Four centuries of soil carbon and nitrogen change after stand-replacing fire in a forest landscape in the western Cascade Range of Oregon

T.W. Giesen, S.S. Perakis, and K. Cromack Jr.

Abstract: Episodic stand-replacing wildfire is a significant disturbance in mesic and moist Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of the Pacific Northwest. We studied 24 forest stands with known fire histories in the western Cascade Range in Oregon to evaluate long-term impacts of stand-replacing wildfire on carbon (C) and nitrogen (N) pools and dynamics within the forest floor (FF, Oe and Oa horizons) and the mineral soil (0–10 cm). Twelve of our stands burned approximately 150 years ago ("young"), and the other 12 burned approximately 550 years ago ("old"). Forest floor mean C and N pools were significantly greater in old stands than young stands (N pools: 1823 ± 132 $kg \cdot ha^{-1}$ vs. 1450 ± 98 $kg \cdot ha^{-1}$; C pools: 62 980 ± 5403 $kg \cdot ha^{-1}$ vs. 49 032 ± 2965 $kg \cdot ha^{-1}$, mean ± SE) as a result of significant differences in FF mass. Forest floor C and N concentrations and C/N ratios did not differ by time since fire, yet potential N mineralization rates were significantly higher in FF of old sites. Old and young mineral soils did not differ significantly in pools, concentrations, C/N ratios, or cycling rates. Our results suggest that C and N are sequestered in FF of Pacific Northwest Douglas-fir forests over long (∼400 year) intervals, but that shorter fire return intervals may prevent that accumulation.

Résumé : Les feux de forêt épisodiques qui entraînent le remplacement des peuplements sont des perturbations importantes dans les forêts mésiques et humides de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) du Pacific Northwest. Nous avons étudié 24 peuplements forestiers dont l'historique des feux est connu dans le paysage de l'ouest des Cascades en Oregon pour évaluer les impacts à long terme des feux de forêt qui entraînent le remplacement des peuplements sur C et N dans les horizons O_e et O_a de la couverture morte et dans le sol minéral (0–10 cm). Douze peuplements ont brûlé il y a environ 150 ans (« jeunes ») et 12 autres il y a environ 550 ans (« vieux »). Les réserves de C et N dans la couverture morte étaient significativement plus importantes dans les vieux peuplements que dans les jeunes peuplements (réserves de N ± erreur type (ET) : 1823 ± 132 $kg \cdot ha^{-1}$ vs 1450 ± 98 $kg \cdot ha^{-1}$; réserves de C ± ET : 62 980 ± 5403 $kg \cdot ha^{-1}$ vs 49 032 ± 2965 $kg \cdot ha^{-1}$) à cause de différences significatives dans la masse de la couverture morte. Les concentrations de C et N et les rapports C:N dans la couverture morte ne différaient pas en fonction du temps écoulé depuis le feu mais les taux potentiels de minéralisation de N étaient significativement plus élevés dans la couverture morte des vieux peuplements. Dans le sol minéral, les réserves, les concentrations, les rapports C:N et les taux de recyclage n'étaient pas significativement différents entre les vieux et les jeunes peuplements. Nos résultats indiquent que C et N sont séquestrés dans la couche organique des forêts de douglas du Pacific Northwest pendant de longs (~400 ans) intervalles mais que des intervalles plus courts entre les feux de forêt pourraient empêcher cette accumulation.

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Introduction

Pools and dynamics of soil carbon (C) and nitrogen (N) are important drivers of temperate forest ecosystem structure and function and have the potential to be influenced by fire over both short and long time scales (Chapin et al. 2002). Many short-term effects of fire on soils are known: when fire heats soils to 200 °C or more, organic matter begins to combust, and much of the C is oxidized and lost as CO and CO_2. At those temperatures, N in soil organic matter is chemically altered, with some of the N remaining in the soil as ammonium, and with most of these compounds being evolved as gases. Although after the fire there is a short-term boost in available N, in the form of the heat-generated ammonium, within 5 years this available N has been completely depleted. Above 500 °C, most soil organic matter and N are lost (DeBano et al. 1998).

In severe stand-replacing fires, N losses can be large and may persist (Certini 2005). However, the long-term legacy of fire on soils is not often studied and is not well understood. Recent meta-analyses are devoid of studies that address the long-term effects of fire on forest floors and soils (Wan et al. 2001; Johnson and Curtis 2001). Numerous (>16) studies since 2001 have investigated C pools, N pools, and N mineralization and nitrification over long-term periods, but systematic studies of soil and forest floor C and N

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pools and processes across centuries since stand-replacing fire are rare and are lacking entirely for Pacific Northwest forests. Given the potential for globally large C accumulation in Pacific Northwest forests (Smithwick et al. 2002), and calculations that fire may strongly influence regional C stocks (Page-Dumroese and Jurgensen 2006), there is a need to obtain field-based information on long-term wildfire effects on ecosystem C pools in the region.

