2697

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Rapid soil development after windthrow disturbance in pristine forests

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Summary

1 We examined how rapidly soils can change during secondary succession by observing soil development on 350-year chronosequences in three pristine forest ecosystems in south-east Alaska.

2 Soil surfaces, created by different windthrow events of known or estimated age, were examined within each of three forest stands (0.5–2.0 ha plots; i.e. a within-stand chronosequence method). Soil surfaces are more likely to have developed under common climate and vegetation conditions within stands than in the spatially separated ecosystems used in traditional chronosequence studies.

3 We observed rates of change that were higher than those previously reported for secondary succession, and were similar to those described for primary succession. Well-developed spodic and albic (podzol) horizons with characteristic C, Fe, and Al signatures were found in soil surfaces less than 150 years old. Carbon accumulated linearly at 21 g m^{-2} $year^{-1}$; mineral P and N became increasingly immobilized in the spodic horizon as time passed. We found no trend toward an equilibrium in C or N accumulation over the 350-year chronosequences in any of the three stands examined.

4 These rapid changes in soil and a shift in rooting from mineral to organic horizons appeared likely to reduce productive capacity of the soil during a single generation of trees. Windthrow or disturbances that mimic windthrow may be required at intervals of about 200–400 years to maintain soil productive capacity in these ecosystems.

Keywords: C accumulation, chronosequence, disturbance frequency, podzolization, soil development, soil disturbance, windthrow

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Introduction

Changes in terrestrial ecosystems that are independent of human activity, here termed 'baseline' changes, include ecosystem development, succession, soil development, natural disturbances such as fire and windthrow, disease, and evolution or migration of species. Without a thorough knowledge of the causes and rates of baseline change in ecosystems, human-induced change is difficult to detect, predict, or manage. This paper focuses on potential baseline changes in soils during secondary succession, an understanding that will help in developing strategies, for example, to conserve and sequester C (Dixon *et al.* 1994).

Slow, steady baseline changes in soil properties have been demonstrated for some ecosystems. For example, podzols are thought to form in 1000–3000 years (Tamm 1920; Burges & Drover 1953; Olson 1958; Protz *et al.* 1984), and glaciated soils undisturbed by people are assumed to have undergone a slow, steady change since the retreat of continental glaciers (Schlesinger 1990). More often, however, difficulty in detecting changes in soils over short periods, because of inherent variability, has led to the assumption of steady state or nonsignificant change

(34)

over periods less than one century. For example, an analysis of the role of tree growth and harvesting on global C balance assumes no change in storage of C in soil layers (Harmon *et al.* 1990).

Rapid changes in soils have also been reported. Losses of soil organic matter resulting from cultivation of agricultural soils range from 31% in 35 years (Martel & Paul 1974) to 35% in 15 years (Jenkinson & Rayner 1977). Planting pines can reduce soil C by 20% in 5 years in the 0–20-cm layer under *Pinus resinosa* Ait. and *Pinus rigida* Mill. (Bormann *et al.* 1993) and by 40% in 10 years in the 0–10 cm layer under *Pinus caribeae* var. *hondurensis* (Kadeba & Aduayi 1985). Soil maintained without vegetation can have soil C reduced by 40% in 5 years (Bormann *et al.* 1993). Abandonment of fields (Jenkinson 1971) and planting of N_2-fixing trees such as red alder (Tarrant & Miller 1963; Bormann *et al.* 1994) can result in rapid gains of C and N. Conifers can increase podzolic E horizons in several decades (Page 1968). Primary succession studies have found podzolic horizons forming in 100–150 years, C accumulating at 10–100 g m^{-2} $year^{-1}$, and site productivity increasing, especially in the presence of N_2-fixing plants (Tamm 1920; Tisdale *et al.* 1966; Dickson & Crocker 1953; Crocker & Major 1955; Ugolini 1968; Sollins *et al.* 1983; Miles 1985; Bormann & Sidle 1990).

Changes in soil resulting from human activity need to be placed in the context of natural baseline changes. For example, podzolization under conifers in northern Finland is thought to decrease tree growth because of organic matter accumulation and nutrient immobilization (Siren 1955; Miles 1986). In south-east Alaska, widespread succession from forest to bog vegetation (Dachnowski-Stokes 1941; Zach 1950; Lawrence 1958; Ugolini & Mann 1979; Klinger *et al.* 1990) may be partly caused by podzol formation, nutrient immobilization, and lack of soil disturbance (Ugolini & Mann 1979; Bormann & Sidle 1990; McClellan 1991). Soil disturbance, relative to the baseline, is reduced when trees are harvested before they can be windthrown and when disturbance is avoided with suspension-cable yarding systems, practices common in south-east Alaska over the last 30 years. Rates of soil development may be sufficiently rapid for reduced soil disturbance to speed successional changes and lower forest productivity.

In this paper, we examine rate of changes in soil properties during the first four centuries of secondary succession in pristine forests. We chose to use soil surfaces created by windthrow in this study because the age of such surfaces can be estimated, and because windthrow tends to homogenize the soil, making changes in soil properties easy to detect. This technique allows us to explore baseline changes in physical properties of the soil and in accumulation and redistribution of C, N, P, Fe, and Al. The predominance of windthrow and lack of both wildfire (Harris & Farr 1974; Harris 1989) and human activity make forest ecosystems of south-east Alaska an ideal setting for this research.

