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Fire is a major disturbance process in many forests. Long-term studies of the biogeochemical effects of fires, especially on soils, are very rare. Consequently, long-term effects of fire on soils are often hypothesized from short-term effects. In a chronosequence study, I studied 24 western Cascades (Oregon) forest stands thought to have been initiated in fire. Twelve of those burned about 150 years ago ("young" sites), and the other 12 burned an average of 550 years ago ("old" sites). I hypothesized that young stands would have less carbon (C) and nitrogen (N) in forest floor and in 0 -10 cm mineral soil than old stands. I found that forest floor N pools of old sites (average = 1,823 kg/ha ± s.e. = 132 kg/ha) were significantly greater than young sites (1,450 ± 98 kg/ha). Similarly, forest floor C pools of old sites (62,980 ± 5,403 kg/ha) were significantly greater than young sites (49,032 ± 2,965 kg/ha). Greater N and C pools in forest floor of old sites resulted from greater forest floor mass in old sites; concentrations of both N and C, and C:N ratios, did not differ significantly by forest age class. In mineral soil, neither concentrations

nor pools of N and C differed between young and old sites. Despite overall similarity of C:N ratios in young versus old sites, potential N mineralization rates were twice as high in forest floor of old sites (average = 60 ± 7.3 mg N / g soil) than young sites (26 ± 3.5 mg N / g soil), . Nitrate accounted for only 2% or less of total N mineralized in forest floor samples. In mineral soil, potential net N mineralization did not differ by forest age class. The pattern of high net N mineralization and low nitrification in old forests is consistent with other studies of fire-prone forests, yet contrasts with many studies of forests that lack fire, and suggests that ammonium is not the sole control over nitrification in fire-prone ecosystems. Overall, fire appears to impart a long-term legacy of reduced forest floor N and C pools in this western Oregon Cascades landscape, which suggests that current fire-suppression activities in the region may increase forest floor N and C storage over historical conditions within several centuries. The differences in forest floor and soil N cycling processes that I observed by forest age class raise the further possibility that fire exclusion in these forests may change the relative abundance of soil inorganic N forms to favor ammonium over nitrate. Such changes may have unknown consequences for relative competitive abilities of plant and microbial species that rely preferentially on different N-forms to meet N nutrition requirements.

While forest floor N and C pools increase from young to old stands, forest floor and soil N and C pools are not different, or decline, between 450 year old stands and the oldest stands at 800+ years, That, and other, anomalous changes in values from ~450 to 800+ years, suggest possible changes in ecosystem functions, and may indicate that this landscape could be a fruitful study area for examinations of a mature, steady-state ecosystem.

Four Centuries of Soil Carbon and Nitrogen Change After Severe Fire in a Western Cascades Forest Landscape

by
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Thomas William Giesen, Author

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued).

LIST OF TABLES

LIST OF FIGURES

Four Centuries of Soil Carbon and Nitrogen
Change after Severe Fire in a
Western Cascades Forest Landscape

Introduction

The importance of nitrogen and carbon

Pools and dynamics of soil carbon (C) and nitrogen (N) are important general controls over temperate forest ecosystem structure and function, and have the potential to be influenced by fire over both short and long time scales (DeBano et al. 1998, Neary et al. 1999, Certini 2005). C is both the major component of the structure of organisms, and a source of energy as well. In soils, C is essential in soil organic matter for soil structure, as a cation exchange medium, for aeration and water holding capacity, as a substrate for the nutrient-cycling microbial communities, and in many other ways. The conversion of CO_2 to carbohydrates in plants, through photosynthesis, with O_2 as a product, is essential to the maintenance of life. The ability of forests to sequester C in live and detrital biomass is important for the control of CO_2 in the atmosphere causing global warming. N is an essential element in proteins and in DNA. Though abundant as dinitrogen in air, N is sometimes the limiting resource for plant life, and the recycling of N in natural ecosystems is a critically important process (Brady and Weil 2002, Chapin et al. 2002). N is demonstrably a limiting resource in many forests in the Pacific Northwest

(Peterson and Hazard 1990). N is a link with carbon: N influences turnover of soil carbon (Chapin et al. 2002).

Fire: a major disturbance process

Fire is a major disturbance process in many Oregon forest ecosystems (Agee 1993). Fire alters forests both above-ground and below-ground. The above-ground effects are those most often reported, and involve fire's various effects on vegetation. Most commonly reported are fires which consume a lot of fuel, including the crowns of trees, killing most vegetation and initiating secondary succession (Agee, 1993).

Fire studies are limited

Wan, et al. (2001), in a meta-analysis involving 185 data sets from 87 studies, investigated changes in N pools and processes in response to fire. Forest types studied included both broadleaf and coniferous, and fire types included prescription fire, slash fire, and wildfire. The meta-analysis did not analyze forest floors; just mineral soils. The data sets studied dealt with soils generally much less than 20 cm in depth, and for periods after fire of no more than 5 years, and mostly much less. They found that N pools in all fuels diminished with fire; ammonium levels increased (94%) in soils post-fire, and nitrate levels increased (154%) in soils, but more slowly than ammonium levels, and persisted longer. They did not find any effect on soil nitrogen pools from fire. None of the fire studies studied fire in Douglas-fir forests. In only one coniferous forest wildfire study was soil N measured, and it was an Alaskan site. In only two coniferous forest slash fires was soil N measured, and these were sub-boreal spruce and eastern pine/hardwood forests. The very small representation of slash and wildfire fires in coniferous forests in Wan et al (2001) may indicate that the bulk of fires studied were low or moderate severity burns, without heat enough to alter soil N. Wan et al. (2001) conclude by acknowledging that a key research need is understanding how fire-induced changes in N pools and processes influence the structure and function of ecosystems over the long-term (defined here as at least > 10 years, but mainly over centuries).

Johnson and Curtis (2001), in another meta-analysis, studied the effects of forest management on soil C and N storage. Fire was included as a management effect, and 13 of the studies they analyzed involved fire. Three of the 13 were wildfires. Forest floors were not included in the analysis. Johnson and Curtis found that, considering all 13 fire studies, fire had no significant immediate effect on soil C or N. However, they found a significant effect ten years after fire: C and N pools had increased. They also reported an anomalous result that prescribed fires diminished soil N and C, and that wildfire increased soil N and C. The latter, counter-intuitive result was attributed to retained charcoal, a retained recalcitrant hydrophobic organic layer resulting from fire, and the invading, N-fixing shrub vegetation. In this meta-analysis study, as in the Wan et al. (2001) study, the data sets used were mostly short term (defined here as < 10 years).

These two meta-analyses demonstrate that wildfire effects on soils are seldom studied, and seldom studied long term.

Long term studies

Long term studies of fire and soils are not common, particularly for coniferous forests subject to fire, but a few are available. DeLuca et al. (2002) studied a 352 year fire chronosequence in northern Sweden, analyzing nitrogen mineralization, nitrification, and phenol accumulation. They found that N mineralization decreased with time since fire, as did nitrification. Free phenols increased. The decrease in nitrification, they suggested, is possibly due to free phenols which somehow inhibit nitrification. Charcoal, a powerful adsorbent, enters soils after a fire, and charcoal adsorbs phenols. As charcoal adsorbs over time, it loses its ability to adsorb new phenols, free phenols increase, and nitrification diminishes as a result. As an experiment, glycine (a labile source of N) was added to all soils to accelerate N mineralization in older soils. N mineralization did increase in older soils, but the expected consequence of increased nitrification did not occur. As a second, related experiment, charcoal was added to soils and nitrification did increase slightly in response. The authors hypothesized from these experiments that charcoal plays a key role in controlling nitrification by adsorbing free phenols, although this mechanism was not shown conclusively, MacKenzie et al. (2005) studied forest floors along a fire chronosequence (132 years) in second growth forests in western Montana, and found a similar pattern in decreased nitrification over succession. Forest floors increased in thickness, and forest floor C and N pools increased with time since fire. Ammonium and potentially mineralizable N increased with time, but NO_3^- content diminished significantly. DeLuca et al. (2005) performed laboratory experiments with soils from Ponderosa pine forests in western Montana, testing charcoal and nitrification theories related to long-term studies of fire and forests. They added NH_4^+ to soils, testing the conventional wisdom that the control over nitrification is its substrate, NH_4^+, and they found that nitrification did not increase in response to the additions. They also added new charcoal, taken from the forest after a recent fire, and found greatly increased nitrification, and diminished concentrations of phenolics in the soil. They thus demonstrated that the nitrification process in these soils is not substrate-limited. MacKenzie et al. (2005) studied a 130 year chronosequence in western Montana testing the consequence of forest succession (in this case, time-since-fire) on soil biogeochemical processes and microbial activity. They found that decomposition diminished with age, as did N mineralization, nitrification, and labile C pools, indicating a decrease in substrate quality and microbial activity. They conclude that N availability in Ponderosa pine ecosystems is dependent on fire and successional status.

Increasingly, computer simulation models of ecosystem dynamics are attempting to account for impacts of fire on soil C and N dynamics, and represent one among the few approaches available for extrapolating short-term impacts of fire on C and N dynamics over longer time scales. Some of these models are primarily heuristic, and focus on theoretical implications of fire for maintenance of N-limitation in fire-prone regions (Vitousek 1998). However, other more highly parameterized models (e.g., Bachelet et al. 2004) seek to understand potential interactions of climate, fire and ecosystem biogeochemistry more quantitatively in order to guide forest ecosystem management and policy decisions. Field verification of model results that address long-term fire impacts is generally lacking, however.

Fire effects: above and below ground

Fire affects soils both through combustion of forest floor and soil organic matter, and through the effects of soil heating (DeBano et al. 1998, Neary et al. 1999, Certini 2005). The potential for fire to affect soils is determined by the temperature to which the surface of the soil is exposed, and by the duration of the exposure. The range of potential temperatures and time exposures is large, from the low temperatures and short time exposure of a swiftly–moving surface fire burning through low densities of fine surface fuels, to the high temperatures and long duration of a fire burning through large amounts of small-to-large fuels piled on and near the forest floor, which may take many hours to burn. A more concentrated, if very localized instance of soil heating, is through below-surface smoldering and glowing combustion. This slow moving (< 3 cm/hr), non-flaming combustion occurs in densely-packed organic matter such as Oe and Oa horizons in forest floor, or buried dead wood and roots (DeBano et al. 1998, Neary et al. 1999, Certini 2005).

A wide array of change in soils may result from fire (DeBano et al. 1998, Neary et al. 1999, Certini 2005). A primary change is the loss of organic matter through distillation and combustion. Depending on the severity of the loss and the degree of soil heating, this loss may be accompanied by a host of other changes, including nutrient loss; diminished soil structure, porosity, and aeration; increased bulk density; reduced water-holding capacity; diminished biotic abundance and diversity; increased likelihood of hydrophobicity; increased susceptibility to wind and water erosion; decreased infiltration rates and increased runoff; and a deposition of charcoal into forest floor and mineral soil from both above-ground and below-ground combustion. In addition, a loss of vegetative cover and/or forest floor cover (exposing mineral soil), may increase soil temperatures, decrease transpiration, and increase evaporation. This suite of changes may radically alter the below-ground environment, but most of the changes are often thought to be resolved toward pre-fire conditions in less than 10 years. (DeBano et al. 1998, Neary et al. 1999, Certini 2005).

Fire effects on soils

Long-term fire-caused changes in soils include alterations in pools of N and C, in cycling processes, in the composition and biomass of the biotic community, and in charcoal contents in the forest floor and mineral soil (Certini 2005, DeBano et al. 1998). Soil temperatures at which these components are altered by fire have been studied in the lab and (less often) in the field (DeBano et al. 1998).

However, generalizing from short-term laboratory and field studies to N and C losses in wildfire is very difficult. Fire is a stochastic process, which changes, moment by moment, through alterations in wind direction and speed; the nature and amount of fuels; moisture content in air, soils and fuels; solar heating; and the topography of the landscape through which it is burning (Agee 1993, DeBano 1998). This high level of variability in fire produces a high level of variability in effect on N and C. The effects of fires are often termed “patchy” or “spotty.” But the distribution of fire-induced combustion and elevated temperatures in soils is simply not known: the spatial distribution of fire effects on soils has not, to the best of my knowledge, ever been studied and/or mapped**,** much less related (if such is possible) to above-ground fire intensity or severity. The distinctively heterogeneous (“patchy”) nature of fire’s effects on the landscape is reflected in the literature regarding fire intensity and severity in soils (DeBano et al. 1998, Neary et al. 1999, Certini 2005). The terminology of forest fire intensity and severity, above- and below-ground, reflects the complex interactions between fire, heat energy, vegetation, soil and a number of environmental variables. Fire intensity describes energy released per unit of length of fire front, above-ground. Fire severity describes the effects of fire on forest constituents, either above- or below-ground. Intensity is just an above-ground descriptor; severity applies to both above- and below-ground, but with a different meaning in each place. Above-ground fire severity describes effects on vegetation. Below-ground fire severity describes not only the effects on forest floor and below-ground (living and dead) vegetation, but also the effects on nutrients, organisms, moisture, and the physical and chemical nature of the soil (DeBano et al. 1998, Neary et al. 1999, Certini 2005).

That fire effects on naturally burnt soils are irreglarly distributed is clear in Certini's characterization of them as "chaotic mosaics" of little affected areas alternating with seriously impacted areas (Certini 2005).

In a local area (a "patch"), fire effects on soils are classified (Hungerford 1996, DeBano et al. 1998, Neary et al. 1999, Certini 2005) as follows:

- Low fire severity: Soil temperatures at 1 cm in mineral soil are less than 50 degrees C. Litter mostly consumed; duff still present. Lethal to all organisms to about 1 cm.

- Moderate fire severity: Soil temperatures at 1 cm reach 100-200 degrees C. Litter consumed and duff charred or consumed. Coarse woody debris mostly consumed, except for logs, which are charred.
- High fire severity: Litter and duff consumed; soil surface visibly altered in color. Organic material in mineral soil may be either consumed or charred to 10 cm or more. Near-mineral soil surface biota greatly diminished. Logs can be consumed, and ground char can be very deep under fuel concentrations (logs, slash piles, etc.). Shrub stems consumed. Temperatures at 1 cm > 250 degrees C.

This “patch” fire-effects-on-soils system is then used to define burned forest soils in broader areas (Wells 1979):

- Low-severity burn: < 2% severely burned; < 15% moderately burned, and the balance is low severity or unburned;
- Moderate-severity burn: < 10% severely burned; > 15% moderately burned, and the balance is low severity or unburned;
- High-severity burn: > 10% severely burned; over 80% moderately or severely burned, and the balance burned with low severity.

A common description of a severe fire is a stand-replacing fire, an above-ground-based description (Brown 2000). However, there is no model as yet relating below-ground fire effects to levels of fire intensity and severity above-ground (DeBano, et al. 1998) (see Methods section for a detailed discussion of this problem).

For any fire-induced soil temperature and time of exposure, the variables determining the degree of effects on soil include at least (DeBano et al. 1998, Neary et al. 1999):

- Soil moisture: below-surface temperatures are limited (to ~ 100 C) until moisture has been vaporized;
- Bulk density: lower bulk density implies better insulating properties and less heat penetration; and
- Organic content provides more fuel for the fire but, on the other hand, at low temperatures, contributes to low bulk density and is good insulation.

When a fire heats soils to 200 ^{o} C or more, organic matter is combusted, and much of the carbon is oxidized and lost as CO and CO_2. At those temperatures, nitrogen in soil organic matter is chemically altered, with some of the nitrogen remaining in the soil as ammonium (NH_4^+), but most (up to 99% in laboratory studies) going off as dinitrogen (N_2) (Certini 2005, DeBano et al. 1998). Above 500 ^{o} C most soil organic matter and N have been lost (Neary et al. 1999).

Four elements of fire effects on N pools; fire effect budget

The likelihood of detecting long-term effects of fire on soil C and N pools can be evaluated by constructing a hypothetical N budget that considers 1) losses at the time of the fire, 2) loss of litter input, 3) draw-down of mineral soil pools in the re-growth of the stand, and 4) fire-occasioned N fixation, and other nitrogen inputs. Each of these will be discussed below, with the focus on nitrogen.

First, losses of N at the time of the fire depend, in part, on the amount available to be lost. Pools of nitrogen in western Cascades coniferous forests of Washington and Oregon are shown in Table 1, below. Also, from the literature, amounts (percentages and pools) of N losses from fire can be found for ecosystems in this coniferous biome. Barnett (1984) found N losses from severe slash burns on a highly productive Oregon Coast range site of 150 kg N/ha in forest floor and 550 kg N/ha in mineral soils, for a total of 700 kg N/ha. Grier (1975) reports N losses from a stand-replacing wildfire in a Washington east-side mixed conifer forest to be 817 kg N/ha in forest floor and 90 kg N/ha in mineral soils, for a total of 907 kg N/ha. That loss is 39% of total N (2,310 kg N/ha) in forest floor plus mineral soil. N in forest floor plus mineral soil of sites in Table 1, above, is an average of 4,505 kg N/ha. If N losses through fire in Table 1 sites were proportional to that observed in Grier et al. (1975), the N loss in forest floor and mineral soil (to 36 cm) on sites in this present study would be 1,757 kg N /ha. This extrapolation may not be entirely appropriate due to differences in sampling time and depth.