We studied, through space-for-time substitution (Pickett 1989), soil C and N pool and process changes over a period of four centuries. To conceptualize those changes, we created a hypothetical N budget covering 400 years that considers losses at the time of the fire, transfer of mineral soil N into regrowing vegetation, N fixation, atmospheric N inputs, and leaching. To compare our conceptualized changes with field observations, we studied Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in the western Cascade Range in Oregon, which developed after severe stand-replacing fire an average of 150 years ago (young stands) or an average of 550 years ago (old stands). We also evaluated changes in potential net N mineralization and nitrification through laboratory incubations. These stands have not been subject to recent (<150 years) anthropogenic disturbance, but did experience some amount of fire and other disturbance by Native Americans.

Methods

Sites

We studied a 180 km^2 area around and including the H.J. Andrews Experimental Forest in the Willamette National Forest in Oregon (Fig. 1). The sites (Table 1) are on the western slope of the Cascade Range about 75 km east of Eugene, Oregon, range in elevation from about 400 m to 1550 m, and have a maritime-influenced climate, with wet, mild winters and dry, cool summers. Mean low-elevation temperatures range from 1 °C in January to 18 °C in July. Precipitation is concentrated from November through March, averaging from 230 cm/year at lower elevations to over 355 cm/year 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 fluvial and colluvial processes have formed a steep, dissected landscape. Soils are mainly Inceptisols, with some areas of Alfisols and Spodosols (Willamette National Forest 2003). A more detailed description of soils is not available.

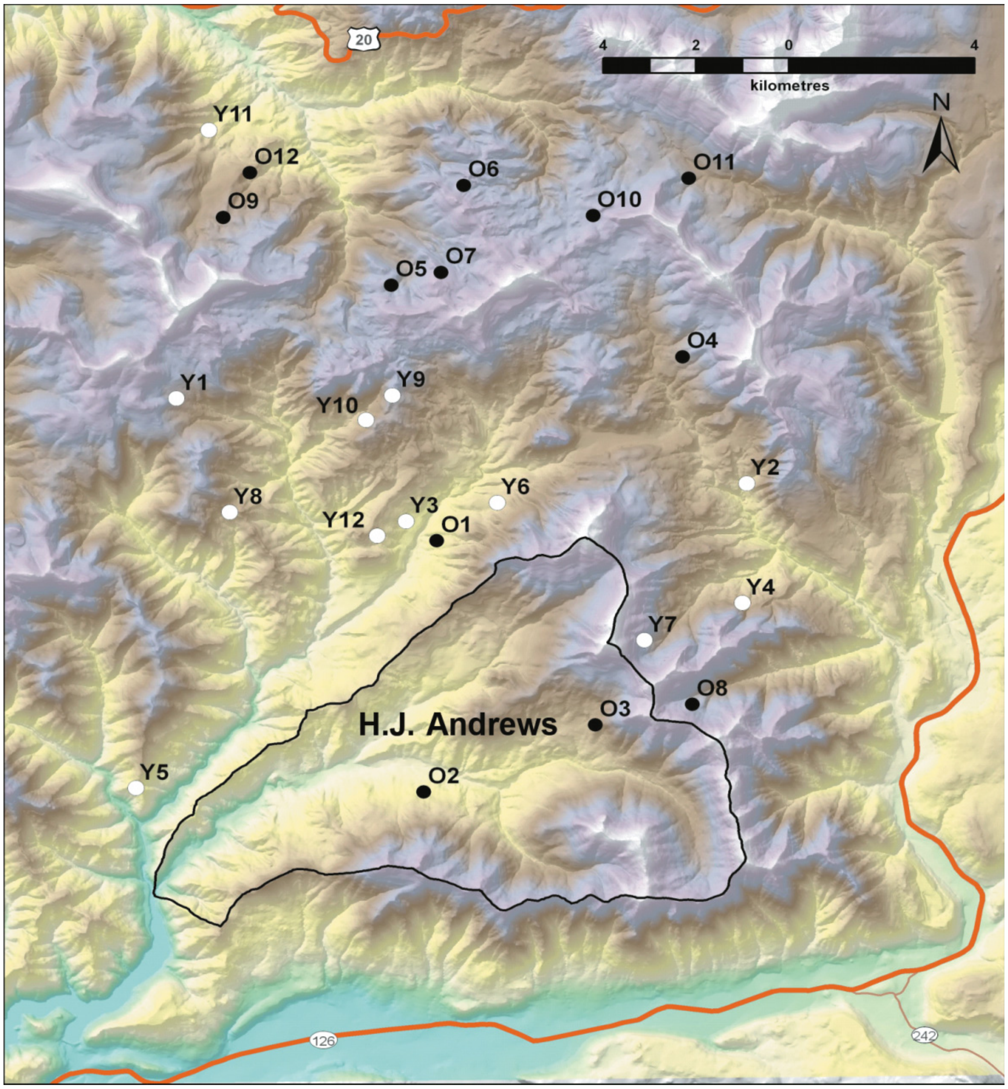
Our sites were previously studied for fire history by Weisberg (1999). Weisberg studied stumps in clearcuts to find dates of fire scars and tree origin. We sought stands of live trees located near Weisberg's clearcuts that appeared to be of the same age as the stands that had been clear cut, on the assumption that fire histories would be the same. Weisberg considered a fire to be a high-severity stand-replacing fire if few stumps predated the fire and if evidence of regeneration of postfire species met minimum standards. We selected sites based on their history of stand-replacing fire and assumed these sites had experienced a high-severity fire. "Young" sites sustained a stand-replacing fire within the past 200 years and may have experienced less severe fires before that time. "Old" sites sustained a stand-replacing fire more than 400 years ago and 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 400 years to more than 800 years before the present (Weisberg 1999).