Methods

SITE DESCRIPTION

Three stands were chosen in the northern part of south-east Alaska. Precipitation, evenly distributed throughout the year, averages 1370 mm $year^{-1}$ at the nearest official collection station at the Juneau airport. 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. Stands were chosen that had roughly similar windthrow disturbance histories, vegetation, and soils. Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) are the dominant trees; *Vaccinium* spp. and various mosses are common understorey plants. On all stands, young, recently disturbed soils were described as Ochrepts, older more-developed soils as Humic Cryorthods, and scattered low-lying areas as Cryosaprists. Disturbances such as recent colluvial or alluvial action, fire, burrowing mammals, or earthworms were not found on these stands. The effect of frost under the thick vegetative canopy and humus and moss layers is evidently of little consequence; permafrost does not form at the elevation of these stands (Loewe 1966; Ugolini 1968). Windthrow appears to be the most important disturbance agent in these forest ecosystems. All three sites were affected to various extents in about 1830 by a large windthrow event.

The Hawk Inlet stand (58°8′N, 134°44′W) is a 2-ha plot on Admiralty Island, 27 km south-west of Juneau. The stand lies on a gently sloping bench formed from till and colluvial deposits. Soils are deep, well-drained, gravelly silt loams. The 1830 windthrow event released understorey hemlock and allowed a new spruce cohort to germinate on the newly created mineral mounds (Deal *et al.* 1991). Only 20% of the 58 trees we cored predated the 1830 windstorm, and many of these ‘residuals’ were, at the time of the windthrow, young, advanced-regeneration hemlocks. Based on ages and heights we measured, the height of the largest spruce trees at age 50 is predicted to be about 25 m (Farr 1984).

The Outer Point stand (58°18′N, 134°40′W) is a 0.5-ha plot on Douglas Island 17 km west of Juneau. The stand is on a very gently sloping raised beach terrace containing a mix of glacial till and bedrock-derived slate fragments (Alexander *et al.* 1993). This stand appears cooler and wetter than the two other stands; peaty areas are present in and near the stand, and at times of heavy rainfall, intermittent streams traverse the stand. Of the 66 trees we cored, 23% predated the 1830 windstorm. These residual hemlocks are larger and older than those present on the Hawk Inlet or Juneau stands, suggesting that this stand was not as severely affected as the others. The height of the largest spruce trees at age 50 is predicted to be about 15 m (Farr 1984; Deal *et al.* 1991).

The Juneau stand (58°22′N, 134°34′W) is a 1.5-ha plot, 2 km north-east of the Juneau airport. The stand lies on a nearly level, glacial-marine till bench deposited about 9000 years ago. The spruce–hemlock stand developed on the site after the 1830 windthrow which left abundant pit and mound microrelief. Only 10% of the 202 trees we cored predated the 1830 windstorm. The height of the largest spruce trees at age 50 is predicted to be about 24 m (Farr 1984).

THE WITHIN-STAND WINDTHROW CHRONOSEQUENCE METHOD

Windthrow mounds in young, mid-aged, and old age-classes were used to assess changes in soil over time (Fig. 1). An abundance of windthrow mounds of each age-class made replication possible within stands. We were able to find at least four replicate mounds of each age-class in each stand, giving a total of 39 mounds sampled. Because climatic and vegetative conditions are more similar within than between stands that may be widely separated, the within-stand chronosequence approach avoids some of the criticism of traditional methods that have used spatially separated stands to represent different stages of succession (Stevens & Walker 1970; Pickett 1989).

Good estimates of soil-surface age are essential to the within-stand chronosequence method. Reconstructing any event from a century or more ago is difficult, and we accumulated a variety of evidence, some circumstantial, to allow us to estimate the date of windthrow events and soil-surface ages. The best evidence, obtained on most of the young and some of the mid-age mounds, was from scars on standing-live trees made by the treefall that created the mound. Scars were examined on wedges cut from these live trees. For older mounds, dates were frequently deduced from the age of trees growing on top of the mound (Zeide 1981). Alternatively, dates were estimated from the age of trees growing on wind-thrown logs, the ring-width response (release) of trees adjacent to gaps above the mounds, or radiocarbon dating. The first of these techniques may under-estimate age because seedlings may or may not establish rapidly after the treefall (Dynesius & Jonsson 1990). For many of the apparently older mounds, where none of these techniques worked, we calculated mean residence time (MRT) of the humic material in the Bh horizon by using ^{14}C dating. Estimated MRT for mid-aged mounds, known to be about 160 years old, ranged from 20 to 100 years BP; MRT for old-mound Bh's ranged from 50 to 210 years BP. Given the uncertainty with this technique (Stuiver & Becker 1986; Goh 1991), we took the maximum difference between MRT and actual age (140 years) for mid-aged mounds, and added that to the oldest estimated MRT for old mounds to estimate the maximum age of the old mounds (350 years BP). We used 350 years BP as a conservative (upper-end) estimate of age for all old mounds where other evidence was lacking.

SAMPLING OF SOIL SURFACES

Soil sampling was limited to the top or side of the mound opposite the windthrown log. Where these logs were no longer present, a soil profile was exposed on the edge, perpendicular to the long axis of the mound, to determine the side to sample. Older mounds frequently lacked any evidence of a wind-