Table 1. Nitrogen pools in roots, forest floor and mineral soil reported in four studies of western Cascades forests in Oregon and Washington. Sites: * H.J. Andrews Experimental Forest in 450 year-old old-growth; ** Western Cascades forests in Oregon and Washington. Sources: 1: Grier et al. 1974; 2: Sollins et al. 1980; 3: Edmonds et al. 1992; 4: Remillard 1999.

N pools (kg/ha)

Sites	Roots	Forest floor	Soil (100 cm)	Total N	Reference
A*	162	434	4,300	4,896	1
B*	197	256	3,724	4,177	2
C*	140	445	4,560	5,145	3
D**	not included	700	3,100	3,800	4
Average	166	459	3,921	4,505	

At best, the Barnett study and the Grier study are suggestive, with losses ranging from 700 kg N/ha (Barnett 1984) to 907 kg N/ha (Grier 1975), so that N loss from forest floor and 0 -100 cm mineral soil due to fire in the sites in of Table 1 could reasonably be 800 kg/ha or much more.

Note that Grier's samples were taken just two weeks after the fire, and showed that N in the 6 cm to 36 cm depth of soils increased post-fire, by almost 10%. This is consistent with the view that some of the organic N is transformed in fire by heat into NH_4^+, and moves deeper into the soil (DeBano et al. 1998). The fate of this new ammonium, if not adsorbed, or taken up by microbes or vegetation, is to be lost within a year or two through nitrification and leaching (or denitrification) (DeBano et al. 1998, Neary et al. 1999, Certini 2005). Hence the overall N loss through fire in Grier's study, long-term, is likely greater than losses they measured after just two weeks.

Second, loss of litterfall N results from stand-replacing fire. Johnson, et al. (1982) (following Grier and Logan (1977)) estimate N in above-ground vegetation at 488 kg/ha. With removal of vegetation, the annual input of portions of that N through litterfall is lost. Until full re-vegetation, the full pre-fire annual N input to forest floor in fine litter and foliage, estimated by Sollins et al. (1980) at 20.2 kg/ha/yr, is missing. However, the dynamics of that loss, partially offset by the onset of litterfall from revegetation, appears unstudied, and the loss is not included in the post-fire budget.

Third, secondary succession after fire draws down the mineral soil N pool.` Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the dominant species in the stands in the present study (Weisberg 1999). Initiation of the regrowth of a stand of western Washington Cascades Douglas-fir following stand-replacing disturbance can take place over just 21 years (Winter 2000). Douglas-fir is a shade-intolerant species and does not grow well in the shade of other species, germinates well on mineral soil, and is a pioneering species after disturbance (Hermann and Lavender undated). Nitrogen required to grow such a stand of Douglas-fir (that does not come from fixation or deposition) must come from mineralization of organic N remaining in the soil after fire. In a chronosequence study of afforestation in abandoned agricultural areas in New England, Hooker and Compton (2003) reported a transferof 12 kg/ha/yr from mineral soil to above-ground N in biomass (Hooker and Compton 2003). Estimates of the average need for N from mineral soils, above the amount from other sources, to grow a new stand of Douglas-fir, are in the range of 20-25 kg/ha/yr over about 70 years (Cole and Bledsoe 1976, Cole and Johnson, 1981, Johnson et al. 1982). Note that is about the same amount as the loss in litterfall (20.2 kg/ha/yr) noted above,

Fourth, after fire, there are numerous inputs of N to soils, listed in Table 2, below. These include continuous atmospheric deposition and non-symbiotic fixation in soils and woody debris, periodic symbiotic fixation in *Alnus rubra* and/or *Ceanothus velutinus,* and symbiotic fixation in *Lobaria oregana* beginning 200 years after stand re-initiation. Of these, atmospheric deposition, non-symbiotic fixation in soils and woody debris, and symbiotic fixation in *Lobaria oregana* are uniformly distributed over the stand, while symbiotic

Table 2. N inputs in western Cascades Douglas-fir forests after fire.

Nitrogen inputs (kg/ha/yr)					
Source	Amount kg/ha/yr	Reference	Amount used kg/ha/yr	Kind (Key note 1)	Distri-bution (Key note 2)
Atmospheric deposition	2.0	Sollins et al. 1980	2	C	U
	1.6 - 2	Vanderbilt, et al. 2003			
Non-symbiotic fixation	2-10	Chen and Hicks 2003 (post-logging)	2	C	U
	0.7 - 1	Hicks et al. 2002			
Symbiotic fixation with *Alnus rubra* or *Ceanothus velutinus*	101	McNabb and Cromack 1983	25	E	P
	20	Zavitkovsky and Newton 1968			
	54 - 73	Binkley et al 1992			
Symbiotic fixation with *Lobaria oregana*	2.5-16	Antoine 2003	3.5	E	U
	2.8	Sollins et al. 1980			

Key note 1
C = continuous
E = episodic

Key note 2
U = uniform coverage
P = partial coverage

Table 3. 600 year nitrogen budget for burned and unburned stands.

Forest stand nitrogen budget: burned vs unburned				
Input or loss:	Nitrogen kg/ha	Time yr	Burned stand	Unburned stand
Fire loss (FF + mineral soil)	-800.0	1	-800	0
Regrowth loss per year	-22.5	70	-1575	0
Fixation per year				
non-symbiotic (in soil and detritus)	2.0	600	1200	1200
symbiotic (Alnus or Ceanothus)	25.0	40	1000	0
symbiotic	3.5	600	0	2100
(Lobaria orgegana)	3.5	400	1400	0
Atmos. Depos per year	2.0	600	1200	1200
Leaching per year	-0.5	600	-300	-300
200 year totals			2125	4200
Difference (kg/ha)				2075

fixation in *Alnus rubra* and/or *Ceanothus velutinus* are considered to be only over parts of the stand area.

A budget depicting the difference in N-status between hypothesized burned and unburned stands over the first 600 years since stand-replacing fire is in Table 3, above. Unburned and burned stands begin at the same point, but, starting with the fire in the burned stand, the next 200 years are markedly different. At about 200 years, after the assumed re-initiation of N fixation by the cyanolichen *Lobaria oregana* at that age of the burned stand (Antoine 2003), the N pools for the two stands again follow a parallel track, as indicated in Figure 1, below..

In the 200 year budget, short-term effects (< 10 years) are ignored. The effects short-term include, as noted above, the fire-induced transformation of some organic N to NH_4^+, and its relocation deeper into the soil, where it may be nitrified to NO_3^- and lost through leaching. The loss of N through elevated leaching of NO_3^- after fire has been most often noted through hydrological studies, and is often studied in conjunction with a different disturbance, clear-cutting and slash burning (McClain et al. 1998, Gresswell 1999). While the effect may raise nitrate leaching levels to 500% of normal for as long as five years, it is not clear that the effect would follow wildfire in the same amounts. For these western Cascades forests, nitrate leaching is likely less than 1 kg/ha/yr (Vanderbilt et al. 2003), and hence the total effect for a fire event is less that 5 kg/ha.

Chronosequence issues

Note in Figure 1, below, that two stands, one burned and the other unburned, begin at equal pools of nitrogen, and separate to different tracks only when one stand is disturbed by fire. These patterns of N accumulation or loss over 600 years are idealized to illustrate potential effects of a single severe fire on western Cascades soils. Actual patterns across the landscape are likely to be more complex due to non-fire events, and the actual, shorter interval of stand replacing fire reported for other locations in this landscape (Weisberg 1999). This, the assumption of idealized behavior as shown in Figure 1, is characteristic of chronosequence studies (Pickett 1989). Such studies substitute space for time, and assume that two events widely separated in time can be studied using two places representing conditions assumed to be the same as those separated by time. The fundamental assumption in SFT studies is that temporal and spatial variations are equivalent. That assumption cannot be verified in the present, and corrections to the conclusions of SFT studies may only come with actual long- term studies (Pickett 1989).

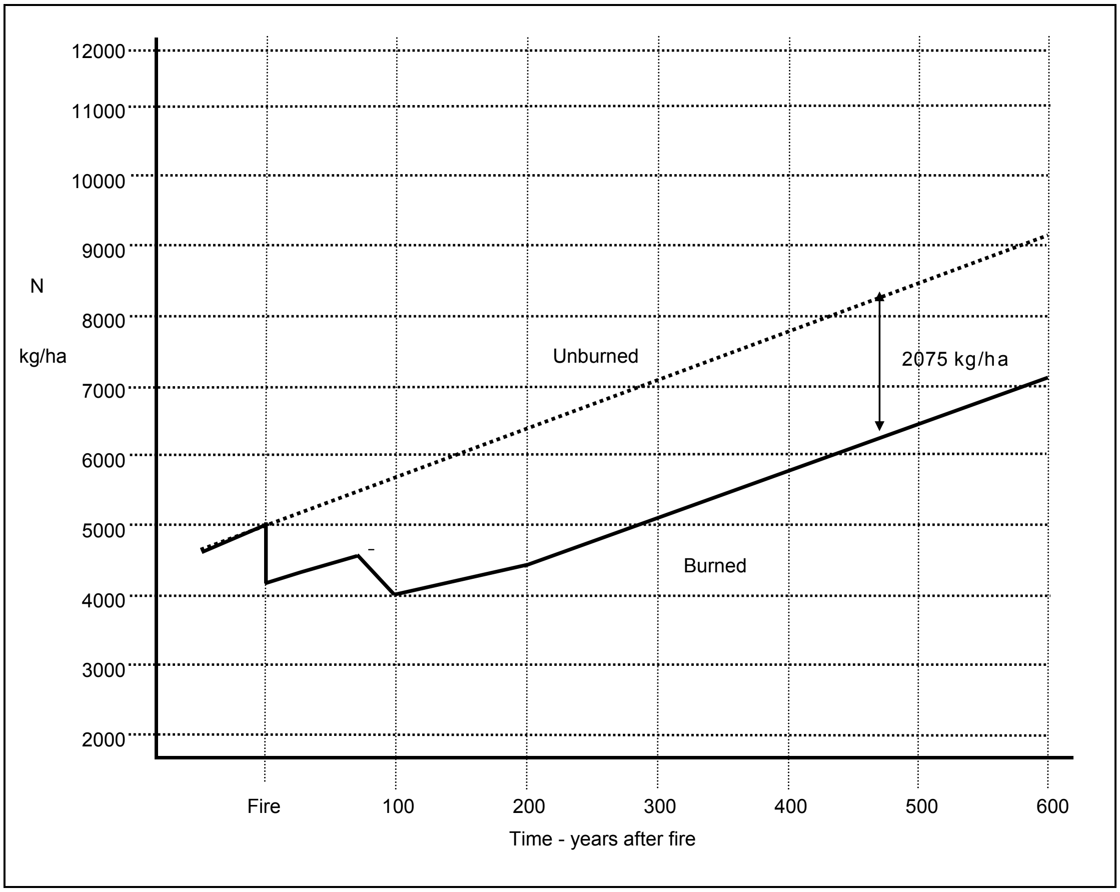

Figure 1. Nitrogen pool status for burned versus unburned stands over 600 years since fire.

Nitrogen cycling

While pools of N are of interest over time and through disturbance, the cycling of those pools by plants and microbes has more direct implications for ecological processes in forests. Rates of cycling are a measure of whether N is actually available to plants and microbes in forms they can decompose and assimilate. Rates of cycling are also a reflection of the interaction of N with other soil constituents and conditions as well.

Nitrogen mineralization

Microbial and plant needs for N are supplied by dissolved organic N and by inorganic N forms (Schimel and Bennett 2004). Dissolved organic N (DON) is produced by the depolymerization of insoluble organic matter by exoenzymes secreted by microbes. Plant-available forms of DON haves two primary fates: direct uptake by microbes or plants, or mineralization into NH_4^+ (Schimel and Bennett 2004). Net nitrogen mineralization (the NH_4^+ mineralized from DON in excess of that taken up by microbes for their own needs) in N-rich environments is said to be controlled by a complex interaction of microbes and their substrate, expressed as the substrate ratio of carbon to nitrogen (C:N) (Chapin et al. 2002). Carbon-limited aerobic microbes decompose DON via exoenzymes, and utilize the carbon skeleton to support their energy and maintenance needs. The N from the decomposed DON is released by microbial activity into the soil as NH_4^+, available for microbial or plant uptake. The $NH_4^{+,}$ plus NO_3^- found available in the soil, is termed net mineralized nitrogen. If the C:N ratio of a plentiful DON substrate is high, microbes respond to the increasing availability of carbon by growing to take advantage of the abundance. However, they then need nitrogen for growth, and they become N-limited rather than C-limited. In that case, the NH_4^+ produced by the microbes tends to be used preferentially by the microbes themselves for new biomass rather than being available for plants. The critical substrate C:N ratio at which the net NH_4^+ produced diminishes is the point of limitation of net mineralization, often considered to be C:N = 25 (Chapin et al. 2002). Hence net mineralization is thought of as controlled by the C:N ratio of the microbial substrate.

Many authors have studied net N mineralization (and net nitrification) during succession in forests subject to periodic wildfire. Most of those authors have found that net N mineralization in boreal or sub-arctic forests decreased with succession (DeLuca, et al 2002, Berglund 2004, DeLuca et al. (in press)). These sites are characterized by large reservoirs of organic N, due to slow decomposition rates in cold environments. On the other hand, MacKenzie, et al (2004), in a 10 day aerobic laboratory incubation of forest floor, found net N mineralization to increase along a 132 year fire chronosequence in samples from a low-elevation Douglas-fir forest in western Montana. The lack of longer chronosequence studies of fire-affected forests make sit difficult to know whether changes in N mineralization would persist beyond the 132 years observed by MacKenzie et al. (2004).

Nitrification

Nitrification refers to the microbially-mediated transformation of NH_4^+ to NO_3^-. Nitrification is important in that NO_3^- is a preferred form of N for some plant species. NO_3^- is also important because, unlike the positively charged NH_4^+, NO_3^- is not retained on cation exchange sites, and is often leached from the rooting areas of plants with potential to deplete essential base cations as well. NO_3^- in anaerobic environments is denitrified, releasing N as N_2 and NO_x (Chapin et al. 2002).

Nitrification has two forms – autotrophic and heterotrophic. Most nitrification in soils is autotrophic, performed by a specific suite of organisms which oxidize NH_4^+ and gain energy in the process. Heterotrophic nitrifiers also process NH_4^+ into NO_3^-, but the rates are said to be very small (Chapin et al. 2002). In either case, nitrification is described as controlled by the abundance of NH_4^+, from which NO_3^- is derived: more NH_4^+ produces more NO_3^- (Chapin et al. 2002). However, rapid immobilization rates can mask high rates of gross nitrification, resulting in low measured net nitrification (Stark and Hart 1997).

Rates of net nitrification are often found to diminish with succession or time-since-fire (Rice and Pancholy 1973, Wardle et al. 1998, Stark and Hart 1997, Sjkemstad et al. 2001, DeLuca et al. 2002, MacKenzie et al 2004, Berglund 2004). The presence of charcoal (a powerful adsorbent) is thought to be a direct control on nitrification (DeLuca et al. in press), but the mechanism is as-yet unknown. Some interaction of polyphenols, charcoal, and allelopathy have been thought by many to limit nitrification late in succession (Rice and Pancholy 1973, Wardle et al. 1997, Sjkemstad et al. 2001, DeLuca et al. 2002, MacKenzie et al 2004, Berglund 2004), but again, the mechanism is not yet known. It is not clear if nitrification rates continue to diminish after the time periods previously studied, or reflect another outcome.

Objectives and hypotheses

I studied Douglas-fir stands in the western Oregon Cascades which developed after severe fire an average of 150 years ago (young stands) or an average of 550 years ago (old stands). My objective was to study the legacy of fire on N and C pools and processes over many centuries in a chronosequence study.

A hypothesis for this study is that a difference in C- and N-status should be observable between young stands and old stands. In the formulation of a hypothesis for the extent of severe effects on soils, some rough estimates were made, as the areal distribution of severe fire effects on soils has never been studied. The estimate for this study is that, in a stand-replacing fire in a western Cascades Douglas-fir-dominated forest, fire would cause high severity burns in soils over a percentage of the area such that the average loss in N, across the entire burned site, would be 10%. A high severity burn in soils is defined such that at least 10% of the area burned has experienced high fire severity. Losses in the balance of the fire-affected area would be much less than in the high fire severity area, because N losses begin at 200 ^{o} C, and moderate fire severity areas have temperatures of just 100 – 200 ^{o} C. If the sampling protocol used in this study captures that 10% proportionately, then the observed result should reflect 10% (or more – not all losses are temperature-related) of the hypothesized difference in N pools of 2,075 kg/ha, or 208 kg/ha. As N losses are related, in part, to soil organic matter losses, C losses are expected to be somewhat proportional, but larger as a percentage, as there is no equivalent in C processes for N fixation, which mitigates losses of N in fire.