We found that 51 sites from Weisberg's study, as well as a stand in the historic (1912) Carpenter fire (not studied by Weisberg), met our criteria for stand-replacing fire and age-class. From those 52 candidate sites, we found 24 to be suitable: 12 young and 12 old. Some of those sites were directly adjacent to the clearcut studied by Weisberg, while others were 200 to 900 m from the reference clearcut. Minimum size for our study stands was 150 m × 250 m so that the 100 m transect we used would always be at least 75 m from any edge to avoid edge effects (Hayes 2002). Most often the transect orientation was set by the need for staying 75 m from the edge of the stand; otherwise, the direction was set randomly. Each site had one transect of 100 m, sampled along a centerline each 10 m. At the 5 m mark between centerline samples, a sample was gathered off of the centerline in alternate directions, at a random distance of 1–5 m. The 20 samples per transect were grouped by adjacent four samples along the transect, resulting in five composite samples of forest floor and five composite samples of mineral soil per site. All sample collection was done by one individual in one season (19 July through 23 September 2004). Data collected onsite included GIS coordinates, elevation, and aspect; soil type and slope were later determined through GIS processes (Table 1).

Nitrogen budget

We constructed a long-term forest N budget to develop a hypothesized estimate of severe-fire effects on forest floor and soil C and N (Table 2). We hypothesized that stand-replacing fire produced high-severity burns in soils (the most severe fire disturbance to soils (DeBano et al. 1998)) and would result, averaged over the site, in a loss of 10% of forest floor and surface soil N. This value (10%) represents the lower bound for a high-severity burn. Nitrogen losses in less-than-severe-burn areas would be much less than those in the high-fire-severity burn area, because N losses begin at 200 °C, and only high-severity burns reach temperatures over 200 °C (DeBano et al. 1998). Losses of N at the time of the fire vary with the amount of N within the forest floor and soil. Previous studies in the Pacific Northwest (Grier et al. 1974; Sollins et al. 1980; Edmonds et al. 1989; Remillard 1999) found forest floor and soil N pools of 3800 to 5145 kg·ha^{-1}, with a mean of 4505 kg·ha^{-1}. There are two reports of actual losses of N through fire. On a highly productive Oregon Coast Range site, Barnett (1984) found N losses from severe slash burns of 150 kg·ha^{-1} in forest floor and 550 kg·ha^{-1} in mineral soils, for total losses of 700 kg·ha^{-1}. Grier (1975) reported N losses of 817 kg·ha^{-1} from the forest floor and 90 kg·ha^{-1} from the mineral soil (total = 907 kg N·ha^{-1}) from a stand-replacing wildfire in a mixed-conifer forest on an eastern Cascade slope in Washington, which is a drier, less productive site than those in this study. We therefore estimated N loss from forest floor and 0 –10 cm mineral soil at the time of the fire as an average of those two studies (~800 kg·ha^{-1}). Another decrease

Fig. 1. Sampling sites within the study area, where Y indicates young sites, and O indicates old sites. “H.J. Andrews” is the H.J. Andrews Experimental Forest within the Willamette National Forest, Oregon.



in N pools in soils occurs through secondary succession, as N for regrowth of the forest is transferred from the mineral soil N pool to vegetation (Turner 1975) (Table 2). We hypothesized that a difference in mean C and N pools should exist between young stands and old stands, with more C and N in the old stands. If our sampling protocol accurately captured the 10% of soils that experienced a high-severity burn, we should find a difference in N pools of 10% of ~2075 kg·ha^{-1} (Table 2), which is ~200 kg·ha^{-1}. Since N losses and soil organic matter losses are related, C losses are expected to be somewhat proportional.

Nitrogen fixation is an important N input, as fixation contributes well over 2000 kg·ha^{-1} to both burned and unburned stands over a period of 400 years (Table 2). Amounts used in the budget for N-fixation inputs (Table 3) are estimated from the literature and vary widely depending on site quality, density of the fixing species, aspect, and other factors. These estimates are used only for hypothesis development.

We used quantitative sampling to characterize the stocks and chemistry of partially and well-decomposed Oe and Oa forest floor horizons. We did not sample the Oi horizon because it is strongly affected by short-term stand dynamics, whereas our focus was on longer-term C and N pools and dynamics. After brushing away the Oi material, we sawed a 10 cm square, lifted out the Oa and Oe forest floor material, brushed soil from the bottom, placed the sample in a Ziploc bag, and stored the samples in coolers. In the laboratory, we weighed each bag; removed all intact cones, larger rocks, and twigs; broke up the material with finger pressure and passed it through a 9.5 mm sieve; and reweighed the samples. A subsample (about 10 g) was weighed in preweighed sample cups, dried for 48 h at 65 °C, and then reweighed to calculate the percentage of moisture in the original sample. Another subsample of ~10 g of each composite sample was passed through a 2 mm sieve, dried for 48 h at 65 °C, ground on a roller grinder until the particles were about the size of talcum powder, redried for 24 h at 65 °C, and then weighed and wrapped in foil for analysis of total C and N using an elemental combustion analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, California). Forest floor C and N are expressed on an ash-free dry-mass (AFDM) basis, with ash content determined on 1 g of dry

Table 1. Site data: site identification, date, elevation, aspect, slope, glacial study site GIS location information.