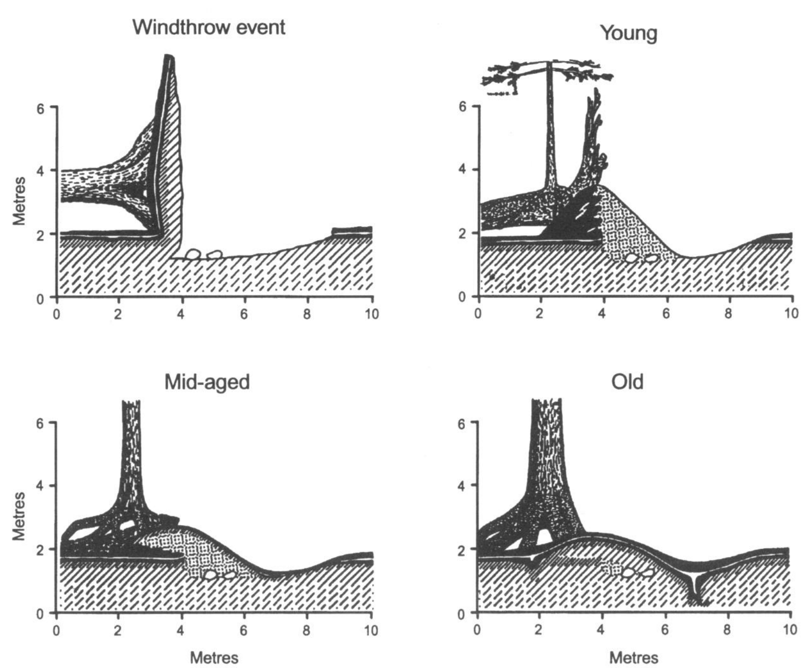

Fig. 1 Schematic drawings of mound evolution, the basis for the within-stand windthrow chronosequence method. Soil surfaces – within a forested stand, created by windthrows of different ages – were used as a chronosequence. Multiple windthrows of similar ages allowed for replication within stands.

thrown log but usually retained the characteristic oblong shape and evidence of buried horizons. Forest floor (O horizon) and mineral soil were sampled with a sharpened 30-cm-diameter steel ring inserted perpendicular to the soil surface. Soil was removed, by horizon, until B material, visibly unaltered by current soil development processes, was encountered. Soils were air-dried for storage before analysis.

We estimated average thickness of O, E, and Bh horizons across the stands by sampling at at 2-m intervals along three transects within each plot, giving 153 (Hawk Inlet), 82 (Outer Point), and 123 (Juneau) sampling points. Horizon thickness was measured on a small, excavated profile; in a few cases where mineral soil was difficult to access, a tube sampler was used. Only 1–2% of sampling points were not measured because trees or large roots blocked access. Sampling points were also classified as either being part of a large (greater than 0.6-m-high) mound and associated pit, or not.

CHEMICAL ANALYSES

The < 2-mm soil fraction was chemically analysed. Total C, N, and P were determined on finely ground soil samples, N and P with a Kjeldahl digest and Technicon Autoanalyzer II (D'Elia *et al.* 1977), and C by dry combustion with a Leco Automatic Carbon Analyser. (The use of trade names does not imply endorsement by the US Department of Agriculture.) We interpret Kjeldahl P to include most primary mineral P because the samples were finely ground and then digested in strong acid. All other analyses were on unground < 2-mm soil samples. Weights are reported on an oven-dry, 105 °C basis. Soil pH was determined in a 1:1 soil:water ratio. The Fe and Al complexed with humic compounds was extracted with 0.1-M sodium pyrophosphate extraction (McKeague *et al.* 1971; Wada 1977). Loosely bound, presumably readily available, organic P was extracted with 0.5-M sodium bicarbonate at pH 8.5 for 16 h (Olsen & Sommers 1982). Humic acid was separated from Bh samples from seven old mounds and two mid-aged mounds with HCl and NaOH, using the method of (Goh 1991) for analysis of ^{14}C.

BASIS FOR EXPRESSING SOIL CHANGES

In nutrient cycling studies, soil variables are traditionally expressed on a depth and area basis (e.g. Mg C 10 cm^{-1} ha^{-1}). Pedologists describe soils by horizons and usually express variables as concentrations (e.g. kg C $horizon^{-1}$ Mg^{-1}). We combine these approaches to express horizon values on an area basis (e.g. kg C $horizon^{-1}$ m^{-2}). To compare profiles of different ages, bulk densities, and organic matter contents, we included horizons from the surface downward to a fixed cumulative mass of mineral soil (ashed to remove organic matter) rather than to a fixed depth, similar to the method of Jenkinson (1971). A fixed cumulative mass of mineral soil was established for each stand, Juneau (150 kg m^{-2}), Hawk Inlet (110 kg m^{-2}), and Outer Point (60 kg m^{-2}), based on the mass of mineral soil in the O, E, and Bh horizons of the single profile with the deepest Fe and Al penetration.

This approach seeks to maximize our ability to detect changes in total C, N, and P by limiting our analysis to the upper horizons involved in soil development after windthrow, and minimize sampling variation by avoiding combining horizons with greatly different elemental concentrations into a single fixed-depth sample. We assume, with this approach, that mineral content of these horizons is not changing substantially over the periods studied. Dense moss cover appears to prevent erosion once mounds are about 50 years old; significant weathering or leaching losses are unlikely to be detectable in this time frame. Changes in pH and Fe and Al concentrations were evaluated against cumulative mineral mass rather than depth to assure that the same amount of mineral particles are being compared through time.

STATISTICAL ANALYSIS

Linear regression was used to test for significance in slope of C, N, and P contents over time. Comparison of regression lines was used to test for differences in slope between stands (Neter & Wasserman 1974). Simple parametric statistics were used to describe variation in sampling of soil variables.

Results

DEVELOPMENT OF WINDTHROW MOUNDS AND SOIL HORIZONS

Windstorms before 1700 and around 1830 and 1930 provided most of the sampled surfaces and allowed us to group windthrow mounds into three replicated age-classes of soil surfaces – young, mid-aged, and old – within each of three forested stands (Table 1). The young age-class averaged 56 years old; the mid age-class averaged 148 years old; and the old age-class averaged 331 years old. Mid-aged mounds, associated with what we believe was a region-wide windstorm about 165 years BP (*c.* 1830), were more common than young or old mounds. The age of most older mounds was estimated with less certainty.