Related objectives are to determine the course of net N mineralization and net nitrification rates after fire, over succession – in this case, in the period 150 years after fire until 550 years after fire. My intent is to determine net N mineralization and nitrification rates early and late in succession, to ascertain whether these rates, over four centuries, extend the pattern in the literature of fire-prone forests of diminished net N mineralization and greatly diminished nitrification with time-since-fire, or exhibit some other pattern.

Methods

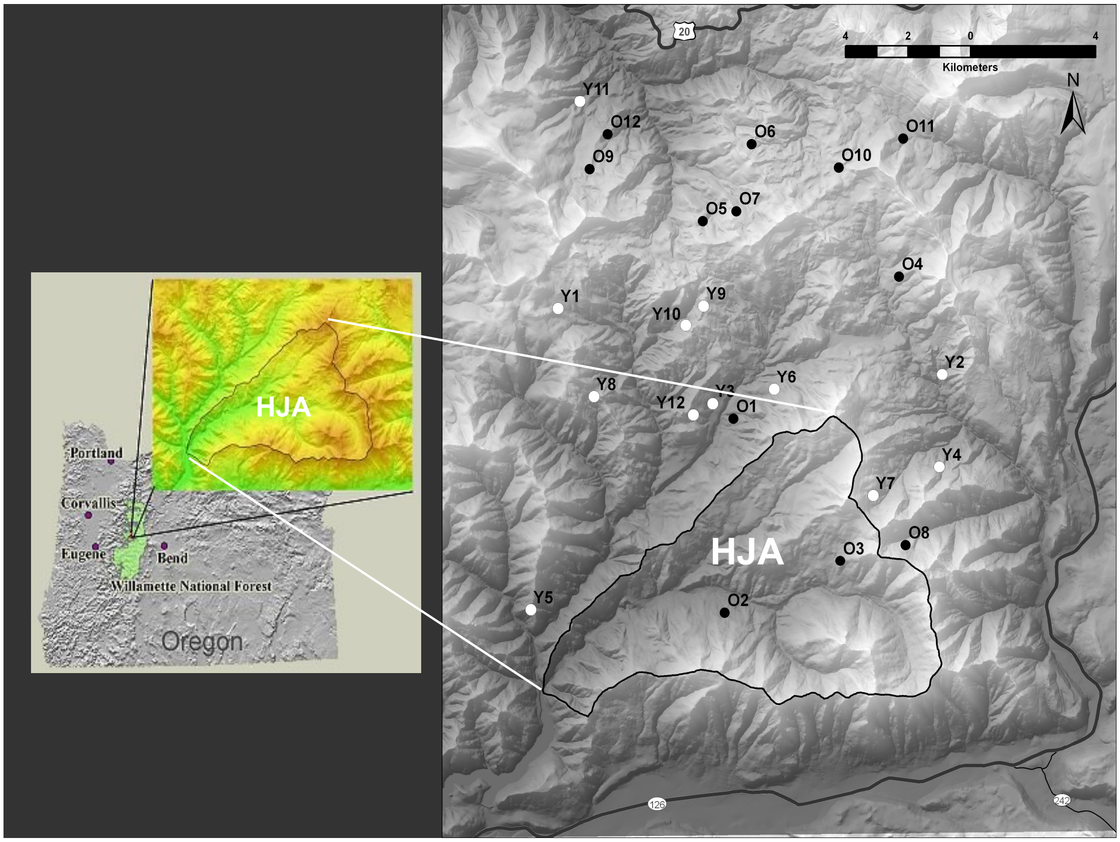

Figure 2. Study area location, and sampling sites as distributed in the study area, where Y = young sites and O = old sites.

Sites

I studied forests in a 450 km^2 area adjacent to and including the HJ Andrews Experimental Forest in the Willamette National Forest in Oregon. The sites are located on the western slope of the Cascade Range about 75 km east of Eugene, Oregon. They range in elevation from about 400 m to 1,550 m, and have a maritime-influenced climate, with wet, mild winters and dry, cool summers. At the lower elevations, the average monthly temperature ranges from about 1 °C in January to 18 °C in July. Precipitation is concentrated from November through March and increases with elevation, averaging about 230 cm per year at lower elevations to over 355 cm at upper elevations, falling as rain at lower elevations and snow at upper elevations. The lower elevations of the study area are composed of volcanic rocks in mudflow, ash flow, and stream deposits. On upper slopes and benches, bedrock is Miocene andesite lava flows and younger High Cascades rocks. Glacial action, landslides, and alluvial and colluvial processes have produced a dissected and steep landscape. Soils developed from these parent materials are mainly Inceptisols with some areas of Alfisols and Spodosols (Anonymous 2003).

For this study, it was necessary to find sites which had a high severity burn as a result of forest wildfire either fairly recently (0-200 years ago; termed “young sites”) or quite some time ago (> 400 years ago; termed “old sites”). I used a fire history done by Peter Weisberg (Weisberg 1999) covering the upper McKenzie and South Santiam watersheds in the west side of the central Cascade Mountains in Oregon. This is a 450 km^2 area just west of the north-south section of US Highway 126, north of Belknap Springs, OR, and including the H.J. Andrews Experimental Forest. I also used a second summary study conducted by Sheryl Giglia (Giglia 2004). This work summarized, consolidated and expanded fire history data on super-old-growth (SOG) (stands and trees originating > 550 years before the present) from Peter Weisberg’s and two other earlier studies. Peter Weisberg's fire history (Weisberg 1999) was selected for use in site selection, as his work had a large number of sites (137) and the greatest number of samples (33) per site of the three studies done in the general area. In addition, his sites had the advantage of being fairly accurately located using GIS coordinates.

A search of the literature failed to find practical tests which would indicate that soils had experienced a high severity burn. Stand-replacing fire, the most intense and severe fire event above-ground, was used as a surrogate for such a test for a high severity burn in soil. This was done despite evidence that there is no direct relationship between stand-replacing fire and high severity burn in soils (Neary et al. 1999, DeBano et al. 1998). Hence, sites selected for this study are stratified on the basis of time since stand-replacing fire. Weisberg terms stand-replacing fire "high severity fire." Other classifications used by Weisberg include low severity, low severity/underburn, and moderate severity fire (Weisberg 1999). These lesser levels of fire severity seem less likely to produce a high severity burn (DeBano et al. 1998, Neary et al. 1999) though documentation is sparse. Using stand-replacing fires as the sole indicator of a high severity burn in soils is fraught with uncertainty, but other choices do not seem superior.

To examine N and C pools and processes resulting from natural fire disturbance, this study required stands of live trees, undisturbed since the last stand-replacing fire, located near Weisberg’s study sites. Weisberg’s fire history used fire scars and dates of tree origin found through the study of tree stumps in clearcut logging units. In order for a fire site to qualify as a high severity (stand-replacing) fire, few, if any, trees studied there could predate the fire, and regeneration of post-fire seral species had to meet minimum standards. Weisberg quantified this, using a calculation he termed the proportion of regeneration (PropRegen), whereby:

$$\text{PropRegen} = \frac{\text{basal area (PSME + ABPR)}^{1}}{\text{basal area (PSME + ABPR)}^{2}}$$

Notes:

1) basal area generated in first 40 years since the fire

2) basal area in 1) plus basal area from oldest to time of fire

PSME is *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir)

ABPR is *Abies procera* Rehd. (Noble fir)

The basal areas represent those trees surviving from the fire until clearcut in the period 1965-1995.

For a high severity fire, PropRegen had to be 70% or greater – describing a stand in which fewer than 30 % of the trees survived the stand-replacing fire. Using this definition of high severity fire, I selected sites on the basis of fire history. Young sites were selected as having high severity fire within the past 200 years, and may have experienced less severe fires before or since. Old sites were selected as having high severity fire more than 400 years ago, may have experienced a low severity fire more than 100 years ago, or a medium severity fire more than 200 years ago; or may have no sign of fire, with stand origin date over 550 years to more than 800 years before the present (Weisberg 1999). In this study area, and throughout the western Cascades, many of the stand-replacing fires are aggregated in the mid-sixteenth century and again in the nineteenth century (Weisberg 1999). The most recent stand-replacing fire on the landscape of this study was the historical Carpenter Fire in 1912 (Weisberg and Swanson 2001).

Fire histories such as Weisberg's rely on fire scars, and on dates and percentages of regeneration, to reconstruct fire history. However, non-stand-replacing fire does not always leave a record in the form of scars or of partial stand-replacement (Weisberg 1999), and the fire history may be incomplete. However, this study only uses stand-replacing fire, as the most intense and severe fire event. Any missing fire records (no record on scars or cohorts of trees) would be related to low- or moderate-intensity fire, and these were not used as criteria in this study. Hence, any missing fire information does not seem relevant to this study, and the missing record, if any, was ignored.

Another possible error in using fire history would be the event that stand-replacement occurred from another disturbance, such as wind-throw. However, Weisberg required fire evidence from scars on survivors to validate fires, so all scar-dated stand-replacement events are highly likely to simply be fire events. The four oldest stands bear no evidence of the disturbance which originated them, and could have had a non-fire cause of origin.

Fire dates were aggregated by century by Giglia in her SOG study (Giglia 2004), and this study follows her lead rather than using approximate fire history dates developed by Weisberg (Weisberg 1999). Giglia chose that method of aggregated dates in response to a study by Peter Weisberg and Fred Swanson of likely errors in fire dating in Weisberg's study (which was not cross-dated), indicating that the use of actual dates might be misleading (Weisberg and Swanson 2001).

Fifty-one sites from Weisberg's study, plus the Carpenter fire, which was not in his study, were identified as suitable as regards stand-replacing fire and age-class. Each of the 52 sites was visited to see if there was an adjacent remnant stand fitting the description of the stand described by Weisberg from the evidence in the clearcut. Many of the 52 sites were found unsuitable due to:

- lack of a remnant stand clearly fitting the description;
- a remnant stand too small in one or both dimensions, or too irregular;

- an uncertain location for the studied clearcut (GIS coordinates indicated for the Weisberg clearcuts often seemed to be off by at least 200 meters);
- an inability to determine which remnant stand fit the stand studied in the clearcut. Often, at higher elevations (> 1100 meters), or on ridge tops, it was difficult to ascertain which remnant stand matched the description of the clearcut stand.

After elimination of sites based on the above criteria, twenty four suitable sites were found: 12 were young, and 12 were old. Eleven of those sites were directly adjacent to the reference clearcut. Six were within 200 meters of the clearcut, and seven were somewhat remote, ranging from 200 to 900 m from the reference clearcut. Minimum study stands were about 150 m x 250 m, so that a 100 m transect would always be at least 75 m from any edge (see Figure 2) to avoid edge effects. Edge effect describes possible changes in vegetation, pools, and processes resulting from the differences in light levels, moisture, wind and temperature that occur across a transect from the interior of a stand to a stand edge at a road, clearcut, stream, or natural gap (Chen et al. 1995, Hayes 2002). Most often the direction of the transect was set by the need to stay 75 m in from the edge of the stand, but, if not, the direction was set randomly.

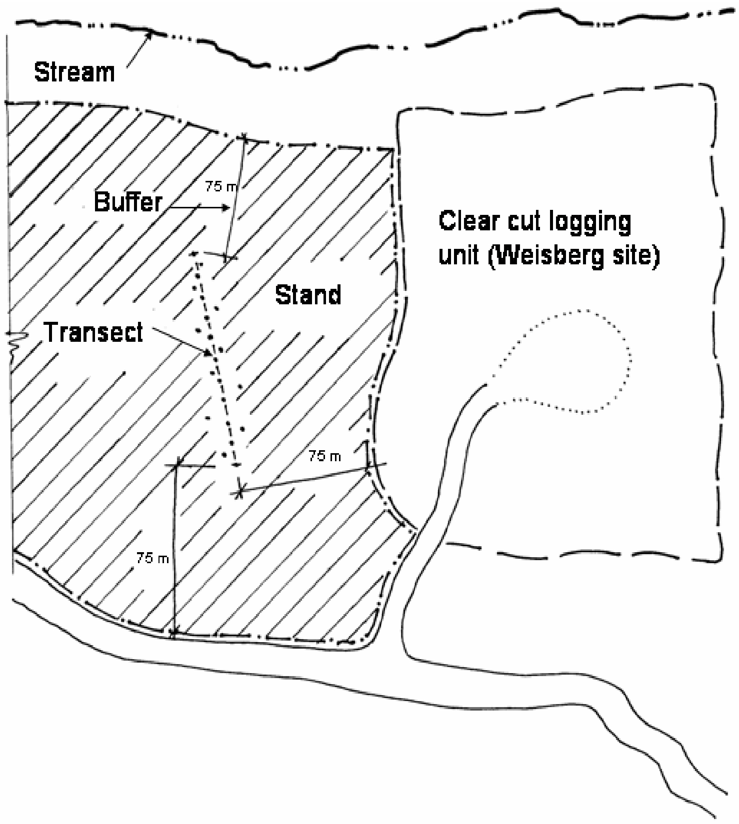

Figure 3. Schematic site layout, depicting an example of a clear-cut studied by Weisberg for fire history, adjacent remnant stand (hatched area) used in this study, transect, and buffers.

Samples and analysis

In each site I established one transect of 100 m. The transect was sampled on centerline each 10 m. At the 5 m mark between centerline samples, the transect was sampled off-centerline in alternate directions, at a random distance of 1-5 m, for a total of 20 collections per transect. These collections were composited by adjacent four samples along the transect, making 5 bags, each containing 4 samples, of forest floor and soil, for each site. All sample collection was done by one person (Tom Giesen) in one season (7/19 through

9/23/2004), using the same procedures. One set of sampling equipment was used throughout. Data collected onsite included elevation and aspect, and soils and slope were later ascertained. See table of site information in Appendix 1.

Forest floor (defined here as Oe and Oa, but not including Oi horizons) was sampled by:

- removing the Oi layer via brushing it away with a gloved hand;
- measuring and marking a 10 cm x 10 cm square in the remaining material;
- sawing the outline using a coarse-toothed folding limbing saw;
- lifting out the Oe and Oa horizon, often as an intact “brownie;”
- inverting the sample and brushing off the mineral soil, if any; and
- placing the sample in a Ziploc bag.

Samples were kept cool in the field until housed in the USGS 4 ^{o}C cooler in the Forest Service Laboratory within Oregon State University in Corvallis, OR. In preparation for analysis, each bag was weighed; sorted, with all intact cones, larger rocks, and twigs removed and discarded; broken up with finger pressure and passed through a 9.5 mm sieve; returned to the sack; and re-weighed.

Following this preparation, a subsample (about 10 g) was weighed into pre-weighed sample cups, dried for 48 hours at 65 ^{o}C, and then reweighed to calculate percentage moisture in the original sample. Another subsample of ~ 10 g of each composite was passed through a 2 mm sieve in preparation for grinding for total C and N analysis. Sieved subsamples were dried for 48 hours at 65 ^{o}C, and ground on a roller grinder until reduced to the size of talcum. These ground subsamples were placed in vials and re-dried for 24 hrs.at 65 ^{o}C, then placed in a desiccator preparatory to weighing and wrapping in foil for analysis of total N and C using an elemental combustion analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA).

Dried, ground forest floor samples remaining were tested for ash content by drying for 24 hours at 65 ^{o}C, and then compositing subsamples of the 5 forest floor samples per site to make one composite sample for each of the 24 sites. Approximately 1 g was weighed out from each site composite, added to a pre-weighed ceramic crucible, placed in a muffle furnace, allowed to heat slowly over 30 minutes as the temperature was raised, and then kept at 450 – 550 ^{o}C for 4 hours to ash the sample. The samples were then allowed to cool, placed in a desiccator, weighed. The mass remaining is ash; the mass lost is the organic portion. The object is to calculate the ash free dry weight (AFDW), which is:

$$\text{AFDW} = \frac{\text{(initial weight - weight of ash)}}{\text{initial weight}} \text{ x 100 (in \%)}$$

Immediate processing of forest floor samples for potential N mineralization was not possible, so incubations were pre-leached to remove any NH_4^+ and NO_3^- which was there initially or which may have accumulated during cold storage. About 10 g (dry weight) of forest floor from each composite was weighed into Falcon Filters. Initial available N was removed by leaching with 200 ml 4 mM CaCl prior to the start of one 28 day incubation. At the end of 28 days, the forest floor was flushed again with 100 ml CaCl, and samples of the leachate were retained for analysis of available N as NH_4^+ and NO_3^-, using a Lachat QuikChem 8000 Series FIA+ Flow Analyzer System (Lachat Instruments, Loveland, CO). Nitrate was analyzed colorimetrically following cadmium reduction (Lachat method #10-107-04-1-B, and Method #10-107-04-1-J); and ammonium was analyzed colorimetrically by sodium salicylate (Method #10-107-06-2-J). Net mineralized N is the sum of NH_4^+ and NO_3^-, and expressed per gram of forest floor and per gram of forest floor N.

Soils were sampled in the same manner as forest floor, with the following exceptions: soil was sampled by removing the forest floor, inserting a 6.8 cm diameter x 14 cm long steel tulip bulb planter to 10 cm, excavating around the sampler to prevent loss of soil from the bottom, and placing the sample in a Ziploc bag, and compositing from 20 collections to 5 samples per transect per site; all soil in each bag was passed through a 2 mm sieve; a sub-sample (about 30 g) was used for moisture calculations; and about 30 g (dry weight) of soil from each composite was used for incubations, as above.

