sitka spruce forests and, if so, silvicultural systems must be modified to assure soil mixing.

Research Objectives

This study was an attempt to test the following general hypothesis: In western hemlock-sitka spruce forests of southeast Alaska, a natural soil development process, podzolization, leads to a rapid decline in potential site productivity by limiting the supply of nutrients available for tree growth. The following specific hypotheses were tested:

1. Recently-disturbed soils on windthrow mounds provide more favorable environments for decomposition than do pit soils of comparable age.
2. Development of illuvial horizons reduces site productivity by limiting nutrient availability.
    A. Litter and soil organic matter (SOM) decomposition decrease with increased soil age or illuvial horizon development.

B. Nutrients accumulate in illuvial horizons and are less available for plant uptake.

(1) Nutrients accumulate in illuvial horizons.

(2) The proportion of the total soil nutrient content that is in plant-available forms is less in illuvial horizons than it is in less-developed soils.

(3) Soil biological activity is reduced in illuvial horizons.

(4) Root and fungal exploitation of nutrients within the illuvial horizon is limited.

(5) The total amount of nutrients contained in illuvial horizons is significant in terms of general stand nutrition.

Method of Investigation

Processes such as soil development that require decades or centuries to produce significant change usually are studied with the chronosequence method, in which space is substituted for time (Pickett 1989). The soil science and ecological literature contain many examples of chronosequence studies on datable soil surfaces, including glacial deposits, mudflows, sand dunes, uplifted beach terraces, etc. Jenny (1941) describes studies of soil formation on building materials, volcanic ash, moraines, dunes, and dikes.

My study of the effects of podzolization employed multiple age classes of wind-throw mounds as within-stand soil surface chronosequences. In three stands I identified at least four mounds in each of three age classes, ranging from roughly 60 to 400 years. Earlier workers have suggested this approach to the study of soil development. Stephens (1956), noting that horizons in his oldest mounds (450 to 550-years-old) had returned nearly to normal, obscuring the effects of the windthrow disturbance, suggested that the age sequence of mounds represented "the development of a soil profile over time," and that study of soil physical and chemical properties on such a sequence could be used to study changes associated with soil development. Gennadiyev (1983) studied the development of soils in the Caspian lowlands, USSR, using manmade mounds and trenches ranging from 500 to 4500-years-old. He used the manmade system to model the changes occurring in natural mounds and pits.

Within-stand windthrow mound chronosequences have several advantages over multi-site chronosequence studies. Multi-site chronosequence studies have been criticized for failing to meet their primary assumption: that time (or its surrogate, space) is the only factor that varies between sites (Pickett 1989). But sites may differ in many ways, ranging from local adaptations of populations to differences in elevation, aspect, landform, slope position, or parent material. Long-term climate change or local microclimatic variation also may confound the interpretation of between-site differences. Different initial conditions due to variable disturbance intensity may be especially important in secondary succession studies along chronosequences. Although within-site chronosequences are vulnerable to changing climate and variable disturbance intensity, they lack the between-site variability that can compromise results from multi-site chronosequence studies.

STUDY SITES AND SOIL SURFACE DATING

Site Descriptions

Site reconnaissance and selection spanned 1985 and 1986. I considered potential sites near the Juneau, Alaska, road system, and on Douglas, Admiralty, and Chichagof Islands. I had hoped to find a chronosequence of even-aged stands of windthrow origin, but found very few suited to my purpose; particularly scarce were even-aged stands greater than 150 years-old. I decided then to seek stands with multiple cohorts of trees established following windthrow events roughly 50, 150, and 300 (or more) years-ago. Sites were required also to have reasonably deep soil, relatively uniform stands of mixed hemlock and spruce, and no evidence of timber harvesting.

The Heintzleman Ridge site, on the mainland 15 km NW of Juneau, lies on a level, glacial-marine till bench deposited about 9000 years ago. Soils are moderately deep, well-drained, gravelly silt loams. Precipitation, evenly distributed throughout the year, averages 1368 mm yr^{-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 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. Light, chronic disturbance has occurred since then. A group of younger trees (90-100 yrs-old) is present in the N corner of this plot; the young trees established on landslide material. Additional site data are in Table 1 and Table 2.

The Hawk Inlet site, on Admiralty Island 27 km SW of Juneau, lies on a gently sloping bench formed from colluvial or till deposits. Soils are deep, well-drained, gravelly silt loams. Climatic data for this site are unavailable, but should not differ greatly from those of the Heintzleman Ridge site. Spruce growing on mounds at Hawk Inlet are taller and larger in diameter than those growing on unmounded soils. Many hemlocks have shattered, decaying interiors; breakage is frequent and many trees have twin tops with branches starting at approximately 9 m. It appears that in 1835 the hemlock was 9 m high, having established itself around 1780 as an understory to a spruce stand. In 1835 a large windthrow event released the understory hemlock and allowed a new spruce cohort to germinate on the newly created mineral mounds (C.D. Oliver, personal communication).

Table 1. Study site locations and topography

Site	Latitude/ Longitude	Elevation (m)	Aspect	Slope (deg)
Heintzleman Ridge	58°22'N, 134°34'W	75	SW	0
Hawk Inlet	58°8'N, 134°44'W	100	W	10
Outer Point	58°18'N, 134°40'W	10	NW	0-5

Table 2. Stand data for study sites

Site	Spruce			Hemlock		
	DBH (cm)	BA (m^2/ha)	Density (t/ha)	DBH (cm)	BA (m^2/ha)	Density (t/ha)
Heintzleman Ridge	62.4	27	76	39.5	49	333
Hawk Inlet	85.7	21	32	60.2	49	162
Outer Point	68.7	8	20	40.8	65	397

The Outer Point site, on Douglas Island 17 km W of Juneau, is on a very gently sloping uplifted beach terrace. Soils are moderately deep and gravelly, containing many slate fragments. This site appeared cooler and wetter than the two previous sites; mucky areas were present in and near the site, and at times of heavy rainfall, intermittent streams traversed the site. An old-growth hemlock-spruce stand occupied the site. A major disturbance (presumably a windthrow event) around 1820 caused the release of residual hemlocks. Of 41 trees sampled, 18 (44%) originated 150-170 years B.P. (before present), 6 (15%) originated 190-210 years B.P., and 5 (12%) originated 120-129 years B.P. Remaining trees were of various ages, indicating continuing disturbance (R.L. Deal, personal communication). On all sites, young, recently disturbed mound soils probably were Ochrepts; older, more developed soils were Humic Cryorthods, except for scattered low-lying areas containing Cryosaprists.

Mound Dating

Many methods for dating windthrow events have been reported: historical records of storms (Veneman *et al.* 1984) and land use (Beatty and Stone 1986); stand management records or recollections of land managers (Beatty and Stone 1986); determining the age of trees growing on mounds of interest (Lutz and Griswold 1939, Denny and Goodlett 1956, Beatty and Stone 1986) or on adjacent mounds (Veneman *et al.* 1984); stand reconstruction (Stephens 1956); orientation of mound-pit axis (Veneman *et al.* 1984, Lyford and MacLean 1966, Denny and Goodlett 1956); decay class of stump or bole of uprooted tree (Denny and Goodlett 1956); degree of soil development on mound or pit (Denny and Goodlett 1956). Fire or other stand-replacing events limit techniques based on living or dead trees (e.g., Lyford and MacLean 1966).

Denny and Goodlett (1956) estimated mound ages from the age of trees growing on mounds, the decay class of stumps or boles of uprooted trees, the degree of soil development on mounds or in pits, and the orientation of mounds. They found on slopes most trees fell downhill, but in other areas, mound orientation appeared random. With individual treefalls, orientation was usually random; where major storms uprooted groups of trees, their orientations were similar.

Zeide (1981) dated mounds from the age of hardwoods occupying the top of treefall mounds. These trees develop stilted root systems as the mounds subside. Zeide assumed the position of the root collar marked the original height of the mound and developed a model of exponential decline of mound height over time. He noted that this dating method underestimates the mound's age due to the lag in seedling establishment following mound creation. The original mound height is probably underestimated as well.

Fires that swept their study area in 1875 and 1900 prevented Lyford and MacLean (1966) from using tree-based dating methods. They suggested that common, small-scale windthrows were associated with local thunderstorms; larger areas were affected by hurricanes with 50-100 yr return intervals. They observed many mounds with the same general NW-SE orientation and concluded these were produced by large storms noted in the historical record.

Veneman *et al.* (1984), in their study of a single pit-mound pair, nicely illustrate an approach combining several independent estimates of a mound's age. The ages of three

hemlocks growing on top of adjacent mounds provided a minimum age estimate for the mound (113 yr); they estimated the maximum age at 500 yr, because the discontinuous soil horizons observed in the mound would have become uniform by that age. They noted also that a tornado was recorded in 1834, when many forests were blown down from SW winds. Because the bole axes of the pit-mound pairs ran E-W, with the pits W of the mounds, they concluded the 1834 storm was responsible.

For the present study, mounds were dated using several techniques and multiple independent age estimates were used to corroborate or reject each treethrow date. Annual growth rings were counted on increment cores taken from trees growing on mounds or on fallen boles associated with mounds. This method slightly underestimates the time since treethrow because of the delay in seedling establishment on mound crests and fallen boles and because of the time required to grow to breast height, where the cores were typically taken. Where falling trees hit and scarred surviving trees, the new growth surrounding the scar was cored and aged to find the time elapsed since the injury. Highly decayed fallen boles were identified by removing moss and litter from the forest floor and tracing the decayed wood from the mound. Decay-resistant pitchy branch stubs and fiber orientation provided clues to the size, position, and alignment of these decayed boles. Periods of accelerated diameter growth (i.e., wider annual rings) were sought in increment cores or wedges taken from surviving trees, on the assumption that survivors would respond with greater growth to treethrow-created canopy openings.

Several general mound and fallen bole characteristics were used to corroborate the estimated age of mounds. Young mounds tended to have thinner forest floors, greater height and steeper microrelief, less decayed exposed roots and boles, and less profile development than older mounds. Some mounds were rejected due to evidence of further disturbance following the original treethrow event. For example, trees established on mounds often topple, destroying the upper mound surface, or sometimes the decaying root mass collapses upon the developing mound.

Three age classes of mounds were identified at each site: young (50-60 yr), medium (150-160 yr), and old (300-350 yr). Ages of young and medium-aged mounds are reliable estimates based on multiple pieces of evidence. The ages of old mounds are based on the ages of residual trees and should be considered rough estimates. Four

mounds in each of the three age classes were selected at each site and were used in all subsequent analyses.

Improved age estimates forced the reclassification of several mounds used in this study. At Heintzleman Ridge, one 'medium' aged mound was found to be only 82 years-old; an old mound was estimated to be only 200 years-old. These mounds were dropped from all analyses based on age class, as was one old mound at Hawk Inlet. In addition, at Hawk Inlet one old mound was reassigned to the medium age class and another old mound was rendered useless when a deer died on top of it.

SOIL ENZYMES

Introduction

The polymeric constituents of plant and animal detritus must be broken down to subunits before microbial assimilation and plant uptake of energy-rich compounds and nutrients can occur. The requirement for degradation before uptake demands a system of extracellular enzymes. The source of enzymes may be plant roots, mycorrhizal or saprophytic fungi, bacteria, and other living soil organisms, besides the pool of stabilized, long-lived enzymes present in many soils (Ladd 1978).

Soil enzyme activities have been used as a measure of microbial activity and growth (Frankenberger and Dick 1983), although the relation of enzyme activity to actual process rates is disputed: enzyme activities and process rates are variously reported to be highly-correlated or not at all correlated. Several studies have confirmed the association between soil respiration, microbial biomass, and the activity of some soil enzymes. In conifer litter, Spalding (1977) found amylase activity well correlated ($r = 0.71$) with respiration measured *in vitro*. Frankenberger and Dick (1983) studied a diverse group of ten Californian soils and found that several enzymes (alkaline phosphatase, amidase, α-glucosidase, and dehydrogenase) were highly-correlated with respiration in soils amended with glucose, but they found no significant correlation between enzyme activity and soil respiration in unamended soils. Microbial biomass determined by the chloroform fumigation-incubation method was significantly correlated with alkaline phosphatase, amidase, and catalase activities. Studies of ectomycorrhizal fungal mats in western Oregon forest soils showed mat soils to have higher respiration, microbial biomass, and enzyme activities than did the adjacent non-mat soils (Caldwell *et al.* 1989, Griffiths *et al.* 1990).

I hypothesized that if podzolization leads to reduced decomposition and a general slowdown of nutrient cycling and organic matter turnover, this effect would manifest itself in reduced enzyme activity in older soils. To test this idea I measured the activity of cellulase, xylanase, amylase, acid phosphatase, peroxidase, and phenol oxidase in soil chronosequences at Heintzleman Ridge and Outer Point. I attempted to study protease activity, using the method of Ladd and Butler (1972), but I found this assay did not work

well due to colorimetric interference at 700 nm from dark-colored material extracted from the soils by the assay reagents.

Cellulase catalyzes the hydrolysis of cellulose, an important structural polysaccharide of plant cell walls that makes up roughly one-half of the global NPP. Cellulose is aerobically and anaerobically degraded; fungi produce most of the cellulase in well-drained soils (Ljungdahl and Eriksson 1985). Cellulase is long-lasting and somewhat stable in soil; it is constitutive, but induction is necessary for high concentrations to be produced (Saddler *et al.* 1986, Paul and Clark 1989).

Xylanases catalyze the hydrolysis of xylans, structural polysaccharides comprising $\beta(1,4)$ polymers of D-xylose and other components. Xylans are hemicelluloses and are second only to cellulose in abundance as polysaccharide cell wall constituents. Xylans are often associated with lignin.

Amylases catalyze the hydrolysis of the storage polysaccharides starch and glycogen. Both starch and glycogen are $\alpha(1,4)/\alpha(1,6)$ polymers of D-glucose; starch is common in higher plants; glycogen is found in bacteria, fungi, and animals (Lewis 1986).

In the polysaccharide assays, I colorimetrically determined the reaction product of dinitrosalicylic acid and the reducing sugars (Spalding 1977) released during enzyme-catalyzed hydrolysis of substrate solutions (carboxy-methylcellulose, xylan, and starch).

Peroxidase catalyzes the oxidation of various substrates (S) by the following reaction, in which hydrogen peroxide (H_2O_2) is the H-acceptor:

$$S_{red} + H_2O_2 \rightarrow S_{oxid} + H_2O \qquad (1)$$

Several peroxidases are involved in fungal degradation of lignin (Kirk and Farrell 1987). This process is oxidative, produces quinones, and is inhibited by anaerobiosis. Peroxidases may degrade flavonoids (Barz and Hoesel 1979) and also may participate in cellulase regulation (Ljungdahl and Eriksson 1985). I used the peroxidase assay of Bartha and Bordeleau (1969), in which peroxidase catalyzes the oxidation of *o*-dianisidine by H_2O_2. Substrate oxidation is followed colorimetrically by the absorbance increase at 460 nm.

Phenol oxidases catalyze the oxidation of phenolic hydroxyls to carbonyl groups. The particular phenol oxidase that I studied was *p*-diphenol oxidoreductase — also known as laccase — which catalyzes the following reaction:

$$p\text{-}diphenol + \tfrac{1}{2}O_2 \rightarrow p\text{-}quinone + H_2O \quad (2)$$

Quinones produced in this reaction may polymerize to form a brown product. This is the common browning reaction of injured plant tissues. Quinones also react with nitrogenous compounds (R-NH_3, amines) to form brown humic substances (Stevenson 1986).

I used a phenol oxidase assay in which *p*-diphenol oxidase catalyzes this reaction:

$$hydroquinone + \tfrac{1}{2}\ O_2 \rightarrow p\text{-}quinone + H_2O \quad (3)$$

The quinone produced is subsequently reduced by 2-Nitro-5-thiobenzoic acid (TNB) to hydroquinone, reversing the above reaction. The TNB is oxidized and decolorized in the process. The concentration of the reduced form of TNB is measured colorimetrically at 412 nm.

Phosphatases catalyze the hydrolysis of esters or anhydrides of H_3PO_4. Acid and alkaline phosphatases (orthophosphoric monoester phosphohydrolases) catalyze this reaction:

$$R\text{-}PO_4^{-2} + H_2O \rightarrow R\text{-}OH + PO_3OH^{-2} \quad (4)$$

Acid phosphatase is dominant in acidic soils; alkaline phosphatase dominates in alkaline soils (Tabatabai 1982). I used the assay of Tabatabai and Bremner (1969), in which phosphatase cleaves sodium *p*-nitrophenyl phosphate, releasing *p*-nitrophenol, which under alkaline conditions forms the yellow phenolate ion, the concentration of which is measured colorimetrically.

Methods

Soil sampling

At each site three mounds in each age class (young, medium, and old) were selected. Heintzleman Ridge mounds were sampled on September 8 and 12, 1988. Outer

Point mounds were sampled on September 27 and October 6 and 12, 1988. (Outer Point samples were also used for soil respiration study.)

The upper soil profile was exposed by digging one randomly-located soil pit in the pit-facing side of each mound. Samples were taken of each distinct organic horizon and each mineral horizon to 15 cm below the organic-mineral boundary. I also collected a 1 cm-thick slice at the transition from organic to mineral soil and at the transition from E to Bh (where present). Where visible horizonation of the mineral soil was absent, samples were collected for each 5 cm, to 15 cm. Samples were stored in plastic bags at 4°C until processed.

Preparation of soil samples for enzyme assays

I put 5.0 g of fresh, sieved ($\leq$ 2 mm, all visible stones and roots removed) soil in a small blender jar, added 50 ml of acetate buffer (0.1 M, pH 3.9), and stirred the mixture for 30 s with a household blender set to its lowest speed. A magnetic stirrer kept the soil homogenate in suspension while I withdrew aliquots for analysis.

To find the mass of dry soil per unit volume of homogenate, I pipetted 3 consecutive 1.0-ml aliquots (total 3.0 ml) of each sample into a dried weighing dish. This was dried to a constant weight at 105°C and weighed to the nearest 0.01 mg. Soil dry masses were corrected for the mass of buffer in solution.

After removing the soil homogenate for the phosphatase, cellulase, xylanase, and amylase assays, I centrifuged the remaining homogenate for 20 min to produce the supernatant used in the peroxidase and phenol oxidase assays. The filled centrifuge tubes were refrigerated before and after centrifugation.

Peroxidase assay

The peroxidase assay was a modification of the method of Bartha and Bordeleau (1969). I added 1.0 ml of supernatant and 1.7 ml of acetate buffer to a 15×85 mm glass culture tube and then warmed the tube to 30°C in a water bath. After adding 50 µl *o*-dianisidine reagent (3-3'-dimethoxybenzidine, Fast Blue B Base, Sigma D-9143, 0.5% (w/v) in reagent-grade methanol) and quickly mixing the contents with a vortex mixer, I measured the absorbance increase over 2 minutes at 460 nm. This measurement was the

sample blank. To the same tube, I then added 300 µl of H_2O_2 (0.06% in acetate buffer), remixed the contents, and measured the absorbance increase as before.

The reagent blank contained 2.7 ml of acetate buffer and 50 µl *o*-dianisidine reagent. The absorbance change before and after the addition of H_2O_2 was measured as with the sample tubes.

Phenol oxidase assay

To assay diphenol oxidases, 2-Nitro-5-thiobenzoic acid (TNB) was prepared by suspending 0.0198 g of 5,5'-Dithio-bis(2-nitrobenzoic acid) (Sigma D-8130) in 10.0 ml distilled water and then adding 0.030 g of sodium borohydride. This mixture was allowed to react for 1 h at room temperature. To each sample tube I added 1.0 ml of supernatant and 1.7 ml of acetate buffer and then warmed the tube to 30°C in a water bath. The spectrophotometer was set to read absorbance at 412 nm, with the zero set with the assay mixture (supernatant + buffer). After adding 30 µl of TNB to the assay tube and rechecking the absorbance to ensure that it remained on scale, I added 300 µl of 0.02 M hydroquinone (1,4-benzenediol, Sigma H-9003), mixed, and then recorded the decrease in absorbance over 2 minutes. Because the absorbance change always was negative, results were transformed to the absolute value of the absorbance change to ease interpretation of the data. The reagent blank contained 2.7 ml buffer, 30 µl TNB, and 300 µl of hydroquinone.

Phosphatase assay

I used the phosphatase assay of Tabatabai and Bremner (1969). For each sample, 1.0 ml of soil homogenate and 1.0 ml of 50 mM p-nitrophenyl phosphate (PNPP) in buffer (Sigma 104 Phosphatase Substrate, 104-0 (PNPP) were added to a culture tube, mixed, and then incubated at 30°C. Reagent blanks contained 1.0 ml of PNPP and 1.0 ml of buffer; sample blanks contained 1.0 ml of homogenate and 1.0 ml of buffer. After 1 h, 0.5 ml of 0.5 M $CaCl_2$ and 2.0 ml of 0.5 M NaOH were added to each tube, which was then mixed and centrifuged for 10 min (or until clear). I measured the absorbance of the supernatant at 410 nm. Working curves were prepared with tubes containing 0-400 µl of 10 $\mu mol \cdot ml^{-1}$ *p*-nitrophenol (PNP) standard (Sigma 104-1), made up to 1.0 ml with buffer.

Polysaccharidase assays

The polysaccharidase assay of Spalding (1977) was modified slightly. Substrate solutions containing 2% polysaccharide in buffer were prepared using carboxymethyl-cellulose (sodium salt, low viscosity, Sigma C-8758) for the cellulase assay, soluble starch (Mallinckrodt 8188, reagent grade) for the amylase assay, and xylan (from larch, Sigma X-0376) for the xylanase assay. The DNSA reagent was prepared by dissolving 1.0 g of 3,5-Dinitrosalicylic acid (Sigma D-1510) in 20.0 ml of 2.0 M NaOH and then adding 30.0 ml distilled water. I then added 30 g of potassium sodium tartrate, 4-hydrate (J.T. Baker 3262-1) and brought the volume to 100.0 ml with distilled water.

Assay tubes contained 1.0 ml of soil homogenate and 1.0 ml of polysaccharide substrate solution. Substrate blanks contained 1.0 ml of polysaccharide solution and 1.0 ml of buffer; sample blanks contained 1.0 ml of soil homogenate and 1.0 ml of buffer. Each tube received 100 µl of toluene (J.T. Baker 9460-01) to inhibit bacterial growth. The tubes were stoppered and incubated at 30° C. After 24 h, the tubes were centrifuged and 1.0 ml of supernatant was removed and mixed with 1.0 ml of DNSA reagent. This mixture was steamed for 10 min to develop the color, cooled at room temperature, and recentrifuged. The absorbance at 540 nm was then measured. Working curves were prepared from tubes containing 50-1000 µl of glucose standard solution (3 mg glucose (EM Science DX0145-1) per ml of buffer) per ml.

Statistical analyses

Descriptive statistics were calculated by site, soil horizon, and age class. To test the effect of soil age on enzyme activity, I calculated weighted mean enzyme activities for the organic layer and for the upper 15 cm of mineral soil (for all enzymes except protease). Each horizon rate was weighted by the horizon thickness. Inhomogeneous variances indicated a logarithmic transformation of data was needed before performing the ANOVA. I used the following transformation for all rates:

$$\alpha' = \ln(1+\alpha) \tag{5}$$

where α is the original variate and α' is the transformed variate.