About 50 years after the windthrow, mounds averaged 1.0 m in height, and no new E or Bh horizons had formed (Table 1). Organic material accumulated above a buried profile on a previously adjacent area of undisturbed soil on the tree side of these mounds (e.g. Fig. 2a). The pit side of the mound tended to be a homogenized assemblage of deeper soil (mostly Bs), organic matter, and E and Bh material, here termed an Ap horizon. Only a thin organic horizon had

Table 1 Morphology of mounded soil surfaces in the windthrow chronosequences and of all soil surfaces in stand-wide transects (means ± standard deviations)

Stands	*N*	Age (years)	Mound height (m)	Horizon thickness (cm) O	E	Bh
Young mounds						
Hawk Inlet	4	54 ± 7	1.1 ± 0.3	3.5 ± 1.0	NP	NP
Outer Point	4	59 ± 23	1.1 ± 0.3	5.0 ± 2.0	NP	NP
Juneau	4	54 ± 7	0.8 ± 0.6	9.3 ± 4.5	NP	NP
Mid-aged mounds						
Hawk Inlet	5	160 ± 11	0.4 ± 0.2	5.4 ± 1.5	1.9 ± 1.1	3.3 ± 1.7
Outer Point	4	165 ± 2	0.6 ± 0.2	9.0 ± 3.4	0.6 ± 0.6	2.1 ± 2.7
Juneau	4	121 ± 35	1.1 ± 0.6	7.6 ± 5.3	0.5 ± 0.6	2.3 ± 1.9
Old mounds						
Hawk Inlet	4	350 ± –*	0.3 ± 0.2	8.3 ± 3.2	1.3 ± 0.4	3.8 ± 1.1
Outer Point	5	328 ± –	0.3 ± 0.1	11.1 ± 1.6	1.9 ± 1.3	4.0 ± 1.7
Juneau	5	320 ± –	0.6 ± 0.2	10.4 ± 2.3	3.0 ± 1.1	3.8 ± 0.9
Combined-site mound averages						
Young	12	56 ± 3	1.0 ± 0.4	5.9 ± 3.5	NP	NP
Mid-aged	13	148 ± 3	0.7 ± 0.5	7.1 ± 3.0	1.1 ± 1.0	2.6 ± 1.9
Old	14	331 ± –	0.4 ± 0.2	10.0 ± 2.4	2.1 ± 1.1	3.8 ± 1.2
Stand averages based on transects						
Hawk Inlet	153	NE	NE	6.2 ± 9.0†	1.3 ± 1.6	2.2 ± 2.2
Outer Point	82	NE	NE	11.5 ± 9.7	3.1 ± 3.0	3.2 ± 3.6
Juneau	123	NE	NE	11.7 ± 5.6	0.9 ± 2.7	2.0 ± 3.9

NP = no horizon present.
*No variance was calculated because some ages were estimated roughly.
†O horizon thickness on transects does not include rotten wood which averages 13 cm across all stands.
NE = not estimated on transects.

developed, resting on a homogeneous and very permeable A and Ap. Fine roots were found throughout the mound, often concentrating in buried organic horizons.

After only 150 years, the E horizon had developed to an average thickness of 1.1 and the Bh to 2.1 cm (Table 1). In many of the dissected mounds, a buried E and Bh horizon were still present in the lower profile. Mound height decreased from 1.0 m in young mounds to 0.7 m in mid-aged mounds. The windthrown logs associated with mid-aged mounds were usually difficult to locate because these logs had become fully incorporated into the soil. In the example profile for mid-aged mounds (Fig. 2b), the organic matter on the tree side was mostly decomposed, partly compacted, and was buried under collapsed mineral material. Larger roots were present throughout the profile; smaller roots seemed to be concentrated in the upper soil horizons and in the buried Bh horizon.

Substantial E and Bh horizons developed within 350 years, averageing 2.1 and 3.8 cm in thickness, respectively (Table 1). Old mounded surfaces decreased to just 0.4 m high and displayed a very subdued shape, partly because of adjacent, younger windthrows that deposited material on the sides of the old mounds. A faded E horizon is all that was left on the windthrown-log side of some mounds; buried organic and Bh horizons disappeared (Fig. 2c). Roots were mostly confined to the O and E horizons. Field observations indicated that the Bh horizon is poorly permeable, with most of the water running laterally rather than vertically after heavy rain (Bowers 1987).

SOIL-FORMING PROCESSES

Podzolization was the dominant mechanism of soil formation, as shown by the evolution of the soil morphology and the downward movement of C, Fe, and Al (Fig. 3). Outer Point soils had the most pronounced podzolization, with dramatic depletion of Fe and Al in the E horizon and accumulation in the Bh and Bs horizons. Displacement of Fe and Al was deeper, but less pronounced, in Hawk Inlet soils compared to Outer Point. In the Juneau stand, Fe and Al were depleted from the E horizon but little appeared to accumulate in the Bh. Differences in these patterns between stands may have been related to differential permeability and averageing of replicated profiles.