Statistics

For each site, 5 composited samples each of forest floor and mineral soil were analyzed, and the arithmetic mean of those 5 was used in the statistical analysis, where n = 24, 12 per age class. Predictor variables include site elevation (meters above sea level, determined via wrist altimeter and verified with GPS locator), aspect (warm (SE-S-SW-W-NW) or cold (NW-N-NE-E-SE)), soils (glacial till or not), slope (percentage slope, taken from topography via computer) and age-class (young or old).

I used multiple linear regression to analyze relationships in the data. Akaike's Information Criteria (AIC) was used as a model-selecting tool in multiple regression analysis of data. AIC is one of several formulations designed to assist in model selection for regression analysis including multiple predictor variables, all of which can potentially affect a response (Ramsey and Schafer 2002). This procedure quantifies model variability and includes a penalty for the inclusion of too many variables. Suitable models would not include non-predictive variables, as these have large variability not related to the fit of the model. Similarly, a suitable model would include only those predictors which are most useful in predicting fit – hence, the calculations in the model-selecting formulas penalize models with large numbers of variables. The formula for Akaike's model selecting formulation is:

$$\mathrm{AIC} = n \times \log(\sigma(\mathrm{est})^2) + 2p$$

Where n = number of sites, p = number of coefficients in the model and $\sigma(\mathrm{est})^2$ is the estimate of the variance.

A low AIC implies a balance of good fit and a low number of coefficients, and models are selected on the basis of the lowest AIC value (Ramsey and Schafer 2002). The analytical computer program used for evaluations was S-Plus, Version 6.2 for Windows, Academic Site Edition, revised 12 Jan 2004 (build 6713), by McRae Software International, Incorporated. S-Plus (Venables and Ripley 1999) was used to make the calculations generating AIC for a stepwise sequence of models. S Plus calculates AIC for a fully parameterized model (including potential interactions) for deletions and additions of single variables and interactions, until all possible, non-interacting combinations are exhausted. It provides AIC values for each model with a significant result, ending with the model with the lowest AIC. The model with lowest AIC may be unusable because it describes a statistically-significant interaction (in which the major effects p-values cannot be interpreted), however, and in that case the model with the next best AIC is used. This is stepwise analysis of models, using both additions and deletions until the model with the lowest AIC is found (Krause and Olson 2002, Ramsey and Schafer 2002).

Many interactions were encountered in the analysis of the data for this study, and these are noted in Appendix 2, along with a complete listing of models used and rejected, with their AIC values. An interaction is said to exist when an effect is modified or qualified by another effect. This does not imply causality, but simply reflects the fact that in regression the data indicate a relationship between the interacting variables. Interactions can involve more than two variables. The limitations due to a small dataset and a consequent degree-of-freedom problem made it impossible to evaluate all predictor variables in a single model.

P-values < 0.10 were considered important as a trend, while p-values < 0.05 were considered to be significant.

Results

The mean of forest floor ash-free-dry-weight (AFDW) fraction (% of organic content in forest floor) was significantly larger in old forest (64.8 ± 4.1%) than young forest (53.0 ± 2.2%) (p-value = 0.02; r^2 = 0.23). The mean of forest floor mass per area (g AFDW/cm^2) trended higher (p-value = 0.10) in old sites (1.21 ± 0.11 g/cm^2) than in young sites (1.00 ± 0.07 g/cm^2). Mineral soil bulk density was not significantly different between old sites (1.38 ± 0.06 g/cm^3) and young sites (1.46 ± 0.12 g/cm^2). See Table 4, below.

Forest floor N and C concentrations, adjusted to reflect only the organic fraction (AFDW) in forest floor, were virtually identical in old and young sites. Old site N and C concentrations in mineral soil were not significantly different from those in young sites.

In forest floor, there were significantly larger pools of N and C in old sites versus young sites (p-value = 0.03). N pools in forest floor were 1,450 ± 98 kg/ha in young sites and 1,823 ± 132 kg/ha in old sites. C pools in forest floor were 49,032 ± 2,965 kg/ha in young sites and 62,980 ± 5,403 kg/ha in old sites. See Figures 3 and 4. Pools of N and C were numerically larger but not significantly larger in soils in old sites. Differences in forest floor mass, not concentration, explains higher C and N pools in old sites.

Table 4. Physical parameters for forest floor and mineral soils by age group. Significance tested via simple linear regression of response site means against age class.

Physical parameters	Young	Old	p-value	r^2
Forest floor (g/cm3)	1.90	1.96	0.01	0.29
Standard error (+/-)	0.13	0.22		
Forest floor % organic	0.53	0.65	0.02	0.37
Standard error (+/-)	0.02	0.04		
Forest floor (g/cm2, adjusted to AFDW)	1.00	1.21	0.10	0.12
Standard error (+/-)	0.07	0.11		
Soil bulk density (g/cm3)	1.46	1.38	0.35	0.00
Standard error (+/-)	0.12	0.06		

Table 5. Mean values and standard errors by age-group, and p - values and r^2 for differences between age-groups, for N and C pools and C:N. Note 1: statistical analysis using stepwise multiple linear regression. See table 6 for all significant stepwise regression equations. See Appendix 2 for all models considered, with associated AIC.

	N kg/ha	C kg/ha	N mg/g soil	C mg/g soil	C:N
Forest Floor					
Young	1,450	49,032	15.50	523	34.2
S.E.	98	2,965	0.53	4.3	1.3
Old	1,823	62,980	15.45	524	34.3
S.E.	132	5,403	0.63	9.1	1.4
p-value (age)	**0.03**	**0.03**	0.95	0.93	0.94
r^2	0.19	0.19	0.00	0.00	0.00
Note:	1	1	2	2	2
Soils (10 cm)					
Young	5,893	182,619	2.88	88	32.5
S.E.	591	11,950	0.05	9.77	2.0
Old	6,203	193,806	3.07	96	31.7
S.E.	418	12,539	0.03	7.26	1.5
p-value (age)	0.67	0.53	0.70	0.53	0.76
r^2	0.01	0.02	0.00	0.02	0.00
Note:	1	1	2	2	2

Table 6. Significant stepwise multiple regression equations for significance of the difference of means of dependent variables versus all predictors (age, elevation, slope, aspect and soils). See Appendix 2 for all models with associated AIC. Boxed equations = multiple predictor variables in a significant regression. PLUS means equation carried to next lines.

Dependent Variable		Intercept		Coefficient	Independent Variable
Forest floor N mass kg/ha	=	1,450	+	373	age
Standard error		116		164	
p value		< 0.001		**0.03**	
r^2				0.19	
Forest floor C mass kg/ha	=	49,033	+	13,947	age
Standard error		4,357		6,162	
p value		< 0.001		**0.03**	
r^2				0.19	
Forest floor N Min mg/g	=	26	+	34	age
Standard error		6		8	
p value		< 0.001		< 0.001	
r^2				0.45	
Forest floor N Min mg/g N	=	1,659	+	2,189	age
Standard error		340		481	
p value		< 0.001		**< 0.001**	
r^2				0.49	
Forest floor NO_3^- mg/g	=	1	+	-1	age
Standard error		0		0	
p value		1		0.084	
r^2				0	

Table 6, Continued.

Forest floor NO_3^- mg/g N	=	32.7	+	-29.9	age
Standard error		11.5		16.3	
p value		0.01		0.08	
r^2				0.13	
Non age-related relationships					
Soil N mass kg/ha	=	1653	+	4.32	elev
Standard error		1642		1.59	
p value		0.32		**0.01**	
r^2				0.25	
Forest floor C:N	=	44.9	+	-0.011	elev
Standard error		4.33		0.004	
p value		< 0.001		**0.02**	
r^2				0.22	
Forest floor N mg/g	=	9.62	+	0.006	elev
Standard error		1.74		0.002	
p value		< 0.001		**0.00**	
r^2				0.35	
Soil N mg/g	=	12.59	+	0.079	elev
Standard error		27		0.026	
p value		0.65		**0.01**	
r^2				0.29	
Soil C mg/g	=	33.9	+	0.211	elev
Standard error		27		0.026	
p value		0.65		**0.01**	
r^2				0.29	

Table 6, continued:

Soil N min mg/g	=	-0.013	+	0.000	elev
Standard error		0.010		0.000	
p value		0.65		**0.05**	
r^2				0.167	
Soil N min mg/g N	=	-0.108	+	0.000	elev
Standard error		0.058		0.000	
p value		0.08		**0.01**	
PLUS			+	0.040	aspect
				0.022	
				0.08	
Soil Nitrification mg/g N	=	-0.042	+	0.000	elev
Standard error		0.033		0.000	
p value		0.27		0.08	
PLUS			+	-0.023	age
				0.015	
				0.13	
Forest floor N min mg/g	=	54.98	+	-0.55	slope
Standard error		10.3		0.28	
p value		>.001		0.59	
PLUS			+	18.5	soil
				10.8	
				0.10	

Table 6, continued.

Forest floor N min mg/g N =	3448	+	1240	soil
Standard error	628		658	
p value	>.001		0.07	
PLUS		+	-34	slope
			17	
			0.06	

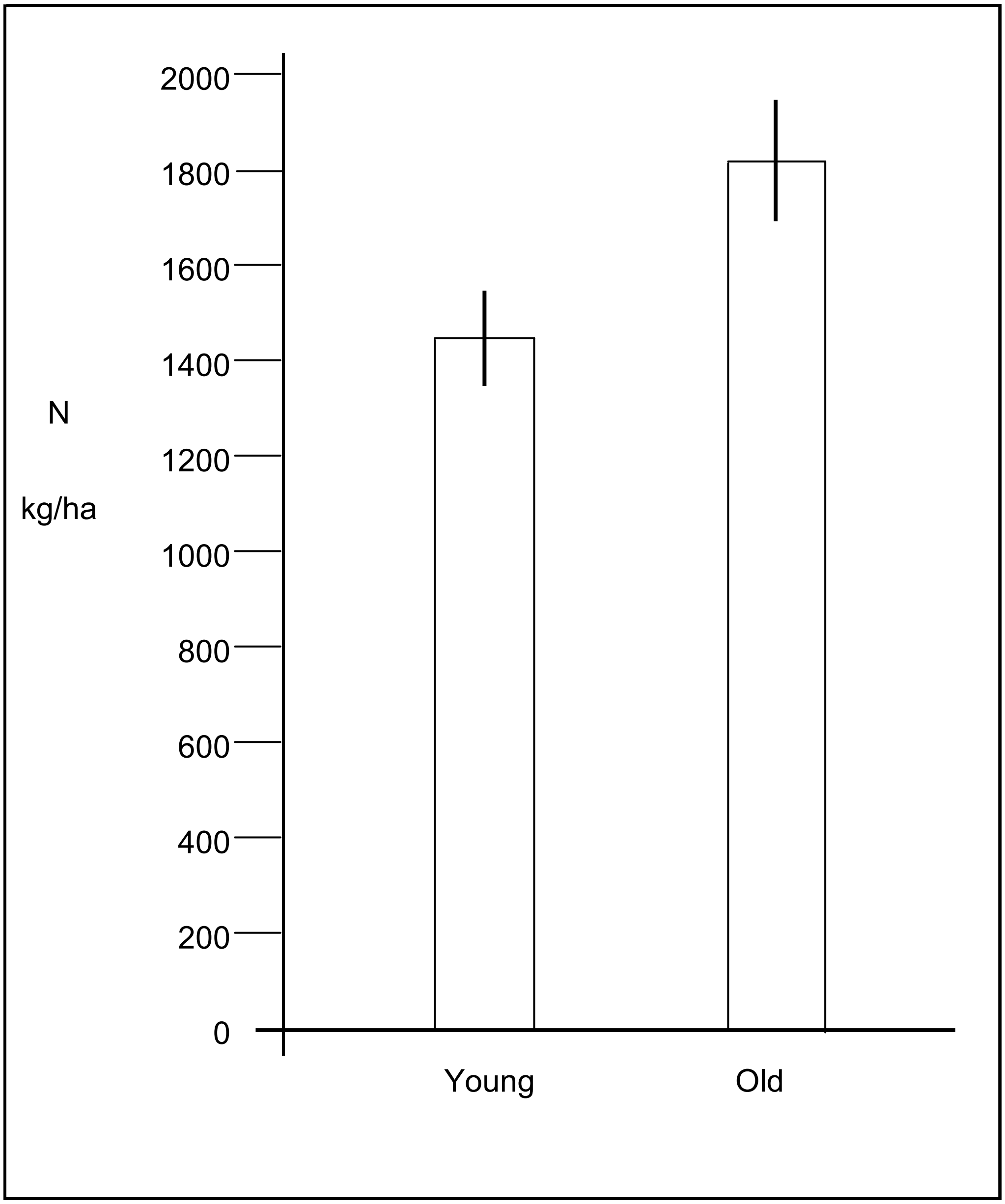

Figure 4. Forest Floor N pools (kg/ha) in young sites versus old sites. Values are arithmetic means, and vertical lines are +/- 1 standard error. See table 6 for stepwise regression equation, where $p = 0.03$ and $r^2 = 0.19$.

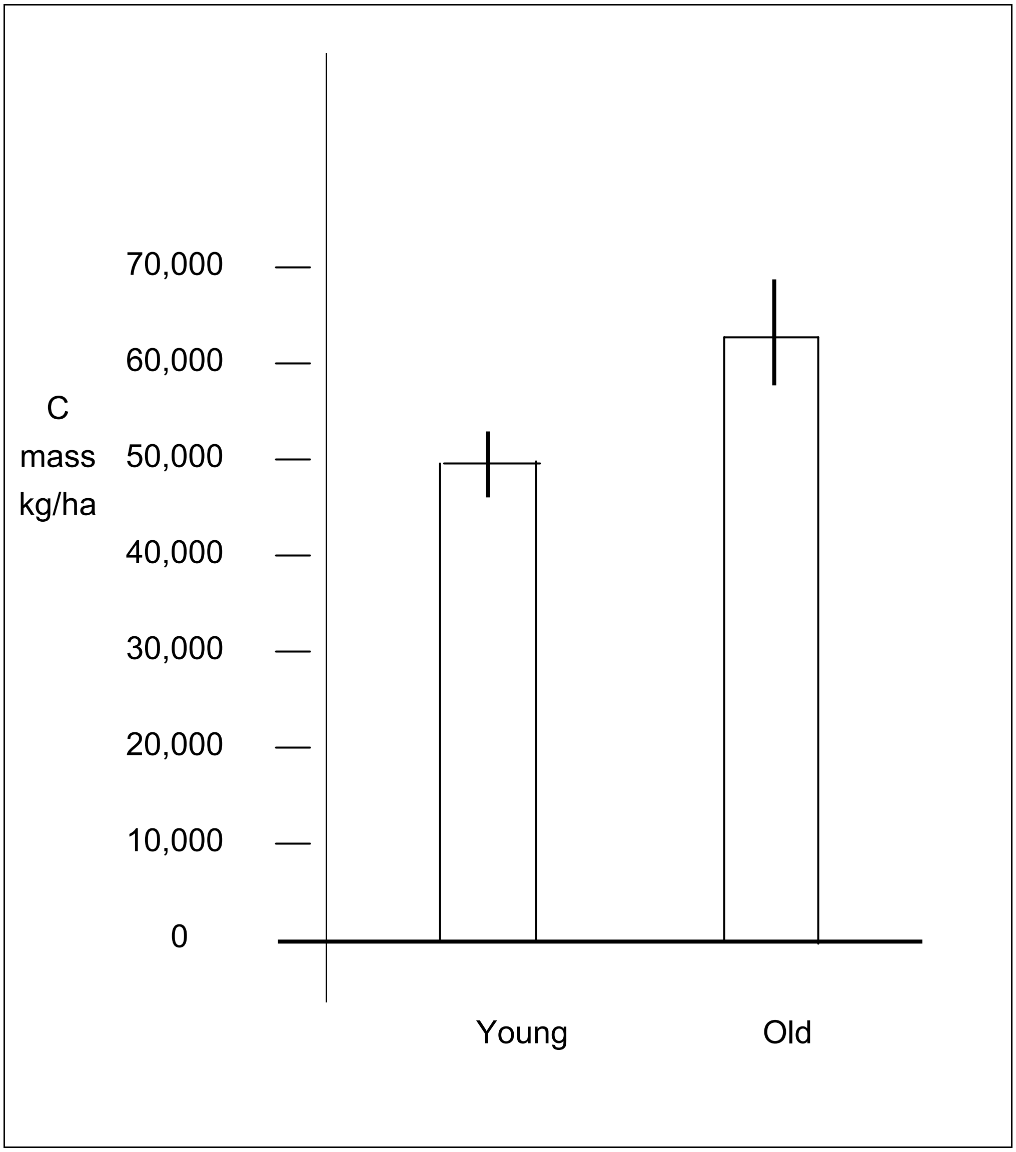

Figure 5. Forest Floor C pools (kg/ha) in young sites versus old sites. Values are arithmetic means, and vertical lines are +/- 1 standard error. See table 6 for stepwise regression equation, where $p = 0.03$ and $r^2 = 0.19$.