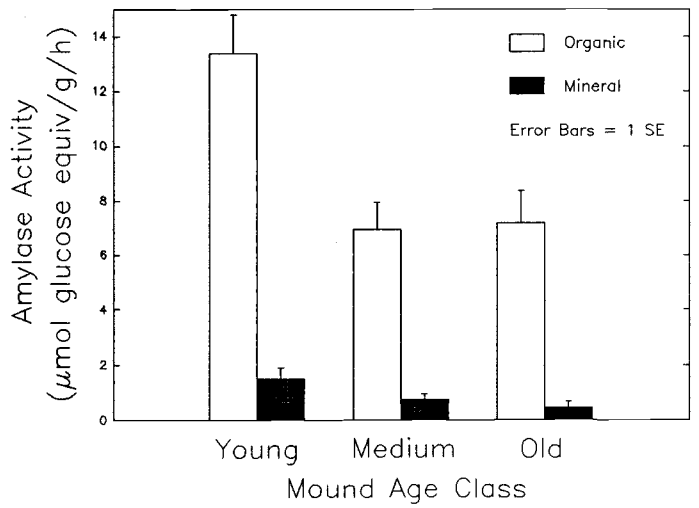

Figure 1. Amylase activity in Heintzleman Ridge soils

Results

Detailed breakdowns of enzyme activity by site, mound age class, and soil horizon may be found in the Appendix. Amylase, cellulase, and xylanase activity decreased with increased soil age; phosphatase, peroxidase, and phenol oxidase activity did not. Amylase activity was measured only at Heintzleman Ridge. Activity dropped dramatically from young to medium-aged soils in both the organic and mineral layers, and then continued to decline in older mineral horizons (Figure 1). Amylase activity increased slightly from medium-aged to old organic horizons. For combined organic and mineral data, the effect of age was highly significant ($F = 9.96$; $df = 2,12$; $p = 0.003$); interactions were not significant.

At Heintzleman Ridge, mean cellulase activity declined with age in both the organic and mineral layers; in both layers at Outer Point, however, slight increases from young to medium age were followed by declining activity in old soils — to levels lower than in the young soils (Figure 2). ANOVA showed a significant age effect in the combined organic and mineral data ($F = 4.20$; $df = 2,24$; $p = 0.027$). Interactions were not significant.

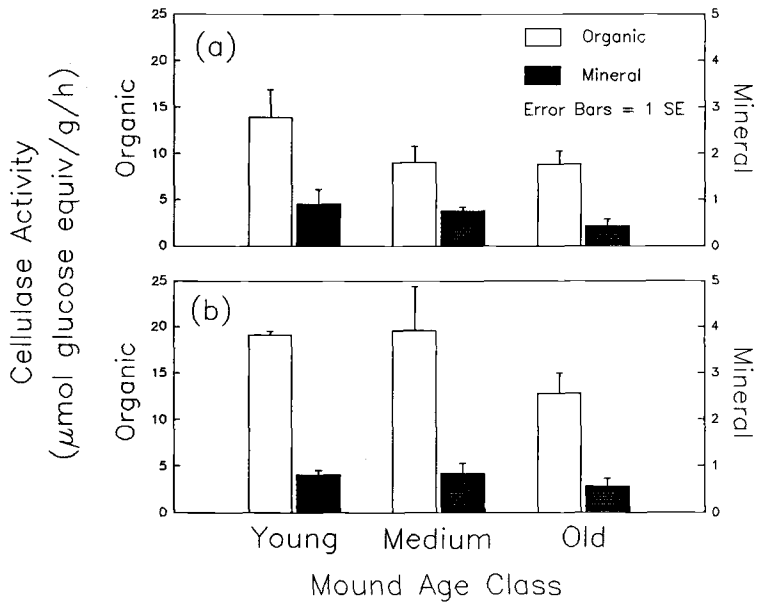

Figure 2. Cellulase activity in Heintzleman Ridge (a) and Outer Point (b) soils. Note that the scales of organic and mineral values differ.

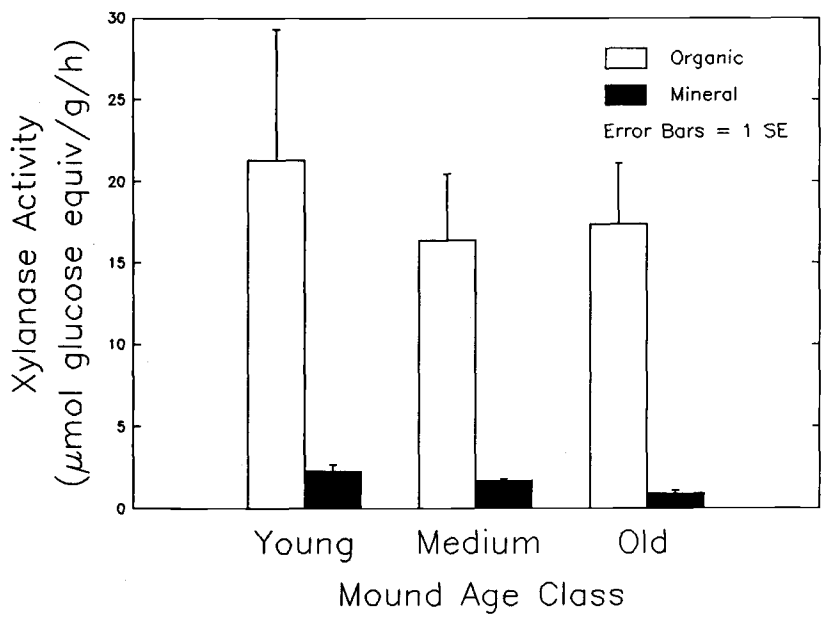

Figure 3. Xylanase activity in Heintzleman Ridge soils

Xylanase activity also was measured only at Heintzleman Ridge. As with amylase, xylanase activity declined from young to medium-aged soils in both the organic and mineral layers; then continued to decline with age in mineral soils, but increased slightly in the organic horizons (Figure 3). The ANOVA showed a significant age effect in mineral horizons ($F = 8.15$; $df = 2,6$; $p = 0.02$), but not in the combined ($F = 0.56$; $df = 2,12$; $p = 0.58$) or organic-only data ($F = 0.02$, $df = 2,6$; $p = 0.98$).

Mean phosphatase activity declined with age in all organic layers and in the mineral soil at Heintzleman Ridge; in the Outer Point mineral soil, phosphatase activity declined slightly from young to medium-aged soils and then increased in older soils (Figure 4). ANOVA using combined data from the organic and mineral samples revealed no significant age effect ($F = 1.43$; $df = 2,24$; $p = 0.26$) and no significant interactions.

Mean peroxidase activity declined with age in the organic layer at both Heintzleman Ridge and Outer Point, but the mineral soils showed general increases in activity with age at both sites (Figure 5). These age trends were not significant ($F = 0.42$; $df = 2,21$; $p = 0.66$) and I detected no significant interactions, despite the apparently different trends by layer.

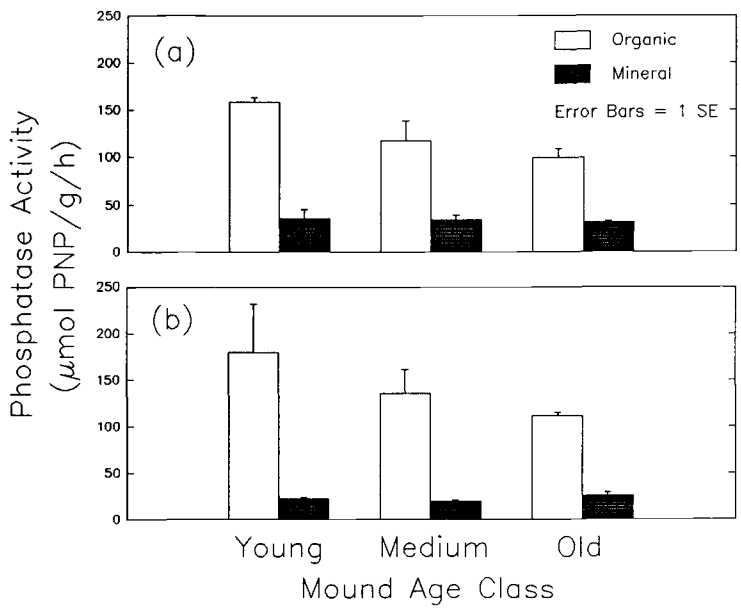

Figure 4. Phosphatase activity in Heintzleman Ridge (a) and Outer Point (b) soils

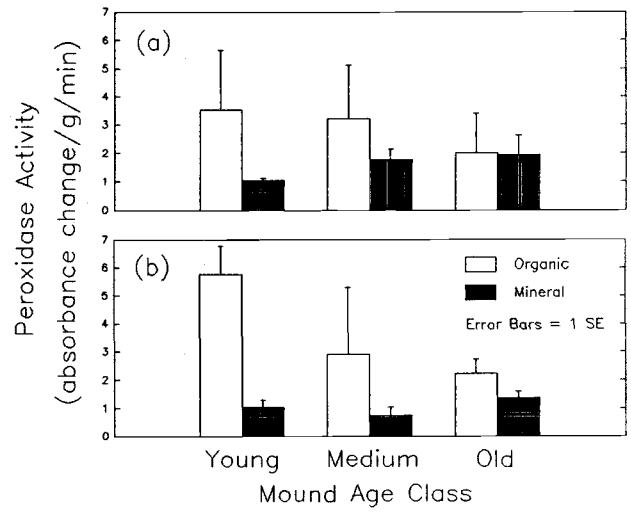

Figure 5. Peroxidase activity in Heintzleman Ridge (a) and Outer Point (b) soils

Phenol oxidase activity was measured only at Outer Point. In the organic layer, mean activity declined with age (Figure 6) in the mineral soil, rates declined from young to medium-aged soils and then increased in old soils to a level slightly greater than in young soils. The ANOVA didn't detect any significant effect of soil age ($F = 0.84$, $df = 2,12$; $p = 0.45$) or any significant interactions.

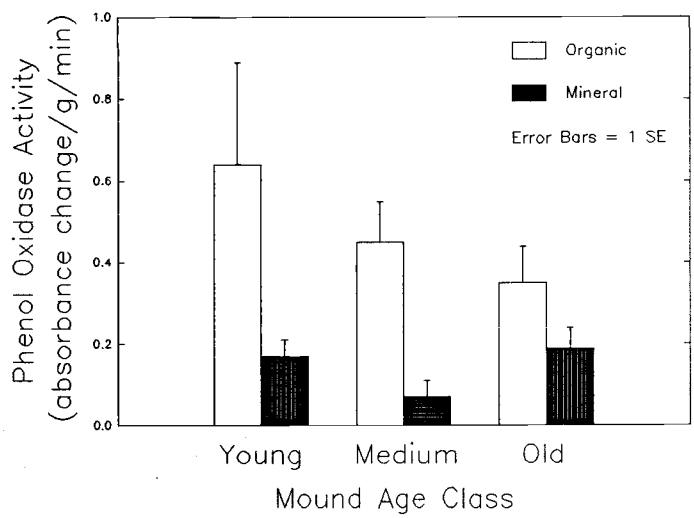

Figure 6. Phenol oxidase activity in Outer Point soils

Discussion

Enzyme activity

Amylase activity was comparable to that found in conifer forests in the PNW. Organic horizon values ranged from 15.2 - 4.0 μmol/g/h, profile means were 7.0 - 13.4. These results are similar to those found by Spalding (1977) in conifer litter collected at several sites in Oregon (4.2 - 23.5, 10.4 mean). Note that he removed all woody and non-foliar material from his litter samples, which may have skewed his results upward. Amylase activity in the upper 15 cm of mineral soil varied from 0.45-1.5; average A horizon rates (4.0) were similar to those found in the upper 5 cm of nonmat mineral soil (3.22) by Caldwell *et al.* (1989, and personal communication). The decreased amylase activity with decreased SOM and increasing depth is consistent with results noted elsewhere (Ladd 1978). Romeiko *et al.* (1968) also found that amylase activity decreased with depth in a sod-podzolic soil in the order: humus > podzolic > illuvial (O > E > Bh).

Cellulase activity in organic horizons was slightly lower (mean 8.8-19.6) than that found by Spalding (1977); his values for litter varied from 12.9-52.9, with a mean of 26.4. My cellulase values for the upper 15 cm of mineral soil varied from 0.43-0.90. These values are lower than those reported by Caldwell *et al.* (1989, and personal communication) — 1.34 in nonmat mineral soil, 3.25 in mat soils — but their values are for the upper 5 cm only. I found cellulase activity within A horizons to vary from 1.8 to 2.1, which compares favorably with the Oregon results.

Xylanase activity in organic horizons was lower than that found by Spalding (1977); he measured rates of 25 to 207 (mean 78) in conifer litter; I found organic horizons averaged 16 to 21. Mineral soil rates were about the same or slightly higher than those of Caldwell *et al.* (1989, and personal communication): 3.04 nonmat, 1.65 and 6.19 in mats versus 0-15-cm rates of 0.9-2.3, A horizon average of 4.9. E and Bh horizons were lower, 1.47 and 1.35, respectively.

I cannot compare the peroxidase and phenol oxidase activities to those found in other studies, because these activities are expressed in units of absorbance change. These rates are useful only for comparative purposes within the scope of this study.

Phosphatase activity within mineral soils was high compared with those found in other studies. The rates in the upper 15 cm of soil (20-35) met or exceeded those found

by Caldwell *et al.* (1989, and personal communication) in the upper 5 cm (22 nonmat, 48-58 mat). Activity within the A horizon was twice that measured in nonmat soils in the Oregon study. The 0-15-cm rate was roughly 20-fold higher than the highest rate found by Frankenberger and Dick (1983) (2.1, recalculated from their data) in uncultivated, 0-15-cm A1 horizons in California.

Soil surface age effects

All three polysaccharidase activities declined with age in both organic and mineral horizons. Amylase activity is clearly declining with age. Activity within horizons (e.g., Oi) on old mounds was much less than in equivalent horizons on young mounds. As soils aged, they were more likely to develop horizons with very low amylase activity, e.g., Oa, E, and Bh horizons. The greatest decline occurred between the young and medium age classes, raising the question of how much higher, if at all, are rates in soils younger than 40 years-old?

Romeiko *et al.* (1968) found that plowing — by mixing and bringing E and B material to the surface — increased mineral soil amylase activity to levels comparable to those of the humus layer. They also found that burial of humus material increased its amylase activity. This phenomenon may be a manmade analogue to the 'plowing' of my sites by uprooting, and is consistent with my finding greater amylase activity in young, more recently-disturbed soils. Although the youngest mounds studied were over 40 years-old, continued collapse of the upturned root system and soil sustains soil disturbance well past the initial uprooting. This may explain the relative longevity of the disturbance effect. The ecological significance of the declining amylase activity is uncertain without a better understanding of the source and role of amylase in these soils (see discussion in correlation section, page 59); it is reasonable to suppose, however, that it indicates a decline in either root or fungal activity and biomass.

The decline of structural polysaccharidase activity (cellulase and xylanase) with soil age probably reflects a concurrent decline in substrate availability. With age, highly-decomposed sapric material comprises more of the organic horizons, reducing the average cellulose and hemicellulose concentration. I have observed an apparent decline in rooting within the mineral soil in older mounds. Because roots are probably the primary source of cellulose and hemicellulose within the mineral soil, it is reasonable to associate their

scarcity with low cellulase and xylanase activity. Cellulase activity is higher in rhizosphere soil than in the general soil, and its seasonal peak varies with plant cover and condition (Kiss *et al.* 1978). By mixing soil and breaking up less-permeable illuvial horizons, uprooting may have promoted greater cellulase activity in young mound soils. Cellulase activity has been observed to increase with improved drainage of wet soils and with plowing (Kiss *et al.* 1978).

Although significant age differences in phosphatase activity were not detected, the generally-declining trend runs counter to some previously published findings. Phosphatase activity has previously been shown to increase with increasing SOM, total N, organic P, and with $NaHCO_3$-soluble organic P; decreased phosphatase activity is associated with increasing orthophosphate concentration and soil depth (Speir and Ross 1978).

Amylase and xylanase activities were measured only at Heintzleman Ridge; phenol oxidase was measured only at Outer Point. The variation with soil age of several other properties changed significantly between sites, so it is possible, even likely, that other patterns of enzyme activity exist.

SOIL NITROGEN

Introduction

Estimates of Nitrogen Availability

Poor N availability frequently limits forest productivity in conifer forests in the Pacific Northwest. Any attempt to understand the effect of soil development on forest productivity must identify changes in plant-available soil N that accompany temporal changes in the soil's chemical and physical character.

The need for a reliable estimate of plant-available soil N has led to the development of many chemical and biological assays. Measurement of mineralizable N (NH_4^+, NO_3^-, and NO_2^-) in the soil solution and on exchange sites underestimates the pool of N available to plants and is subject to wide fluctuations over time (Powers 1980). On the other hand, total soil N includes N in forms that are essentially unavailable to plants. Keeney (1982) recommends the biological index of Waring and Bremner (1964), which entails the incubation of a waterlogged soil sample at 40° C. and measurement of NH_4^+-N mineralized over a period of 7-14 days. The technique is simple and a good predictor of available soil N. Smith *et al.* (1981) compared N mineralization assays on several forest and agricultural soils. Their study included anaerobic and aerobic incubations lasting one and two weeks. For forest soils, they found anaerobic incubations were less variable than aerobic incubations, attributing this to the more uniform conditions with the anaerobic assay.

Mineralizable N and site fertility

Several studies have used the anaerobic incubation as a measure of soil fertility or predictor of fertilizer response. Binkley and Reid (1984) compared N-fertilized Douglas-fir plantations with unfertilized controls and found that N mineralization in the upper 15 cm of soil from fertilized plots was roughly double that on the control plots. Increased N mineralization was associated with higher litter N, increased leaf area, and increased stem growth per unit leaf area. In a study of Australian eucalypt forests, Adams and Attiwill (1986) found the highest anaerobic N mineralization rates in the soils of the most

productive forests. Anaerobic N mineralization appears generally to increase with site NPP (r^2 = 0.42, calculated from data presented by Myrold [1987]).

Geist (1977) found that including a measure of organic N improved a model of orchardgrass N uptake and yield. The N mineralized during anaerobic incubation was a better predictor of plant response than total N, SOM, or N mineralized during aerobic incubation. Shumway and Atkinson (1978) studied the fertilizer response of young, unthinned Douglas-fir in Oregon and Washington and found that N mineralized during anaerobic incubation of samples from the upper 15 cm of soil yielded the best prediction of average tree diameter growth response to N fertilization (r = -0.82). They found also that site index and N mineralization were significantly correlated. Powers (1980) found that N mineralized in a 14-day anaerobic incubation of mineral soil sampled at 18-22-cm correlated well with long-term *in situ* mineralization, and was related to *Pinus ponderosa* L. site index, yield, and foliar N concentration.

In contrast, Radwan and Shumway (1983) didn't find a strong correlation between N mineralization and western hemlock response to N fertilization in western Washington. They concluded that low P availability, not N availability, probably was limiting tree growth. Miller *et al.* (1989) concluded that data from anaerobic N mineralization soil tests add little to the ability to predict Douglas-fir fertilizer response beyond that already afforded by more easily-collected stand data.

Relation of mineralizable N to soil microbial biomass

Myrold (1987) tried to identify the source of N mineralized during the standard anaerobic N mineralization assay. He compared N mineralized from forest soils in the anaerobic incubation with microbial biomass N and C, determined by the chloroform fumigation-incubation method. He also labelled microbial biomass with ^{15}N and measured the atom % ^{15}N released by the two methods. N released by anaerobic incubation was well-correlated with the N flush from chloroform fumigation-incubation, with microbial biomass N, and with microbial biomass C. The isotopic labelling of mineralizable N and N released during chloroform fumigation-incubation were well-correlated. Myrold concluded that mineralizable N released during anaerobic incubation is derived from, and is a measure of, microbial biomass N.

Objectives

My primary objective was to find if soil development affected the amount and distribution of mineralizable N. Although it is not usually done, I included N mineralization in organic horizons after observing extensive rooting there and noting the significant changes in organic horizons with mound age. In addition, I wanted to know the fraction of the total soil N that was mineralizable, the amount of mineralizable N per unit area, and how these variables changed with soil development. Additional data on the amount and distribution within profiles of extractable mineral N would be gathered incidentally. Because anaerobically-mineralizable N is derived primarily from microbial biomass, I sought to test its relation to processes such as soil respiration and decomposition of cellulose and litter, and to soil attributes such as enzyme activity and nutrient concentrations.

Methods

Soil sampling

In 1987, I collected soils for the analysis of mineralizable N and extractable NH_4^+-N and NO_3^--N from Hawk Inlet (August 6), Outer Point (August 27), and Heintzleman Ridge (September 30). At Hawk Inlet and Outer Point, I used a large diameter corer with removable plastic sleeves (7-cm inside diameter × 50-cm length) to sample four mounds in each age class. Four cores were taken at random from each mound. One core was subsampled for the mineralizable N assay and the remaining cores were used to estimate root biomass. The capped sleeves kept the soil cores intact during transport to the lab. At Heintzleman Ridge, subsamples were removed from the soil blocks collected for the soil respiration assays (see respiration methods, page 43, for more details). All soil cores or blocks were refrigerated at 3°C until they were subsampled by horizon for the N mineralization assay. I sieved the fresh soil, discarding the coarse (> 2 mm) fraction, and removed roots > 1 mm in the remaining fine soil. The fine soil was subsampled for gravimetric moisture determination, extraction of NH_4^+ and NO_3^-, and estimation of mineralizable N.

Mineralizable-N assay

I used a slightly-modified version of the biological index of available N recommended by Keeney (1982). I mixed 8.0 g of fresh mineral soil (ca. 5 g oven-dry soil) with 12.5 g of deionized water in a 17×150-mm test tube, which was then stoppered and incubated at 40° C. Because of the low density of forest floor samples, 5.0 g of solids and 12-15 g of water were used; this mixture was incubated in 50-ml screw-top jars. After 7 d, the soil-water mixture was quantitatively transferred to a 125-ml bottle for the extraction of NH_4^+.

Extraction of exchangeable mineral-N

NH_4^+-N and NO_3^--N contents of fresh and incubated soils were determined from soil extracts prepared by the method of Keeney and Nelson (1982). In a 125-ml Nalgene bottle, samples were mixed with KCl extractant in a ratio of 10 ml 2 M KCl:1 g oven-dry soil. The mixture was shaken for 1 h and allowed to settle for 30 min before the supernatant was poured-off and filtered through Whatman No. 42 paper. The filtrate was stored, in capped plastic test tubes, refrigerated or frozen until express-shipped to the OSU Soils Lab for analysis. NO_3^--N was determined by an automated cadmium reduction colorimetric method; NH_4^+-N was determined by an automated salicylate-hypochlorite colorimetric method. Mineralizable-N is the NH_4^+-N content of incubated soil minus the NH_4^+-N content of fresh soil.

Statistical analyses

Descriptive statistics were calculated by site, mound age class, and soil horizon. To test the effect of soil age on N mineralization, for each mound I calculated the weighted mean mineralizable-N for the total organic horizon and for the upper 15 cm of mineral soil. I calculated similar weighted means for the percent of total soil N mineralized and for the amount of N mineralized per unit area ($g\ N \cdot m^{-2}$). Due to inconsistent sampling depths at Hawk Inlet, I chose to eliminate mineral soil values from that site from all tests of age effects. Organic values were retained, however, allowing a two-way ANOVA (site × age) spanning all three sites. A three-way ANOVA (site × layer × age), including data from only Heintzleman Ridge and Outer Point, also was done on weighted means for each variable. Before the ANOVAs, I log-transformed all variates (Eq. (5)) due to apparently

non-homogeneous variance between and within layers. Fisher's protected LSD test (p = 0.05) was used to test age differences between means within site × layer groups.