Site id.	Date[a]	Elev. (m)	Aspect[b]	Slope[c] (%)	Glacial till[d]	Transect origin point[e] *x*	*y*	Transect azimuth
Young								
Y1	8/12	1181	1	17.5	0	559 490	4 906 749	S
Y2	7/19	918	1	46.9	0	571 780	4 904 737	S15E
Y3	8/13	778	1	25.5	0	564 438	4 903 834	W45S
Y4	7/20	1027	0	35.8	0	571 682	4 901 895	N130E
Y5	8/4	753	1	59	0	558 620	4 897 500	N45W
Y6	9/23	930	1	25.5	1	566 406	4 904 277	N25E
Y7	8/3	1200	1	51.5	1	569 571	4 901 011	S20W
Y8	8/12	926	1	10.4	0	560 639	4 904 046	W
Y9	9/3	1230	1	10.4	0	564 147	4 906 825	N10E
Y10	8/12	1031	0	63.3	0	563 577	4 906 239	N25E
Y11	8/23	786	1	58.5	0	560 190	4 913 123	S45W
Y12	8/18	891	1	37.4	0	563 820	4 903 491	N35E
Old								
O1	7/21	741	1	13.6	0	565 097	4 903 382	N50E
O2	8/5	709	0	16	0	564 820	4 897 416	N80E
O3	8/4	1000	1	36.7	1	568 516	4 899 006	N15W
O4	8/18	1128	1	18.4	1	570 396	4 907 750	N
O5	9/7	705	1	43	0	564 125	4 909 450	S
O6	9/23	1260	1	8.7	0	565 680	4 911 820	N10W
O7	9/6	1346	0	29.2	0	565 194	4 909 754	ESE
O8	8/3	1259	0	35.2	0	570 605	4 899 499	N60W
O9	8/16	1142	0	6.2	0	560 499	4 911 059	N30E
O10	8/18	1280	1	12.9	1	568 467	4 911 099	N
O11	8/17	1134	0	56.2	1	570 529	4 911 986	N70W
O12	8/2	951	1	35.8	1	561 080	4 912 119	N15W

[a]Dates are given as month/day; all dates are in 2004.
[b]1, warm; 0, cold. Warm is clockwise, SE to NW; cold is NW to SE.
[c]Slope is taken at transect origin from topographic maps, by computer.
[d]1, indicates the presence of glacial till.
[e]Values are UTM coordinates, where *x* values are in Zone 10.

Table 2. Nitrogen gains and losses for burned and unburned stands over a ~400 year period, illustrating a net difference in N pools.

Input or loss	N ($kg \cdot ha^{-1}$)	Time (years)	Burned ($kg \cdot ha^{-1}$)	Unburned ($kg \cdot ha^{-1}$)
Loss at time of fire from high-severity burn in soils (FF+mineral soil)	–800.0	1	–800	0
Regrowth loss (per year)	–22.5	70	–1575	0
N fixation[a] (per year)				
Nonsymbiotic (in soil and detritus)	2.0	400	800	800
Symbiotic (*Alnus* and (or) *Ceanothus*)	40	25	1000	0
Symbiotic (*Lobaria oregana*)	3.5	400	0	1400
	3.5	200	700	0
Atmospheric deposition (per year)	0.5	400	200	200
Leaching (per year)	–0.5	400	–200	–200
~400 year total			125	2200
Net difference ($kg \cdot ha^{-1}$)				2075

[a]Note that fixation amounts were estimated with various methods and also vary widely with succession and other factors. Amounts shown are for hypothesis development only.

subsample heated in a muffle furnace at 450–550 °C for 4 h (McDowell and Fisher 1976).

Soils were sampled in the same manner as the forest floor, with the following exceptions: soil was sampled with a heavy walled (~2.2 mm), 6.9 cm diameter × 14 cm long, straight-sided cylindrical sampler, beveled and sharpened on the exterior of the lower edge. The sampler was inserted in the mineral soil to a 10 cm line. Soil was then excavated

Table 3. Nitrogen inputs to stands in the western Cascade Range, showing amounts indicated in literature cited and amounts used in the budget in Table 1.