C:N ratios in forest floor or mineral soil do not differ between old sites and young sites.

Incubations for net N mineralization and nitrification showed wide differences between young and old sites despite similar forest floor and mineral soil C:N. Total N mineralized in forest floor was significantly greater (p-value < 0.001, $r^2 = 0.45$) in forest floor in old sites (60 ± 7.3 mg/g) than in young sites (26 ± 3.5 mg/g). See Table 7, below. N mineralized per gram of N was also significantly greater (p-value = < 0.001, $r^2 = 0.48$) in forest floor in old (3.847 ± 0.432 mg/g) versus young sites (1.659 ± 0.210 mg/g). Neither total N mineralized mg/g soil nor mg/g soil N were different in mineral soil in old sites from amounts in young sites.

While net N mineralization increases from young to old sites, net nitrification shows the reverse pattern in both forest floor and soils. In mg/g of AFDW-adjusted mass of forest floor, nitrification trends lower (p-value 0.08, $r^2 = 0.13$) in old sites (0.046 ± 0.027 mg/g) than in young sites (0.551 ± 0.28 mg/g).

Table 7. Data for 28 day temperature and moisture controlled incubation of N mineralization and nitrification in forest floor and soils per gram of forest floor or soil and per gram of forest floor or soil N. Statistical analysis used stepwise multiple linear regression of each response variable against all predictors, but all AIC-selected models were simple linear regression. See Table 6 for significant models with regard to age; see Appendix 2 for all models evaluated via AIC.

	Min N mg/g	Nitri- fication mg N/g	Min N mg/g N	Nitri- fication mg N/g N
Forest Floor				
Young	26	0.55	1.659	0.033
S.E.	3.52	0.28	0.210	0.016
Old	60	0.05	3.847	0.003
S.E.	7.32	0.03	0.432	0.002
p-value (age)	**< 0.001**	**0.08**	**< 0.001**	**0.08**
r^2	0.45	0.13	0.48	0.13
Soils (0-10cm)				
Young	0.007	0.0036	0.06	0.024
S.E.	0.004	0.0027	0.02	0.015
Old	0.007	0.0007	0.06	0.007
S.E.	0.002	0.0003	0.01	0.003
p-value (age)	0.96	0.30	0.73	0.26
r^2	0.00	0.05	0.01	0.06

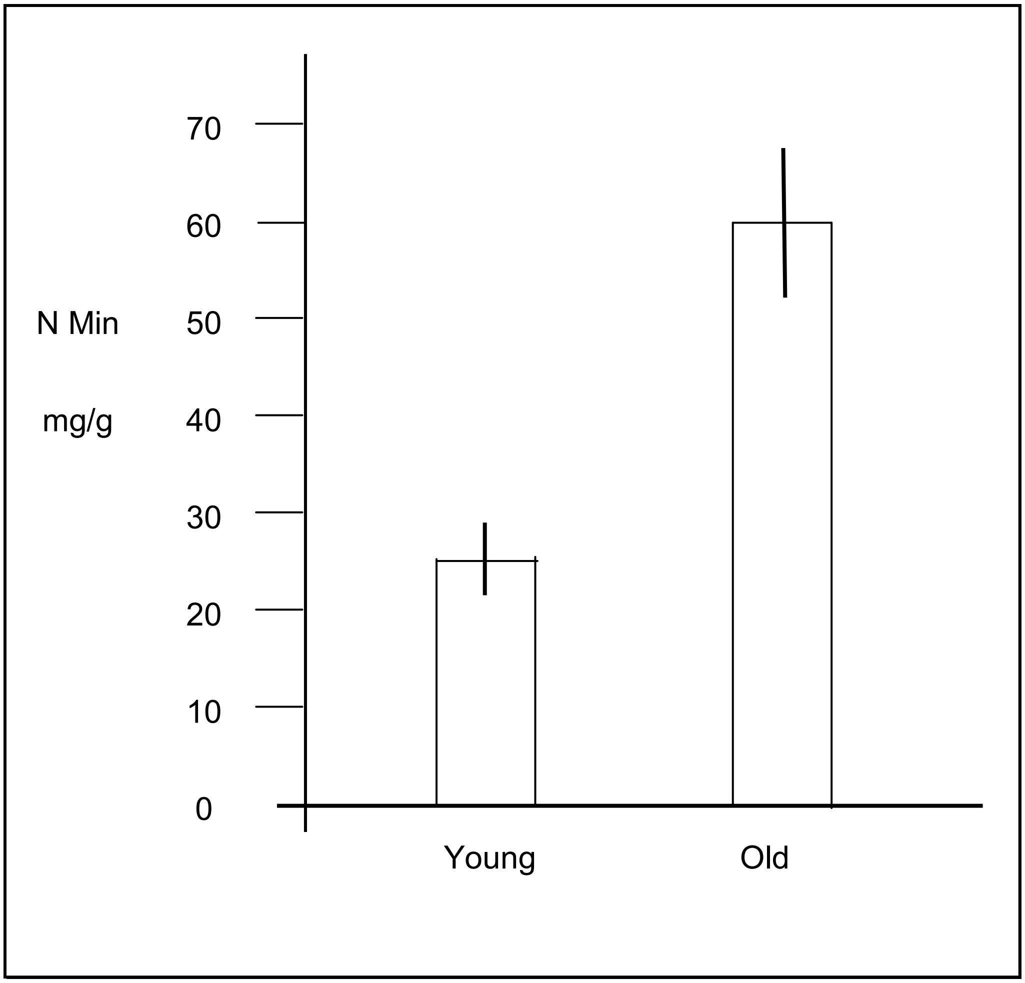

Figure 6. Forest floor net N mineralization in young versus old sites. Values are arithmetic means, and vertical lines are +/- 1 standard error. See table 6 for stepwise regression equation, where $p < 0.001$ and $r^2 = 0.45$.

Nitrification (mg/g) is not different between young and old sites in soils. In forest floor but not in soil, nitrification in mg/g N trends (p-value = 0.08) lower in old sites than in young.

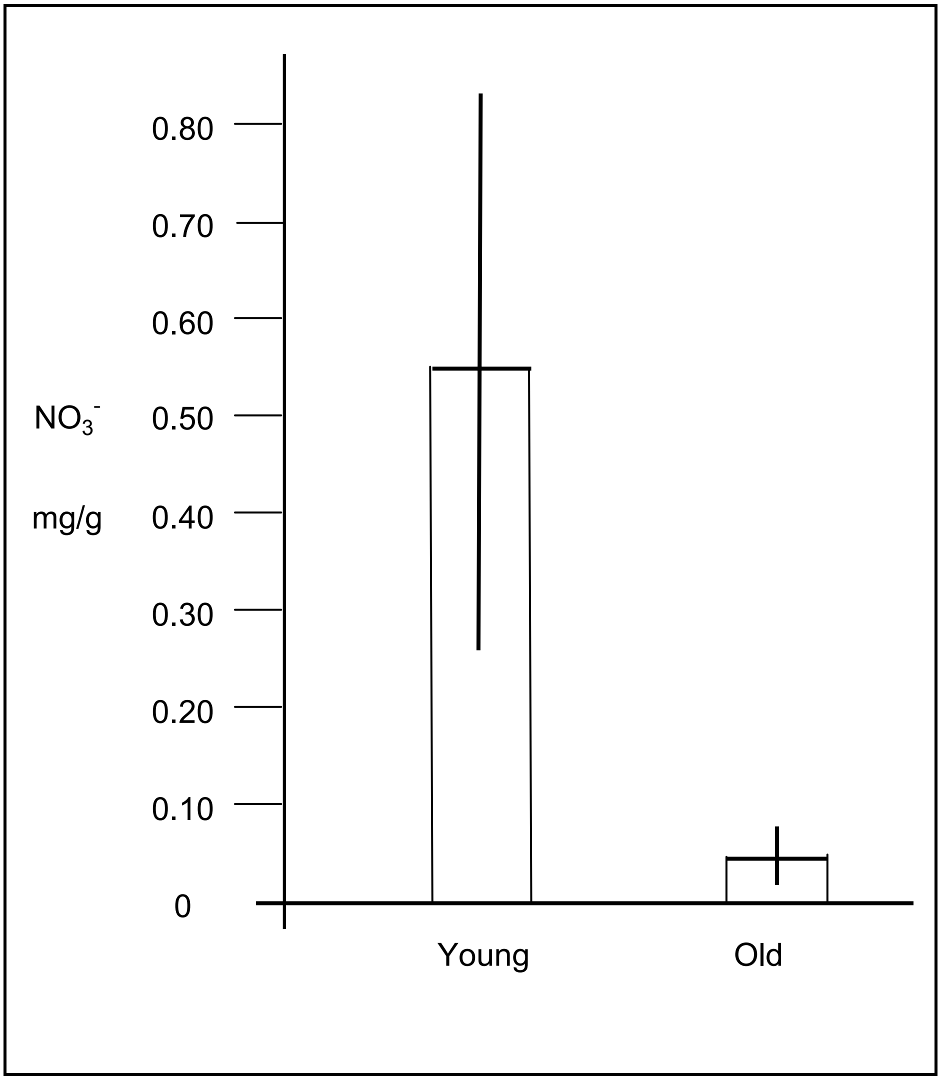

Figure 7. Forest floor net nitrification in young versus old sites. Values are arithmetic means, and vertical lines are +/- 1 standard error. See table 6 for stepwise regression equation, where $p = 0.08$ and $r^2 = 0.13$.

Rates of nitrification and mineralization were vastly different between forest floor and mineral soil. Process rates are higher in forest floor than in soils. The greatest percentage change in C and N pools occurs in forest floors..

While sites in this study fall primarily into short-time-since-fire and long-time-since-fire groupings, there are actually, as noted above, potentially three groupings – average age 150, average age 450, and age indeterminate, but likely 800 or more years. The values and statistical information for forest floor and soil N and C pools for those three age groups are shown in Table 8 and Figures 7, 8, 9 and 10, below. These figures show a consistent pattern of increase in N and C pools in forest floor and mineral soils, from ~150 year old stands to ~ 450 year old stands, followed by steady state or decline from ~ 450 year old sites to 800+ year old sites. I only have data points at ~150 years, ~ 450 years, and 800+years, do not know when values peak (before or after ~ 450), and can not test linearity.

Table 8. Arithmetic means of site means for three age groups (150 years, 450 years, and 800+ years. Key: ff = forest floor; s = mineral soil; Nit = nitrification; N min = N mineralization. Statistical analysis of difference between ~450 and 800+ was done using simple linear regression of response against age class.

	Approximate age, years				
	~ 150	~ 450	800+	p-value	r^2
Pools and C:N					
ff N kg/ha	1,420	1,916	1,636	0.34	
ff C kg/ha	49,033	63,648	61,645	0.87	
s N kg/ha	5,893	6,752	5,104	**0.06**	0.31
s C kg/ha	182,619	201,035	179,351	0.44	
ff C:N	34.2	32.8	37.5	0.11	
s C:N	32.5	29.6	35.8	**0.05**	0.33
Concentrations					
ff N mg/g	16	16	15	0.54	
ff C mg/g	523	512	547	**0.07**	0.30
s N mg/g	88	99	90	0.59	
s C mg/g	238	266	243	0.59	
Process Rates					
ff N min mg/g	26	68	44	0.48	
ff Nit. mg/g	0.55	0.06	0.02	0.47	
s Nit. mg/g	0.0036	0.0007	0.0008	0.88	
s N min mg/g	0.007	0.008	0.004	0.24	
ff Nit. mg/g N	32.7	3.6	1.0	0.44	
ff N min mg/g N	1,659	4,369	2,806	**0.09**	0.26
s Nit. mg/g N	0.240	0.007	0.007	0.99	
s N min mg/g N	0.06	0.08	0.04	0.14	

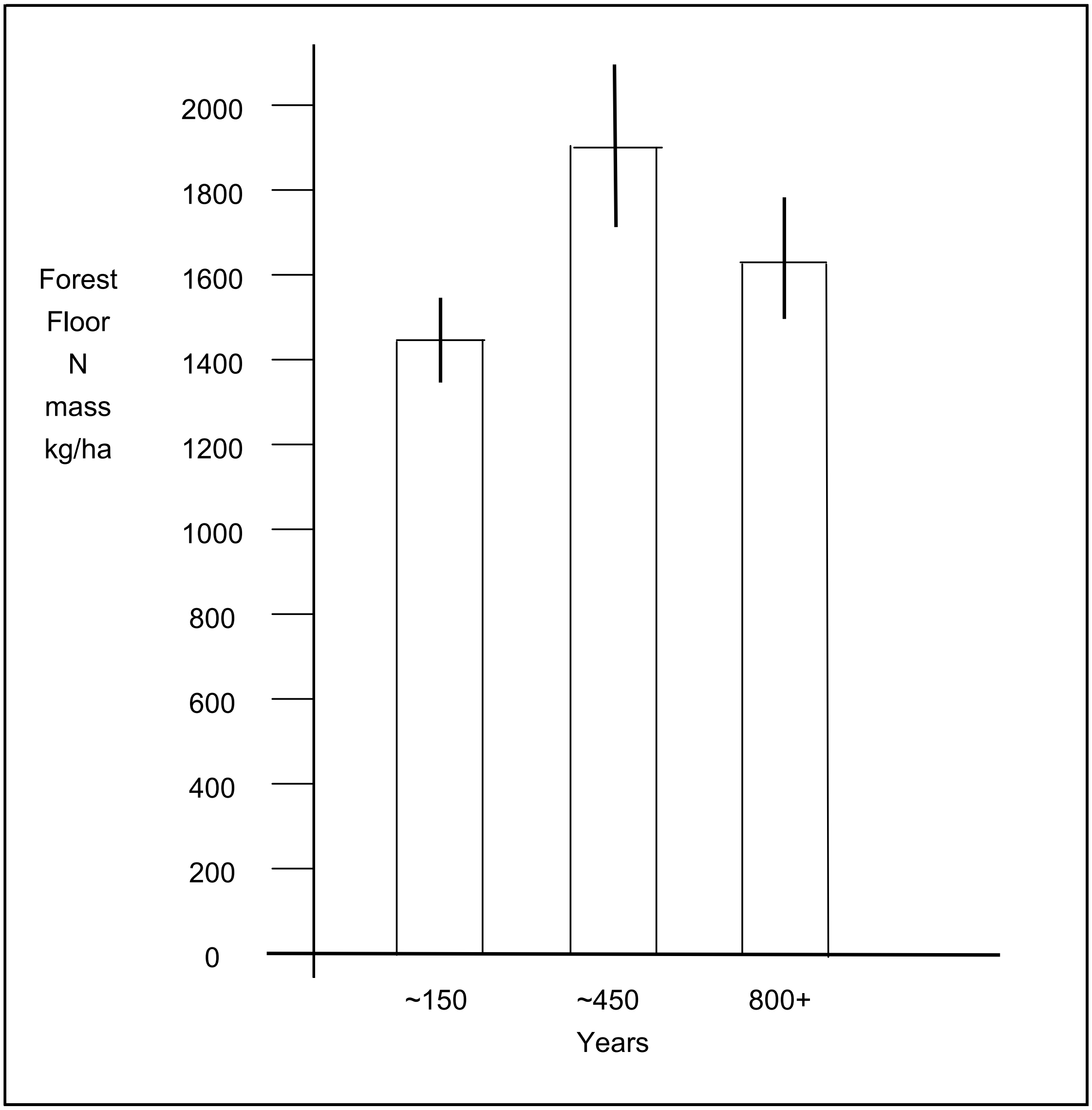

Figure 8. Forest floor N pools for ~ 150, ~ 450 year old, and 800+ year old stands. Values are arithmetic means, and vertical lines are +/- 1 standard error. See Table 8 for numerical values, and for results of regression of values for ~450 against ~800+, where p = 0.0.87