At Outer Point, the B horizon was rich in silt from the breakdown of the slate parent material. This finer material slowed percolation and had a higher surface area, leading to precipitation of Fe and Al higher in the profile. Coarser soils, as found in the Hawk Inlet and Juneau stands, allowed rapid percolation and deeper penetration of Fe and Al and dilution of organic matter. The apparent lack of Fe and Al accumulation in the Bh at the Juneau stand may be explained by variable development in profiles being averaged. Accumulation of Fe and Al in an upper mineral horizon of a profile with slow percolation

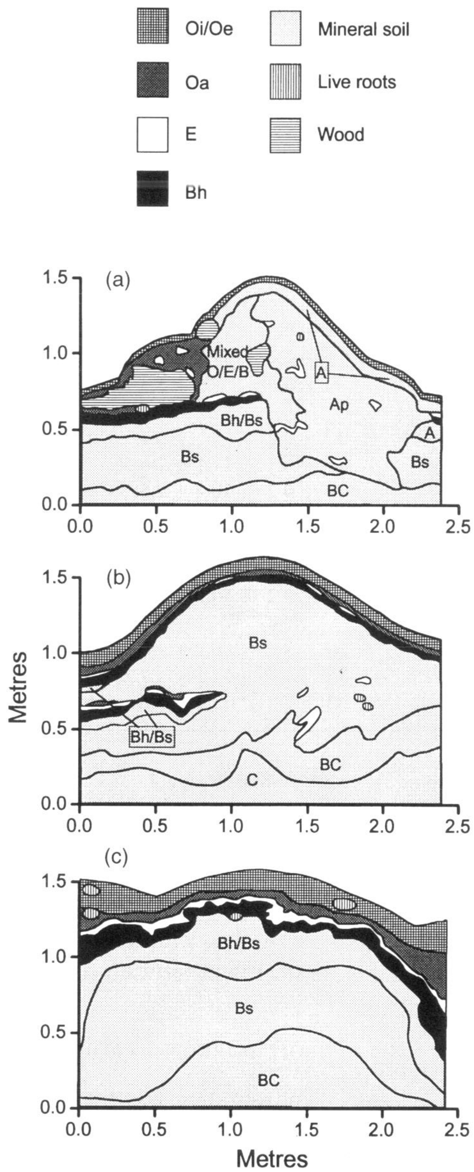

Fig. 2 Drawings of soil profiles on selected windthrow mounds at the Juneau stand. The soil-surface ages are 55, 97, and 350 years for the young, mid-aged, and old age-classes, respectively.

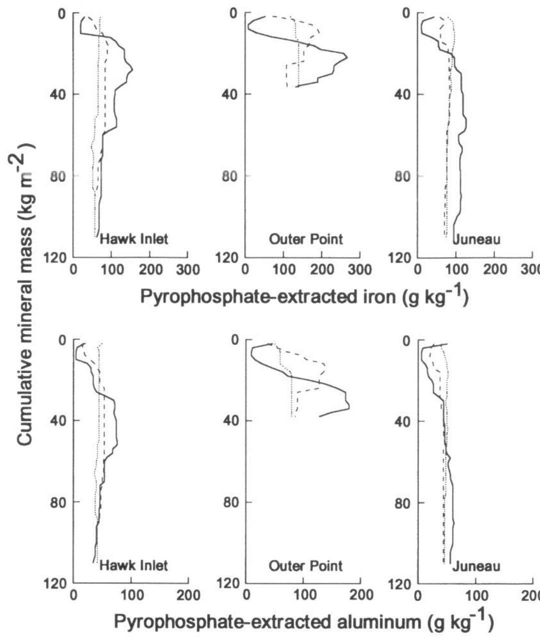

Fig. 3 Comparison of changes in pyrophosphate-extracted Fe and Al with cumulative mineral soil mass between young (·····), mid-aged (– – –), and old mounds (——) on three stands. Values are averages of all surfaces in a given age-class. Cumulative mineral soil mass is proportional to a depth corrected for changes in organic matter content, rooting, or bulk density. Organic horizons averaged roughly 8 cm kg^{-1} m^{-2}, and mineral soils average less than 0.25 cm kg^{-1} m^{-2}.

may have cancelled out depletion of Fe and Al in a corresponding horizon of another profile with more rapid percolation. Depletion and accumulation are readily seen in individual soil profiles (Table 2).

Highly acidic conditions (pH 3.5) appeared in the uppermost soil organic layers in the youngest (50 years old) surfaces sampled (Fig. 4). This condition represents a drop of 1.5 pH units, if we assume that the mound was initially homogenous and that the deeper soil on young mounds represents initial conditions at the surface. The decline was strongly influenced, however, by the change from mineral to organic matter. Further decline in the uppermost soil layer was small, achieving pH 3.3 in 350 years. A decline of 0.5 pH units was evident in about 100 years from young to mid-aged mounds in the zone where the E horizon forms (~ 10 kg m^{-2}). In about 200 years, pH also declined by 0.5 in the zone where the Bh formed from mid-aged to old mounds. Acidification proceeded from the top down, and rate of acidification slowed with depth.

CHANGES IN TOTAL C AND N

The accumulation of C in soil horizons was very rapid and linear, averageing 21 g m^{-2} year^{-1} ($R^2 = 0.526$; Fig. 5). The slope of this regression line, combined for all stands, was significant ($P < 0.01$); slopes for individual stands did not differ ($P > 0.05$) from one another. About 37% of the C accumulated in the O horizon (8 g m^{-2} year^{-1}), 31% in the Bh horizon (7 g m^{-2} year^{-1}), and the remainder in other mineral soil horizons (Fig. 6). The relative importance of the Bh as a sink increased with time. Accumulations of N paralleled C, with an annual rate of 0.6 g m^{-2} year^{-1} ($R^2 = 0.417$; $P < 0.01$); again, stands did not differ ($P > 0.05$) from one another. The rate of N accumulation was similar in the O and Bh (about 0.3 g m^{-2} year^{-1}). We found no sign that an equilibrium of C or N had been reached within the first 350 years.