Source	Amount ($kg \cdot ha^{-1} \cdot year^{-1}$)	Reference	Budgeted ($kg \cdot ha^{-1} \cdot year^{-1}$)	Type	Distribution
Atmospheric deposition (150–550 years BP)	0.5	Galloway et al. 2004	0.5	C[a]	U[c]
Nonsymbiotic fixation	2–10	Chen and Hicks 2003	2	C[a]	U[c]
Symbiotic fixation with *Alnus rubra* or *Ceanothus velutinus*	101	McNabb and Cromack 1983	40	E[b]	P[d]
	20	Zavitkovski and Newton 1968			
	54–73	Binkley et al. 1982			
Symbiotic fixation with *Lobaria oregana*	2.5–16	Antoine 2004	3.5	E[b]	P[d]
	2.8	Sollins et al. 1980			

Note: N-fixation contributions are highly variable by species, site conditions, succession, and other factors. Amounts shown are rough estimates for hypothesis development only.

[a]Continuous.

[b]Episodic.

[c]Uniform.

[d]Partial.

around the sampler to facilitate access and to prevent loss of soil from the bottom of the sampler as it was tipped; the end of the sampler was then covered, and the sample was placed in a Ziploc bag. In the laboratory, all soil in each bag was passed through a 2 mm sieve, and a subsample (about 30 g) was dried to estimate moisture content, as above.

We conducted laboratory incubations for inorganic N mineralization and nitrification using a modification of the procedure outlined in Nadelhoffer (1990). We weighed 10 g of forest floor or 30 g of mineral soil (dry mass equivalents) from each composite into Falcon filter units fitted with Gelman A/E glass fiber filters. Initial available N was removed by leaching (leachate discarded) with 200 mL 4 $mmol \cdot L^{-1}$ $CaCl_2$ prior to the start of the incubation. Incubations ran for 28 days at 25 °C and 60% water-holding capacity. We modified the method of Nadelhoffer (1990) by using only $CaCl_2$ rather than a full nutrient solution to remove accumulated inorganic N, since nutrient replenishment was not needed in our short-term (28 days) incubation. At the end of 28 days, the incubating samples were flushed again with 100 mL $CaCl_2$, and samples of the leachate were retained for analysis of available N as ammonium and nitrate, using a Lachat QuikChem 8000 Series FIA+ Flow Analyzer System (Lachat Instruments, Loveland, Colorado). Nitrate was analyzed colorimetrically following cadmium reduction (Lachat method Nos. 10-107-04-1-B and 10-107-04-1-J), and ammonium was analyzed colorimetrically by sodium salicylate (method No. 10-107-06-2-J). Net potential mineralized N is the sum of ammonium and nitrate, expressed per gram of sample and per gram of sample N for both forest floor and mineral soil.

Statistics

For each site, we used the arithmetic mean of five composite samples each of forest floor and mineral soil in statistical analyses, where n = 24 forest stands, 12 per age-class. While our primary interest was in comparing pools and processes of C and N between age-classes, we were also interested in determining whether other variables, in addition to age, influenced differences in C and N. The variables considered were site elevation (metres above sea level, determined via wrist altimeter and verified with GPS locator), aspect (warm: SE clockwise to NW, or cold: NW clockwise to SE), soil type (glacial till or not), and slope (percent slope, taken from topography via computer). We used multiple linear regression to analyze relationships in the data, and Akaike information criterion (AIC) as a model-selecting tool, using S-Plus, version 6.2 for Windows, (Academic Site Edition, revised 12 Jan. 2004, by McRae Software International, Inc.). We considered that p values < 0.10 indicated trends, whereas p values < 0.05 were considered significant. After model selection, the only remaining significant predictors of C and N pools and process rates were age (old or young) and elevation. We expected elevation to be a significant predictor because decomposition rates vary with elevation, with slower decomposition rates occurring at higher elevations. As the mean elevation of young and old sites was not different (p = 0.17, t test, difference of means), elevation effects are not reported.

Substituting space for time

Our study substitutes space for time and assumes that sampling multiple sites of different ages today provides a proxy for sampling a single site at various times in the past (Pickett 1989). Essential to that assumption is strong similarity in the sites today. One means of testing an effect of time alone is to determine whether other state factors (parent material, biota, climate, and topography) (Jenny 1941) are similar among all the sites. If so, the sites are likely to have the same ecosystem structure and functioning (Chapin et al. 2002). In addition, anthropogenic changes must be considered. All our sites have similar parent material — breccias and tuffaceous materials with minor amounts of andesites and basalts. Some soils (5 of 24) developed differently through glacial tilling, but in the regression analysis, C and N pools did not differ between the five glaciated sites and the nonglaciated sites. The mean elevations of old (1054 ± 67 m) and young (971 ± 48 m) sites do not differ (p = 0.17, t test for difference of means). More of the young sites (10 of 12) than old sites (7 of 12) are on the warm aspects of slopes, and the mean value of slope is 37% on young sites versus 26% on old sites, but the differences are not statistically significant (t test for difference of means). Douglas-fir dominates the stands at all sites (Weisberg 1999), and the climate is essentially the same over the study area. Hence, for these factors, the sites are arguably the same. However, several differences exist related to time and human activity. The mean temperature in the last 150 years has been 0.6–0.8 °C above that for the period 1450–1600 AD (Mann et al. 2003). These are not large changes (about 0.7 °C of warming), but they represent a difference that might influence soil C and N accumulation. Forest fire severity, extent, and incidence varied from 1400 to the present and have been characterized into four intervals (Weisberg 1999): a period of high-severity, widespread fire from 1475 to 1620; reduced frequency, area, and severity of fire from 1620 to 1830; high-severity, frequent, and widespread fires from 1830 to 1910, and reduced fires from 1910 to present. The fire patterns appear to be linked to historic patterns of human activity (Weisberg 1999). Another time-related problem is the absence of historical recordings for certain disturbances, such as low- and medium-intensity fires and widespread blowdowns (Lynott and Cramer 1966). Therefore, possible differences between the periods 1450 to 1600 and 1850 to the present are related to climate, unusual events, and unrecorded disturbances.