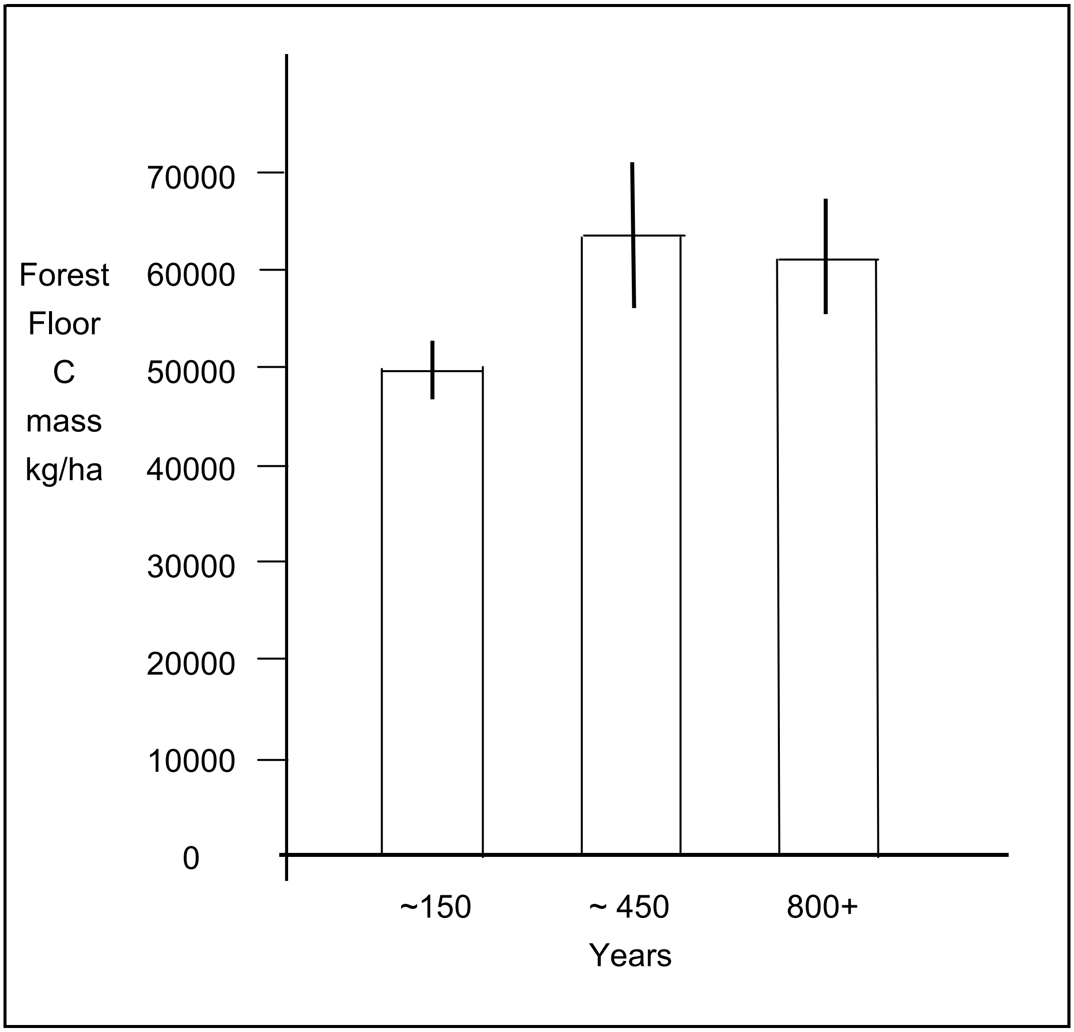

Figure 9. Forest floor C pool for ~ 150, ~ 450 year old, and 800+ year old stands. Values are arithmetic means, and vertical lines are +/- 1 standard error. See Table 8 for numerical values, and for results of regression of values for ~450 against ~800+, where p = 0.34

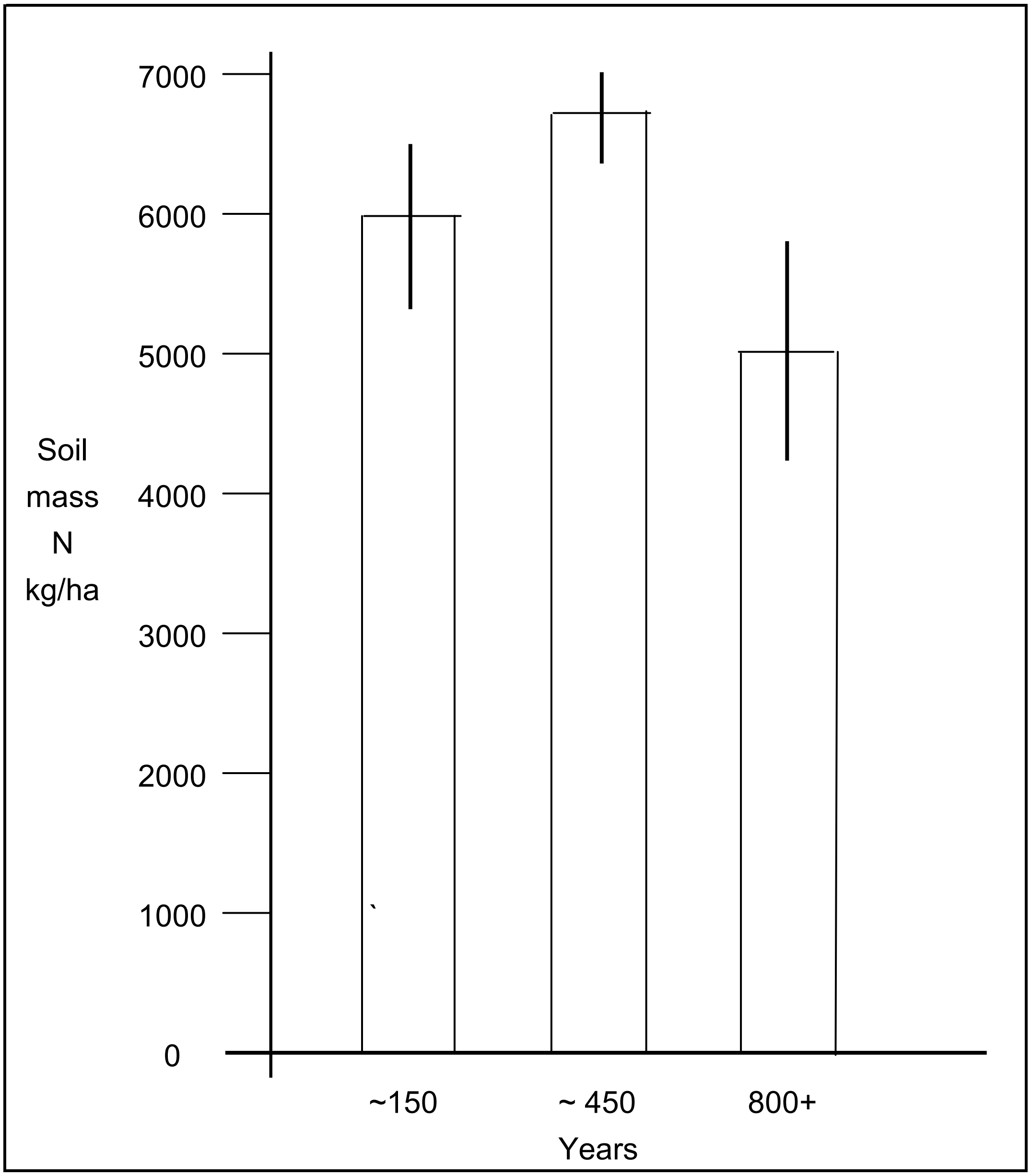

Figure 10. Soil N pools for ~ 150, ~ 450 year old, and 800+ year old stands. Values are arithmetic means, and vertical lines are +/- 1 standard error. See Table 8 for numerical values, and for results of regression of values for ~450 against ~800+, where $p = 0.06$ and $r^2 = 0.31$.

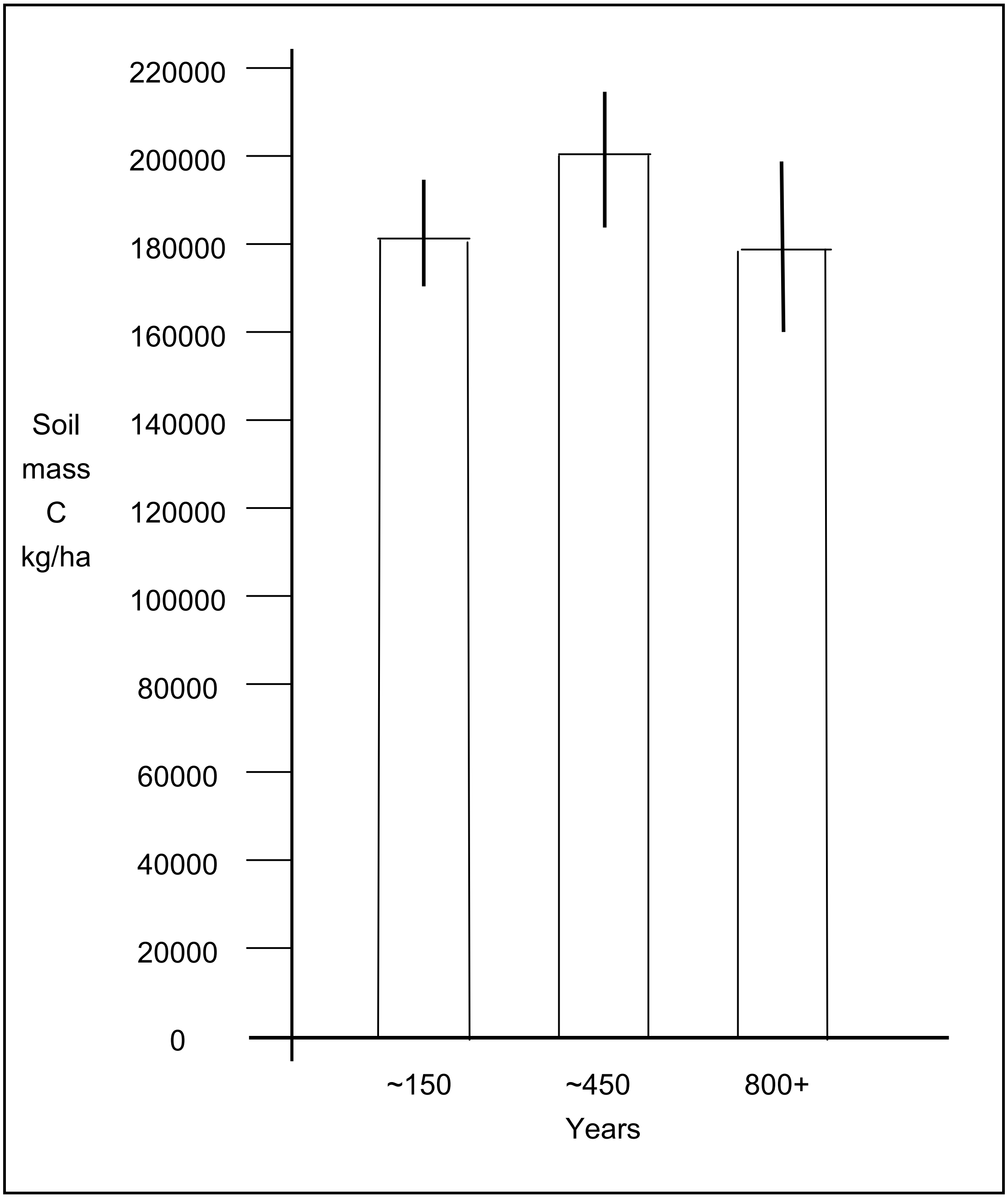

Figure 11. Soil C pools for ~ 150, ~ 450 year old, and 800+ year old stands. Values are arithmetic means, and vertical lines are +/- 1 standard error. See Table 8 for numerical values, and for results of regression of values for ~450 against ~800+, where p = 0.44

Discussion

Chronosequence studies

This chronosequence study assumes that two sets of sites sampled today are equivalent to one site sampled at two different times. Use of this chronosequence assumption, as in this study, imposes an obligation to discuss the equivalence of the two sites in the present, and also any differences between sites today and what they might have been like at the time for which the present substitutes (Pickett 1989).

The first question is: are all of the sites similar today? A means for doing that is to ask if Hans Jenny's state factors (Jenny 1941) are similar for all the sites. Hans Jenny developed the five state factors (topography, time, parent material, potential biota, and climate) to advance the understanding of soil development, but they subsequently have been applied in a more general manner to understand biogeochemical changes over ecosystem development. Sites with the same state factors are likely to have the same ecosystem structure and functioning (Chapin et al. 2002). An additional factor beyond Jenny's five is an anthropogenic factor: has human activity changed over the time of the study in some manner such as to influence either the state factors or the differences being studied?

All of the sites have similar parent material – breccias and tuffaceous materials with minor amounts of andesites and basalts, and there is no systematic bias of parent material types across fire history classes. Some soils (5 sites of 24) may have developed differently, due to topography, as they aged, through glacial tilling. In regression analysis, when sites were not segregated by time-since-fire the five glaciated sites were not different than non-glacially-tilled sites in pools of N and C.

The young and old sites are not statistically different in elevation. The means of the elevations of old (1054 ± 67m) and young (971 ± 48m) sites do not differ significantly (p-value = 0.32) (t-test for difference of means). However, more of the young sites (10 of 12) than old sites (7 of 12) were are on the "warm" aspects of slopes. The mean value of slope is 37% on young sites versus 26% on old sites, but the difference is not statistically different (t-test for difference of means).

Biota was not catalogued by site, but all sites are conifer-dominated. While not measured, Douglas-fir appears to represent a large component in the stands on all sites.

The climate is essentially the same over the study area, save for differences related to topography. The sites are arguably the same today. That leaves time and anthropogenic influences as factors yet to address.

There are several differences related to time and human activity. Northern hemisphere climate 550 to 400 years before the present (i.e., from 1450 – 1600 AD) is thought to have been 0.2 ^{o}C cooler than the preceding climate. In contrast, the most recent 150 years (especially the last 50 – 100 years) has been influenced by anthropogenic global warming, which has raised temperatures perhaps 0.6 – 0.8 ^{o}C above those in the period 1450-1600 AD (Mann et al. 2003). While these are not large changes (0.2 ^{o}C cooler, then ~0.7 ^{o}C warmer), they still represent a difference in northern hemisphere climate history that could have potentially influenced long-term patterns of soil N and C accumulation.

Perhaps more important than macro-climatic trends, forest fire severity, area and incidence have changed substantially from 1450 to the present. The incidence of forest fire is thought of as related to three factors: climate; cyclic stand development-related fuel accumulations; and human influence (Weisberg 1999). Four distinct patterns of fire were found by Weisberg: a period of high-severity, widespread fire from 1475-1620; a period of reduced frequency, area and severity of fire from 1620-1830; a period of high severity, frequent and widespread fires 1830-1910, and reduced fire 1910-present (and especially 1940-present) (Weisberg 1999). The pattern of more severe, frequent and widespread fire does not appear to be consistent with a cooler hemispheric climate in the period 1450-1600, possibly because local climate changes are often out of sync with hemispheric patterns (Mann et al. 2003).

The observed patterns of fire, however, appear fairly well linked to hypothesized patterns of human activity (Weisberg 1999). These are: high levels of native American burning from 1450 until the time of population decreases in native Americans, thought to have been caused by Euro-American-introduced disease; high levels of fire occasioned by settling and settler-traveling; and low levels of fire in the post-1910 fire suppression period (Weisberg 1999).

Another time-related problem in chronosequence studies is the problem of unrecorded history, specifically for low and medium intensity fires. In addition, there may be other, more significant unrecorded events. For example, the oldest four sites have no record of fire, and the trees and cohorts that mark the generation of those oldest stands may have had non-fire origins. In 1962, in the Columbus Day windstorm, there were timber blow-downs totaling 11 billion board feet in Oregon and Washington, resulting from a severe tropical storm (winds to 260 km/hr) moving through northwest Oregon (Lynott and Cramer 1966). Such a storm, or some other event, could have occurred in the period 1200 – 1600 without having left a physical or historical record (oral or otherwise) of which we are aware.

Differences, then, between the periods 1450 – 1600 and 1850 – present, do exist and are related to climate, time (as regards local climate regimes versus hemispheric; the various human influences on fire severity, area, and frequency; missing history; and global warming), and perhaps differences related to the unstudied site biota. At least as regards those issues, the substitution of space for time in this study is not exact. But it seems close: none of the unequal factors appears to loom large enough to detract from the study conclusions.

Other studies of C and N pools:

Comparisons of carbon and nitrogen pools in this study with those developed in other studies in the same landscape or similar landscapes are shown in Table 9, below. In general, values for pools of N and C in forest floors and mineral soils established in this study fall within the range of those from other studies. Differences may be related to differences in sampling techniques, and to forest floor and soil elements retained for analysis. For example, Remillard (2000) included undecomposed litter in her treatment of forest floor, where this study omitted loose, identifiable material. Remillard also included undecomposed cones and wood that was within the body of her forest floor samples, where again that material was excluded in this study. In her study the samples were prepared for analysis via processing in a blender, whereas in this study samples were sieved in a .95 cm sieve, with subsamples sieved

Table 9. N and C concentrations (%) and pools (kg/ha) reported in other Oregon and Washington studies. Key: WC = western Cascades in Oregon; HJA = HJ Andrews Experimental Forest, Oregon; CR 89 = 89 sites in the Coast Range in Oregon and Washington. * Jana Compton, personal communication.