Results

Extractable ammonium and nitrate

Ammonium-N extracted from soils varied widely (Table 4), but a few generalizations may be made. Organic layers consistently contained more extractable NH_4^+-N than did mineral soils within the same site and age class. Among organic layers, Oe layers contained the most NH_4^+-N. Very few samples of decayed wood were analyzed, and their NH_4^+-N content was highly variable. Among mineral horizons, Bh NH_4^+-N contents exceeded those of E horizons, and occasionally those of A horizons. Extractable NO_3^--N was below detection limits at both Heintzleman Ridge and Outer Point. At Hawk Inlet, NO_3^--N in mineral horizons frequently exceeded that extracted from organic horizons, in contrast to the results for extractable NH_4^+-N (Table 3).

Table 3. Extractable soil nitrate-N by age and layer, Hawk Inlet only

	Mound Age Class		
Layer	Young	Medium	Old
		mg NO_3^--N· kg $soil^{-1}$	
Oi	0.05 ± 0.05 (4)†	0.16 ± 0.06 (4)	0.14 ± 0.14 (3)
Oe	0.07 ± 0.07 (2)	0.15 ± 0.09 (4)	0.18 ± 0.09 (3)
Oa	--	--	0.18 ± 0.18 (2)
Wood	--	--	0.63 (1)
A	0.08 ± 0.05 (4)	0.22 ± 0.22 (2)	--
E	--	0.10 (1)	0.71 ± 0.66 (3)
Bh	--	1.6 ± 1.6 (2)	1.1 ± 1.1 (3)
Bs	--	0.00 (1)	1.2 ± 1.1 (3)

† Mean ± standard error (number of observations)

Table 4. Extractable ammonium-N by site, age, and layer

Layer	Mound Age Class		
	Young	Medium	Old
		mg NH_4^+-N · kg $soil^{-1}$	
		Heintzleman Ridge	
Oi	23.4 ± 4.3 (3)†	30.2 ± 12 (3)	17.4 ± 7.2 (3)
Oe	38.8 ± 22 (2)	19.4 ± 4.0 (3)	26.7 ± 17 (3)
Oa	--	7.33 (1)	29.0 ± 14 (3)
Wood	--	--	44.6 (1)
A	15.2 ± 8.3 (3)	4.02 ± 0.40 (2)	--
E	--	4.43 (1)	6.12 ± 0.57 (3)
Bh	--	7.51 (1)	12.9 ± 0.74 (3)
Bs	--	--	8.20 ± 3.5 (2)
BC1	6.59 ± 1.3 (3)	3.24 ± 0.46 (3)	--
		Hawk Inlet	
Oi	7.50 ± 2.7 (4)	10.5 ± 3.7 (4)	11.2 ± 3.5 (3)
Oe	9.77 ± 0.68 (2)	14.6 ± 2.8 (4)	11.6 ± 5.1 (3)
Oa	--	--	2.72 ± 2.7 (2)
Wood	--	--	2.85 (1)
A	1.52 ± 1.0 (4)	2.96 ± 1.8 (2)	--
E	--	2.15 (1)	2.93 ± 2.0 (3)
Bh	--	9.00 ± 8.0 (2)	4.15 ± 2.3 (3)
Bs	--	0.00 (1)	6.52 ± 1.8 (3)
		Outer Point	
Oi	6.34 ± 3.1 (4)	11.0 ± 4.5 (4)	10.2 ± 2.5 (3)
Oe	7.80 (1)	8.02 ± 2.6 (4)	11.6 ± 4.0 (4)
Oa	--	--	4.22 ± 1.0 (3)
Wood	--	--	25.3 (1)
A	0.45 ± 0.45 (3)	9.34 ± 8.5 (2)	--
E	--	--	4.57 ± 2.6 (3)
Bh	--	1.83 ± 0.04 (2)	4.86 ± 1.9 (4)
Bs	--	0.00 (1)	5.24 ± 1.3 (3)
BC1	1.62 ± 1.0 (3)	4.59 (1)	13.2 (1)

† Mean ± standard error (number of observations)

Mineralizable N

Except for the Oa horizons at Hawk Inlet, organic horizons contained far more mineralizable-N than any of the mineral horizons examined (Table 27, Appendix). Within the forest floor, N mineralization generally declines in the order Oi > Oe > Oa. N mineralization from decayed wood is variable, but usually similar to that of sapric (Oa) material.

Few generalizations about N mineralization from mineral horizons apply to all sites. Rates of N mineralization within A horizons are comparable at all sites, but rates within E and Bh horizons are much higher at Hawk Inlet and Outer Point than at Heintzleman Ridge — sometimes exceeding A horizon rates at those sites.

Soil surface age effects

Table 5 contains the mean N mineralization rates (per unit soil mass) for the forest floor and upper mineral soil. Soil age did not significantly affect N mineralization within organic layers from all three sites ($df = 2,23$; $F = 0.81$; $p = 0.46$). There was no significant site × age interaction in spite of an apparent site difference in trend (Table 5). I then tested the age effect with organic and mineral values from Heintzleman Ridge and Outer Point and detected a significant interaction of site and age ($df = 2,26$; $F = 4.81$; $p = 0.02$), requiring reanalysis by site. Age significantly affected rates at Heintzleman Ridge ($df = 2,11$; $F = 6.09$; $p = 0.02$) but not at Outer Point ($df = 2,15$; $F = 0.84$; $p = 0.45$). At Heintzleman Ridge, N-mineralization within the organic layers was not significantly different between ages, but N mineralization within the young mineral soil was significantly greater than in the medium and old soils, which did not differ significantly (Table 5).

Figure 7 shows the mean percent of total soil N mineralized from forest floor and upper mineral soils. The proportional mineralization of N from organic substrates was 1.4-3.1 times that from mineral substrates. The disparity between organic and mineral values was greater in medium- and old-aged soils (2.4-3.1 times) than it was in young soils (1.4-1.9 times).

Table 5. N mineralized (mg N· kg^{-1} soil) during 7-day anaerobic incubation of organic layers (O) and upper mineral soil (0-15 cm, M)

	Mound Age Class		
Layer	Young	Medium	Old
		Heintzleman Ridge	
O	271 ± 38 $(3)_a$†	204 ± 17 $(3)_a$	202 ± 4.1 $(3)_a$
M	31.2 ± 6.4 $(3)_a$	15.5 ± 2.5 $(3)_b$	17.6 ± 5.3 $(2)_b$
		Hawk Inlet	
O	189 ± 41 (4)	214 ± 45 (4)	147 ± 11 (3)
		Outer Point	
O	152 ± 8.1 (4)	245 ± 35 (4)	204 ± 25 (4)
M	30.3 ± 11 (2)	28.4 ± 6.9 (3)	34.5 ± 4.9 (4)

† Mean ± standard error (number of observations). Where the F-test detected a significant age effect, means within a single line sharing a common subscript were not significantly different.

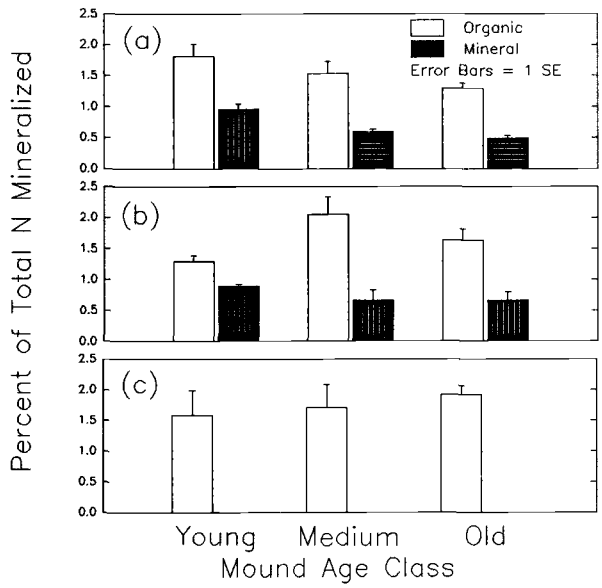

Figure 7. Percent of total soil N mineralized during 7-day anaerobic incubation of soils from Heintzleman Ridge (a), Outer Point (b), and Hawk Inlet (c)

A test of soil age effects on the percent of soil N mineralized from organic layers from all three sites showed no significant effect (df = 2,22; F = 0.40; p = 0.67). Although the pattern of mineralization appeared to differ from site to site (Figure 7), no significant site × age interaction was detected. A second ANOVA, using organic and mineral data from both Heintzleman Ridge and Outer Point, revealed strong site × age class (df = 2,26; F = 3.12; p = 0.06) and layer × age class (df = 2,26; F = 3.16; p = 0.06) interactions, so I reran the ANOVA by site. At Heintzleman Ridge, the percent of soil N mineralized declined very significantly with soil age (df = 2,11; F = 9.38; p = 0.004) and the trend was similar in organic and mineral layers (Figure 7). At Outer Point conflicting trends by layer — apparent in a strong but not significant (p = 0.08) layer × age interaction — yielded no significant age effect. Rerunning the ANOVA by layer showed no significant age effect in either the organic (df = 2,9; F = 3.41; p = 0.08) or the mineral (df = 2,6; F = 0.69; p = 0.54) layers.

Figure 8 shows the mean N mineralized per unit area from forest floor and upper mineral soils. Note that in young soils, the mineral soil from 0-15 cm mineralized more N per unit area than did the forest floor material, but the reverse is true in medium-aged and old soils, which have greater forest floor accumulations.

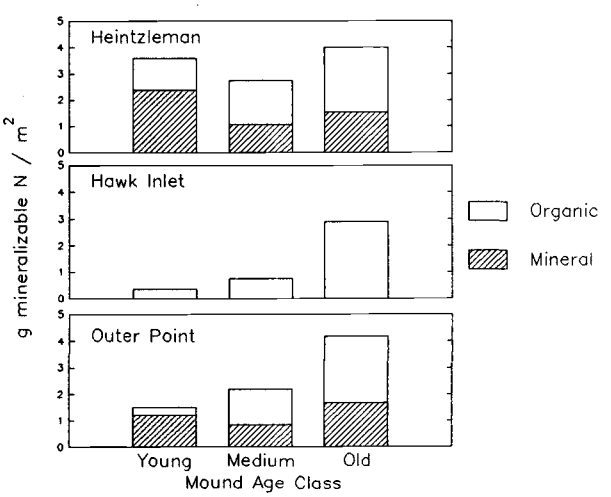

Figure 8. Mineralizable N per unit area

The amount of organic layer N mineralized per unit area increased very significantly with soil age at all sites (df = 2,22; F = 26.26; p = 0.0001). The ANOVA of combined organic and mineral data for Heintzleman Ridge and Outer Point showed that age effect was significant (df = 2,26; F = 6.43; p = 0.005), but so was the layer × age class interaction (df = 2,26; F = 7.80; p = 0.002). Analysis of organic layer values revealed a very significant increase with age (df = 2,15; F = 12.59; p = 0.0006), which merely confirmed results obtained earlier by analyzing data from all three sites. Analysis of mineral layer values showed a strong, but not significant, soil age effect (df = 2,11; F = 2.95; p = 0.09), with mineralization decreasing from young to medium-aged soils and then increasing again in the old soils. This pattern holds at both Heintzleman Ridge and Outer Point.

Discussion

Mineralizable N

Anaerobically-mineralizable N within litter or forest floor is not measured typically, so there are few comparative data available. Binkley (1984) measured mineralizable N in combined F and H layers (roughly comparable to Oe and Oa material) sampled in conifer forests on Vancouver Island and found 400 to 800 mg NH_4^+-N · kg^{-1} soil. These rates are 2-4 times greater than comparable rates in this study. His lowest numbers are from a low-elevation red-cedar/Sitka spruce stand.

The observed decline of mineralizable N with the transition from fibric to sapric organic material is reasonable. Young, somewhat undecomposed fibric litter should support a large microbial community, but sapric organic matter has undergone extensive degradation, leaving only the most highly decay-resistant materials. Microbial populations within sapric materials are probably held at low levels by C limitation; their low biomass is reflected in low mineralizable N values.

Mineralizable N measured in the upper 15 cm of mineral soil (15 - 34 mg NH_4^+-N · kg^{-1} soil) was comparable to values reported for conifer forest soils in the PNW (Geist 1977, Shumway and Atkinson 1978, Smith *et al.* 1981, McNabb *et al.* 1986, Myrold 1987). Shumway and Atkinson (1978) found when mineralizable N was < 25 mg N · kg^{-1}, Douglas-fir stands responded very well to N fertilization and that 25-50 mg N · kg^{-1} yielded

a moderate response. One could conclude, based on data from mineral soil alone, that the S.E. Alaskan soils were moderately-to-very N-deficient by Douglas-fir region standards, but this ignores the contribution of forest floor material, which may make a somewhat greater contribution to the plant-available N pool in southeast Alaskan forests.

Soil surface age effects

With increased soil C storage are associated accumulations of soil nutrient elements, particularly N. If the relative availability of soil N decreases over time, the percentage of the total soil N mineralized should decline with soil age, but mineralizable N and N mineralized per unit area could decrease, remain constant, or increase at a slower rate than that expected, based on increases in soil N capital. There was some evidence that N availability declined.

The lack of any consistent trend in the percentage of total N mineralized from organic layers appears to support the null hypothesis that N availability is not declining. Still, two other trends suggest N availability is declining. Mineral soils at both Heintzleman Ridge and Outer Point consistently mineralized less of their total N with age and the ratio of the percentage of total N mineralized in organic layers to that in mineral layers increases with age (Figure 7). I interpret the lower percentage of total N mineralized as an indicator that more of the mineral soil N is tied up in resistant, humified organic materials, whereas organic layer N is more likely to be contained in microbial biomass or more-readily degraded plant litter. The increasing gap is largely due to decreased mineralization in the mineral soil, not to increases within the organic layers. It therefore appears that as soils age, N is found increasingly in forms resistant to mineralization.

The only significant change with soil age of anaerobically-mineralized N was a decline at Heintzleman Ridge, suggesting that N availability declined more quickly than soil N could increase. This trend was not supported by the nonsignificant trends at Hawk Inlet and Outer Point.

The patterns of mineralizable N per unit area resembled those of respiration per unit area (compare Figure 8 to Figure 11, page 48); this is consistent with Myrold's (1987) suggestion that the source of mineralizable N is the microbial biomass. Even though the mineralizable N per unit area increased significantly with soil age, the decline in the

proportion of N mineralized leads me to conclude that older soils have reached a point of diminishing returns, beyond which N is increasingly immobilized in poorly-available forms. This is likely to lead to an eventual absolute decline in plant-available N.

SOIL RESPIRATION

Introduction

I hypothesized that soil organic matter (SOM) in older soils, illuvial horizons, and sapric organic horizons would be more recalcitrant than that in young, A, and Oi soil horizons. I proposed respiration expressed per unit of SOM or total soil C as a measure of recalcitrance or resistance to decomposition. Nearly all the total soil C should have been organic C, because acidic, highly leached soils such as these should contain little inorganic C and the rarity of wildfire should make charcoal scarce.

Van Cleve *et al.* (1979) tested several laboratory methods of respirometry and found that a flow-through system employing an infrared gas analyzer (IRGA) for CO_2 measurement gave the highest respiration estimates and the lowest minimum sensitivity, so I chose this as my respirometry method. I did not remove roots or soil fauna from respiration samples. It may have been feasible to remove larger roots from mineral soil samples, but removal of very fine roots and mycorrhizal hyphae would have been impossible, and one is always faced with the question: Where does the root stop? Litter layer samples would have been impossible to free of roots and microfauna without excessive manipulation that would have introduced artifacts of its own. By removing nothing, I reasoned that I could estimate the total soil biological activity. Macfadyen (1963) stated that roots contribute up to 50% of forest soil CO_2 production.

I was not over-concerned with accurately estimating absolute respiration rates; I wanted an unbiased measure of relative respiratory activity to estimate the effects of soil development. Estimating actual *in situ* rates is best done from field measurements with systems requiring least manipulation of the soil.

Methods

Soil sampling

I collected soil samples for respiration assays at Hawk Inlet on September 25, 1987, at Heintzleman Ridge on September 30, 1987, and at Outer Point on September 27, October 6, and October 12, 1988. In each age class, four mounds were sampled at Hawk

Inlet and Heintzleman Ridge, three mounds at Outer Point. From each mound sampled at Hawk Inlet and Heintzleman Ridge I cut soil blocks, roughly 25-cm on each side, wrapped them in plastic, and transported them intact to the lab. At Outer Point, soil samples were collected from each horizon in freshly-exposed profiles. This sampling method disrupted the soils more than the block method, but I attempted to remove intact peds as much as possible. I also measured the enzyme activity of this sample set. All samples were stored at 3°C until analyzed.

Respirometry apparatus

The soil CO_2 evolution rates were measured in the laboratory with an apparatus similar to one described by Anderson (1982). CO_2-free air was drawn through a temperature-controlled sample chamber and the CO_2 evolution was calculated from the CO_2 content of air leaving the chamber, as measured with an infrared gas analyzer (IRGA).

My apparatus supported five sample streams. Air was drawn into the system at 25-30 $ml \cdot s^{-1}$ by either a vacuum pump (during preaeration) or by the IRGA pump (during CO_2 analysis), both located downstream from the sample chambers.
Air entering the apparatus first passed through CO_2 scrubbers, 2.5×30-cm tubes packed with indicating granulated soda lime. The air was then cooled as it flowed through 8 m of copper tubing submerged in water kept at 10°C. Finally, the air was humidified by passing through an airstone submerged in a stoppered 250-ml flask partly-filled with CO_2-free (boiled) distilled water.

Sample chambers constructed from 2-in. PVC pipe were plugged at each end with rubber stoppers fitted with glass tubes connected to the air lines, and plastic foam filter disks confined the soil samples within the chamber. Each chamber had a thermistor access hole drilled at its midpoint. Sample chambers were cooled to 10°C within an incubator (1987 measurements) or by submersion in a water bath (1988 measurements).

Thermistors within the sample chambers measured temperatures at the center of each soil sample. The thermistors were inserted through rubber stoppers to ensure a gas-tight seal with the chamber wall. In 1987 I used 5 calibrated LI-COR 1000-15 Soil Temperature Sensors (LI-COR, Inc., Lincoln, NE); temperatures were recorded automatically by an LI-1000 datalogger. In 1988 I used 5 YSI-418 penetration thermistor probes (Yellow Springs Instruments), read manually with an analog YSI Model 46 TUC Telether-

mometer. Thermistors were calibrated with a VWR ASTM mercury-in-glass reference thermometer.

The IRGA used was an LI-6200 Portable Photosynthesis System equipped with an LI-6250 CO_2 Analyzer. I calibrated the IRGA with either a LI-COR 6000-01 gas calibration cylinder and 99.99% CO_2 (Scott Specialty Gases) or with prepared standard gas mixtures (Scott Specialty Gases). I measured barometric pressure with a digital barometer.

Respiration measurement

At the time of analysis, the soil blocks were unwrapped and subsampled by horizon. I removed all green leaves and stems from Oi samples, but did not remove roots from any samples. Samples were packed uniformly into the center of the sample chambers, taking care to eliminate channels that would allow the airstream to bypass the sample. Each chamber contained 5-15 g (dry mass) of organic or 10-30 g of mineral material; this did not fill the chambers, so I used foam plugs to prevent the samples from shifting.

Filled chambers were connected to the respirometry system and preaerated for 40 min. During preaeration, CO_2-free air flowed through the chamber, stripping accumulated CO_2 from the sample and warming the soil to 10°C. Preliminary tests showed that 40 min. of preaeration was sufficient to achieve stable CO_2 evolution rates. At 2 min before the CO_2 measurement, I switched the sample stream to the IRGA. During the 5 minute measurement period the IRGA sampled CO_2 ppm and gas flow once per second and then averaged and stored these values once per minute. Temperatures were recorded once per minute.

After each run of 5 samples, the material was removed from the chamber and its dry mass was determined after drying at 105°C for 24 h. Dried samples were sieved and masses were obtained for the fine (< 2 mm) and coarse (> 2 mm) fractions. The SOM content of the fine fraction was determined from mass lost on ignition at 500°C for 6 h. Soil C was determined by dry combustion on a separate set of soil samples taken from the same mounds.

Data reduction and analysis

Respiration rates were calculated and expressed as μg of CO_2 produced hourly per g of fine soil (< 2 mm), or per g of SOM or C in the fine soil fraction. Because the chamber temperatures were not always exactly 10°C, I standardized the observed rates with Eq. (6), assuming a Q_{10} of 2.

$$R_{t_0} = \frac{R_{t_1}}{e^{k(t_1 - t_0)}} \tag{6}$$

R_{t0} is the standardized respiration rate, R_{t1} is the observed respiration rate, k = 0.06931, t_0 is the standardized temperature (10°C), and t_1 is the actual sample temperature.

Descriptive statistics were calculated by horizon for each site and mound age class. To test the effect of soil age on soil respiration, I first calculated mean respiration rates for the organic layer and mineral layer (0-15 cm) of each mound. I did this for respiration on dry soil, SOM, and soil C basis. The treatment variances did not appear equal, so before testing the age effect with a three-way (site × layer × age) ANOVA, I transformed individual variates with Eq. (5). Where the age effect was significant, rate differences between ages were tested with Fisher's protected LSD test (p = 0.05).

Results

Table 28 (Appendix) contains CO_2 evolution rates per unit soil mass, broken down by site, soil layer, and mound age class; Table 29 (Appendix) contains rates per unit SOM. The BC1 layers are not comparable between age classes — they are layers of soil with little or no visible soil development; in young mounds they occur below the A horizon; in older mounds the BC1 was typically found below the Bh or Bs horizon. Comparisons between Outer Point, Heintzleman Ridge, and Hawk Inlet should be made with caution, because the time and method of sample collection at Outer Point differed from the latter two, although the rates appeared similar.

Respiration per unit soil mass declined with depth in young soils and in most medium-aged soils, but in the oldest soils, respiration within the Bh horizons was always

greater than in the overlying E horizon (Table 28). Respiration of the A horizon was similar at all sites, but respiration of the Bh at Heintzleman Ridge was only half that measured at Hawk Inlet and Outer Point. I also observed that E horizon respiration was much lower than that of the A horizon at Heintzleman Ridge and Outer Point, but the difference was less pronounced at Hawk Inlet. As expected, no respiration rate (soil basis) measured within the mineral horizons equalled or exceeded the respiration of organic samples.

Respiration per unit of SOM, which can be interpreted as a measure of the relative availability of C within SOM, was lower in some Oa horizons and pockets of decayed wood than in mineral soil. In young soils, respiration per SOM declined with depth, but in medium-aged and old soils, respiration sometimes increased below the Bs horizon. Usually, Bh and Bs horizons had the lowest respiration per unit SOM.

Soil surface age effects

Figure 9 and Figure 10 show the mean respiration rates (soil and SOM basis, respectively) for organic and mineral (0-15 cm) layers, by site. The ANOVA of rates based on soil revealed a nearly significant age effect (df: 2,41; $F = 2.70$; $p = 0.08$), but a strong site × age class interaction (df: 4,41; $F = 2.50$; $p = 0.06$) demanded a reanalysis by site. I found that respiration declined significantly with age only at Heintzleman Ridge (df: 2,13; $F = 14.25$; $p = 0.0005$). I observed various trends at Hawk Inlet and Outer Point, but age differences were not significant.

Respiration per unit SOM was significantly affected by soil age (df: 2,41; $F = 5.88$; $p = 0.006$; Figure 10). Site × age class and layer × age class interactions were not significant. Within organic horizons, respiration per unit SOM generally declined with age, as it did in the mineral soil at Heintzleman Ridge. At Hawk Inlet and Outer Point, respiration per SOM peaks in medium-aged soils and then declines with soil age, although this effect was significant only at Outer Point.