CHANGES IN PHOSPHORUS

Total P (g m^{-2}), summed for the profile, did not vary with soil age, suggesting that root uptake, erosion, leaching, and weathering effects were offsetting, absent, or undetectable. Nevertheless, some vertical

Table 2 Changes in concentration of total C, Kjeldahl N and P, bicarbonate-extracted P (P_{BE}), and pyrophosphate-extracted Fe and Al (Fe_{PE} and Al_{PE}) for the horizons of three selected profiles at the Juneau stand: young (55 years); mid-aged (97 years); old (350 years). Profiles correspond to drawings in Fig. 2. Data for individual profiles are presented here because averaged data (e.g. Fig. 3) can hide patterns of accumulation and depletion where the rate of development is not the same in averaged profiles

Horizon	Thickness (cm)	Concentration (g 100 g^{-1})					
		Total C	Total N	Total P	P_{BE}	Fe_{PE}	Al_{PE}
Young mound							
O	5.7	44	1.58	0.14	0.022	0.23	0.20
A	3.1	14	0.68	0.19	0.015	0.43	1.57
B1	19.0	5	0.21	0.10	0.006	0.89	1.56
B2	3.2	2	0.12	0.12	0.004	0.79	1.26
B3	2.4	2	0.09	0.12	0.003	0.65	1.06
Mid-aged mound							
O	12.0	44	1.32	0.10	0.014	0.16	0.19
E	0.1	7	0.37	0.04	*	*	*
Bh	4.1	7	0.49	0.08	0.008	0.34	1.08
B1	10.3	3	0.15	0.09	0.003	0.84	1.32
B2	3.4	2	0.13	0.10	0.003	0.76	1.31
B3	2.4	2	0.10	0.11	0.003	0.68	1.29
Old mound							
O	8.1	48	1.77	0.12	0.018	0.18	0.15
E	1.9	5	0.22	0.02	0.003	0.12	0.11
Bh	4.0	9	0.50	0.07	0.010	0.62	1.75
Bs	2.2	6	0.27	0.07	0.008	0.77	2.17
B1	8.0	4	0.18	0.10	0.005	1.30	1.86
B2	3.2	3	0.15	0.10	0.004	1.08	1.20
B3	1.1	2	0.11	0.09	0.003	0.86	0.51

*Insufficient sample for analysis.

redistribution of total P (g 100 g^{-1}) within profiles was evident (Table 2). Trends suggest an initial upward redistribution of total P into organic matter followed by a decline in the E horizon.

Bicarbonate-extracted P (g m^{-2}) increased with soil age in mineral soil horizons (Fig. 7). The rate of increase was more rapid in Hawk Inlet soils than Outer Point soils ($P < 0.05$); Juneau samples were not analysed. The increase of bicarbonate-P, mainly in the Bh horizon (Table 2), probably resulted from reduced root uptake, because few roots were observed in well-

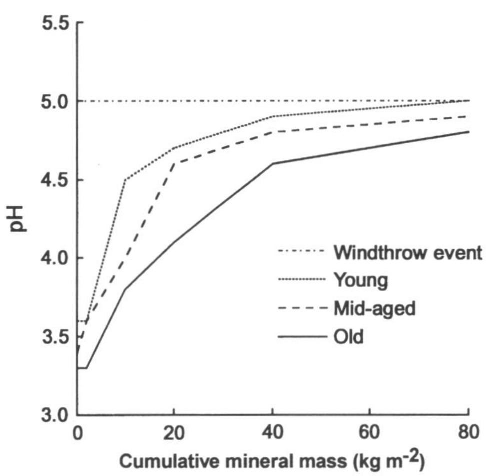

Fig. 4 Comparison of pH as a function of cumulative mineral soil mass in young, mid-aged, and old windthrow mound surfaces. Cumulative mineral soil mass is proportional to a depth corrected for changes in organic matter content, rooting, or bulk density. Values of pH are calculated from average H^+ concentrations for each age-class across all stands.

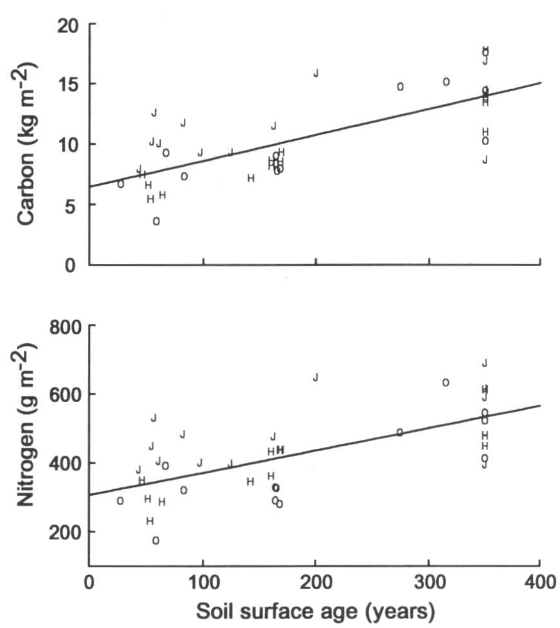

Fig. 5 Changes in C and N on within-stand chronosequences. Letters denote stands: O for Outer Point; H for Hawk Inlet; and J for Juneau. Note that the cumulative mineral mass was fixed for each stand and varied across stands; thus the interpretation should be limited to slope. Regression lines from each stand are combined into a single line because slopes were not significantly different ($P > 0.05$).

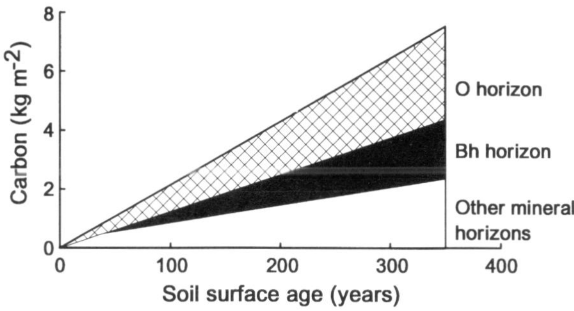

Fig. 6 Distribution of C added to within-stand chronosequences. Slope coefficients from significant ($P < 0.01$) regressions of mound age and C in the O and Bh horizons were subtracted from the total-profile C regression coefficients. *Y* intercepts were set to zero to represent accumulation from initial post-windthrow conditions, except for the Bh regression that had a negative *Y* intercept because it did not appear until roughly age 60.