Results

The forest floor AFDM fraction (i.e., percent organic content) was significantly larger ($p = 0.02$, $r^2 = 0.23$) in old forest (64.8 ± 4.1%, mean ± SE, $n = 12$) than young forest (53.0 ± 2.2%, $n = 12$) (Table 4). Forest floor mass per area tended to be higher ($p = 0.10$) in old sites (1.21 ± 0.11 g AFDM·cm^{-2}) than in young sites (1.00 ± 0.07 g AFDM·cm^{-2}). Mineral soil bulk density was not significantly different between old (1.38 ± 0.06 g·cm^{-3}) and young sites (1.46 ± 0.12 g·cm^{-3}).

In the forest floor there were significantly larger pools of C and N in old sites than in young sites ($p = 0.03$ for both C and N). Nitrogen pools in the forest floor were 1823 ± 132 kg·ha^{-1} in old sites and 1450 ± 98 kg·ha^{-1} in young sites. Carbon pools in the forest floor were 62 980 ± 5403 kg·ha^{-1} in old sites and 49 032 ± 2965 kg·ha^{-1} in young sites (Table 5 and Fig. 2). Site age did not significantly influence mineral soil pools of C and N, nor concentrations of N, C, and C/N ratios in either forest floor (AFDM) or mineral soil.

Laboratory incubations for potential N mineralization and nitrification showed wide differences between young and old sites. Total inorganic N mineralized in the forest floor was significantly greater in old sites (60 ± 7.3 mg·g^{-1}) than in young sites (26 ± 3.5 mg·g^{-1}), and the same pattern held when mineralization was expressed per gram of soil N (Table 6, $p < 0.001$). Overall, N mineralization rates in forest floor were much greater than rates in mineral soil, and there were no significant effects of site age on mineral soil N mineralization rates ($p > 0.73$).

While potential net N mineralization increased from young to old sites, potential net nitrification diminished. Nitrification, when expressed as milligrams N per gram of AFDM-adjusted forest floor, was lower ($p = 0.08$, $r^2 = 0.13$) in old sites (0.046 ± 0.027 mg·g^{-1}) than in young sites (0.551 ± 0.28 mg·g^{-1}). Soil nitrification was not different between young and old sites ($p = 0.30$).

Table 4. Mean (with standard errors in parentheses) physical parameters of forest floor (FF) and mineral soils for young and old sites.

	Young	Old	p^a	r^2
FF (g·cm^{-2})	1.90 (0.13)	1.96 (0.22)	0.71	na
FF (% organic)	53 (2.2)	65 (4.1)	0.02	0.37
FF(g·cm^{-2}, adjusted to AFDM^b)	1.00 (0.07)	1.21 (0.11)	0.10	na
Soil bulk density (g·cm^{-3})	1.46 (0.12)	1.38 (0.06)	0.35	na

[a]Significance values from t test for difference between means.
[b]Ash-free dry mass.

Discussion

We found reasonably close agreement between our hypothetical N budget and our field measurements evaluating long-term effects of wildfire on forest floor and mineral soil N pools. With the assumption that 10% of the soil surface area experienced severe fire effects (see Methods), our N budgeting approach suggested that forest floor and mineral soil in older stands should contain ~200 kg·ha^{-1} more N than young stands. Field measurements found a difference in forest floor N pools of 373 kg·ha^{-1}, and a total difference in forest floor plus mineral soils of 683 kg·ha^{-1}. Our values for N (and C) in forest floor and mineral soil are within the range reported for other Douglas-fir forests of the Pacific Northwest (Binkley et al. 1992*a*; Means et al. 1992; Hart 1999; Remillard 1999; Prescott et al. 2000). This suggests that the difference between budgeted and measured N losses is likely attributable to an underestimate in our assumption of the areal extent of severe fire effects on soils and (or) errors in our hypothetical N budget. Severe fire effects on 33% of the soil area (versus our assumed 10%) could account for this discrepancy. Both our N budget analysis and field studies support the idea that severe wildfire can have multicentury impacts on N pools in forests of the Pacific Northwest.