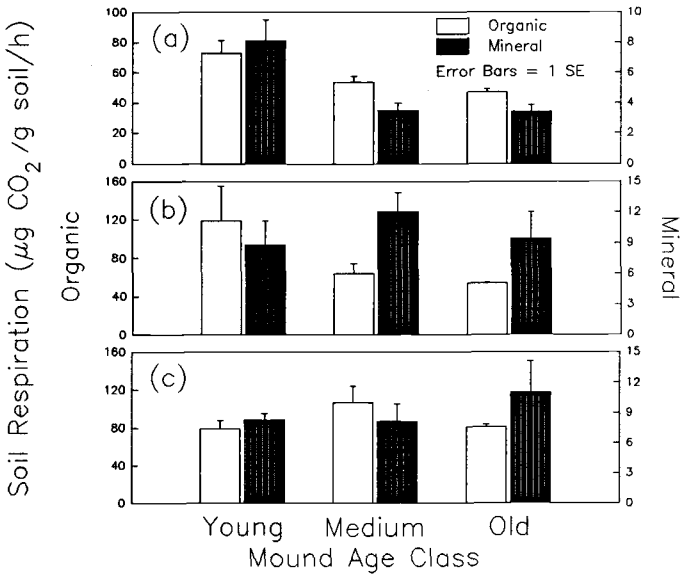

Figure 9. Soil respiration per unit of whole soil (< 2 mm) in Heintzleman Ridge (a), Outer Point (b), and Hawk Inlet (c) soils. Note that the scales of organic and mineral values differ.

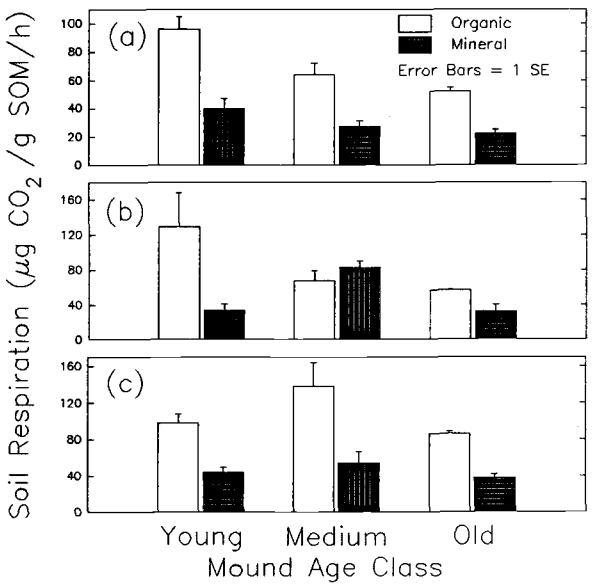

Figure 10. Soil respiration per unit SOM in Heintzleman Ridge (a), Outer Point (b), and Hawk Inlet (c) soils.

Figure 11 shows the respiration rates per unit area (RPA). Organic horizon RPA contributed 29-54% of the total RPA in young mounds, but this share increased to 61-73% in older mounds. The mineral soil RPA declined slightly with age at Heintzleman Ridge and Outer Point, but not at Hawk Inlet. The slight reductions in mineral soil RPA were more than offset by increased organic layer RPA: total (organic + mineral). RPA increased with age at all sites, but most dramatically at Hawk Inlet.

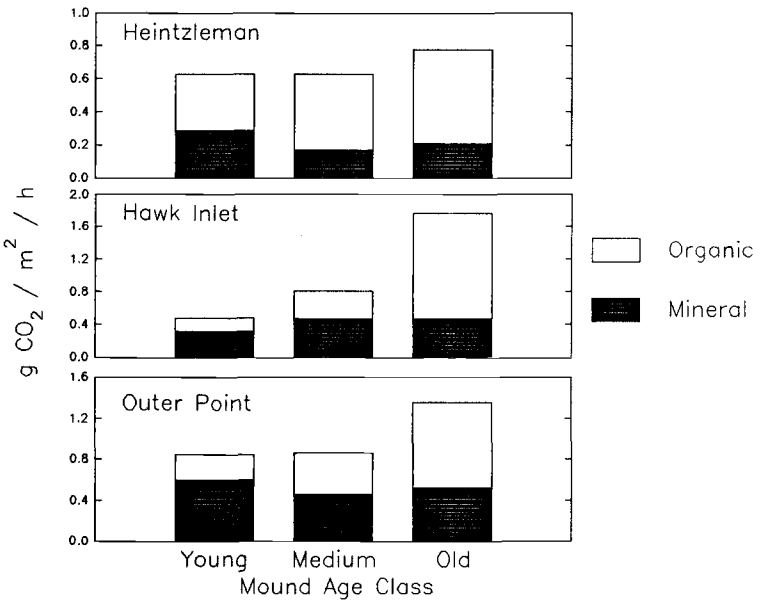

Figure 11. Contributions of forest floor and mineral soil (upper 15 cm) to total soil respiration per unit area: variation with site and soil surface age

Discussion

Soil respiration rates

The soil respiration rates probably represent maximal rates, due to the large sample-airstream CO_2 gradient — *in situ* soil is exposed to much lower CO_2 gradient, leading to slower removal. Relative comparisons are still valid; there is no evidence of a systematic bias in the rates. Comparisons between studies of soil respiration are made difficult by the lack of standardization of factors known to influence rates, including incubation temperature, sample moisture content, sample-headspace CO_2 gradient, and sample preparation and storage.

Organic layer respiration was similar to rates measured in conifer litter in the PNW, but low in comparison with rates measured in hardwood litter in Alaska and Alberta. Respiration rates of mineral soil were low compared with some forest soils, but high compared with agricultural soils.

I found respiration rates for the Oi and Oe horizons to be at the low end of the range of rates reported by Coxson and Parkinson (1987) for aspen litter and soil in SW Alberta; the Oa and A horizon rates were roughly one-third of their values. Van Cleve *et al.* (1979) reported rates for combined O1, O21, and O22 horizon (Oi, Oe, and Oa) samples from a paper birch (*Betula papyfera*) stand in Alaska that were 2 to 5 times greater than rates that I observed. Both studies used incubation temperatures, sample moisture, and respirometry apparatus similar to mine, with the exception that their aeration stream contained ambient concentrations of CO_2.

Caldwell *et al.* (1989, and personal communication) found that mineral soils in Douglas-fir stands in Oregon produced 6 $\mu g\ CO_2 \cdot g^{-1} \cdot h^{-1}$, close to values I observed in E horizons and roughly half those I observed in A horizons. Their highest rate, measured in soil from an ectomycorrhizal mat, was nearly three times the rate I observed in A horizons. Their rates were measured in a closed system at unspecified field temperatures.

All composited organic layer respiration values were within the range reported by Spalding (1977) for conifer litter, following transformation of his values. Transformation, assuming $Q_{10} = 2$, was necessary because he incubated his samples at 23°C. His transformed mean (79 $\mu g\ CO_2 \cdot g^{-1} \cdot h^{-1}$) was just slightly higher than that of the organic layer

of young mounds at Heintzleman Ridge and Hawk Inlet young organic — about 2/3 of the Outer Point rate.

Frankenberger and Dick (1983) measured respiration in uncultivated A1 horizons in California. They did not specify the incubation temperature, but if it was 20° C., their rates would vary between 2.2 and 9.5 $CO_2 \cdot g^{-1} \cdot h^{-1}$, roughly 2/3 of the rate I observed in the upper 0-15 cm of mineral soil.

Soil surface age effects

As the mound soils develop, carbon accumulates in the forest floor and mineral soil. With increased C storage comes increased soil respiration per unit area, primarily due to dramatically increased respiration within the accumulating forest floor. The data for respiration per unit of SOM suggested that respiration was not keeping pace with C buildup; C in old organic and mineral horizons appeared to be less efficiently converted to CO_2. The Oa and Bh horizons common in older soils generally had very low rates of respiration in proportion to the amount of C contained within them. Sapric material is the product of extensive decomposition and probably comprises highly-humified and decay-resistant organic residues. Illuvial horizons contain humic and fulvic acids that are inherently resistant to decomposition, besides being complexed with Al and Fe, making them even more recalcitrant. This decline is not attributable solely to the formation of new types of horizons: respiration per unit SOM declined with age within Oi, Oe, Oa, E, Bh, and Bs horizons, when averaged over all sites (Table 29).

The results for respiration per unit soil were more equivocal, but note that in only one instance — the mineral soil at Outer Point — was the average respiration per unit soil highest in the oldest age class, despite the oldest soils having the highest C contents.

Of the three perspectives on soil respiration — area, soil, and SOM bases — I believe the trend of soil respiration per unit SOM to be the most instructive, because it clearly shows that C turnover is slowing with increased soil age, a trend that will lead to increased nutrient immobilization in SOM.

CORRELATIONS AMONG SOIL CHEMICAL AND BIOLOGICAL PROPERTIES

Methods

Soil Chemistry

Soil samples, including forest floor and mineral soil, were removed from within a 30-cm steel ring (0.0707 m^2) that had been driven into the soil. All soil within the ring was removed, by visible horizon, until visibly unaltered BC material was encountered. Soils were air-dried for storage before analysis.

Total N and P were determined by the Kjeldahl method, SOM by mass loss on ignition at 900° C., total C by dry combustion, and pH was determined in water (1:1 soil:water ratio). A series of extraction procedures was used to remove selectively various soil fractions. A sodium pyrophosphate extraction (0.1 M $Na_4P_2O_7$) was intended to remove Fe and Al complexed with organic compounds, e.g., fulvic acids (McKeague *et al.* 1971, Wada 1977). A separate set of sequential extractions also was done on most soils. A single soil sample (unground soil, ≤ 2 mm fraction) was subjected to extraction by sodium bicarbonate (BIC), oxalate (OX), citrate-dithionate (CD), and finally hydrochloric acid (HCl) solutions.

The bicarbonate extraction (Olsen and Sommers 1982) used 0.5 M $NaHCO_3$ at pH 8.5 for 16 h, and yielded a dark solution. The P contained in this is mostly organic P. This fraction is considered a measure of readily-available organic P. The subsequent oxalate extraction (0.2 M, pH 3.0, 4 h duration), dissolved organic-P, allophane, imogolite, and noncrystalline hydrous oxides of Fe and Al, plus organically-complexed Fe and Al (Wada 1977), yielding a clear extract. A dithionate-citrate extraction followed (pH 7.0), dissolving crystalline Fe oxides and hydroxides (Olson and Ellis 1982). Sodium dithionate ($Na_2S_2O_4$) reduces Fe and sodium citrate ($Na_3C_6H_5O_7$) complexes Fe and buffers the solution. This removes non-silicate, total free Fe (organically-bound, amorphous hydrous oxides, and crystalline forms), i.e., it dissolves any non-silicate Fe remaining after the other extracts and some additional SOM. The HCl (0.1 M) extraction was intended primarily as a check or cleanup; it removes some easily-weathered primary minerals. All extraction procedures were standard methods used in soil survey and classification. Birkeland (1984) noted that these extracts are not as specific for Al fractions as they are for Fe. The

extract concentrations of Si, Al, Fe, P, Ca, Mg, Mn, and K were determined by inductively coupled plasma optical emission spectrometry (ICP-OES). The P values determined by ICP-OES may vary ± 10%.

Data Analysis

I calculated Pearson coefficients of linear correlation among all enzymes (except protease), respiration rates (soil and SOM basis), and N mineralization. Data for organic and mineral samples were analyzed separately. In the same manner, I calculated linear correlation coefficients for the above variables with the following soil properties: total N, extractable NH_4^+-N, extractable NO_3^--N, C:N ratio, SOM, total C, total P, bicarbonate-extractable P, oxalate-extractable P, citrate-dithionate-extractable P, the sum of extractable P, C:P ratio, N:P ratio, pH, and hydrogen ion concentration.

As noted earlier, in determining soil enzymes, respiration, and N mineralization, I sampled the forest floor by horizon (Oi, Oe, etc.) if horizons were visible. Most soil chemical analyses were done on the bulk forest floor, yielding fewer samples, lower resolution, and fewer significant correlations than in the corresponding mineral horizons.

Table 6 Linear correlation matrix for soil enzyme activities, soil respiration, and mineralizable-N, measured within organic horizons

	Cellulase	Xylanase	Peroxidase	Ph. oxidase	Phosphatase	Resp/soil	Resp/SOM	N-mineralized
Amylase	0.77 (26)†	0.75 (26)	0.43 (26)*	--	0.71 (26)	0.69 (21)	0.72 (21)	0.49 (22)*
Cellulase		0.93 (26)	0.66 (49)	0.60 (24)	0.74 (50)	0.57 (45)	0.53 (45)	NS
Xylanase			0.67 (26)	--	0.65 (26)	0.67 (21)	0.67 (21)	NS
Peroxidase				0.65 (23)	0.45 (49)	0.46 (44)	0.45 (44)	NS
Phenol oxidase					0.69 (24)	0.56 (24)	0.52 (24)	NS
Phosphatase						0.76 (45)	0.72 (45)	0.38 (42)
Respiration (per unit soil)							0.96 (73)	0.40 (62)
Respiration (per unit SOM)								0.34 (62)

† Pearson correlation coefficient (r) and (number of observations). All coefficients are significant at the 1% level or better, except those marked * (5%) or NS (not significant). Ph oxid: phenol oxidase, Resp/soil: respiration per unit soil, Resp/SOM: respiration per unit SOM.

Table 7. Linear correlation matrix for soil enzyme activities, soil respiration, and mineralizable-N, measured within mineral horizons

	Cellulase	Xylanase	Peroxidase	Ph. oxidase	Phosphatase	Resp/soil	Resp/SOM	N-mineralized
Amylase	0.75 (34)†	0.84 (34)	NS	--	0.59 (34)	0.95 (21)	0.61 (21)	0.56 (21)
Cellulase		0.92 (34)	NS	NS	0.63 (66)	0.36 (53)	NS	0.40 (39)
Xylanase			NS	--	0.80 (34)	0.74 (21)	NS	0.62 (21)
Peroxidase				0.58 (29)	0.36 (62)	NS	NS	NS
Phenol oxidase					0.58 (32)	NS	NS	NS
Phosphatase						NS	NS	NS
Respiration (per unit soil)							0.63 (86)	0.37 (57)
Respiration (per unit SOM)								NS

† Pearson correlation coefficient (r) and (number of observations). All coefficients are significant at the 1% level or better, except those marked NS (not significant). Ph. oxid: phenol oxidase, Resp/soil: respiration per unit soil, Resp/SOM: respiration per unit SOM.

Results

Linear correlations among enzyme activities, respiration, and N mineralization are reported in Table 6 (organic horizons) and Table 7 (mineral horizons). Correlations between enzymes or N mineralization and respiration were generally better when respiration was expressed per g of soil rather than per g of SOM. This may merely reflect the expression of both enzyme activity and N mineralization on a soil mass basis.

Within organic horizons, phosphatase was most highly correlated with soil respiration; amylase was second. Within mineral horizons, amylase was very highly correlated with respiration ($r=0.95$) and xylanase was second, but the correlation with phosphatase was not significant. Surprisingly, N mineralization was associated only weakly with respiration in both layers. N mineralization was associated most closely with polysaccharidases: amylase in the organic horizons; xylanase in the mineral horizons.

Considering the enzymes involved in degrading structural polymers: xylanase was highly-correlated with cellulase in both organic and mineral horizons; peroxidase, which is involved in the breakdown of lignin, is reasonably-well correlated with cellulase and xylanase in the organic horizons, but not in the mineral horizons (all correlations were NS).

Linear correlations of enzyme activities, respiration, and N mineralization with soil properties are reported in Table 8 (organic layers) and Table 9 (mineral horizons). In the organic layers, there were no significant correlations with amylase or xylanase. In the mineral horizons, there were no significant correlations with peroxidase or respiration per g SOM. Of the soil properties tested, the following were not significantly correlated with any enzyme, respiration, or N mineralization within the organic layers: extractable NO_3^--N, SOM, total C, total P, bicarbonate-extractable P, citrate-dithionate-extractable P, sum of extractable P, and C:P ratio. Within mineral soil samples, the following were not significantly correlated with any enzyme, respiration, or N mineralization: extractable NO_3^--N, C:N ratio, oxalate-extractable P, C:P ratio, and N:P ratio.

Amylase and xylanase activity within the mineral horizons correlated best to bicarbonate and citrate-dithionate extractable P, and to measures of organic matter (total N and C, SOM). Cellulase activity decreased with increasing total N within organic layers, but increased with increasing total N within the mineral horizons.

Table 8. Linear correlation matrix for soil enzyme activities, soil respiration, and mineralizable-N versus soil organic layer chemistry

	Total N	C:N	NH_4^+-N	Oxal-P	N:P	pH
Cellulase	-0.58 (18)†	0.53 (18)	NS	0.71 (12)	NS	NS
Peroxidase	NS	NS	NS	0.88 (12)	-0.60 (18)	NS
Phenol oxidase	-0.69 (9)	NS	NS	NS	NS	NS
Phosphatase	NS	NS	NS	NS	-0.50 (18)	0.51 (18)
Respiration (per unit soil)	NS	NS	NS	0.44 (20)	-0.45 (31)	0.51 (31)
Respiration (per unit SOM)	NS	NS	NS	NS	-0.50 (31)	0.63 (31)
Mineralizable-N	NS	NS	0.25 (75)	NS	NS	NS

† Pearson correlation coefficient (r) and (number of observations). All coefficients are significant at the 5% level or better, except those marked NS (not significant). Total N, total soil N; C:N, soil C:N ratio; NH_4^+-N, extractable soil ammonium-N; Oxal-P, oxalate-extractable soil P; N:P, soil N:P ratio; pH, soil pH (in water).

Table 9. Linear correlation matrix for soil enzyme activities, soil respiration, and mineralizable-N versus mineral soil chemistry

	Total N	NH_4^+-N	SOM	Total C	Total P	Bic-P	CD-P	Sum P	pH
Amylase	0.72 (34)	NS	0.72 (34)	0.74 (34)	0.58 (34)	0.83 (9)	0.72 (9)	NS	-0.50 (32)
Cellulase	0.67 (65)	-0.31 (40)	0.52 (65)	0.62 (65)	0.41 (65)	0.42 (40)	NS	0.36 (40)	-0.38 (63)
Xylanase	0.73 (34)	NS	0.73 (34)	0.75 (34)	0.52 (34)	0.78 (9)	0.72 (9)	NS	-0.45 (32)
Phenol Oxidase	0.40 (31)	NS	NS	NS	NS	NS	NS	NS	NS
Phosphatase	0.42 (65)	NS	NS	0.32 (65)	NS	NS	NS	NS	-0.30 (63)
Respiration (per unit soil)	0.41 (83)	NS	0.42 (83)	0.42 (83)	0.31 (83)	NS	NS	NS	NS
Mineralizable-N	0.55 (67)	NS	0.50 (67)	0.53 (67)	0.35 (67)	0.41 (43)	NS	0.34 (43)	NS

† Pearson correlation coefficient (r) and (number of observations). All coefficients are significant at the 5% level or better, except those marked NS (not significant). Bic-P, bicarbonate-extractable soil P; CD-P, citrate-dithionate-extractable P; Sum P, sum of extractable soil P; pH, soil pH in water.

Peroxidase was most closely linked with P, increasing with increased levels of oxalate-extractable P (the highest enzyme/soil-property correlation found) and declining with higher N:P ratios. Phenol oxidase was significantly correlated only with total N: in organic layers phenol oxidase activity increased with total N; in mineral horizons activity decreased weakly with increased total N. In mineral soil, phosphatase activity was not correlated (positively or negatively) with any tested measure of soil P; in the organic horizons, phosphatase weakly declined with increasing N:P ratio.

No single soil property stood out as associated with respiration rates: the correlation with pH was best in the organic layers; measures of organic matter were best in the mineral soil (total N and C, SOM). None of these were very highly correlated with respiration. No tested soil property was strongly associated with N mineralization; in the mineral horizons, measures of organic matter (total N and C, SOM) were weakly and positively associated with N mineralization.

Of the two measures of soil acidity, pH was better correlated (linearly) with enzyme activity, respiration, and N-mineralization, than was hydrogen ion concentration. This was true in both organic and mineral samples. Within organic horizons, most activities increased with pH, though not all correlations were significant; within mineral horizons most activities declined with increasing pH.

Discussion

Correlations among measures of soil biological activity

The poor correlation between mineralizable N and respiration is surprising, given that mineralizable N is a measure of the microbial biomass present (Myrold 1987). I have noted earlier the similar patterns of activity presented by mineralizable N and respiration (Figure 8 and Figure 11). A poor correlation could result if the anaerobic incubation mineralized differing proportions of the microbial biomass in different horizons or if some microbes were in a quiescent state, due to nutrient or carbon limitation, thus changing the relative respiratory activity per unit of biomass. Griffiths *et al.* (1990) measured respiration, fumigation-incubation CO_2 release, and mineralizable N in fungal mat and nonmat soils and found that the ratio of mat to nonmat respiration was more closely matched by the fumigation-incubation CO_2 release ratio than by that of mineralizable N. They suggested that the fumigation method best estimated biomass in acid forest soils.

My findings of significant associations of enzyme activity and respiration are consistent with other studies. Frankenberger and Dick (1983) found significant correlations between acid phosphatase, α-glucosidase, and respiration of amended soils with fumigation-incubation microbial biomass. The excellent correlation of amylase and respiration that I found agrees with the findings of Spalding (1977), but not with those of Caldwell *et al.* (1989, and personal communication), who found that respiration increased from non-mat to mat soils but amylase activity decreased.

The amylase results are interesting. Not only was the amylase-respiration correlation strong, but the absolute amylase activity, in terms of reducing sugars released, was similar to that of cellulase and only slightly less than that of xylanase. The raises the question: What is the function of this amylase? Spalding (1977) states that conifer foliage litter contains very little starch, so it is unlikely that amylase is directly useful for foliage litter breakdown.

Amylase could originate in plant roots; conifer fine roots contain significant starch reserves at the time of their formation (Marshall and Waring 1985) and amylase would be required to mobilize starch in response to respiratory demand. To the extent possible, roots were excluded from enzyme preparations but not from respiration assays, suggesting

that the amylase is of microbial origin. Amylase activity also could arise from enzymes released from senescent roots and stabilized by association with humic substances or clay, but the strong correlation with respiration suggests that the enzyme is associated with currently active biomass.

Amylase of microbial origin might be used by root pathogens exploiting plant root starch reserves; amylase activity is reasonably-well correlated with cellulase and xylanase, enzymes used to degrade plant cell walls. Amylase also catalyzes the hydrolysis of glycogen, a storage polysaccharide present in ascomycete and basidiomycete mycorrhizal fungi (Lewis 1986). Amylase might be produced by fungi for their internal use in the mobilization and translocation of stored glycogen reserves, or by fungal parasites or saprophytes for the breakdown of glycogen in fungal tissues.

The strong correlation of amylase activity and respiration is potentially useful. Reliably estimating soil respiration is difficult: it requires complex and expensive equipment, it is time-consuming, and it is subject to many artifacts. In contrast, enzyme assays are done easily. If amylase activity could be shown to correlate well with *in situ* soil respiration under a wide range of conditions, it would be a useful technique in the analysis of ecosystem C cycling. Further analysis is required to determine the source of amylase, its longevity and stability in forest soils, the primary enzyme function (i.e., hydrolysis of starch or glycogen), and the seasonal variation of absolute activity and activity in relation to respiration and microbial biomass. It will be necessary also to discover the limits of this technique — the conditions under which the relationship is no longer valid. This is a promising area for future research.