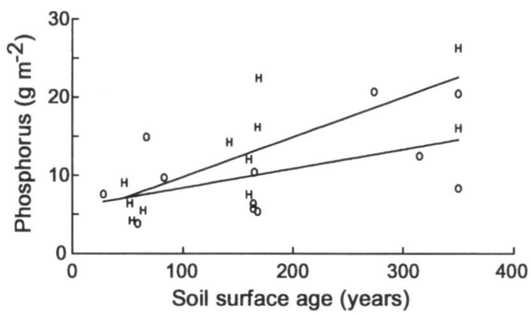

Fig. 7 Change in loosely bound phosphorus (bicarbonate extraction) in the mineral soil over time. Letters denote stands: O for Outer Point and H for Hawk Inlet. Juneau stand soils were not analyzed for bicarbonate-extracted P.

developed Bh horizons. Bicarbonate-extracted P (g m^{-2}) in the O horizon, which was not affected by soil age, averaged about 1 g m^{-2} across all sites.

Discussion

CHANGE IN SOIL ON AN ECOSYSTEM BASIS

The main focus of our study was soil development on windthrow mounds, and the potential for extrapolation to ecosystems may be limited. Extensive transects, however, indicated that windthrow mounds greater than 0.6 m high and their associated pits – likely to be young to mid-aged surfaces – make up 41% (Hawk Inlet), 53% (Outer Point), and 32% (Juneau) of the stand areas. Unmounded areas – including small older mounds, but not pits associated with larger mounds – had average O and E horizons that were 13% thicker than old mounded surfaces. The Bh horizons on unmounded surfaces were thicker than on old mounds at Outer Point, but thinner than on old mounds at Hawk Inlet and Juneau. Most unmounded areas were likely to be old windthrow surfaces being buried by more recent windthrows (Fig. 2c). Burial of the edges of older mounds by more recent windthrows appeared responsible for some of the decline in mound height with time (Table 1).

Accumulation of C in soils not sampled may be greater or less than the soils included in our sample. Sampling was confined to the top or side of mounds away from the largest deposits of organic matter, and thus, on a stand basis, increases in C may have been partly offset by decomposition of buried organic material. These buried layers, however, appear to decompose most rapidly during the first 50 years and had often more or less disappeared by 160 years. Also, litter was redistributed from mounds to adjacent lower areas, suggesting more rapid C accumulation on nonmound soils (McClellan *et al.* 1990). Observed increases in soil C may have been partly offset by a net decrease in rotting wood. Rotting wood fragments were abundant, averageing 13 cm deep (Table 1). Most of this wood may have come from the 1830 windstorm because windthrown logs associated with old mounds were completely absent. Surfaces that had a combined O + Bh thickness greater than the average for old mounds accounted for 21–30% of the land area, and these surfaces may or may not be accumulating C as rapidly as other surfaces. Observations of reduced rooting in well-developed mineral horizons suggested reduced root litter input.

On balance, these factors suggest ecosystem rates of soil C accumulation somewhat lower than the 21 g C m^{-2} $year^{-1}$ we calculated for mounded surfaces. Our estimated rate, however, is still 13 times more rapid than the rate estimated by Protz *et al.* (1984) for northern Canada, and nearly double the maximum C accumulation rate reported by Schlesinger (1990). Thus, stand soil C accumulation on our sites should be considered as an upper-end of possible rates of soil C accumulation in forest ecosystems undergoing secondary succession.

The rate of soil C accumulation we estimated was five times slower than reported rates in the alder phase and half as rapid as in the spruce phase of the primary succession at nearby Glacier Bay, Alaska (Bormann & Sidle 1990). A climatic explanation for this difference in rates is difficult because stands included in our study were about 60 km south of Glacier Bay and had only slightly warmer summer and winter temperatures (Loewe 1966). The lack of N_2-fixing species, such as red alder (*Alnus rubra* Bong.) or Sitka alder (*A. sitchensis* (Regal) Rydb.) might help to explain less rapid C accumulation in our secondary succession soils; N_2-fixers are known to enhance mineral soil C content through the formation of stable organo-mineral complexes (Bormann *et al.* 1994). Another reason may be the slower decomposition of the O horizon during the spruce phase in Glacier Bay, where the O horizon averaged 14 cm on a 160-year-old surface compared to 7 cm on our 160-year-old secondary succession surfaces. Hemlock trees, found throughout our secondary-succession stands but nearly absent from Glacier Bay stands, are thought to efficiently extract nutrients from organic substrates (Harmon & Franklin 1989). Thus, presence of hemlock might explain rapid decomposition of the O horizon. The rate of N accumulation in our secondary succession chronosequence was about four times precipitation input (Bormann *et al.* 1989) and about three times the observed N accumulation rate in the spruce phase of the primary succession chronosequence at Glacier Bay (Bormann & Sidle 1990). Less rapid N accumulation at Glacier Bay may also slow decomposition, resulting in more rapid C accumulation in the O horizon than in our secondary succession chronosequence.