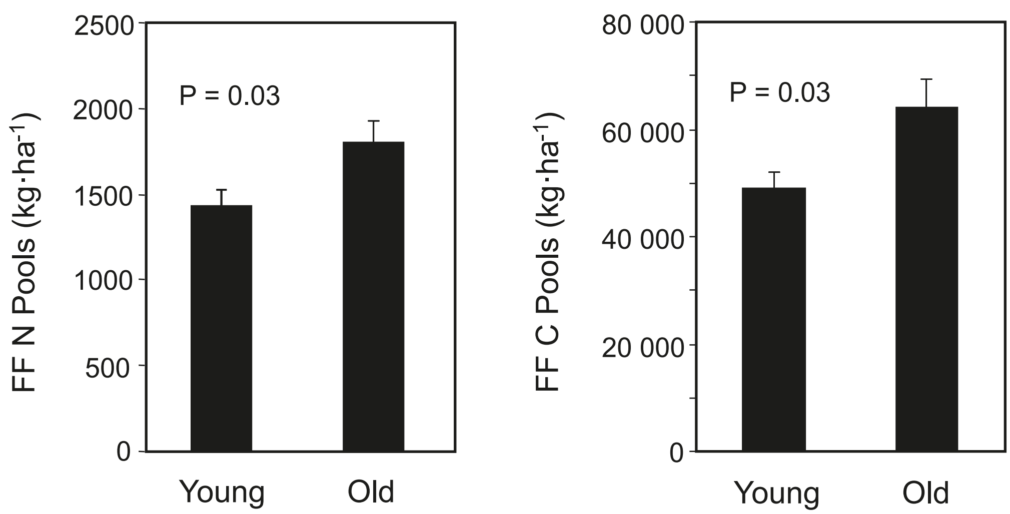
We could not measure C and N losses at the time of fire, as these fires occurred about 150 years ago at our young sites and about 550 years ago at our old sites. The 683 kg N·ha^{-1} difference we measured between young and old sites likely underestimates N losses at the time of fire, owing to some N replacement by postfire N fixation (Table 2). It is unclear whether forest ecosystems would be dramatically affected by this magnitude of N loss at 400 year intervals, which is equivalent to slightly less than 9% of total N we measured in forest floor and mineral soil. However, mean fire return intervals in our study area are much shorter than 400 years: reported means range from 151 years (Cissel et al. 1999) to 197 years, excluding low-severity fires (Weisberg 1999). As our estimates indicate that mean N losses from severe fire cannot be restored in 150–200 years, we suggest that N accumulation in our study area may be limited by fire disturbance at historic frequencies. Previous empirical and theoretical studies have also shown that wildfire can have multicentury impacts on forest N budgets (Johnson et al. 1998, 2004).

Table 5. Mean (with standard errors in parentheses) N and C pools, concentrations, and C/N ratio in the forest floor and soil of young and old stands.

	N (kg·ha^{-1})	C (kg·ha^{-1})	N (mg·g^{-1})	C (mg·g^{-1})	C/N
Forest floor					
Young	1450 (98)	49 032 (2965)	15.5 (0.53)	523.1 (4.28)	34.2 (1.29)
Old	1823 (132)	62 980 (5403)	15.45 (0.63)	524 (9.09)	34.3 (1.36)
p (age)[a]	0.03	0.03	0.95	0.93	0.94
r^2	0.19	0.19	<0.01	<0.01	<0.01
Mineral soil (0–10 cm)					
Young	5893 (591)	182 619 (11 950)	88.21 (9.77)	237.6 (26.32)	32.5 (1.99)
Old	6203 (418)	193 806 (12 539)	95.95 (7.26)	258.5 (19.57)	31.7 (1.53)
p (age)[a]	0.67	0.53	0.53	0.53	0.76
r^2	<0.01	0.02	0.02	0.02	<0.01

[a]Stepwise multiple linear regression using Akaike information criterion.

Fig. 2. Forest floor N and C pools (kilograms per hectare) in young and old sites. Values are arithmetic means, and vertical bars are ±1 standard error.



It is generally thought that forests display decreases in N availability over long-term succession following wildfire (Wardle et al. 1997, 2003, DeLuca et al. 2002; DeLuca and Sala 2006; MacKenzie et al. 2006). Some forests, however, display increased N availability late in succession after fire (White et al. 2004; Yermakov and Rothstein 2006) and others show no clear trend (Brais et al. 1995). Our finding of twofold greater potential N mineralization in older forests may be affected by our choice of a laboratory incubation, since at least one postfire chronosequence has shown complex and seemingly contradictory patterns of N availability in forest floor versus mineral soil when comparing laboratory versus field rates (MacKenzie et al. 2004, 2006). Although laboratory potential and field assays of N mineralization agree qualitatively in forests of the Pacific Northwest (Binkley et al. 1992*b*), actual patterns of N availability with succession in our forests await further study under field conditions.

Nitrogen availability often is cited as the most important control of nitrification rates in soils (Chapin et al. 2002), a pattern that also has been observed in Douglas-fir forests (Sinkhorn 2007), yet we found that N availability was negatively related to nitrification in our samples. This suggests that other factors, such as pH (Aber 1991), labile C supply (Hart et al. 1994), and the presence of charcoal (DeLuca et al. 2006), possibly could be influencing nitrification rates since time of fire. We did not measure available C in soils and in the forest floor, and the similarity in overall soil C/N ratios of young and old forests at our sites did not reveal obvious differences in C quality with time since fire, but we cannot fully evaluate this hypothesis. The average forest floor pH of a nearby Cascade Range Douglas-fir forests is slightly higher in unmanaged 150-year-old stands (pH 5.74) than in old-growth forests (pH 5.45) (S.S. Perakis, unpublished data), yet both are well above pH 4.5, which has been identified as a threshold of nitrate production in Douglas-fir forest floors (Prietzel et al. 2004). Moreover, nitrification rates in surface soils under Coast Range Douglas-fir actually increase with decreasing soil pH across the range of 4.2–5.9 (Sinkhorn 2007), suggesting that pH alone is unlikely to explain the nitrification differences that we observed.