The strong correlations among cellulase, xylanase, and peroxidase within the organic horizons are evidence of a cooperative system of enzymes involved in the degradation of structural polymers in plant litter. Spalding (1977) found a similar strong correlation between cellulase and xylanase in conifer litter, but no significant correlation with peroxidase. In his study, peroxidase was significantly correlated with levels of extractable phenolics; I found a good correlation of peroxidase and phenol oxidase. Caldwell *et al.* (1989, and personal communication) found significant increases in cellulase and xylanase activities from nonmat to *Hysterangium* mat soil, but amylase decreased.

Soil biological activity versus soil properties

Cellulase appears related to biomass and SOM within mineral soil, and with the relative 'C richness' vs. 'N richness' of the organic layer. With high C:N ratios, large amounts of cellulose are available but N is scarce; cellulase may be needed to digest the cellulose cell wall matrix of litter to improve access to N-containing cell materials.

The negative correlation of cellulase and phenol oxidase with total N in the organic horizons probably relates to the transition from Oi to Oa, where C is respired, relative N content increases, and C:N declines. This effect is seen in the positive correlation of cellulase and C:N ratio. Within the mineral soil, all significant correlations of biological activity with total N, SOM, total C were positive, probably because these properties are surrogate measures of biomass.

The superiority of extractable P over total P as a predictor of biological activity (polysaccharidases, peroxidase, and respiration) was expected, because not all P in soil is equally available. Orthophosphate is a competitive inhibitor of phosphatase activity (Tabatabai 1982), so I expected a negative correlation of phosphatase and easily extractable P; this was not observed. It is likely that much of the easily-extractable P is complexed with organic compounds.

Frankenberger and Dick (1983) also found that acid phosphatase declined (-0.51, NS) with increased pH. Several enzyme activities declined with pH. This could be a direct effect of pH, but note that pH probably increases with depth, as does SOM and soil biomass, which are more likely to be the causal factors for the declining enzyme activity. Within the organic horizons, activities generally increased with pH, probably because the more highly-decomposed sapric material has both lower pH and lower substrate availability.

CELLULOSE DECOMPOSITION IN SOUTHEAST ALASKAN FORESTS: EFFECTS OF PIT AND MOUND MICRORELIEF AND BURIAL DEPTH

Abstract

McClellan, M.H., Bormann, B.T., and Cromack, K.,Jr. 1990. Cellulose decomposition in southeast Alaskan forests: effects of pit and mound microrelief and burial depth. Can. J. For. Res. 20:1242-1246.

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-yr decomposition of confined cellulose filter paper placed in the organic horizon and at the organic-mineral interface on both treethrow 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.

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.* 1989a). 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, treethrow mounds are favored microsites for tree establishment (Lutz 1940, Denny and Goodlett 1956, Lyford and MacLean 1966, Schaetzl *et al.* 1989a); 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 index, a strong positive relation exists between the degree of uprooting disturbance and site index, and the basal area/ha 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, unpublished 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 (*Lysichiton 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 treethrow 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).

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.

Methods

Site descriptions

The Heintzleman Ridge site (58°22' N, 134°34' W), 15 km NW 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 SW aspect. Precipitation, evenly distributed throughout the year, averages 1368 mm yr^{-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 NW of Juneau, Alaska. This site lies on a NE-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 over 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.

Filter paper packs

Five cellulose filter papers (ca. 1.85 g ovendry, 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 airdry mass of the enclosed filter paper; the ovendry mass was estimated by subsampling each box of filter papers.

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 treefalls occurred 50 to 160 years ago . Mounds and pits from the same treefall 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.

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 five of the twelve 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 one 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):

$$X_t = X_0 \cdot e^{-kt} \tag{7}$$

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).

Table 10. ANOVA table for 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: 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 boundary vs. organic-mineral boundary; Error C, residual error. Each F has as its denominator the following error MS. Each observation is the mean of three packs in one treatment combination.

Results and Discussion

Decomposition rates were not significantly different ($p = 0.39$) between pits and mounds (Table 10, Figure 12). 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 (Figure 12). 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 10). The declining decomposition with depth agrees with the results of Clymo (1965) and Binkley (1984) (Table 11), and may be attributed to cooler temperatures and more frequent water saturation at depth.

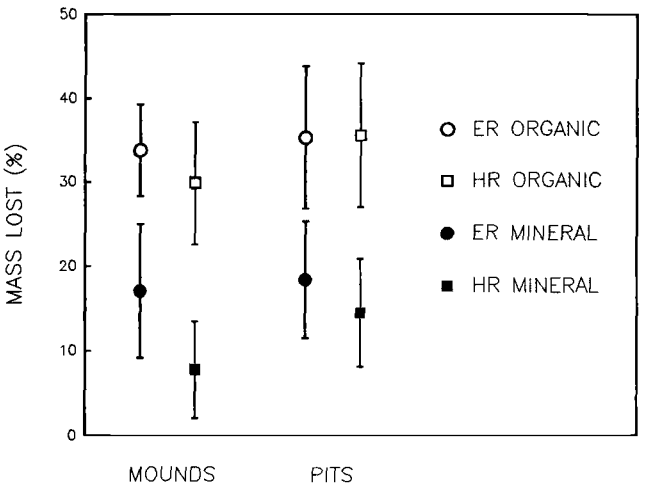

Figure 12. One-year mass loss of filter papers at the Oi-Oe (organic) and O-mineral (mineral) boundaries on mound and pit microsites at the Eagle River (ER) and Heintzleman Ridge (HR) sites. Error bars represent 95% confidence intervals.

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 clearcut 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 10). 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 11. Summary of field studies of cellulose filter paper decomposition

Location	Vegetation	Depth	Time	Loss	k	Reference
Vancouver Is., Canada	*Thuja plicata/Picea sitchensis*	Oi/Oe boundary	0.17	0.069	0.428	Binkley 1984
		Oe/Oa boundary		0.028	0.170	
		Oa/mineral boundary		0.031	0.189	
	Tsuga heterophylla/Pseudotsuga menziesii	Oi/Oe boundary		0.109	0.691	
		Oe/Oa boundary		0.106	0.671	
		Oa/mineral boundary		0.091	0.571	
	Tsuga mertensiana/Abies amabilis	Oi/Oe boundary		0.338	2.470	
		Oe/Oa boundary		0.250	1.723	
		Oa/mineral boundary		0.166	1.087	
N. England, UK	*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, USA	*Populus tremuloides*	Base of Oe (6.2 cm)	1.06	0.904	2.213	Fox and Van Cleve
	Betula papyrifera	Base of Oe (6.5 cm)		0.886	2.051	1983
	Picea glauca	Base of Oe (7.0 cm)		0.603	0.872	
	P. glauca	Base of Oe (13.4 cm)		0.537	0.727	
	Picea mariana	Base of Oe (12.3 cm)		0.412	0.501	
	P. mariana	Base of Oe (12.5 cm)		0.204	0.215	
Oregon Cascades, USA	*T. mertensiana*	Base of Oe	1.17	0.670	0.950	Waring *et al.* 1987
S.E. Alaska, USA	*T. heterophylla/P. sitchensis*	Oi/Oe boundary	1.04	0.337	0.396	(The current study)
		O/mineral boundary		0.145	0.151	

NOTE: Time, duration of experiment, in years; loss, proportion of mass lost; k, annual decay constant, from Eq. (7).

Table 11 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 did 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 to 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 yr) 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, $s = 3.39$, $n = 10$) than on the mounds (6.7 cm, $s = 3.16$, $n = 10$). 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 litterfall 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 litterfall data. Assumption of homogeneous litter distribution in these stands would yield substantial underestimates for k in pit microsites.

Acknowledgments

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SOIL AGE EFFECTS ON DECOMPOSITION OF LITTER AND CELLULOSE PACKS

Methods

Pack construction

Five cellulose filter papers (VWR Quantitative Grade 74, 7-cm diameter) were weighed and sewed into 9×9-cm nylon mesh (1-mm mesh size) packs. I assigned each pack a unique number and recorded the air-dry mass of the enclosed paper. Dry mass of each filter paper pack was estimated by subsampling each box of filter papers and determining the mass loss of the subsample after drying 24 h at 105°C. Each pack contained approximately 1.84 g of oven-dry paper.

I collected western hemlock and Sitka spruce litter from sapling- and pole-sized trees at three sites on Douglas Island. The oven-dry (55°C) litter was mixed thoroughly, then 5.00 g of litter was enclosed in each 12×12-cm nylon mesh (1-mm) litter bag. The litter was primarily needles, with some small twigs, branches, and reproductive structures; most of the needles were from western hemlock. Litter nutrient content was as follows: N: 0.60%, P: 0.05%, and K: 0.11%. Sequential fiber analysis showed the litter to contain 50.6% acid-detergent fiber, 28.9% lignin, 21.4% cellulose, and 0.31% residual ash.

Pack installation

At each site, I selected four mounds within each age class: young (40-60 years), medium (140-165 years), and old (precise ages unknown, but probably 300 years or more). Mound dating and selection techniques are described elsewhere (page 15). Packs were installed at Hawk Inlet on Aug. 20, 1986; Heintzleman Ridge on Sept. 14, 1986; and Outer Point on Sept. 16, 1986.

On each mound, I put six cellulose packs on the forest floor surface, six at the Oi-Oe (fibric-hemic) boundary, six at the organic-mineral soil boundary, and six at the top of the Bh horizon, if present. Buried packs were oriented parallel to the forest floor surface. Nearby — usually within 1 m — I put three litter bags on the forest floor surface and buried three litter bags at the Oi-Oe (fibric-hemic) boundary, parallel to the surface. To ease retrieval, surface packs were tethered with nylon fishing line and the locations of buried packs were mapped and marked with flags.

A few needles were inevitably lost from each litter bag during handling, transport to the field, and during placement and retrieval. To correct for this loss, I took a few bags to each site, installed them as I did the others, and immediately retrieved and reweighed them. From the average handling loss of this subset (ca. 2.8%), I estimated the corrected initial litter mass to be 4.86 g per bag.

Pack retrieval and processing

The cellulose and litter packs remained in place for slightly over one year: Hawk Inlet packs were retrieved Sept. 9, 1987 (385 d in place); Heintzleman Ridge on Sept. 21, 1987 (372 d); and Outer Point on Sept. 23, 1987 (372 d). At retrieval, I measured the burial depth of buried packs and, for surface packs, classified the degree of contact with the forest floor (1 = ≥75% of area in close contact, 3 = <50% in close contact) and estimated the percent litter cover.

All collected packs were stored frozen before final processing, when they were thawed and cleaned of roots and adhering soil material. Cellulose packs were then dried at 105° C and weighed. Packs in contact with mineral soil (mineral and upper Bh), were subsampled by mound and ignited at 450° C for 5 h to estimate the average mineral contamination. Final oven-dry masses, corrected for mineral contamination where necessary, were subtracted from initial oven-dry masses (m_0) to yield the mass lost (Δm). Litter packs were dried at 55° C and weighed. Final oven-dry masses were subtracted from 4.86 g (m_0) to yield the mass lost (Δm). Decomposition rates were calculated using the days in place, t_{days} (Eq. (8)).

$$Decomposition\ Rate = \frac{\Delta m}{m_0} \times \frac{365}{t_{days}} \qquad (8)$$

Data analysis

Effects of site, soil age, and substrate position on cellulose and litter decomposition rates were tested with ANOVA, using the SAS General Linear Models (GLM) procedure (SAS Institute, Inc. 1987). In this nested-crossed experimental design, individual packs are nested within mounds and mounds are nested within their age class at their site. Because the Bh horizon was absent from many medium-aged mounds and all the

young mounds, only data from the surface, mid-organic, and organic-mineral positions were included in the ANOVA. The effect of Bh development was tested by determining the correlation between cellulose decomposition and several measures of Bh development, including Bh thickness, total mass of Bh per unit area, and mass of the ≤ 2 mm Bh fraction per unit area.

To test whether cellulose and litter decomposition were related, I calculated Pearson correlation coefficients, pairing mean rates by position (surface or organic) within mounds. Similar tests were made for the decomposition rates of similar substrates placed at the surface or buried.

Decomposition correlations with soil properties

I calculated Spearman's rank-order correlation coefficient, a nonparametric measure of association, for cellulose and litter decomposition rates with the following soil properties: pH, total C, N, and P, C:N, C:P, nitrate- and ammonium-N, mineralizable-N, enzyme activities, respiration, and extractable P, Al, Fe, Si, Mg, Mn, Ca, and K. Correlations were determined for each substrate × position combination, over all sites, and for each site × substrate × position combination. Surface cellulose and litter decomposition was tested with organic horizon data; mid-organic cellulose and litter decomposition was tested with data from the organic horizon and from the uppermost mineral horizon, usually an A or E horizon; decomposition of cellulose at the organic-mineral boundary was tested with data from the organic, upper mineral, and Bh horizons (if present); E-Bh cellulose decomposition was tested with upper mineral (E) and Bh horizon data. In all, I examined roughly 2530 separate correlations. I rejected all correlations where $n \leq 5$ or $p > 0.05$.

I used a nonparametric statistic for several reasons: the parametric Pearson's correlation coefficient assumes a bivariate normal distribution, Spearman's does not; Spearman's coefficient does not assume a linear relationship between variables; and nonparametric methods are nearly as efficient as parametric methods in small samples ($n \leq 10$) (Steel and Torrie 1980).

Results

Cellulose and litter decomposition rates

Figure 13 through Figure 15 and Table 12 contain the decomposition rates of cellulose and litter, respectively. Table 30 (Appendix) contains detailed cellulose loss data. Cellulose losses varied far more than litter losses, and cellulose at the surface and mid-organic positions lost 41.1% of their mass, compared to 35.2% from litter in similar positions. Note that several mean cellulose decomposition rates are very low: sometimes less than 10% of the mass was lost in 1 year. Low cellulose losses at the surface were associated with poor contact with the forest floor (Spearman's correlation coefficient, $r_S = -0.53$, $p = 0.001$, $n = 36$) and with sparse litter coverage of the pack ($r_S = 0.63$, $p = 0.004$, $n = 19$). Age class differences are more pronounced in the cellulose data, but the ANOVA didn't detect any significant age effect over all sites and positions in either cellulose ($p = 0.22$) or litter ($p = 0.80$).

For cellulose decomposition, site and position main effects were highly significant (both $p < 0.001$); significant interactions included site × age, age × position, and site × age × position (all $p < 0.05$). These interactions, which are apparent in Figure 13, Figure 14, and Figure 15, preclude generalizations about the age effect. Tests of age effects within sites and positions (Table 13) revealed only three instances where soil age significantly affected the cellulose decomposition rate. For litter, site was the only main effect approaching significance ($p = 0.07$).

On mounds with Bh horizons present, cellulose decomposition at the organic-mineral boundary was negatively-correlated with Bh horizon thickness (Pearson's correlation coefficient, $r_P = -0.68$, $p = 0.01$, $n = 13$, Figure 16). Cellulose decomposition at the upper Bh horizon boundary was related also to the Bh horizon total mass, but this relation was weak ($r_P = -0.37$, $p = 0.24$, $n = 12$); the combined Bh and Bs horizon thickness related slightly better ($r_P = -0.41$, $p = 0.14$, $n = 14$).

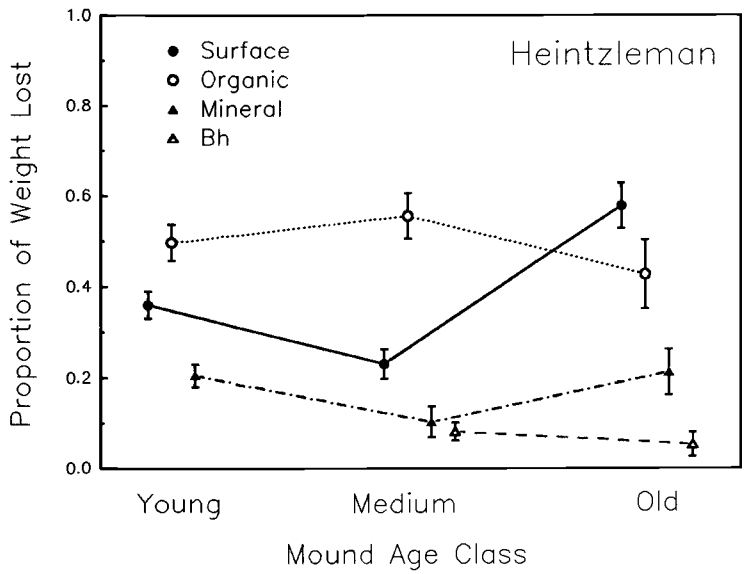

Figure 13. Cellulose decomposition at Heintzleman Ridge, 1986-87

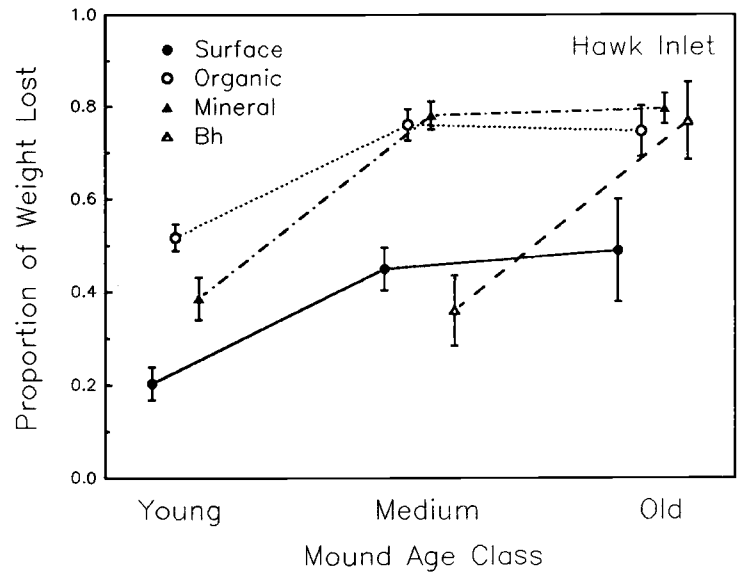

Figure 14. Cellulose decomposition at Hawk Inlet, 1986-87

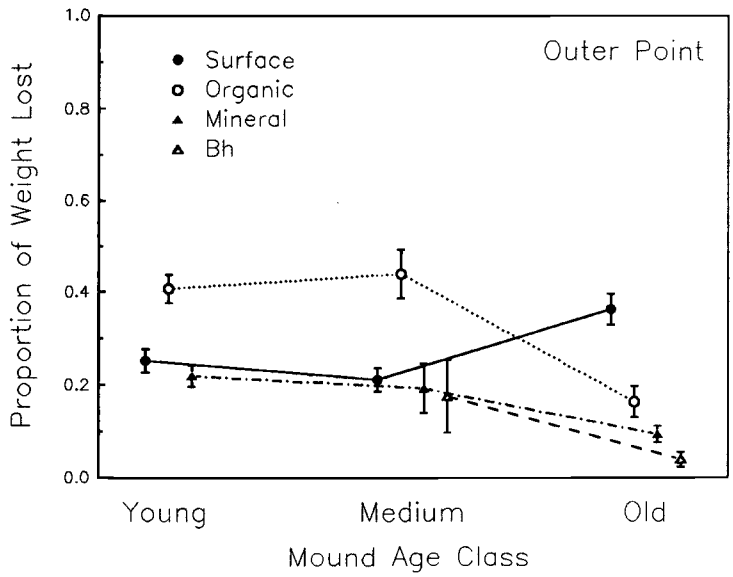

Figure 15. Cellulose decomposition at Outer Point, 1986-87

Table 12. Proportion of mass lost from litter packs during 1 year: breakdown by site, mound age, and pack position

Position	Young	Medium	Old
		Heintzleman Ridge	
Surface	0.358 ± 0.010 (12)†	0.313 ± 0.016 (9)	0.359 ± 0.020 (9)
Organic	0.320 ± 0.011 (12)	0.362 ± 0.023 (9)	0.326 ± 0.010 (9)
		Hawk Inlet	
Surface	0.295 ± 0.011 (12)	0.317 ± 0.017 (15)	0.308 ± 0.008 (3)
Organic	0.381 ± 0.016 (12)	0.379 ± 0.015 (15)	0.375 ± 0.027 (3)
		Outer Point	
Surface	0.399 ± 0.018 (12)	0.390 ± 0.015 (12)	0.396 ± 0.012 (12)
Organic	0.383 ± 0.016 (12)	0.314 ± 0.011 (12)	0.340 ± 0.028 (10)

† Mean ± standard error (number of observations)

Table 13. ANOVA tests of age class effect on cellulose decomposition, by site and position

Position	df	MS	F	p
		Heintzleman Ridge		
Surface	2	0.556	7.75	0.017
Organic	2	0.076	0.25	0.786
Mineral	2	0.071	1.04	0.403
Bh	1	0.004	0.13	0.756
		Hawk Inlet		
Surface	2	0.400	1.54	0.289
Organic	2	0.378	3.37	0.104
Mineral	2	1.167	5.73	0.041
Bh	1	0.968	1.66	0.420
		Outer Point		
Surface	2	0.149	3.22	0.088
Organic	2	0.545	7.05	0.014
Mineral	2	0.105	0.97	0.416
Bh	1	0.089	6.66	0.082

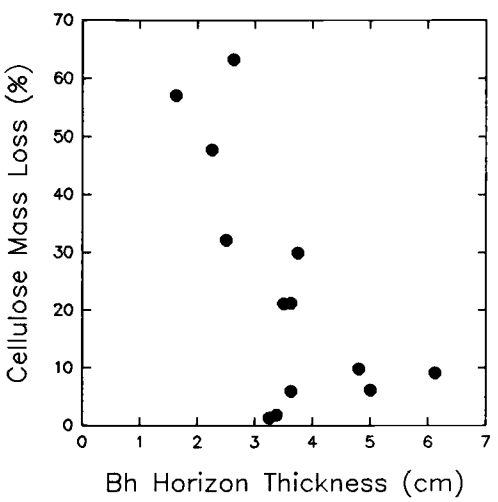

Figure 16. Relation of cellulose mass loss (1986-87) to illuvial horizon (Bh) thickness

Decomposition rates of litter and cellulose in similar positions were unrelated: at the surface $r_P = 0.03$, $p = 0.85$, and $n = 36$; at the mid-organic $r_P = 0.27$, $p = 0.11$, and $n = 36$. The poor correlations were not due to non-linearity of the relations. Comparisons of surface and buried litter packs detected no relation between their respective decomposition rates, but comparisons of surface and buried cellulose packs showed weak but significant relations between the surface and mid-organic positions ($r_P = 0.46$, $p = 0.004$, $n = 36$) and between the surface and organic-mineral positions ($r_P = 0.51$, $p = 0.002$, $n = 36$). Correlations among buried cellulose packs were much better: all were between 0.68 and 0.77 with all $p < 0.01$.

Decomposition correlations with soil properties

All correlations of litter or cellulose decomposition with soil properties where $p \leq 0.05$ and $n > 5$ are contained in Table 31 through Table 35. Note that cellulose decomposition rates were significantly correlated more often with soil properties than were litter rates at the same position and that buried substrates had more significant correlations with soil properties than surface substrates. I will present some general observations first and then turn to a discussion of results for each substrate × position combination.

Decomposition of cellulose increased with soil respiration; buried cellulose decomposition increased with phosphatase and cellulase activity, decreased with amylase activity in organic horizons; and surface cellulose decomposition decreased with increased cellulase activity in organic horizons. Extractable P, total P, and P per unit area were associated positively with cellulose and litter decomposition, and high C:P ratios were associated with slower decomposition of cellulose. I found only one significant correlation between measures of soil N and all buried cellulose decomposition rates.