By estimating ecosystem soil-C content, we can compare short-term (50–350 years) and long-term (9000 years) C accumulation rates. We estimated the ecosystem soil-C content by multiplying the stand-average degree of development – based on O + Bh thickness from stand transects – by the ratio, on sampled soils, of C content per unit area to O + Bh thickness. Because average stand O + Bh thickness was 10% lower than the thickness of older, mounded surfaces, we calculated the ecosystem soil C across all stands to be about 90% of that calculated for older mounds, or about 12 kg C m^{-2}. Doubling this amount to account for C in woody debris and C deeper in the profile, we roughly estimated 24 kg C m^{-2}. This C has accumulated in about 9000 years after the glaciers left these sites, for a long-term rate of only 2.6 g C m^{-2} $year^{-1}$, similar to the long term rate proposed by Schlesinger (1990). The potential rate of accumulation for the ecosystem over our 50- to 350-year chronosequence is 6.3 kg C m^{-2}, over one-fourth of the total ecosystem soil C. Thus, wide fluctuations in soil C, caused by extensive windthrow, appeared to be possible within a long-term, slower soil C change.

MECHANISMS OF CHANGE

The initial phase (0–50 years) was characterized by rapid organic matter accumulation into the top of the mineral soil, active rooting deep into the profile, and a dramatic decline in upper mineral soil pH. Recently formed mounds were not available for sampling on our sites, so we do not know the rate of C and N accumulation or loss during this phase, but the rapid disappearance of buried horizons during this period strongly suggested rapid decomposition of C in disturbed O and Bh horizons. Observations of dense fungal growth on Bh horizons exposed by windthrow supported this conclusion.

In the second phase (50–250 years), E and Bh horizons form, accompanied by a downward shift in Fe and Al and reduced pH at increasing depths. Rooting in mineral soil horizons appeared to persist during this period and bulk density was maintained or may even have decreased slightly. Carbon accumulated rapidly throughout the profile but with increasing allocation to the Bh.

During the third phase (250–350 years), C and N accumulation appeared to continue at the same rate as in phase 2, although surface dating was less certain. Beyond 350 years, C and N are likely to continue to increase because inputs of aboveground litter will continue. Because root litter may decline as roots become fewer and more confined to the upper O horizon, total accumulation may decline.

A wide range of mechanisms might have brought about these dramatic changes. The cool, hyper-humid climate appeared to be conducive to moderately high rates of primary productivity and decomposition. Decomposition of detrital C should have proceeded rapidly in this climate because both summer drought and extended periods of freezing, especially when soils are covered by snow, were lacking. Abundant coniferous litter appeared to decompose fairly rapidly at first, but intermediate products of decomposition appeared to have great stability. This pattern was confirmed by the continual buildup of C in the lower O and Bh horizons (Fig. 6). The chemistry of spruce–hemlock detritus was probably related mechanistically to incomplete decomposition. Incomplete decomposition and podzolization may also have been due to the lack of effective short-term mixing agents. The only earthworm we saw was a litter-confined enchetraed. Gophers, moles, and other mammals that disturb soils extensively are also notably absent from this region (Hall & Kelson 1959).

The frequency of windthrow disturbance appeared, by default, to be the primary mechanism for decomposing the intermediate products that accumulated in the O and Bh horizons. The small O and Bh fragments that make up young mounds were largely decomposed in 50 years. Rotten wood fragments and buried Bh horizons had mostly disappeared by 150 years (Fig. 2). Organic matter buried by windthrow is likely to have decomposed rapidly because of several factors; e.g. replacement by surface litter was eliminated, although root litter may continue or increase; the pH increased and chemistry was altered by contact with sub-soil; and the cation and phosphorus supply and root and mycorrhizae activity was likely enhanced. The low bicarbonate-extracted P in the young mounds can be interpreted as efficient root uptake (Fig. 7).

We propose a general model of C accumulation and decomposition for these soils in this region. The amount and type of soil C varied with the frequency of windthrow-induced soil disturbance. With repeated large windthrows, soil C fluctuated with periods of accelerated decompostion and periods of rapid accumulation. A longer-term upward or downward trend may be related to windthrow frequency. The greater the frequency, the lower the rate of C accumulation as the period of rapid decomposition (0–50 years) became more frequent. A threshold of about

200–350 years was apparent, after which roots became confined to the O horizon and windthrow would not disturb well-developed mineral soil horizons. This threshold would be crossed when some mechanism – such as diseases that cause trees to snap off above ground or tree-felling – prevented soil disturbance.

Crossing this threshold may lead the ecosystem on a dramatically different trajectory that could result in thick organic horizons and a downward trend in productivity. Bog formation may sometimes be the end result. Spruce stumps and logs buried under upland bogs in this region (Dachnowski-Stokes 1941) led Zach (1950) to conclude that bogs are the climax vegetation for this region. Although podzolization and lack of mineral soil disturbance may change the trajectory toward bog formation, other secondary mechanisms, such as invasion by *Sphagnum* sp. (Noble *et al.* 1984; Klinger *et al.* 1990), are also likely to contribute.

This model of soil development and disturbance has implications for management policies in these forests. The continued accumulation of nutrients in the O and Bh horizons, and decreasing nutrient availability along with immobilization in biomass are likely to lead eventually to nutrient deficiency. The rapidity of this immobilization appears to reduce net primary productivity over a single generation (Bormann & Sidle 1990). Concern over the effect of soil disturbance on streamwater quality and conifer regeneration has led to careful logging practices on managed forests in the region. Logging, however, eliminates windthrow by removing trees before they can be windthrown. Successive rotations without soil disturbance may cause the site to become excessively organic and reduce the productive potential of the soil, as has been found in Northern Finland (Siren 1955; Miles 1986). Accumulation of C in soils is likely to be maximized by soil disturbance at a frequency of about 200–350 years. More frequent disturbance may cause declining soil C and more productive vegetation; lower frequency may alter the trajectory of ecosystem development toward organic soils and less productive vegetation.

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