The cumulative effects of severe fire on N pools, over the historic period 1400–2000 AD, with a fire return interval of ~150 years (omits low-intensity fires), is likely to limit N accumulation on these sites. Since N pools are large, a single instance of N loss is unlikely to have a significant effect on long-term ecosystem processes. However, the C losses in

Table 6. Mean (with standard errors in parentheses) net N mineralization and nitrification for forest floor and soil.

	N mineralization ($mg \cdot g^{-1}$)	Nitrification ($mg \cdot g^{-1}$)	N mineralization ($mg \cdot (g\ N)^{-1}$)	Nitrification ($mg \cdot (g\ N)^{-1}$)
Forest floor				
Young	26 (3.52)	0.55 (0.28)	1.66 (0.21)	32.7 (16.3)
Old	60 (7.32)	0.05 (0.03)	3.85 (0.43)	2.7 (1.5)
p (age)[a]	<0.001	0.08	<0.001	0.08
r^2	0.45	0.13	0.48	0.13
Mineral soil (0–10 cm)				
Young	0.007 (0.004)	0.0036 (0.0027)	0.06 (0.02)	0.024 (0.015)
Old	0.007 (0.002)	0.0007 (0.0003)	0.06 (0.01)	0.007 (0.003)
p (age)[a]	0.96	0.30	0.73	0.26
r^2	0.00	0.05	0.01	0.06

Note: Results are from a 28 day controlled (temperature and moisture) laboratory incubation.

[a]Multiple linear stepwise regression using Akaike information criterion.

Table 7. Pools and processes for forest floor (FF) and mineral soil for three age groups, with analysis of differences from ~450 to 800+ years.

	Approximate age (years)				
Item	~150 (*n*=12)	~450 (*n*=8)	800+ (*n*=4)	p^a	r^2
Pool ($kg \cdot ha^{-1}$)					
FF N	1 420	1 916	1 636	0.34	
FF C	49 033	63 648	61 645	0.87	
Soil N	5 893	6 752	5 104	0.06	0.31
Soil C	182 619	201 035	179 351	0.44	
C/N					
FF C/N	34.2	32.8	37.5	0.11	
Soil C/N	32.5	29.6	35.8	0.05	0.33
Concentration ($mg \cdot g^{-1}$)					
FF N	16	16	15	0.54	
FF C	523	512	547	0.07	0.30
Soil N	88	99	90	0.59	
Soil C	238	266	243	0.59	
Rates ($mg \cdot g^{-1}$)					
FF N miner.	26	68	44	0.48	
FF nitrif.	0.55	0.06	0.02	0.47	
Soil N miner.	0.007	0.008	0.004	0.24	
Soil nitrif.	0.0036	0.0007	0.0008	0.88	
Rates ($mg \cdot (g\ N)^{-1}$)					
FF N miner.	1.66	4.37	2.81	0.09	0.26
FF nitrif.	32.7	3.6	1.0	0.44	
Soil N miner.	0.06	0.08	0.04	0.14	0.26
Soil nitrif.	0.024	0.007	0.007	0.99	

[a]Significance for *t* test of means of ~450 vs. 800+ years.

a single severe-fire event are quite large and are likely to be a significant addition to atmospheric CO_2 concentrations (Campbell et al. 2007). Thus, historic mean fire intervals (~100 years, all fires) may limit C sequestration on these sites, although a significant amount of C may be converted and stored as charcoal (DeLuca and Aplet 2008). Hence, a return to historical fire regimes may reduce the differences between old and young sites, since low to moderate fires may be more frequent, thereby reducing forest floor mass accumulation. Such changes also may influence plant nutrition and competition, since successional age appears to limit nitrification, and hence, may favor plants that use ammonium preferentially.

Our 12 old sites did not have a random distribution of data in line with expected trends, so to examine longer-term C and N accumulation patterns, we further divided our 12 old sites into two groups: ~450 years (n = 8) and 800+ years (n = 4). We found that forest floor and surface mineral

C and N pools accumulate from 150 to ∼450 years, then stabilize or decrease sometime before 800+ years (Table 7). The evidence that C and N do not continue to accrete throughout the 450 to 800+ year period is an interesting phenomenon that needs further study, as we are unaware of a tested explanation for this phenomenon. Our insight into long-term biogeochemical processes may have been limited because our data for the oldest age group (800+ years) were gathered from only four sites. Our results suggest that further study of sites composed of the dominant age-class in Pacific Northwest Douglas-fir old-growth (∼450 years) and comparisons between these sites and older sites (800+ years), may reveal long-term biogeochemical patterns not observed previously.

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