Decomposition of buried cellulose and litter usually declined with increased extractable Fe and Al in the organic and Bh horizons, but increased with increased extractable Fe and Al in the upper mineral (A or E) horizon. Conversely, surface cellulose and litter decomposition both increased with increased extractable Al or Fe in the organic horizons. Decomposition of cellulose, but not litter, declined with increased H^+ activity. Litter decomposition at the surface was correlated positively, albeit weakly, with only five organic horizon properties: oxalate-extractable and bicarbonate-extractable Al, bicarbonate-extractable Fe and P, and total N (Table 31).

Cellulose at the surface (Table 32) was correlated positively with pyrophosphate-extractable and bicarbonate-extractable Al, total N and N per unit area, and total P per unit area. Surface cellulose decomposition correlated negatively with cellulase activity and extractable Mn in organic horizons. Decomposition of litter buried at the mid-organic horizon was correlated positively with H^+ activity and C:N ratio in the organic horizons, negatively with extractable Ca in the uppermost mineral horizon at Heintzleman Ridge, and negatively with total N, bicarbonate-extractable Al, and pyrophosphate-extractable Fe within the organic horizons.

Cellulose decomposition at the mid-organic position (Table 33) correlated positively with respiration (whole soil basis), P (oxalate-extractable, total, and total per unit area), cellulase and phosphatase activity, bicarbonate-extractable Si, and extractable Ca in the uppermost mineral horizon. With one exception, decomposition was correlated negatively with extractable Fe and Al, H^+ activity, and amylase activity within organic horizons, but it was positively correlated with extractable Al in the uppermost mineral horizon. Decomposition was negatively associated with the C:P ratio in the uppermost mineral horizon.

Decomposition of cellulose placed at the organic-mineral interface (Table 34) was strongly and negatively correlated with extractable NH_4^+-N in the mineral horizon immediately below. This was the only significant correlation between buried cellulose decomposition and measures of soil N. Cellulose decomposition at this position was correlated positively with respiration (per unit SOM) in organic horizons layer above, and with phosphatase activity, C:P ratio, and extractable K and Mg in the uppermost mineral horizon. I found negative correlations with H^+ activity in the organic horizons above, C:P ratio in the Bh, extractable Al and Fe in the organic or Bh horizons, and with extractable Ca, Mn, and Si in the Bh horizon.

Cellulose decomposition at the deepest position — the boundary between the E and upper Bh horizons — correlated positively with extractable P (oxalate-extractable P best), total P, extractable Al, Fe, Ca, Mg, Mn, and Si in the horizon above (usually an E), and with extractable Ca and Mn in the Bh horizon (Table 35). I found negative correlations between E-Bh cellulose decomposition and the H^+ activity and C:P ratios of soils above and below, and with extractable Fe, Al, and Mg in the Bh horizon.

Discussion

Decomposition of litter and cellulose

I did not expect that cellulose decomposition rates would surpass those of litter, because the latter contains nutrients, simple carbohydrates, an established microflora, and readily soluble components. The more rapid decomposition of cellulose was probably due to a greater surface-to-volume ratio and the absence of decay-resisting components such as lignin, a waxy cuticle, and polyphenols. Note that litter lost 35% of its mass, on average, even though its cellulose and lignin contents were only 21% and 29%, respectively.

Cellulose decomposition rates show considerable yearly variation. In a study of cellulose decomposition at Heintzleman Ridge during 1985-86, McClellan *et al.* (1990) found cellulose decomposition rates on mounds of 30% at the mid-organic position and 8% at the organic-mineral interface. Comparable 1986-87 rates at the same site on young mounds were 50% and 21%, respectively. Materials and methods used were nearly identical and the mounds were very similar. Warmer summer weather during 1987 was most likely responsible for the dramatic rate increase. This result suggests that single-year decomposition studies may lead to erroneous conclusions.

Site differences in cellulose decomposition may be explained by temperature and moisture differences. Hawk Inlet had the greatest general rate and it has a western exposure, and the stand appears more open and drier. The least decomposition occurred at Outer Point, which has a N aspect and is cool and wetter. But, total litter decomposition was highest at Outer Point; rates at Hawk Inlet and Heintzleman Ridge were about equal. The decline of decomposition with depth may be attributable to lower temperature, less biological activity.

Soil surface age effects

Why didn't soil age significantly affect litter pack and cellulose pack decomposition? It appears that litter decomposition responds primarily to physical conditions, which changed little over the range of ages studied. Cellulose decomposition rates are highly variable; packs placed within a single soil horizon within 50 cm of each other frequently decomposed to radically different degrees. Such extreme within-treatment variability makes it very difficult to detect any but the most gross treatment effects with reasonable

sample sizes. In addition, there does not even appear to be a consistent trend across all sites. Only Outer Point data conforms to the hypothesis that decomposition slows with increasing soil age. At Heintzleman Ridge patterns conflict between horizons, and at Hawk Inlet, rates appear to level in the older age classes — it is uncertain what will happen next: a continued steady state, decline, or increased decomposition. Note that only one mound was available in the oldest age class at Hawk Inlet; one should not put undue emphasis on this value.

The differing trends with soil age may be attributed to site microclimate. Hawk Inlet appears to be the warmest and driest site, Outer Point the wettest and coolest. Podzolization is favored by cool, wet conditions, and I think Outer Point showed the earliest and most extreme development of a general trend, although this cannot be directly confirmed. The finding that cellulose decomposition slowed with increased Bh development suggests that decomposition will decrease with increased soil development.

Decomposition may follow a pattern I have observed in other data in this study, increasing during the early stages of mound soil development and then declining following Bh establishment. The general mean cellulose losses for the upper three positions (excluding Bh) were as follows: young, 34%; medium 44%; and old, 34%.

Estimation of Litter Decomposition — A Critique

The poor correlation between decomposition of cellulose and litter packs raises the question: Which substrate, if either, is the best predictor of actual decomposition of native litter? It is possible that they estimate only their rate of decomposition, and that other soil properties — nutrient content, respiration, mineralizable N — may better estimate *in situ* litter decomposition.

I concluded that decomposition of standardized litter responded to the physical conditions — moisture and temperature primarily — of each microsite, and not to chemical conditions. Litter pack decomposition correlated significantly with few soil chemical or biological properties. This is reasonable, for litter contains many nutrients needed by decomposers, requiring few nutrient subsidies from the surrounding soil. The uniformity

of litter decomposition parallels the apparent uniformity of within-site microclimates. I did not take extensive moisture and temperature measurements, but within-site conditions appeared somewhat uniform: frequent cloud cover minimized the effects of canopy gaps; rainfall is abundant and evenly-distributed during the growing season; soil temperatures varied little from mound-to-mound or within the upper 15 cm of the soil profile.

Cellulose decomposition appeared to respond to both physical and chemical conditions. I found many significant correlations between soil properties and decomposition of buried cellulose. Cellulose decomposition at the surface varied significantly with surface contact and litter coverage — variables that relate to physical conditions.

If cellulose decomposition integrates both soil chemical and physical properties of a microsite, isn't this the best estimator of decomposition? The problem with this interpretation is as follows. Tree roots may extend for great distances, preferentially exploiting soil volumes with favorable nutrient status and physical properties. The quality of foliage and branch litter produced by any single tree probably reflects the distribution and accessibility of favorable soil microsites within a broad area. Foliage litter may fall far from its source; a point may receive litter from many trees, integrating soil conditions over a wide area. Microsite soil conditions may control tree root litter quality, also that of understory vegetation with circumscribed rooting. Thus, the chemical composition of litter found on any single mound is partly a function of the aggregate site quality and partly a function of soil conditions on that mound.

On my study sites, mound litter layer nutrient contents are probably less variable than nutrient availability within mound mineral soils. This litter will decompose at a rate determined mostly by its chemical composition and the physical conditions at the microsite; to the extent that foliage litter dominates organic horizons, local soil chemical conditions will exert little direct control over decomposition rates, unless the substrate is very nutrient-deficient, as is pure cellulose.

Because litter quality results from broad-scale integration, I concluded that decomposition of cellulose and standard litter are likely to fail to estimate actual litter decomposition on heterogeneous sites such as ours; still, cellulose decomposition may estimate the relative nutrient supplying capacity of a microsite.

Could cellulose decomposition predict actual litter decomposition? Given a hypothetical series of stands of varying site quality, each with high within-stand soil quality

uniformity, litter decomposition and soil nutrient availability at each microsite should be closely linked. Relative cellulose decomposition rates in such a series should relate to the relative site quality and litter decomposition. On more heterogeneous sites, if you could adequately sample over a site, stratifying by soil nutrient availability and sampling in proportion to each area's contribution to stand litter production, cellulose decomposition could predict litter quality, and therefore, litter decomposition. This is impractical. Also, this assumes that nutrients controlling cellulose decomposition are the same as those promoting high-quality, readily-decomposable litter. An additional assumption is that nutrients available to saprophytes attacking cellulose come from the same pool as those nutrients available to plant roots and mycorrhizal fungi.

Of the soil properties and processes measured, soil respiration and polysaccharidase enzyme activity may be the best predictors of actual litter decomposition. As measured, respiration included microbial, microfaunal, and root respiration. Respiration of the microfauna is probably insignificant in these acid soils. Root activity is likely to be greatest in areas of rapid decomposition and nutrient mineralization. High levels of polysaccharidase activity may suggest high decomposition rates. This set of enzymes catalyzes the breakdown of cell wall components. Cellulase and other polysaccharidases are inducible — produced in response to available substrate under conditions favorable to microbial growth and activity.

A PRELIMINARY CARBON BUDGET

Introduction

Litterfall is a major flux of carbon, energy, and nutrients in forest ecosystems. In boreal and temperate conifer forests, 57-85% of the aboveground NPP ends as litter (Kimmins 1987). Knowing litterfall rates, it is now possible to estimate several other components of ecosystem C cycling (Raich and Nadelhoffer 1989).

I attempted to construct a simple, preliminary C budget for my study sites using litterfall measurements, chronosequence changes in soil C, and laboratory soil respiration measurements, along with several assumptions based on values reported in the literature. My primary goal was to simply compare the sites with forests in other regions, but I realized it was also possible to compare two methods of estimating forest soil respiration.

Methods

Biomass and productivity estimation

The allometric equations of Bormann (1990) were used to estimate the above-ground biomass and aboveground net primary productivity (ANPP) of Sitka spruce and western hemlock on each site. The equations were developed for trees in southeast Alaska and are valid for western hemlocks up to 60 cm in diameter and for Sitka spruce up to 100 cm in diameter. All tree diameters were within that range at Heintzleman Ridge and Outer Point, but not at Hawk Inlet, where more than half the western hemlocks were over 60 cm in diameter.

As a check on the out-of-range equation, I re-estimated the Hawk Inlet ANPP, assuming the following linear relation between litterfall and estimated ANPP (based on data from Heintzleman Ridge and Outer Point).

$$ANPP = (3.79 \times LFALL) - 9.4 \quad (9)$$

ANPP and litterfall (LFALL) units are $Mg \cdot ha^{-1} \cdot yr^{-1}$.

Soil carbon model

I created a simple soil carbon cycling model in a microcomputer spreadsheet. The model had three main parts: the soil C pool (STORAGE), additions to the soil C pool (INPUTS), and removals from the soil C pool (OUTPUTS). INPUTS included above-ground fine litterfall, aboveground coarse woody debris (CWD), and belowground C-allocation. OUTPUTS included soil respiration, leaching of soluble C to the subsoil, and surface transport of particulate C (leaching and surface transport were initially set to 0). The following equation defined the model:

$$\Delta Storage = Inputs - Outputs \quad (10)$$

The mean annual change in soil C per ha (ΔSTORAGE) was estimated from soil C contents of mound chronosequence soils. To eliminate artifacts due to bulk density change, SOM additions, and variable coarse fraction content, the depth of soil equivalent to the upper 55 $kg \cdot m^{-2}$ of ashed soil ($\leq$ 2 mm) was calculated for each mound. This was equivalent to a 25-cm depth, on average. The total C content of this soil, including the organic horizons, was then calculated and a regression of total soil C per unit area over mound age was performed. Because the ages of old mounds were not known, I assigned to them an estimated age of 350 yrs.

Estimation of litterfall, CWD, and belowground C allocation

Litter was collected in traps with wooden frames and wire mesh bottoms (3-cm mesh). The traps were roughly 9-cm deep, with an internal area of 0.53 m^2. Each trap was fitted with a removable liner of non-woven polyester fabric that retained the finest litter, allowed water to drain freely, dried quickly, and did not rot. Unfortunately, the liners also were favored nest material for the local wildlife.

I put twenty traps at each site. The sample size was calculated from the variance reported by Hurd (1971) for his study of litterfall in spruce-hemlock stands in the nearby Mendenhall Valley. At each site (Heintzleman Ridge, Hawk Inlet, Outer Point) I laid out a grid of 1 m cells; the grid varied from 70-100 m on a side, depending on the plot. I selected trap x-y coordinates from a random number table; if it was impossible to put a

trap at the selected point, it was moved 1-2 m in a random direction. The traps were level, with their lowest point at least 5 cm from the ground.

Table 14 contains data on the total collection period and the median time between individual collections. At each collection time, the liners plus litter were removed, bagged, returned to the lab, and dried at 55°C. If drying was delayed, the litter was stored frozen. Each sample was identified by site, trap number, and collection date.

Table 14. Litterfall collection periods

	Heintzleman	Hawk Inlet	Outer Point
Start date	9/14/86	8/20/86	9/12/86
Stop date	10/5/89	9/25/89	10/5/89
Period (d)	1117	1132	1119
Period (yr)	3.06	3.10	3.06
Median interval (d)	76	58	76

Random subsamples of dried litter were sorted and weighed to estimate the relative contribution of conifer foliage and reproductive structures, non-conifer foliage, branches, lichens, and unidentified fine litter. Because the proportions of these components were expected to vary seasonally, collections from all seasons were subsampled and sorted.

In calculating stand litterfall rates, I used only litter weights where the trap liner was disturbed < 5% by wind or animals. Rejecting disturbed traps left, on average, 16.9 traps per collection at Heintzleman Ridge, 17.1 at Hawk Inlet, and 18.3 at Outer Point. For each site, I calculated the litterfall rate per trap and averaged all traps to find the rate per collection period. The average yearly litterfall rate was weighted by the days in each collection period. I truncated the last collection period to yield exactly three years of litter collection (1096 d).

CWD input and belowground C allocation were not measured directly. For CWD inputs, I calculated a value for each site that was 14.1% of the estimated site ANPP. I derived this factor from data presented by Grier (1978) for a 121 yr-old western hemlock-

Sitka spruce stand at Cascade Head on the Oregon coast (ANPP = 19.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$, CWD input = 2.8 $Mg \cdot ha^{-1} \cdot yr^{-1}$). This may be a conservative estimate, based on the range of hemlock-spruce CWD inputs summarized in Harmon *et al.* (1986). In addition, CWD inputs may vary greatly from year to year in response to weather (wind and snow loading) or stand condition (disease, self-thinning, etc.). I used Eq. (11), developed by Raich and Nadelhoffer (1989), to estimate belowground allocation of C from aboveground litter inputs (units are g $C \cdot m^{-2} \cdot yr^{-1}$).

$$\textit{Root Allocation} = (1.92 \times \textit{LFALL}) + 130 \qquad (11)$$

Soil respiration

I compared two methods for estimating yearly soil respiration. The first used laboratory measurements of respiration rates adjusted for average monthly field temperatures; the second used a regression equation developed by Raich and Nadelhoffer (1989) that estimates soil respiration from aboveground litterfall.

Mean monthly temperatures of air (10 m above surface), litter (2 cm below surface), and soil (10 cm below surface) were calculated from daily mean temperatures recorded at Outer Point and Heintzleman Ridge during 1989 using thermistors and automated solid-state data loggers (data on file at the USFS Forestry Sciences Lab, Juneau, AK; provided by Paul Alaback). Temperature readings were taken every 6 s and averaged hourly, with a resolution of 0.3°C. I used Eq. (6) to correct the laboratory-determined respiration rates per unit area (Figure 11) for the observed monthly mean temperature, assuming a Q_{10} of 2. The spreadsheet model included a factor representing the measurement effect on soil respiration. The initial assumption was that lab rates were 10% greater than field rates. The model allows this factor and the Q_{10} to be changed at will.

In the second method, yearly aboveground litterfall rates for each site first were converted to C equivalents assuming a litter C content of 52%. Annual soil respiration was then estimated from annual litterfall C with Eq. (12) (Raich and Nadelhoffer 1989).

$$\textit{Respiration} = (2.92 \times \textit{LFALL}) + 130 \quad \textbf{(12)}$$

Units are g C· m^{-2}· yr^{-1}.

Results

Biomass and productivity

Table 16 contains the estimates of biomass components and aboveground net primary productivity. As expected, the ANPP estimate for Hawk Inlet was very low due to the out-of-range hemlock diameters. In fact, the estimated ANPP was less than the annual aboveground litterfall estimate. The revised Hawk Inlet ANPP estimate, based on the ANPP-litterfall relation, was 9.26 $Mg \cdot ha^{-1} \cdot yr^{-1}$.

Soil carbon

Table 15 contains the measured soil C for each site and mound age class. The estimated age of 350 yrs for old mounds yielded a fairly uniform rate of C accumulation over time. Regressions of soil C ($Mg \cdot ha^{-1}$) over mound age (yrs) produced the following equations:

Heintzleman Ridge: Soil C = 0.09 × Age + 51.4 (r^2 = 0.39)
Hawk Inlet: Soil C = 0.23 × Age + 25.6 (r^2 = 0.72)
Outer Point: Soil C = 0.27 × Age + 27.2 (r^2 = 0.73)

Table 15. Total soil C ($Mg \cdot ha^{-1}$) by site and mound age class

	Young	Medium	Old
Heintzleman	60 ± 7.3 (4)†	60 ± 8.4 (3)	82 ± 9.2 (4)
Hawk Inlet	42 ± 1.8 (4)	58 ± 2.6 (5)	99 ± 18 (4)
Outer Point	64 ± 10.9 (4)	86 ± 5.1 (4)	140 ± 14 (5)
All Sites	55 ± 4.9 (12)	68 ± 4.6 (12)	110 ± 10 (13)

Note: Estimated to soil depth equivalent to 55 kg $ash \cdot m^{-2}$, ≤2 mm fraction. † Mean ± standard error (number of observations)

Table 16. Biomass components and aboveground net primary productivity

	Heintzleman			Hawk Inlet			Outer Point		
	SS	WH	Total	SS	WH	Total	SS	WH	Total
Trees · ha^{-1}	76	333	409	32	162	194	20	397	417
Basal Area (m^2 · ha^{-1})	27.1	48.9	75.9	20.7	49.3	70.0	8.1	65.1	73.2
Diameter (breast ht., cm)	62.4	39.5	NA	85.7	60.2	NA	68.7	40.8	NA
Sapwood (radial, cm)	3.4	NA	NA	3.9	NA	NA	4.3	NA	NA
				Foliage (Mg · ha^{-1})					
Age ≤ 1 yr	0.56	0.70	1.27	0.40	0.91	1.31	0.18	0.90	1.08
1 > Age ≤ 2 yr	0.68	0.69	1.38	0.46	0.53	0.99	0.22	1.13	1.35
Age > 2 yr	27.3	3.8	31.1	21.6	2.9	24.5	8.7	6.2	14.8
Total	28.1	5.0	33.1	22.0	4.1	26.1	9.0	8.1	17.1
				Branches (Mg · ha^{-1})					
Age ≤ 1 yr	0.17	0.48	0.65	0.12	0.76	0.88	0.05	0.32	0.37
1 > Age ≤ 2 yr	0.30	0.15	0.45	0.21	0.11	0.32	0.10	0.16	0.26
Age > 2 yr	18.7	27.3	46.1	14.5	25.6	40.1	5.9	43.6	49.6
Total	19.2	27.5	46.8	14.8	25.8	40.6	6.1	44.0	50.1
Bole (Mg · ha^{-1})	144	216	361	122	234	356	43	294	337
NPP (Mg · ha^{-1} · yr^{-1})	2.66	3.30	5.96	1.86	2.57†	4.42†	0.84	4.09	4.93

Note: SS, Sitka spruce; WH, western hemlock. Boles includes bark. † Probable low estimates due to out-of-range equation.

Litterfall, CWD, and belowground C allocation

Figure 17 displays the litterfall rates for the duration of the study. Litterfall at Heintzleman Ridge and Outer Point varied in unison, as might be expected from their closeness. Hawk Inlet litterfall patterns differed slightly; this may relate to its exposure to different storm systems. The mean annual litterfall rates, estimated belowground C allocation, and estimated CWD inputs are contained in Table 17. Mean annual litterfall over all sites was 4.25 $Mg \cdot ha^{-1} \cdot yr^{-1}$. On average, annual belowground C allocation estimates were 2.5 times greater than aboveground litterfall. Table 18 contains the breakdown of litter by component, averaged over all sites and seasons. The proportion of conifer needles varied by site: Heintzleman Ridge 58.4%, Hawk Inlet 66.7%, and Outer Point 47.9%.

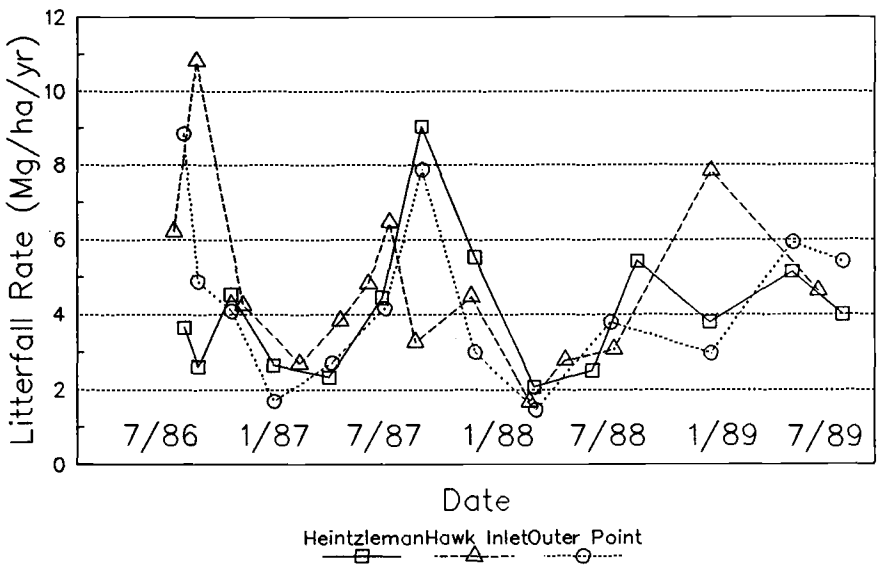

Figure 17. Litterfall rates at Heintzleman Ridge, Hawk Inlet, and Outer Point, 1986-89

Table 17. Aboveground litterfall, estimated root turnover, and estimated CWD inputs ($Mg \cdot ha^{-1} \cdot yr^{-1}$)

	Heintzleman	Hawk Inlet	Outer Point
Aboveground litterfall	4.06	4.92	3.77
Belowground C allocation	10.30	11.95	9.74
CWD	0.84	1.30	0.69
Total	15.20	18.17	14.20

Table 18. Average litterfall composition

Litter component	%
Conifer foliage	57.7
Branches ≤ 2 mm diam.	9.3
Branches > 2 mm diam.	6.1
Conifer reproductive structures	9.7
Non-conifer foliage	1.3
Lichens	0.3
Miscellany	15.6

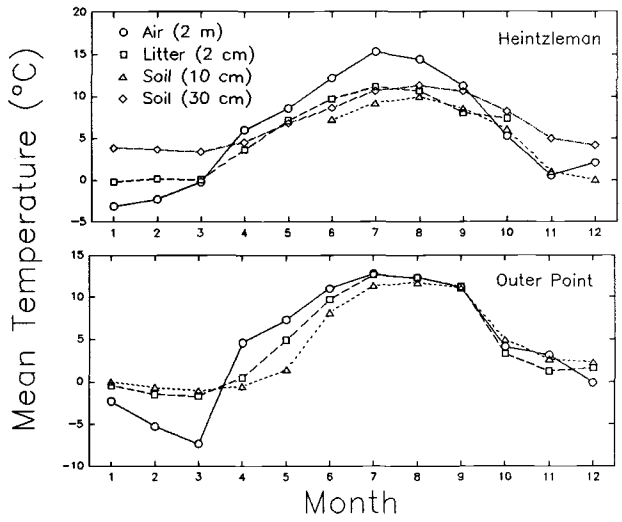

Figure 18. Average monthly temperatures at Heintzleman Ridge and Outer Point, 1989

Soil respiration

Figure 18 shows the 1989 monthly mean temperatures for Heintzleman Ridge and Outer Point. Because I did not have temperature data for Hawk Inlet, I used Heintzleman Ridge data to correct soil respiration values for Hawk Inlet. Table 19 contains soil C budget data. Inputs include aboveground litterfall, CWD inputs, and belowground C allocation. Outputs include only soil respiration, as estimated from adjusted *in vitro* soil respiration rates and from aboveground litterfall. The predicted values for the annual change in soil C storage were calculated using Eq.(10).