Author	Depth (cm)	%	kg/ha	Age	Location
Nitrogen in forest floor					
Means et al. (1992)	NA	NA	662	450	WC
Remillard (1999)	NA	NA	505	450	WC
This study	NA	0.30	1,637	Varies	WC
Carbon in forest floor					
Remillard (1999)	NA	NA	21,000	450	WC
This study	NA	9.2	56,000	Varies	WC
Nitrogen in Soils					
Means et al. (1992)	15	NA	2,000	450	HJA
Binkley et al. (1982)	15	0.21	780	450	HJA
Binkley et al. (1982)	15	0.16	790	Varies	WC
OR Cascades *	10	0.37	NA	Varies	WC
Remillard (1999)	20	NA	2,200	450	WC
This study	10	0.30	3,300	450+	WC
Prescott et al. (2000)	15	NA	6,690	42-70	CR89
Hart (1999)	15	0.33	NA	450	HJA
Carbon in soil					
Means et al. (1992)	15	NA	57,000	450	HJA
Remillard (1999)	20	NA	42,000	450	WC
This study	10	9.20	103,000	Varies	WC
Prescott et al. (2000)	15	5.85	120,000	42-70	CR89
Hart (1999)	15	8.66	NA	450	HJA

to 2 mm and subsequently ground. It appears that the differences in treatment would result, in Remillard's samples, in the inclusion of wood, cones and other material in which the N-content is very low, while in this study those were excluded. The likely result, then, is N concentrations and N masses in forest floor per unit area much lower in Remillard's study than those in this study, and that is what was found. Methods in Prescott et al. (2000) were similar to those used in this study. N pools in the Prescott study forest floors were higher than those in this study. On the other hand, Prescott et al. studied sites in Washington and Oregon coastal sites, which tend to have more N in forest floors and soils (Remillard 1999).

Remillard's processing of soils was complex and was related to her task of separating soils by depth, by size, and by C-bearing and non-C-bearing materials (Remillard 1999). Direct comparisons in mineral soil to the methods of this study do not appear to be useful.

In other studies (Sollins et al. 1980, Means et al. 1992, Binkley et al. 1982) methods of sampling and sample processing are not described in enough detail to make a comparison with this study.

Overall, it appears that the values developed in this study for pools of N and C in forest floor and soils are consistent with and within the range of those developed by others, given sampling, processing and analytical differences.

Pools of N and C

In forest floor, the mean values of N and C pools increased significantly between young and old stands. In soil, the mean values of N and C pools increased between young and old stands, but were not statistically different. The combined pools, forest floor plus soil pools of N and C, increased in N and C with age, but were not statistically different. The hypothesis of this study, that N pools would be 208 kg/ha greater in old stands which had not burned for a long time versus young stands burned recently, is affirmed by the results of this study, in forest floors, as forest floor appears to become the center of pool accumulation, as seen in a comparison of young with old stands. The actual difference in N pools observed in forest floors is 373 kg/ha. The overall increase in N pools, forest floor plus mineral soils, was 683 kg/ha, though that result was not significant.

For perspective, deposition (total N, all forms) is 1.75 kg/ha/yr, while leaching (total N) is 0.59 kg/ha/yr (Vanderbilt 2003). N lost from forest floor from fire over 400 years, in this study, is 0.96 kg/ha/yr. N lost from forest floor plus soils over 400 years, in this study, is 1.71 kg/ha/yr. The loss in forest floor N in this study, 373 kg/ha, must be seen in relation to other N fluxes: a loss of 373 kg/ha is equal to ~ 213 years of western Oregon Cascades atmospheric deposition of N, or ~ 600 years of N (all forms) leaching in western Oregon Cascades old-growth forests. To reiterate a conclusion of Johnson et al (2004), fire disturbance must be a part of all thinking about long-term N and C pools in all fire-prone ecosystems.

Fire as the agent?

This is an observational study in which cause and effect cannot be inferred. In addition, there is no control group. To think that fire is associated with the differences found in N and C pools between young and old stands, it would be better to have young stands not generated by fire as a control – a group of stands of the same average age which were unlikely to have suffered N-loss through fire. However, this is a fire-disturbance-dominated landscape (Weisberg 1999), so the likelihood of finding and verifying stands generated in non-fire disturbances appears to be low: finding a control group to verify a fire effect appears very unlikely.

Variability

Biogeochemical pools and processes in soils have very large variability. Homann et al. (2001) make clear that the great variability in soils produces low statistical sensitivity. On sites in the Siskiyou National Forest in Oregon, they studied statistical simulation and data from 271 soil cores to determine the minimum detectable difference (MDD) between treatments, and found that the MDD for those samples was between 26 and 57% of current soil pools of N and C. For N pools, and considering post-treatment (old) less pre-treatment (young) differences, the MDD is 24%. The difference found in forest floor pools between young and old mean values on the sites in this study is 23% (N) and 25% (C) of the average pool values. Had the result in this study been the hypothesized difference of 208 kg/ha, the difference may well have been statistically insignificant. The theoretical and/or quantitative assumptions made in developing the hypothesis for differences in pools over time-since-fire were likely underestimates for the result to be 373 kg/ha (almost double the hypothesized difference of 208 kg/ha) and to be statistically significant. However, the areal extent and degree of fire effects on soils is unstudied, and I selected an extent consistent with the threshold definition of a high severity burn.

N Mineralization

Rates of net N mineralization are important as an index of N availability to plants in N-rich environments, and are thought to be controlled by processes related to the C:N ratio of the substrate (Chapin et al 2002). In this study, N mineralization increased significantly with age in forest floors but not in soils.

Process rates are much greater (both per unit mass and soil N) in forest floor than in mineral soils.

Forests that periodically burn appear to reflect patterns of net N mineralization different from forests not subject to periodic fire, in that net N mineralization declines with succession (DeLuca, et al. 2002, Berglund 2004, DeLuca (in press)). In contrast, in non-burning forests, net N mineralization increases with succession (Vitousek et al. 1989, Pastor et al. 1994, Chapin et al. 2002). Note that the fire-prone forests in which net N mineralization declines are boreal or sub-arctic. As an exception to the general patterns noted above, MacKenzie, et al (2004), in a 10 day aerobic laboratory incubation of forest floor samples from a Douglas-fir forest in western Montana, found net N mineralization to increase along a 132 year fire chronosequence.

Results in this study are similar to results in MacKenzie et al (2004). In this study, in forest floor, rates of net N mineralization, per gram of ADFW organic matter and per gram of N, are significantly greater in old forests than in young. N cycling process rates are much higher in forest floor than in soils in this study. However, C:N ratios, thought of representing processes controlling net N mineralization (higher C:N is often associated with lower N mineralization (Chapin et al. 2002)), are not different between young stands (34.2) and old stands (34.3). Despite this, there is a large difference in values for N mineralization: rates are much higher in old sites. Below are several theories about how that anomalous behavior might be explained.

One explanation for high rates of N mineralization despite no change in C:N between young and old stands might be due to an increase in ectomycorrhizal (ECM) fungi over succession, if such exists. For the purpose of this hypothesis, I assume ECM fungi are more common and have greater biomass in older forests. ECM fungi are thought of as short-circuiting the usual model in N-rich environments for making N available to plants, which is N mineralization (Read and Perez-Moreno 2003). The "short circuit" method for making N available to plants is a direct method via ECM fungi, which are said to "intervene" in the N cycling process. This intervention has two aspects. The first is through decomposing ECM fungi and the exoenzymes secreted by them. This process differs from the usual process in that ECM fungi receive carbon from their partners in mutualism, the plants with which they exist in symbiosis. They need not scavenge for carbon with NH_4^+ as a byproduct: they can seek N for itself. They appear incapable of producing NH_4^+, and instead are said to decompose, absorb and furnish plant-available dissolved organic N to their plant partners in mutualism. The second aspect of intervention is by not producing NH_4^+, and thereby avoiding immobilization of N in microbes – instead, the N goes preferentially to plants (Reed and Perez-Moreno 2003). The relevance of these processes to N mineralization in late succession (old stands) may that the ECM "short-circuit" provides another, more direct source of N for plants, reducing their need for NH_4^+, diminishing the competition in soil solution for NH_4^+, and hence increasing net N mineralization (Read and Perez-Moreno 2003). But this theory depends on greater or more active ECM decomposing communities in old stands, and this is an unstudied issue.

Yet another facet of hypothesized increased fungal presence in old forests relates to the C:N ratio of fungi, which is greater than that of bacteria (Brady and Weil 2002). That higher C:N ratio enables decomposing fungi to utilize a substrate for their own growth with a higher C:N, as their need for N, in relation to C, is less than that of bacteria (Chapin et al. 2002). That increased ability with succession to create and utilize DON with higher C:N may increase the rate of N mineralization. But, to repeat, this theory depends on greater or more active ECM decomposing communities in old stands, and this is an unstudied issue

A third possible explanation for increased N mineralization with constant C:N over time relates to charcoal. Stands which are subject to periodic fire contain charcoal in forest floor and mineral soil. Charcoal is a powerful adsorbent, with enormous amounts of adsorbing surfaces that are negatively charged at pH < 7 (Berglund 2004). Inorganic N mineralization is thought to occur by breakdown of proteins and amino acids present as soluble organic N in soils (Schimel and Bennett 2004).Decreased sorptive potential of charcoal over long periods without fire may permit greater microbial access to N mineralization precursors in old sites, thus increasing N mineralization at a constant forest floor and soil C:N over succession.

Diminished net nitrification in old sites

As noted in the Introduction, nitrification refers to the microbially-mediated transformation of NH_4^+ to NO_3^-. Nitrification has two forms – autotrophic and heterotrophic. In either case, nitrification is described as controlled by the abundance of NH_4^+: more NH_4^+ produces more NO_3^- (Chapin 2002). Rice and Pancholy (1972) suggest that nitrification will diminish over succession due to the influence of allelopathic chemicals (polyphenols) affecting nitrifiers. Others find decreased net nitrification with stand age (Wardle et al. 1997, Sjkemstad et al. 2001, DeLuca et al 2002, Berglund 2004, MacKenzie et al. 2004). In this study, forest floor net nitrification, per g soil and soil N, trended lower with increasing age, suggesting that net nitrification is not controlled by net NH_4^+ production. The phenomenon of decreasing net nitrification with age, and independent of NH_4^+ availability, appears unique to fire-adapted ecosystems. DeLuca et al. (in press) experimented with post-fire soils from low elevation *Pinus ponderosa* (Ponderosa pine) forests in Montana, by adding NH_4^+, and found no increase in nitrification. Berglund (2004) found that adding charcoal to soils in the laboratory increased nitrification, but could not duplicate that in the field. DeLuca et al. (in press) also experimented by adding charcoal (from a recent nearby forest fire) to soils in a laboratory experiment and found an increase in nitrification versus controls.

Charcoal in soils has been a focus of the work of several researchers for 10 years or more now (Zackrisson et al. 1996, Wardle et al. 1997, Pietikaenen et al. 2000, Sjkemstad 2001, Berglund 2004, DeLuca et al. 2002, Lehmann et al. 2005). They have studied the nature of charcoal, the role of charcoal as an adsorbent, the role of charcoal in nitrification and other processes, and the ways in which the adsorptive capacity of charcoal is altered. But the mechanism(s) by which charcoal and nitrification interact(s) is as yet unclear. Charcoal is a powerful adsorbent, and has large surface area (Berglund 2004). Charcoal appears to saturate with adsorbents and become inactive by about 100 years (Berglund 2004, Zackrisson et al 1996). It is thought that fresh charcoal may adsorb polyphenols or other inhibitory compounds, thus facilitating nitrification soon after fire, at least until the charcoal is “deactivated” by saturation of sorption sites (Berglund 2004, Zackrisson et al 1996). However, the exact inhibitory connection has not been shown. What seems clear, however, from this and other studies of ecosystems subject to fire, is that the availability of ammonium does not appear to be the only control over nitrification in fire-adapted soils.

Changes late in succession

Vitousek and Reiners (1975), suggested that as ecosystems mature, ecosystem biomass (live and dead) would accumulate to a maximum, followed by a steady state, with elemental inputs equal to outputs.

In this study, the forest floor and mineral soil N and C pool arithmetic mean values for the oldest four sites, at age 800+, are less than those for the ~ 450 year old sites, whereas the values at ~450 years are significantly greater than values at ~150 years. In the case of soil N, the mean values indicate a statistically significant difference, a decrease after 450 years. In the other three cases (soil C, forest floor N and C), means at ~450 and 800+ are not different. (The mean values are in Table 8, above, in Results.)

It is surprising that N and C pools do not continue to increase past ~450 years, and it indicates that at some point after ~150 years, N and C accumulation in forest floor and mineral soil pools ceased and may have begun to decline.

Data regarding elemental inputs and out puts for 800+ year-old sites is not available. Hydrologic data for ~ 450 year old sites indicates that N input is quite a bit higher than output: - by 4 - 6 kg/ha/yr (Vanderbilt et al. 2003, Sollins 1980). Some sources (Southwick et al 2001) feel that live biomass in ~450 year old stands has reached a plateau, but detritus pools at that age and older have not been studied (Mark Harmon, personal communication). It is not possible, given the available data, to say if biomass has reached a plateau or if equality in elemental input and output has been reached. These are the conditions of Vitousek and Reiners' hypothesis. My data gives indications of the end of N and C accretion in soils, rising C:N ratios, and some reversals in N process rates, and those may be an important indication that sites such as these may be past maturity, in a steady state, and hence would be a fruitful venue for the testing of ecosystem transitions from accretion to steady state.

At ~450 years, N inputs in these stands exceeds outputs by 4-6 kg/ha/yr (Vanderbilt, et al. 2003). If, as this study suggests, N is not accumulated from ~450 – 800+ years, and inputs and outputs do not change, there must be a substantial un-accounted-for N loss. Low and moderate severity fires do not appear to account for such a large loss, as temperatures in litter and soils are not high enough for substantial N-loss. Shrub losses in fire do not appear great enough either. There appear to be major processes not fully understood implied by the data in this study.

Some differences between values at ~ 450 and 800+ merit discussion. Soil N pools declined significantly, and proportionately more than soil C pools, and hence soil C:N ratios increased. Forest floor C:N ratios also increased, but not as much. With higher C:N ratios, net N mineralization values would be expected to decrease in both forest floor and mineral soils (Chapin et al 2002), and they did. The mechanism for increasing N mineralization from young to old stands, whatever it is, is not dominant as stands reach 800+ years. With less net N mineralization, net nitrification would be expected to diminish (Chapin 2002), and forest floor net nitrification did diminish. Process rates per unit of soil N diminished or stayed the same, whereas the rates for net mineralization, in forest floor and soils, per unit of N, had increased from ~150 to ~450. These process differences reverse some of the trends found with sites divided into just two age-classes, and this reversal lends credence to the suggestion that substantial change may have taken place in ecosystem structure and function somewhere in the course of succession in this study.

Conclusions

Stands burned an average of 550 years ago have significantly more N and C in forest floor pools, and different N cycling process rates in forest floors, than stands burned an average of 150 years ago. While differences in soil N and C were not significant, the means increased with age in each case. Nitrogen cycling in fire-adapted ecosystems is not completely understood, especially in regard to increased N mineralization and diminished nitrification as stands age in the absence of fire. Fire is not just an occasional setback in nutrient pools, but appears, through the legacy of charcoal, to have lasting effects on rates of nitrification. Considering NH_4^+ as the primary control over nitrification does not appear to apply to fire-adapted ecosystems. While forest floor N and C pools increase from young to old stands, forest floor and soil N and C pools are not different, or decline, between 450 year old stands and the oldest stands at 800+ years, That, and other, anomalous changes in values from ~450 to 800+ years, suggest possible changes in ecosystem functions, and may indicate that this landscape could be a fruitful study area for examinations of a mature, steady-state ecosystem.

Results from this study, seen in the context of active fire suppression on fire-prone forest lands in the United States, make it clear that nutrient pools and cycling processes are likely to be altered by fire suppression, due to diminished charcoal inputs, and that fire-suppression related decreases in nitrate and increases in ammonium levels may have implications for the fitness of organisms adapted to low NH_4^+ and high NO_3^- soils.