Table 19. Predicted change in total soil C ($Mg \cdot ha^{-1} \cdot yr^{-1}$)

	Heintzleman	Hawk Inlet	Outer Point
Inputs	7.90	9.45	7.38
	Estimates based on *in vitro* assay		
Soil respiration	11.08	16.07	15.71
ΔStorage	-3.18	-6.62	-8.33
	Estimates based on litterfall		
Soil respiration	7.46	8.77	7.02
ΔStorage	0.44	0.68	0.36

Discussion

The Heintzleman Ridge soil C accumulation results may indicate a problem with the chronosequence. The soil C vs. soil age regression intercepts may estimate the mound soil C content at the time of mound creation. In the case of Heintzleman Ridge mounds, the intercept appears too high and the slope too low when compared with results from Hawk Inlet and Outer Point. This may reveal different initial soil C contents for young mounds versus the medium and old mounds at this site.

Aboveground litterfall rates are underestimates. The lengthy period between collections allowed leaching of soluble substances and some decomposition. Monthly collections would have been better, but were simply not possible given the remote locations. Collections missed litter from short-statured plants (<20 cm), CWD, and root turnover. The estimated CWD input was 18-27% of aboveground fine litter inputs; which is a reasonable range (Harmon et al 1986).

Wind speeds over 13.4 $m \cdot s^{-1}$ are most common in October and November at Juneau, Alaska (Harris 1989, p. 3). This, coupled with the autumnal dieback of foliage, explains the litterfall peak observed in October and November. Annual litterfall was in the middle range of values reported for comparable forests (Table 20).

The lower rates found by Hurd (1971) at nearby sites are consistent with the generally lower productivity of forests on the glacial outwash plain of the Mendenhall Glacier (B.T. Bormann, personal communication). The proportion (59%) of foliage is slightly lower than the 70% suggested by Meentemeyer *et al.* (1982) and higher than the 45% reported by Grier (1976). There is some uncertainty in this proportion. It would be even lower if CWD were included; higher if some of the unknown litter fraction is of foliar origin. In comparison, Hurd (1971) found 65% of the litter to be non-woody.

Table 20. Reported values for litterfall, NPP, and biomass of spruce-hemlock forests

Forest Type	Location	Age	BA	Biomass	ANPP	LFALL	Reference
PISI	Pacific Northwest, USA	NA	NA	NA	NA	0.9	Tarrant *et al.* 1951
TSHE	Pacific Northwest, USA	NA	NA	NA	NA	1.1	Tarrant *et al.* 1951
PISI plantation	North Wales, UK	30	NA	NA	NA	2.1	Owen 1954
PISI/TSHE (54/46%)	Mendenhall Valley, AK	153	69	NA	NA	2.9	Hurd 1971
TSHE/PISI	Outer Point		73	404	4.9	3.8	This study
TSHE/PISI	Heintzleman		76	441	6	4.1	This study
TSHE/PISI	Hawk Inlet		70	422	4.4	4.9	This study
Conifer	boreal	NA	NA	250	8.5	6.0	Kimmins 1987
TSHE/PISI	OR coast	110	98	871	10.3	NA	Fujimori *et al.* 1976
TSHE/PISI (76/24%)	Cascade Head, OR	121	100	NA	19.9	6.1	Grier 1976
Conifer	temperate	NA	NA	300	15	8.5	Kimmins 1987

Note: PISI, Sitka spruce; TSHE, western hemlock; NA, not available.

Use of the Raich and Nadelhoffer equation seemed to yield the better estimates of soil respiration, given the assumptions necessary to construct the soil C model. Soil C accumulated in mound soils at 0.1 to 0.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$. Model estimates of soil C change ranged from 0.4 to 0.7 $Mg \cdot ha^{-1} \cdot yr^{-1}$ using the Raich and Nadelhoffer relation. In contrast, estimates of soil C change ranged from -3 to -8 $Mg \cdot ha^{-1} \cdot yr^{-1}$ using temperature-adjusted *in vitro* soil respiration rates. Clearly the lab-determined estimates are inflated. This may be due to an incorrect Q_{10} value, sample disturbance, or artifacts introduced by the respirometry system. The Raich and Nadelhoffer equation (1989) was based on field measurements of soil respiration in a wide range of sites and seasons. In contrast, my lab measurements of soil respiration were limited to a one-time sample at each site. These results appear to confirm the usefulness of their approach.

The generally greater *in vitro* respiration of Outer Point soils may result from the method of soil sampling. Heintzleman Ridge and Hawk Inlet soils were sampled by removing soil block intact from the field. Soils were separated by horizon only just before the assay. In contrast, Outer Point soils were separated in the field, and in general were more highly disturbed. The added disturbance may have promoted higher respiration rates.

CONCLUSION

Evaluation of the Within-Stand Chronosequence Method

This study demonstrates that it is possible to identify within-stand soil chronosequences that are useful for studying questions about soil development and soil ecology. I have identified several problems in using these chronosequences; some are general, others are specific to their use in the current study.

The range of soil ages studied may have been too restricted: recent windthrows were rare within the study sites, and as a result all the mounds studied were over 40 years-old. Early stages of mound development were ignored and I may have missed important changes occurring shortly after mound creation. The reliance on dendrochronological methods for dating soil surfaces restricted the range of soil development examined; more significant or opposing trends may have appeared if older, but undatable, soils with highly-developed illuvial horizons were included in the study. The mounds studied may have been too young to exhibit changes detectable by my techniques. A more fruitful approach might have been to correlate soil biological processes with the degree of illuvial horizon development, ignoring age.

Failure to detect significant age effects may be attributed to a genuine absence of effects or to the insensitivity of the analytical method. It is possible that the age classes used may not have corresponded to functional classes. Just as space is substituted for time in chronosequence studies, time is substituted for process; the passage of time *per se* changes nothing; only process rates matter. Variation in the rate of change of a process will obscure the effect of development if time is used as the independent analytical variable.

For instance, podzolization may not proceed at the same rate on all soils within an age class: accidents of parent material, microrelief, patterns of canopy throughfall, etc. may affect how rapidly a particular soil develops. This is well illustrated by the variable development of spodic horizons within the medium age class of soils. Also, significant differences in eluvial and illuvial horizon development may be observed within short distances — roughly 10-20 cm. For example, I have observed how soils under thick

deposits of decayed wood seem to show more advanced podzolization than do adjacent soils of the same age on the same mound.

I used mounds to provide datable soil surfaces — a requirement of some of my objectives — but it is possible that soil development rates differ between mounds and the intervening flat areas, because the slope, relief, and orientation of mounds may affect soil water and energy relations. This limits the scope of inference of my results. Limiting sampling to mounds may have reduced the ability to detect podzolization-related changes. If podzolization affects soil processes, part of the effect may be due to reduced permeability of the illuvial horizons and subsequently increased water saturation of overlying horizons. If that is so, mounds may have masked the effect of podzolization, because lateral flow of ground water on steeply-inclined mound surfaces would reduce the saturation of soils overlying the poorly-permeable horizon.

Development of Soils on Windthrow Mounds

It is now possible to present a general description of the first 300-400 years of soil development on windthrow mounds. Although the rate of soil development may have varied slightly between sites, the pattern of development was consistent from site to site. The pattern of biological activity was less consistent and may have reflected between-site variation in microclimate, hydrology, soil parent material, disturbance history, or rate of soil development. The following discussions of very recent and very old windthrow mound soils are based on many observations of mounds not formally included in the current study.

Recent mounds (0-10 yr) are frequently disturbed as the upturned root and soil mass collapses. Plants that become established on the steep and unstable root mass are often dislodged and soil from the collapsing root mass frequently buries young plants and the developing litter layer on the mound surface. No pedogenic horizons can be distinguished in the mound soil, although some layering may be visible from the deposition of varied mineral and organic materials sloughed from the root mass. The sparse surface litter layer and the presence of large amounts of buried organic matter confines most of the soil biological activity to the mineral soil.

Important questions remain regarding the nutrient dynamics of this early stage of soil development. If this stage is marked by rapid mineralization of nutrients contained in

upturned soil horizons, losses of newly-available nutrients are likely if root or microbial uptake is delayed. Further studies are required of nutrient mineralization, root growth, microbial biomass, and leaching losses during the period immediately following mound creation.

Young mounds (40-60 yr) are relatively stable aggrading systems, characterized by the growth of the forest floor and A horizon. A thin forest floor is present, composed primarily of young fibric material, and horizon development in the mineral soil is typically limited to a few centimeters of A horizon. The young mound soils had the highest observed polysaccharidase activities, which suggests that plant residue decomposition proceeds rapidly during this stage of soil development. On the other hand, these soils had the lowest respiration and mineralizable-N per unit area, due to their meager organic matter accumulation. The thin forest floor also lacks the buffering capacity of older, thicker organic horizons, so soil biological activity may vary more than in older soils in response to changing temperature and moisture.

There is some evidence that medium-aged mounds (140-170 yr) may have the most highly productive soils. The forest floor has well-developed fibric and hemic layers, but lacks large accumulations of poorly decomposable sapric material. A moderately-thick forest floor may provide habitat for a more diverse soil fauna and may buffer the soil system from changing physical conditions. The buffering effect is suggested by trends observed in my cellulose decomposition study, which spanned a particularly warm and dry summer. At Hawk Inlet, the warmest and driest site, decomposition increased with age and forest floor development, but at Outer Point, the wettest site, decomposition declined with age.

Mineral soil horizon development is most variable in this age class: some soils have only A horizons but others have well-developed spodic horizons. Clearly the rate of soil development varies even under the relatively uniform conditions within a single stand. Most enzyme activities are lower in this age class compared with those of young soils, but medium-aged soils have the highest rate of soil respiration per unit SOM. High respiration rates coupled with low polysaccharidase levels suggest that this age group may have the greatest root activity.

Old soils (300-400 yr) show some signs of decline, but are still fairly productive. Their thick forest floors are differentiated into fibric, hemic, and sapric horizons, and are

increasingly dominated by sapric material, which is extensively decomposed and humified. Sapric organic matter has very low respiratory and enzyme activity by weight. Mineral soil horizons show well-developed spodic horizons and generally have thick eluvial horizons.

The forest floor, through its accumulation of organic matter, dominates the biological activity of old soils. Younger soils have small pools of organic matter that turn over rapidly, but the old soils have very large pools of organic matter that turn over slowly. As a consequence, soil respiration and mineralizable-N per unit area are highest in old soils, but this is due to the large accumulations of forest floor, not because of greater specific activity. If the trend toward slower turnover of C and N continues as soils age beyond 350-400 yr, it is likely that biological activity per unit area will decline, despite large accumulations of forest floor and SOM.

Some Implications of Rapid Soil Development in Southeast Alaska

From this study, it appears that the rates of visible soil profile development on windthrow mounds (i.e., the appearance of genetic horizons) exceed those previously observed on recessional moraines or on uplifted beach terraces (Chandler 1942, Crocker and Dickson 1957, Ugolini 1968, Ugolini and Mann 1979). For example, half of the medium-aged windthrow mounds (160-yr) had distinct eluvial and illuvial horizons; this precocious development has not been observed previously in this region (see page 3).

In contrast, soil organic C appears to accumulate faster during the early stages of the glacial recession chronosequences (first 100-200 yr) than it does in the windthrow chronosequences. Note that comparisons between studies may be misleading due to different sampling depths, analytical methods, and conversion factors used by the various researchers. Reported early accumulation rates on glacial deposits range from 0.5-1.1 Mg C/ha/yr, dropping to 0.2-0.3 Mg C/ha/yr after 150-200 years (Chandler 1942, Crocker and Dickson 1957, Bormann and Sidle 1990). The rate of C accumulation on windthrow mounds during the first 350 years ranged from 0.1-0.3 Mg C/ha/yr, roughly comparable to accumulation rates observed in the conifer-dominated stages of post-glacial succession. These results -- considering that glacial recession and windthrow chronosequences both start with bare, undifferentiated soils -- suggest that the site vegetation is the primary factor controlling rates of C accumulation in these soils.

This raises the question of what is responsible for the relatively rapid profile development on mound soils. Other pedological studies in this region have examined soils developing during primary succession on freshly exposed glacial deposits or uplifted beach terraces. In contrast, this study reports the development of soils previously exposed to soil-forming factors. Recent-mound soils differ from freshly exposed parent material in several ways; one or more of these factors may explain the accelerated pace of soil profile development observed. First, mound soils at all sites had been weathered to some degree prior to the creation of the mound surface. During previous cycles of soil development they probably lost carbonates and other readily soluble minerals. Second, in the mounds, fresh C horizon mineral soil is mixed with soil from well-developed A, E, and B horizons and with organic matter from the forest floor. Juxtaposition of these materials could facilitate rapid mineral weathering and soil development. Third, the newly-created mound soil surfaces receive organic inputs from the surrounding intact forest vegetation, but primary chronosequences have extended pioneer phases with little or no vegetation cover. Finally, even though windthrow mounds within conifer stands appear to have lower rates of soil C accumulation, the organic matter that is supplied to the soil (conifer foliage, bark, and coarse woody debris) may be more effective at promoting podzolization. It was noted earlier that heavy accumulations of decaying coarse woody debris seemed to be associated with the greatest E-horizon development. Large inputs of conifer CWD would only appear late in the primary succession chronosequences, in contrast to the within-stand chronosequences, where conifer CWD inputs can occur from the very earliest stages.

Clearly, rates of soil development estimated from studies of primary succession must be used with caution if applied to soils developing within long-established stands, but the question remains whether soil development continues at this rapid pace in soils older than 350 years, or does it asymptotically approach some equilibrium condition? Published rates of soil development on primary materials suggest that many soil parameters change rapidly at first, then change more slowly, and ultimately approach some equilibrium value. Examination of presumably older surfaces at my study sites showed that even the oldest mounds studied had not yet approached the maximum possible profile development, thus significant further soil profile development is likely. If the trends of nutrient availability and organic matter turnover observed in this study continue, soil development beyond 350

years will probably reduce soil productivity as nutrients accumulate in poorly-decomposable sapric and spodic horizons.

The rapid soil development observed in this study reminds us that soil cannot be considered a constant during the development of a single stand, much less over multiple rotations. Within the life span of a single tree, soils can develop substantial spodic and sapric horizons that significantly change the physical, chemical, and biological properties of the soil. Thus it appears that maintaining soils in the productive intermediate stage of development requires relatively frequent soil-mixing disturbance, on the order of once every 300-400 years.

Soil Development Effects at the Stand or Ecosystem Level

A serious obstacle to generalizing the results is the variation of the age functions of some soil parameters between sites. The trends of some soil parameters with age actually reverse between sites, allowing only site-specific conclusions in the absence of data explaining the between-site variation. Another difficulty results from the choice of soil surfaces that were studied. At least four types of soil surfaces were present at the study sites: pits, mound fronts (the side opposite the fallen tree), mound backs, and undisturbed areas. Many so-called undisturbed areas contained very old windthrow-disturbed soils where surface evidence of disruption was no longer apparent. Of the several soil surfaces present, only the mound fronts were studied. As discussed earlier, this restriction may limit the inferences that can be drawn from the data. The slope, relief, and orientation of mounds may yield soil development rates different from rates occurring on other surface types, but the overall direction of development, ultimately producing a Spodosol, does not differ. One exception to this generalization is that very old pits sometimes contain Histosols.

Windthrow mound soils exist in a matrix of soils in widely different stages of development. Matter and energy are exchanged between soil bodies through litterfall, root and hyphal translocation, and soil water movement. We need to recognize that mound soils developing in this context probably develop differently from soils developing in more uniform surroundings, but the mixed context is the norm in this region.

The juxtaposition of youthful and mature soils may enhance the overall soil productivity. Undisturbed areas could provide refugia for soil organisms and may be a source of propagules or colonizers. Older soils could enhance stability and buffering through nutrient conservation, moderation of soil moisture, and protection from soil erosion. Recently disturbed areas are areas of accelerated nutrient turnover that may be tapped by plants growing on adjacent older soils or by plants occupying the mound itself. The bare mineral soils of recent mounds and thin forest floors of young mounds contribute to the habitat and substrate diversity within the stand, perhaps increasing overall system productivity.

If the paludification hypothesis of Ugolini and Mann (1979) proves to be correct, the balance between rapid podzolization and the rejuvenation of soils by windthrow will be a key determinant of site productivity. The placic horizons implicated by Ugolini and Mann (1979) were not observed at any of my study sites, but it appears that well developed Bh and Bs horizons also can retard water flow through the soil. For example, soil permeability on mounds at Outer Point and Heintzleman Ridge declined dramatically with soil surface age and spodic horizon development (B.T. Bormann, data on file at the USFS Forestry Sciences Laboratory, Corvallis, OR).

The rapid development of spodic horizons observed in this study could contribute to site paludification over a relatively short time span, particularly at sites where soil drainage is only marginally adequate for good forest growth. From my observations of recent and young windthrow mounds, I concluded that uprooting effectively mixes soils and destroys spodic horizons that might impede drainage. In addition, the elevated mounds provide well drained surfaces within sites that are otherwise excessively wet. Thus it appears that windthrow can effectively limit the contribution of podzolization to site paludification.

Opportunities for Future Research

To answer some of the questions raised by this study, it will be necessary to examine recent windthrow mounds and soils older than 350 years. We need to know how quickly the spodic horizons disappear and the fate of the nutrients released during their decomposition. To evaluate the potential for nutrient loss at this stage, we must under-

stand the dynamics of root ingrowth, plant cover establishment, and the proliferation of microbial biomass in recent mounds. The entire mound system — including the back, front, and pit — should be studied. As discussed above, the need for datable soil surfaces limited the age of soils examined in this study. We need to know if trends identified thus far continue or accelerate in old, highly developed soils. Since soil surface age will be unavailable, the best approach will be to correlate the soil properties of interest with some measure of the degree of soil development.

Controlled-environment, experimental studies of soil disturbance could elucidate the dynamics of spodic horizon breakdown and nutrient release. Such studies could provide information useful in the design of field treatments intended to improve site productivity. Several types of soil disturbance should be included: physical disruption, wetting and drying, freezing and thawing, and mixing with mineral or organic materials. Of course the ultimate test of the effect of soil disturbance on productivity requires field testing at the small-plot or operational scales. Only at this scale can we get a realistic view of plant response to soil disturbance.

As discussed earlier, most forest soils in this region are mosaics of multiple classes of soil surface age and degree of development. This complicates correlating soil development with stand- or ecosystem-level properties such as productivity. By employing some measure of podzolization (horizon development, chemical indices, etc.), extensive sampling, and spatial statistics, it should be possible to generate a meaningful, area-weighted statistic that expresses the overall degree of soil development within a plot, stand, or ecosystem. If the effects of other productivity-influencing variables can be controlled or accounted for, such a statistic could yield real insight into the relation between soil development and productivity at a scale of interest to ecologists and resource managers alike.

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APPENDIX

Table 21. Amylase activity of Heintzleman Ridge soils

Layer	Mound Age Class		
	Young	Medium	Old
	μmol glucose equivalents · g soil^{-1} · h^{-1}		
Oi	15.2 ± 1.9 (3)†	10.6 ± 3.1 (3)	10.0 ± 3.7 (3)
Oe	10.6 ± 2.1 (3)	6.22 ± 1.8 (3)	7.61 ± 0.50 (3)
Oa	--	4.35 (1)	4.03 ± 0.50 (2)
Wood	--	--	4.61 (1)
A	5.39 ± 0.96 (3)	1.84 ± 0.06 (2)	--
E	--	1.61 (1)	0.37 ± 0.16 (3)
Bh	--	1.25 (1)	1.03 ± 0.43 (3)
Bs	--	--	0.67 ± 0.47 (3)
BC1	0.89 ± 0.39 (3)	0.85 ± 0.27 (3)	0.29 ± 0.29 (3)
BC2	0.16 ± 0.04 (3)	0.35 ± 0.19 (2)	0.88 (1)
BC3	0.66 ± 0.22 (2)	0.00 (1)	--

† Mean ± standard error (number of observations).

Table 22. Cellulase activity of Heintzleman Ridge and Outer Point soils

Layer	Mound Age Class		
	Young	Medium	Old
	μmol glucose equivalents · g soil^{-1} · h^{-1}		
	Heintzleman Ridge		
Oi	18.1 ± 6.0 (3)†	16.4 ± 3.3 (3)	20.3 ± 1.8 (3)
Oe	9.94 ± 2.1 (3)	5.70 ± 0.73 (3)	5.07 ± 0.79 (3)
Oa	--	1.63 (1)	2.00 ± 0.66 (2)
Wood	--	--	3.50 (1)
A	2.10 ± 0.34 (3)	1.83 ± 0.75 (2)	--
E	--	1.12 (1)	0.33 ± 0.16 (3)
Bh	--	1.28 (1)	0.48 ± 0.17 (3)
Bs	--	--	0.72 ± 0.35 (3)
BC1	0.73 ± 0.24 (3)	0.78 ± 0.19 (3)	0.37 ± 0.15 (3)
BC2	0.19 ± 0.09 (3)	0.41 ± 0.21 (2)	0.64 (1)
BC3	0.21 ± 0.01 (2)	0.07 (1)	--
	Outer Point		
Oi	24.0 ± 2.7 (3)	27.4 ± 6.4 (3)	29.5 ± 4.8 (3)
Oe	9.46 ± 1.3 (2)	12.8 ± 5.9 (3)	7.57 ± 2.1 (3)
Oa	--	7.83 ± 2.8 (2)	2.23 ± 0.43 (3)
Wood	--	--	6.72 (1)
A	1.77 ± 0.34 (3)	1.82 ± 0.10 (2)	--
E	--	1.67 (1)	0.15 ± 0.10 (3)
Bh	--	1.23 (1)	0.79 ± 0.20 (3)
Bs	--	0.84 (1)	0.80 ± 0.21 (3)
BC1	0.50 ± 0.24 (3)	0.64 ± 0.20 (3)	0.77 ± 0.28 (3)
BC2	0.36 ± 0.20 (3)	0.41 ± 0.10 (2)	0.30 (1)

† Mean ± standard error (number of observations)

Table 23. Xylanase activity of Heintzleman Ridge soils

Layer	Mound Age Class		
	Young	Medium	Old
	μmol glucose equivalents · g soil^{-1} · h^{-1}		
Oi	26.9 ± 10.8 (3)†	27.7 ± 8.4 (3)	37.4 ± 6.3 (3)
Oe	15.0 ± 5.3 (3)	11.6 ± 1.4 (3)	10.1 ± 1.4 (3)
Oa	--	4.71 (1)	5.86 ± 1.9 (2)
Wood	--	--	6.06 (1)
A	5.59 ± 0.38 (3)	3.91 ± 1.8 (2)	--
E	--	2.98 (1)	0.96 ± 0.23 (3)
Bh	--	1.95 (1)	1.15 ± 0.41 (3)
Bs	--	--	1.44 ± 0.61 (3)
BC1	1.75 ± 0.76 (3)	1.65 ± 0.26 (3)	1.02 ± 0.31 (3)
BC2	1.23 ± 0.55 (3)	1.30 ± 0.03 (2)	0.33 (1)
BC3	1.02 ± 0.49 (2)	1.33 (1)	--

† Mean ± standard error (number of observations)

Table 24. Phosphatase activity of Heintzleman Ridge and Outer Point soils

Layer	Mound Age Class		
	Young	Medium	Old
	μmol PNP · g soil^{-1} · h^{-1}		
	Heintzleman Ridge		
Oi	182 ± 8.1 (3)†	149 ± 27 (3)	143 ± 15 (3)
Oe	127 ± 8.1 (3)	110 ± 23 (3)	84.0 ± 3.6 (3)
Oa	--	92.5 (1)	78.5 ± 6.5 (2)
Wood	--	--	59.8 (1)
A	58.6 ± 11 (3)	63.2 ± 25 (2)	--
E	--	45.8 (1)	16.1 ± 2.6 (3)
Bh	--	51.0 (1)	33.6 ± 5.9 (3)
Bs	--	--	44.2 ± 8.5 (3)
BC1	39.6 ± 15 (3)	31.7 ± 9.7 (3)	32.3 ± 4.5 (3)
BC2	21.5 ± 5.7 (3)	24.8 ± 2.0 (2)	23.3 (1)
BC3	19.2 ± 0.4 (2)	30.6 (1)	--
	Outer Point		
Oi	202 ± 43 (3)	172 ± 41 (3)	195 ± 9.2 (3)
Oe	89.0 ± 38 (2)	96.5 ± 13 (3)	99.5 ± 25 (3)
Oa	--	76.9 ± 13 (2)	53.7 ± 4.6 (3)
Wood	--	--	81.3 (1)
A	29.6 ± 0.9 (3)	27.3 ± 1.4 (2)	--
E	--	42.9 (1)	14.3 ± 3.0 (3)
Bh	--	30.4 (1)	35.6 ± 4.3 (3)
Bs	--	24.2 (1)	29.4 ± 3.9 (3)
BC1	21.3 ± 2.9 (3)	14.7 ± 1.5 (3)	24.7 ± 1.8 (3)
BC2	16.4 ± 2.0 (3)	17.9 ± 1.9 (2)	23.3 (1)

† Mean ± standard error (number of observations)

Table 25. Peroxidase activity of Heintzleman Ridge and Outer Point soils

Layer	Mound Age Class		
	Young	Medium	Old
	Units Absorbance Change · g soil^{-1} · min^{-1}		
		Heintzleman Ridge	
Oi	4.50 ± 2.70 (3)†	8.42 ± 6.10 (3)	4.61 ± 2.59 (3)
Oe	2.58 ± 1.68 (3)	0.36 ± 0.06 (3)	0.95 ± 0.81 (3)
Oa	--	1.18 (1)	0.58 ± 0.58 (2)
Wood	--	--	0.22 (1)
A	1.80 ± 0.94 (3)	1.68 ± 0.77 (2)	--
E	--	1.36 (1)	0.33 ± 0.24 (3)
Bh	--	2.82 (1)	1.61 ± 0.02 (3)
Bs	--	--	2.48 ± 0.15 (3)
BC1	0.77 ± 0.56 (3)	2.15 ± 0.18 (3)	2.69 ± 1.56 (3)
BC2	0.18 ± 0.06 (3)	0.86 ± 0.58 (2)	0.50 (1)
BC3	0.58 (1)	0.32 (1)	--
		Outer Point	
Oi	7.27 ± 0.22 (3)	4.22 ± 3.15 (2)	4.83 ± 0.76 (3)
Oe	1.65 ± 0.09 (2)	2.25 ± 1.47 (3)	1.11 ± 0.25 (3)
Oa	--	0.63 ± 0.63 (2)	0.71 ± 0.13 (3)
Wood	--	--	0.68 (1)
A	1.85 ± 0.15 (3)	1.12 ± 0.53 (2)	--
E	--	0.04 (1)	0.22 ± 0.15 (2)
Bh	--	2.58 (1)	2.46 ± 0.51 (2)
Bs	--	1.23 (1)	1.73 ± 0.89 (2)
BC1	0.82 ± 0.16 (3)	0.21 ± 0.09 (3)	1.22 ± 0.55 (3)
BC2	0.65 ± 0.39 (3)	0.99 ± 0.85 (2)	0.21 (1)

† Mean ± standard error (number of observations)

Table 26. Phenol oxidase activity of Outer Point soils

Layer	Mound Age Class		
	Young	Medium	Old
	Units Absorbance Change · g soil^{-1} · min^{-1}		
Oi	0.74 ± 0.22 (3)†	0.51 ± 0.15 (3)	0.56 ± 0.18 (3)
Oe	0.19 ± 0.06 (2)	0.35 ± 0.06 (3)	0.28 ± 0.09 (3)
Oa	--	0.44 ± 0.09 (2)	0.20 ± 0.05 (3)
Wood	--	--	0.52 (1)
A	0.26 ± 0.09 (3)	0.12 ± 0.01 (2)	--
E	--	0.21 (1)	0.14 ± 0.11 (3)
Bh	--	0.24 (1)	0.46 ± 0.19 (3)
Bs	--	0.29 (1)	0.24 ± 0.18 (3)
BC1	0.11 ± 0.04 (3)	0.04 ± 0.04 (3)	0.12 ± 0.07 (3)
BC2	0.12 ± 0.05 (3)	0.07 ± 0.07 (2)	0.18 (1)

† Mean ± standard error (number of observations)

Table 27. Mineralizable soil N, by site, age, and layer

Layer	Mound Age Class		
	Young	Medium	Old
		mg NH_4^+-N · kg $soil^{-1}$	
		Heintzleman Ridge	
Oi	292 ± 48 (3)†	254 ± 42 (3)	235 ± 41 (3)
Oe	247 ± 70 (2)	184 ± 17 (3)	247 ± 40 (3)
Oa	--	165 (1)	141 ± 6.4 (3)
Wood	--	--	128 (1)
A	44.4 ± 8.5 (3)	25.2 ± 0.50 (2)	--
E	--	15.7 (1)	12.4 ± 2.5 (3)
Bh	--	4.3 (1)	9.70 ± 4.0 (3)
Bs	--	--	20.0 ± 3.2 (2)
BC1	29.1 ± 7.2 (3)	14.6 ± 1.6 (3)	--
		Hawk Inlet	
Oi	203 ± 49 (4)	298 ± 16 (4)	208 ± 58 (3)
Oe	123 ± 6.9 (2)	170 ± 48 (4)	182 ± 50 (3)
Oa	--	--	34.3 ± 12 (2)
Wood	--	--	108 (1)
A	34.9 ± 3.9 (4)	50.1 ± 13 (2)	--
E	--	34.2 (1)	23.3 ± 7.8 (3)
Bh	--	69.6 ± 34 (2)	36.9 ± 6.4 (3)
Bs	--	38.1 (1)	54.6 ± 15 (3)
		Outer Point	
Oi	169 ± 19 (4)	264 ± 45 (3)	211 ± 37 (3)
Oe	85.5 (1)	204 ± 46 (4)	242 ± 26 (4)
Oa	--	--	138 ± 12 (3)
Wood	--	--	141 (1)
A	40.8 ± 12 (3)	31.5 ± 16 (2)	--
E	--	--	37.2 ± 13 (3)
Bh	--	37.5 ± 3.2 (2)	45.4 ± 3.9 (4)
Bs	--	25.2 (1)	22.3 ± 4.8 (3)
BC1	21.0 ± 8.6 (3)	40.5 (1)	52.5 (1)

† Mean ± standard error (number of observations)

Table 28. Soil respiration ($\mu g\ CO_2 \cdot g\ soil^{-1} \cdot h^{-1}$) by site, age, and layer

Layer	Mound Age Class		
	Young	Medium	Old
		Heintzleman Ridge	
Oi	83.9 ± 14.8 (4)†	86.7 ± 12.9 (3)	82.9 ± 10.3 (3)
Oe	51.3 ± 7.35 (3)	38.4 ± 1.04 (3)	41.0 ± 1.99 (3)
Oa	--	27.6 (1)	22.3 ± 2.1 (3)
A	17.8 ± 3.14 (4)	6.5 ± 0.20 (2)	--
E	--	4.1 ± NA (1)	3.1 ± 0.35 (3)
Bh	--	4.0 ± NA (1)	5.4 ± 0.44 (3)
Bs	--	--	3.3 ± 0.45 (2)
BC1	6.3 ± 0.86 (4)	2.9 ± 0.39 (3)	--
		Hawk Inlet	
Oi	90.8 ± 13.2 (4)	130 ± 23.0 (5)	104 ± 7.82 (2)
Oe	43.4 ± 0.97 (2)	82.3 ± 13.9 (5)	70.6 ± 0.36 (2)
Wood	--	--	27.0 (1)
A	15.9 ± 3.33 (4)	14.4 ± 1.95 (2)	--
E	--	15.8 ± 1.80 (2)	11.1 ± 5.75 (2)
Bh	--	8.9 ± 2.20 (3)	16.6 ± 7.80 (2)
Bs	--	7.3 ± 0.20 (2)	9.4 ± NA (1)
BC1	7.2 ± 0.69 (4)	7.2 ± 3.28 (3)	--
		Outer Point	
Oi	123 ± 31.0 (3)	77.3 ± 16.3 (3)	102 ± 8.38 (3)
Oe	86.1 ± 49.9 (2)	53.6 ± 1.73 (3)	48.6 ± 17.6 (3)
Oa	--	40.1 ± 9.21 (2)	19.2 ± 7.82 (3)
Wood	--	--	29.4 (1)
A	12.2 ± 0.64 (3)	13.5 ± 0.87 (2)	--
E	--	--	3.4 ± 1.21 (3)
Bh	--	15.2 ± NA (1)	8.3 ± 4.92 (3)
Bs	--	17.1 ± NA (1)	8.1 ± 4.78 (3)
BC1	8.1 ± 4.02 (3)	7.7 ± 1.00 (3)	17.2 ± 2.46 (3)

† Mean ± standard error (number of observations). NA = not applicable.

Table 29. Soil respiration ($\mu g\ CO_2 \cdot g\ SOM^{-1} \cdot h^{-1}$) by site, age, and layer

Layer	Mound Age Class		
	Young	Medium	Old
		Heintzleman Ridge	
Oi	104 ± 12.9 (4)†	94.8 ± 15.3 (3)	89.2 ± 11.4 (3)
Oe	80.0 ± 17.8 (3)	47.7 ± 5.08 (3)	46.7 ± 2.40 (3)
Oa	--	30.7 (1)	26.6 ± 2.92 (3)
A	53.5 ± 11.9 (4)	25.9 ± 3.20 (2)	--
E	--	47.1 (1)	45.2 ± 6.12 (3)
Bh	--	22.7 (1)	23.6 ± 1.52 (3)
Bs	--	--	17.6 ± 4.70 (2)
BC1	37.3 ± 6.02 (4)	26.6 ± 5.11 (3)	--
		Hawk Inlet	
Oi	109 ± 14.7 (4)	150 ± 31.3 (5)	109 ± 8.38 (2)
Oe	61.9 ± 4.42 (2)	123 ± 23.0 (5)	75.2 ± 0.33 (2)
Wood	--	--	27.6 (1)
A	44.8 ± 6.06 (4)	60.4 ± 9.90 (2)	--
E	--	103 ± 5.70 (2)	66.6 ± 20.0 (2)
Bh	--	45.5 ± 9.34 (3)	46.3 ± 14.8 (2)
Bs	--	48.6 ± 2.50 (2)	24.6 (1)
BC1	43.8 ± 7.31 (4)	52.3 ± 25.8 (3)	--
		Outer Point	
Oi	130 ± 34.4 (3)	80.4 ± 17.5 (3)	105 ± 8.42 (3)
Oe	105 ± 59.3 (2)	56.9 ± 2.32 (3)	51.7 ± 18.5 (3)
Oa	--	45.2 ± 9.84 (2)	23.1 ± 8.16 (3)
Wood	--	--	29.8 (1)
A	42.7 ± 7.41 (3)	64.6 ± 17.4 (2)	--
E	--	--	39.7 ± 26.5 (3)
Bh	--	41.7 (1)	17.1 ± 9.29 (3)
Bs	--	42.2 (1)	20.6 ± 11.6 (3)
BC1	32.0 ± 14.6 (3)	69.3 ± 14.9 (3)	55.8 ± 7.53 (3)

† Mean ± standard error (number of observations)

Table 30. Proportion of mass lost from cellulose packs during 1 year: breakdown by site, mound age, and pack position

Position	Young	Medium	Old
		Heintzleman Ridge	
Surface	0.360 ± 0.03 (24)†	0.231 ± 0.03 (18)	0.578 ± 0.05 (18)
Organic	0.497 ± 0.04 (24)	0.556 ± 0.05 (18)	0.427 ± 0.08 (18)
Mineral	0.205 ± 0.02 (24)	0.103 ± 0.03 (18)	0.213 ± 0.05 (18)
Upper Bh	--	0.082 ± 0.02 (6)	0.054 ± 0.03 (18)
		Hawk Inlet	
Surface	0.203 ± 0.03 (24)	0.450 ± 0.05 (30)	0.489 ± 0.11 (6)
Organic	0.517 ± 0.03 (24)	0.764 ± 0.03 (30)	0.746 ± 0.05 (6)
Mineral	0.386 ± 0.05 (24)	0.781 ± 0.03 (30)	0.795 ± 0.03 (6)
Upper Bh	--	0.361 ± 0.08 (18)	0.768 ± 0.08 (6)
		Outer Point	
Surface	0.252 ± 0.02 (24)	0.211 ± 0.02 (24)	0.363 ± 0.03 (24)
Organic	0.407 ± 0.03 (24)	0.440 ± 0.05 (24)	0.164 ± 0.03 (24)
Mineral	0.219 ± 0.02 (24)	0.193 ± 0.05 (24)	0.094 ± 0.02 (24)
Upper Bh	--	0.176 ± 0.08 (6)	0.040 ± 0.02 (24)

† Mean ± standard error (number of observations)

Table 31. Correlations between litter decomposition at the surface and mid-organic horizons and the chemical or biological properties of the organic or upper mineral soil layers

Soil Property	Site	Layer	r_s	p	n
		Surface			
Al_{bic}	All Sites	Organic	-0.50	0.010	25
C:N	Outer Point	Mineral	-0.57	0.050	12
C:N	Heintzleman	Organic	0.65	0.030	11
Ca_{oxal}	All Sites	Mineral	-0.58	0.003	24
Fe_{pyr}	Heintzleman	Organic	-0.59	0.050	11
N_{tot}	Heintzleman	Organic	-0.79	0.004	11
$[H^+]$	Heintzleman	Organic	0.73	0.010	11
		Mid-Organic			
Al_{bic}	All Sites	Organic	0.50	0.010	25
Al_{oxal}	All Sites	Organic	0.56	0.003	25
Fe_{bic}	All Sites	Organic	0.53	0.007	25
N_{ash}	All Sites	Organic	0.34	0.050	33
P_{bic}	All Sites	Organic	0.46	0.020	25

Note: ash, concentration based on ashed soil mass; bic, bicarbonate-extractable; $[H^+]$, hydrogen ion activity; oxal, oxalate-extractable; pyr, pyrophosphate-extractable; tot, total concentration based on unashed soil mass

Table 32. Correlations between cellulose decomposition at the soil surface and the chemical or biological properties of the organic layer

Soil Property	Site	r_s	p	n
Al_{bic}	Outer Point	0.57	0.050	12
Al_{pyr}	Heintzleman	0.75	0.010	11
cellulase	Outer Point	-0.70	0.040	9
Mn_{bic}	Outer Point	-0.68	0.020	12
Mn_{oxal}	Outer Point	-0.61	0.040	12
N_{ash}	Heintzleman	0.74	0.010	11
N_{m^2}	Heintzleman	0.72	0.010	11
P_{m^2}	Outer Point	0.62	0.030	12

Note: ash, concentration based on ashed soil mass; bic, bicarbonate-extractable; m^2, mass per unit area; oxal, oxalate-extractable; pyr, pyrophosphate-extractable

Table 33. Correlations between cellulose decomposition at the mid-organic horizon and the chemical or biological properties of the organic or upper mineral soil layers

Soil Property	Site	Layer	r_s	p	n
Al_{bic}	All Sites	Organic	-0.72	<0.001	25
Al_{c-d}	Outer Point	Mineral	0.69	0.010	12
Al_{HCl}	Outer Point	Organic	0.67	0.020	12
Al_{oxal}	Outer Point	Mineral	0.62	0.030	12
Al_{oxal}	All Sites	Organic	-0.51	0.010	25
Al_{pyr}	Outer Point	Mineral	0.64	0.030	12
Al_{pyr}	All Sites	Organic	-0.54	0.001	33
amylase	Heintzleman	Organic	-0.67	0.050	9
C:P	Outer Point	Mineral	-0.64	0.030	12
Ca_{bic}	All Sites	Mineral	0.51	0.010	24
cellulase	Outer Point	Mineral	0.68	0.040	9
Fe_{bic}	All Sites	Organic	-0.58	0.002	25
Fe_{c-d}	Outer Point	Mineral	0.62	0.030	12
Fe_{c-d}	Outer Point	Organic	0.57	0.050	12
Fe_{HCl}	Outer Point	Organic	0.61	0.040	12
Fe_{oxal}	Outer Point	Mineral	0.66	0.020	12
Fe_{pyr}	Outer Point	Mineral	0.68	0.020	12
Fe_{pyr}	Heintzleman	Organic	-0.61	0.050	11
Mg_{c-d}	All Sites	Mineral	0.52	0.010	24
Mg_{HCl}	Hawk Inlet	Mineral	-0.68	0.030	10
Mg_{HCl}	Outer Point	Organic	0.63	0.030	12
phosphatase	Outer Point	Mineral	0.68	0.040	9
P_{m^2}	Hawk Inlet	Mineral	0.68	0.030	10
P_{oxal}	Outer Point	Mineral	0.60	0.040	12
P_{tot}	Outer Point	Mineral	0.64	0.020	12
R_W	Outer Point	Mineral	0.68	0.040	9
Si_{bic}	Outer Point	Mineral	0.67	0.020	12
$[H^+]$	Outer Point	Organic	-0.59	0.040	12

Note: bic, bicarbonate-extractable; c-d, citrate-dithionate-extractable; $[H^+]$, hydrogen ion activity; HCl, HCl-extractable; m^2, mass per unit area; oxal, oxalate-extractable; pyr, pyrophosphate-extractable; R_W, respiration per unit whole soil; tot, total concentration based on unashed soil mass

Table 34. Correlations between cellulose decomposition at the upper mineral soil boundary and the chemical or biological properties of the organic, upper mineral, or illuvial (Bh) soil layers

Soil Property	Site	Layer	r_s	p	n
Al_{bic}	All Sites	Illuvial	-0.78	0.003	12
Al_{bic}	All Sites	Organic	-0.64	0.001	25
$Al_{c\text{-}d}$	All Sites	Illuvial	-0.57	0.050	12
Al_{HCl}	All Sites	Illuvial	-0.76	0.005	12
C:P	All Sites	Illuvial	-0.58	0.020	15
C:P	Heintzleman	Mineral	0.64	0.040	11
Ca_{oxal}	All Sites	Illuvial	-0.57	0.050	12
Fe_{bic}	All Sites	Illuvial	-0.71	0.010	12
Fe_{bic}	All Sites	Organic	-0.51	0.010	25
Fe_{HCl}	All Sites	Illuvial	-0.83	0.001	12
Fe_{oxal}	All Sites	Illuvial	-0.61	0.040	12
$K_{c\text{-}d}$	All Sites	Mineral	0.51	0.030	19
K_{oxal}	Hawk Inlet	Mineral	0.72	0.020	10
$Mg_{c\text{-}d}$	All Sites	Mineral	0.53	0.010	24
Mn_{HCl}	All Sites	Illuvial	-0.63	0.030	12
NH_4^+-N	Outer Point	Mineral	-0.94	<0.001	10
phosphatase	Outer Point	Mineral	0.85	0.004	9
R_C	All Sites	Organic	0.59	0.001	29
R_O	All Sites	Organic	0.61	<0.001	30
R_W	All Sites	Organic	0.58	0.001	30
Si_{bic}	All Sites	Illuvial	-0.65	0.020	12
Si_{HCl}	All Sites	Illuvial	-0.77	0.003	12
$[H^+]$	All Sites	Organic	-0.59	<0.001	33

Note: bic, bicarbonate-extractable; c-d, citrate-dithionate-extractable; $[H^+]$, hydrogen ion activity; HCl, HCl-extractable; oxal, oxalate-extractable; R_C, respiration per unit soil carbon; R_O, respiration per unit SOM; R_W, respiration per unit whole soil

Table 35. All-site correlations between cellulose decomposition at the upper illuvial soil boundary and chemical properties of the upper mineral or illuvial soil layers.

Soil Property	Layer	r_s	p	n
$Al_{c\text{-}d}$	Mineral	0.89	0.001	10
C:P	Illuvial	-0.55	0.040	14
C:P	Mineral	-0.59	0.030	14
Ca_{bic}	Mineral	0.67	0.030	10
$Ca_{c\text{-}d}$	Illuvial	0.83	0.002	11
$Ca_{c\text{-}d}$	Mineral	0.75	0.010	10
Ca_{HCl}	Mineral	0.81	0.005	10
$Fe_{c\text{-}d}$	Mineral	0.76	0.010	10
Fe_{HCl}	Illuvial	-0.61	0.050	11
Fe_{HCl}	Mineral	0.73	0.020	10
Fe_{oxal}	Mineral	0.79	0.010	10
Fe_{pyr}	Mineral	0.74	0.004	13
Mg_{bic}	Mineral	0.79	0.010	10
$Mg_{c\text{-}d}$	Mineral	0.83	0.003	10
Mg_{HCl}	Illuvial	-0.64	0.040	11
Mg_{HCl}	Mineral	0.67	0.030	10
Mn_{bic}	Mineral	0.75	0.010	10
$Mn_{c\text{-}d}$	Illuvial	0.67	0.020	11
$Mn_{c\text{-}d}$	Mineral	0.82	0.004	10
Mn_{HCl}	Mineral	0.75	0.010	10
Mn_{oxal}	Mineral	0.75	0.010	10
P_{ash}	Mineral	0.61	0.020	14
$P_{c\text{-}d}$	Mineral	0.62	0.050	10
P_{ext}	Mineral	0.79	0.010	10
P_{oxal}	Mineral	0.83	0.003	10
P_{tot}	Mineral	0.71	0.004	14
Si_{HCl}	Mineral	0.76	0.010	10
$[H^+]$	Illuvial	-0.55	0.040	14
$[H^+]$	Mineral	-0.54	0.050	13

Note: ash, concentration based on ashed soil mass; bic, bicarbonate-extractable; c-d, citrate-dithionate-extractable; ext, total extractable; $[H^+]$, hydrogen ion activity; HCl, HCl-extractable; oxal, oxalate-extractable; pyr, pyrophosphate-extractable; tot, total concentration based on unashed soil mass