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Appendices

Appendix 1 – Site Information

Site Data Site ID	Date 2004	Elev. m	Aspect 1= warm 0 = cold	Slope %	Glacial till 1 = yes	Transect origin point x (GIS Coordinates)	y
Young sites							
Y1	8/12	1181	1	17.5	0	559490	4906749
Y2	7/19	918	1	46.9	0	571780	4904737
Y3	8/13	778	1	25.5	0	564438	4903834
Y4	7/20	1027	0	35.8	0	571682	4901895
Y5	8/4	753	1	59	0	558620	4897500
Y6	9/23	930	1	25.5	1	566406	4904277
Y7	8/3	1200	1	51.5	1	569571	4901011
Y8	8/12	926	1	10.4	0	560639	4904046
Y9	9/3	1230	1	10.4	0	564147	4906825
Y10	8/12	1031	0	63.3	0	563577	4906239
Y11	8/23	786	1	58.5	0	560190	4913123
Y12	8/18	891	1	37.4	0	563820	4903491
Old sites							
O1	7/21	741	1	13.6	0	565097	4903382
O2	8/5	709	0	16	0	564820	4897416
O3	8/4	1000	1	36.7	1	568516	4899006
O4	8/18	1128	1	18.4	1	570396	4907750
O5	9/7	705	1	43	0	564125	4909450
O6	9/23	1260	1	8.7	0	565680	4911820
O7	9/6	1346	0	29.2	0	565194	4909754
O8	8/3	1259	0	35.2	0	570605	4899499
O9	8/16	1142	0	6.2	0	560499	4911059
O10	8/18	1280	1	12.9	1	568467	4911099
O11	8/17	1134	0	56.2	1	570529	4911986
O12	8/2	951	1	35.8	1	561080	4912119

Appendix 2

Stepwise Regressions Models

Forest Floor N Pool (ff N mass) analysis using stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors……………………			Interaction terms			
		1	2	3		AIC	p value	R^2
First initial stepwise regression								
1	ff N mass	long	elev	slope	Includes all predictors	3013661		
	Ending @ interaction						0.058	
Second stepwise regression								
1	ff N mass	long	elev	aspect	aspect x long x elev	5812631		
2	ff N mass	long	elev	aspect	aspect x long	5449843		
					aspect x elev			
					long x elev			
3	ff N mass	long	elev	aspect	aspect x long	5087181		
					elev x long			
4	ff N mass	long	elev	aspect	elev x long	4807998		
5	ff N mass	long	elev		elev x long	4462945		
	Ending @ interaction						0.08	
Third stepwise regression								
1	ff N mass	long	elev		long x elev	4213702		
	Ending @ interaction						0.08	
Fourth stepwise regression								
1	ff N mass	long	aspect		aspect x long	4899955		
2	ff N mass	long	aspect		none	4573707		
3	ff N mass	long			none	4245234	0.033	
Fifth initial stepwise regression								
1	ff N mass	soil	slope		Includes all predictors	5330499		
2	ff N mass	soil	slope		none	5096193		
3	ff N mass	slope			none	4842094		
	Ending - non-significant, no p value given							
Sixth initial stepwise regression								
1	ff N mass	long	elev	soil	Includes all predictors	5363759		
2	ff N mass	long	elev	soil	long lev	5170720		
					long soil			
					elev soil			
3	ff N mass	long	elev	soil	long lev	4876002		
					elev soil			
4	ff N mass	long	elev	soil	long lev	4685672		
5	ff N mass	long	elev		long lev	4350727		
	Ending @ interaction						0.0819	
Selected model:								
	ff N mass	long			none	4245234	0.0329	0.19

Forest Floor C Pool (ff C mass) analysis using stepwise multiple linear regression evaluated by AIC
Initial Regressions always include age class

Steps	Response	Predictors……………….			Interaction terms	AIC	p value	R^2
		1	2	3				
First stepwise regression								
1	ff C mass	long	elev	slope	Includes all predictors	4,540,489,876		
Ending - all predictors interact, cannot interpret main effects							0.0441	
Second stepwise regression								
1	ff C mass				aspect x long x elev	7,994,149,572		
2	ff C mass	long	elev	aspect	aspect x long aspect x elev long x elev	7,507,282,971		
3	ff C mass	long	elev	aspect	aspect x aspect elev x long	7,007,852,568		
4	ff C mass	long	elev	aspect	elev x long	6,525,963,070		
5	ff C mass	long	elev		elev x long	6,399,749,687		
6	ff C mass	long	elev		none	6,356,563,384		
7	ff C mass	long			none	6,012,805,522	0.0338	0.19
Third stepwise regression								
1	ff C mass				aspect x long x slope	9,099,938,191		
2	ff C mass	long	slope	aspect	aspect x long aspect x slope long x slope	8,544,744,495		
3	ff C mass	long	slope	aspect	long x aspect slope x long	7,984,447,631		
4	ff C mass	long	slope	aspect	long x slope	7,423,869,226		
5	ff C mass	long	slope	aspect	none	7,017,776,401		
6	ff C mass	long	aspect		none	6,478,789,275		
7	ff C mass	long			none	6,151,029,099	0.0338	0.19
Fourth stepwise regression								
1	ff C mass	long	elev		long x elev	6,161,697,211		
Ending - regression is not significant							0.1653	
Fifth stepwise regression								
1	ff C mass	long	elev		none	6,245,563,293		
2	ff C mass	long			none	5,938,805,462	0.0338	0.19
Sixth stepwise regression								
1	ff C mass	long	soil		Includes all predictors	6,992,283,359		
2	ff C mass	long	soil		none	6,495,262,873		
3	ff C mass	long			none	5,938,805,462	0.0338	0.19
Selected model:								
	ff C mass	long			none	5,938,805,462	0.0338	0.19

Soil N Pool (S N mass) analysis using stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors………………			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	S N mass	long	elev	slope	Includes all predictors	93,658,120		
2	S N mass	long	elev	slope	long x elev long x slope elev x slope	88,450,790		
3	S N mass	long	elev	slope	long x elev elev x slope	82,733,300		
4	S N mass	long	elev	slope	long x elev	77,786,001		
5	S N mass	long	elev		long x elev	72,177,962		
6	S N mass	long	elev		none	69,755,960		
7	S N mass		elev		none	63,919,177	0.0127	0.25
	S N mass	long				Not stepwise	0.6729	

Note: in regressions not including age (long) (regression data not shown), aspect and slope interact. No further stepwise regressions including age but not the combination of aspect and slope, will run due to degree of freedom problems.
Age is not a significant predictor of soil N mass, but elevation is.

Soil C Pool (S C mass) analysis using stepwise multiple linear regression evaluated by AIC value
Initial regressions always include age class

Steps	Response	Predictors			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	S C mass	long	elev	slope	Includes all predictors	51,881,938,953		
2	S C mass	long	elev	slope	long x elev long x slope elev x slope	49,388,603,307		
3	S C mass	long	elev	slope	long x elev elev x slope	46,157,184,827		
4	S C mass	long	elev	slope	elev x slope	43,466,606,969		
5	S C mass		elev	slope	elev x slope	40,695,276,454		
6	S C mass		elev	slope	none	39,179,657,090		
7	S C mass		elev		none	37,076,842,095	0.015	0.24
	S C mass	long				Not stepwise	0.53	

Note: in regressions not including age (long) (regression data not shown), aspect and slope interact. No further stepwise regressions, including age, but not the combination of aspect and slope, will run due to degree of freedom problems.
Age is not a significant predictor of soil C mass, but elevation is.

Forest floor N mg/g (ffn.mg.g) analysis using stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors……………….			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	ffn.mg.g	long	elev	aspect	Includes all predictors	70		
2	ffn.mg.g	long	elev	aspect	longxelev	67		
					longxaspect			
					elevxaspect			
3		long	elev	aspect	longxelev	62		
					longxaspect			
4	ffn.mg.g	long	elev	aspect	longxaspect	58		
	Long x aspect interact						0.08	0.6
5	ffn.mg.g	long	elev		Includes all predictors	79		
	ffn.mg.g	long	elev		none	73		
6	ffn.mg.g		elev		none	70	0.0024	0.35
Second stepwise regression								
1	ffn.mg.g	long		aspect	Includes all predictors	106		
	Ends at interaction						0.157	
2	ffn.mg.g	long	slope	aspect	aspect x slope	106		
3	ffn.mg.g			aspect	none	100	n.a.	
		Nothing significant						

Forest floor C mg/g (ffc.mg.g) analysis using stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors……………….			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	ffc.mg.g	long	elev	aspect	Includes all predictors	18,388		
2	ffc.mg.g	long	elev	aspect	longxelev	17,330		
	ffc.mg.g				longxaspect			
	ffc.mg.g				elevxaspect			
3	ffc.mg.g	long	elev	aspect	elevxaspect	16,197		
	ffc.mg.g				longxaspect			
4	ffc.mg.g		elev	aspect	elevxaspect	14,053		
	Interaction of elevation and aspect is significant						0.02	0.29
Second stepwise regression								
1	ffc.mg.g	long	elev		includes all predictors	17,213		
2	ffc.mg.g	long	elev		none	16,871		
3	ffc.mg.g		elev		none	15,641		
	Nothing significant							
Third stepwise regression								
1	ffc.mg.g		aspect	slope	aspect x slope	15,808		
2	ffc.mg.g		aspect	slope	none	14,680		
3	ffc.mg.g			slope		14,084	0.11	0.11

Soil N mg/g (sn.mg.g) analysis using stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors………………			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	sn.mg.g	long	elev	aspect	Includes all predictors	19,765		
2	sn.mg.g	long	elev	aspect	none	18,973		
	sn.mg.g		elev	aspect	none	17,685		
	sn.mg.g		elev		none	16,879	0.0067	0.29
Second stepwise regression								
1	sn.mg.g		aspect	slope	includes all predictors	27,246		
2	sn.mg.g		aspect	slope	none	25,301		
3	sn.mg.g			slope	none	23,386		
	Nothing significant							
Third stepwise regression								
1	sn.mg.g		slope	soil	includes all predictors	24,030		
2	sn.mg.g		slope	soil	none	22,874		
3	sn.mg.g		elev	soil	none	21,444		
	Nothing significant							

Soil Cmg/g (sc.mg.g) analysis using stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors………………			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	sc.mg.g	long	elev	aspect	Includes all predictors	143,412		
2	sc.mg.g	long	elev	aspect	none	137,669		
	sc.mg.g		elev	aspect	none	128,324		
	sc.mg.g		elev		none	122,477	0.0067	0.29
Second stepwise regression								
1	sc.mg.g		slope	soil	includes all predictors	174,364		
2	sc.mg.g		slope	soil	none	165,978		
3	sc.mg.g			soil	none	155,599		
	Nothing significant							
Third stepwise regression								
1	sc.mg.g	long	aspect		includes all predictors	193,700		
2	sc.mg.g	long	aspect		none	182,949		
3	sc.mg.g	long			none	169,656		
	Nothing significant							

Forest Floor C:N (ffcn) analysis using stepwise multiple linear regression evaluated by AIC
Regressions always include age class

Steps	Response	Predictors………………			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	ffcn	long	elev	slope	Includes all predictors	509		
2	ffcn	long	elev	slope	none	474		
3	ffcn		elev	slope	none	453		
4	ffcn		elev		none	432	0.02	0.22

Second stepwise regression								
1	ffcn		aspect	slope	Includes all predictors	519		
2	ffcn		aspect	slope	none	493		
3	ffcn		aspect		none	486	0.11	0.11
Third stepwise regression								
1	ffcn		aspect	soil	Includes all predictors	571		
2	ffcn		aspect	soil	none	533		
3	ffcn		aspect		none	493	0.11	0.11

Soil C:N (scn) analysis using stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors……………….			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	scn	long	elev	aspect	Includes all predictors	815		
2	scn	long	elev	aspect	none	810		
3	scn		elev	aspect	none	780		
4	scn			aspect	none	760	0.02	0.23
1	scn		aspect	slope	Includes all predictors	847		
2	scn		aspect	slope	none	794		
3	scn		aspect		none	768	0.02	0.23
Second stepwise regression								
1	scn		slope	soil	Includes all predictors	1,038		
2	scn		slope	soil	none	969		
3	scn		slope		none	928	n.a.	n.a.

Forest floor N min mg/g (ffnmin.mg.g) stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors……………….			Interaction terms			
		1	2	3		AIC	p value	R^2
First stepwise regression								
1	ffNmin.mg,g	long	elev	aspect	Includes all predictors	11,131		
2	ffNmin.mg,g	long	elev	aspect	none	10,400		
	ffNmin.mg,g	long	elev		none	10,336		
	ffNmin.mg,g	long			none	10,241	0.0004	0.45
Second stepwise regression								
1	ffNmin.mg,g	elev	aspect	slope	includes all predictors	19,249		
2	ffNmin.mg,g	elev	aspect	slope	none	16,628		
3	ffNmin.mg,g	elev	aspect		none	16,391	0.09	0.13
	Nothing significant							

Third stepwise regression									
1	ffNmin.mg,g	soil	slope	aspect	includes all predictors		17,727		
2	ffNmin.mg,g	soil	slope	aspect	none		16,605		
3	ffNmin.mg,g	soil	slope		none		15,715		
	Slope is a trend					slope		0.0585	

Forest floor Nitrification mg/g (ffnit.mg.g) stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors………………. 1	2	3	Interaction terms		AIC	p value	R^2
First stepwise regression									
1	ffnit.mgg	long	elev	aspect	Includes all predictors		12.5		
2	ffnit.mgg	long	elev	aspect	none		12.3		
3	ffnit.mgg	long	elev		none		12.0		
	long is significant in a regression with elevation					long		0.0481	n.a
						elev		0.18	n.a
Second stepwise regression									
1	ffnit.mgg	soil	aspect	slope	includes all predictors		16.4		
2	ffnit.mgg	soil	aspect	slope	none		15.3		
3	ffnit.mgg		aspect	slope	none		14.2		
4	ffnit.mgg		aspect				13.3		
	Nothing significant								

Soil N min mg/g (snmin.mgg) stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors………………. 1	2	3	Interaction terms	AIC	p value	R^2
First stepwise regression								
1	snmin.mgg	long	elev	aspect	Includes all predictors	0.0023		
2	snmin.mgg	long	elev	aspect	none	0.0022		
3	snmin.mgg		elev	aspect	none	0.0021		
	snmin.mgg		elev		none	0.0021	0.0474	0.167
Second stepwise regression								
1	snmin.mgg	soil	aspect	slope	includes all predictors	0.0020		
	soil x slope x aspect interaction is significant at						0.0136	0.38
Third stepwise regression								
1	snmin.mgg	elev	aspect	slope	includes all predictors			
	elevation x aspect x slope interaction is significant at						0.02	0.48

Soil nitrification mg/g (snit.mgg) stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors………………. 1	2	3	Interaction terms	AIC	p value	R^2
First stepwise regression								
1	snit.mgg	long	elev	aspect	Includes all predictors	0.0012		
2	snit.mgg	long	elev	aspect	none	0.0012		
3	snit.mgg	long	elev		none	0.0011		
	Nothing is significant							

Second stepwise regression									
1	snit.mgg	soil	aspect	slope	includes all predictors		0.0009		
	Soil x slope x aspect interaction is significant at							0.0027	0.46
Third stepwise regression							0.0011		
1	snit.mgg		soil	slope	includes all predictors				
	Slope x soil interaction is significant at							0.059	0.26
Fourtf stepwise regression									
1	snit.mgg		slope	aspect	includes all predictors		0.0013		
2	snit.mgg		slope	aspect	none		0.0013		
3	snit.mgg		slope				0.0012		
	Nothing is significant								

Forest floor N min mg/g N (ffnmin.mg.gN) stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors………………			Interaction terms				
		1	2	3			AIC	p value	R^2
First stepwise regression									
1	ffnmin.mg.gN	long	elev	aspect	Includes all predictors		42,459,410		
2	ffnmin.mg.gN	long	elev	aspect	none		40,134,912		
3	ffnmin.mg.gN	long		aspect	none		37,802,645		
4	ffnmin.mg.gN	long			none		36,356,881	0.0002	0.49
Second stepwise regression									
1	ffnmin.mg.gN	soil	aspect	slope	includes all predictors		65,147,782		
	ffnmin.mg.gN	soil	aspect	slope	none		61,085,689		
	ffnmin.mg.gN	soil		slope	none		58,175,366		
	Two trends					soil		0.0733	n.a.
						slope		0.0616	n.a.
	Neither slope nor soil are significant in single linear regression.								

Forest floor nitrification mg/g N (ffnit.mg.gN) stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors………………			Interaction terms				
		1	2	3			AIC	p value	R^2
First stepwise regression									
1	ffnit.mg.gN	long	elev	aspect	Includes all predictors		43,694		
2	ffnit.mg.gN	long	elev	aspect	none		42,808		
3	ffnit.mg.gN	long	elev		none		41,699		
4	ffnit.mg.gN	long			none		41,187	0.08	0.13
Second stepwise regression									
1	ffnit.mg.gN	soil	long	slope	includes all predictors		45,096		
	ffnit.mg.gN	soil	long	slope	none		42,100		
	ffnit.mg.gN		long	slope	none		40,845		
	Significant relationship					long		0.0331	n.a.
	Other:					slope		0.134	n.a.

Soil N min mg/g N (snmin.mg.gN) stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors……………….			Interaction terms				
		1	2	3			AIC	p value	R^2
First stepwise regression									
1	snmin.mg.gN	long	elev	aspect	Includes all predictors		0.070		
2	snmin.mg.gN	long	elev	aspect	none		0.066		
3	snmin.mg.gN		elev	aspect	none		0.062		
	Elevation is significant in a regrssion with aspect					elev		0.014	n.a.
						aspect		0.082	n.a.
Second stepwise regression									
1	snmin.mg.gN	soil	elev	slope	includes all predictors		0.066		
	Soil x slope x elevation interaction							0.082	0.36
Third stepwise regression									
	snmin.mg.gN	soil	aspect	slope	includes all predictors		0.071		
	Aspect x slope x soil interaction							0.0612	0.3

Soil nitrification mg/g N (snit.mg.gN) stepwise multiple linear regression evaluated by AIC
Initial regressions always include age class

Steps	Response	Predictors……………….			Interaction terms				
		1	2	3			AIC	p value	R^2
First stepwise regression									
1	snit.mg.gN	long	elev	aspect	Includes all predictors		0.035		
2	snit.mg.gN	long	elev	aspect	none		0.034		
3	snit.mg.gN	long	elev		none		0.033		
	Elevation is a trend in a regrssion with long					elev		0.077	n.a.
						long		0.127	n.a.
Second stepwise regression									
1	snit.mg.gN	soil	aspect	slope	includes all predictors		0.030		
	Soil x slope x aspect interaction							0.0069	0.38