

Soil Organic Matter Stability in Intensively Managed Ponderosa Pine Stands in California

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Forest soils comprise a large portion of the global terrestrial C pool, and soil organic matter (SOM) is essential to soil function and forest productivity; however, responses of SOM quality to changes in fertility, moisture availability, or management are not well understood. We tested the effects of two common forest management practices, fertilization and competing vegetation control using herbicides, on surface SOM distribution and stability characteristics in three ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) plantations of differing productivity, soil type, and parent material in northern California by using density fractionation and aerobic laboratory incubation of the surface soils. The treatment effects on pine productivity revealed responses dominated by moisture limitation at the less productive sites and by nutrient limitation at the most productive site. The stability of surface SOM increased with increasing site productivity. Fertilization increased N concentrations and decreased C/N ratios in whole soils and light fractions at the less productive sites, and the effects persisted for more than a decade. Furthermore, fertilization increased soil C mineralization from the intermediate-productivity site during incubation. In contrast, fertilization decreased C mineralization from the most productive site, suggesting that fertilization increased SOM stabilization at this site. Controlling understory vegetation with herbicides reduced N availability, as evidenced by reduced light-fraction N at the poorest site and decreased N mineralization during incubation. Our study demonstrates the importance of site characteristics and the use of a combination of indices in determining the effects of forest management practices on SOM characteristics and dynamics.

Abbreviations: DF, dense fraction; DiN, dissolved inorganic nitrogen; DOC, dissolved organic carbon; DOM, dissolved organic matter; DON, dissolved organic nitrogen; LF, light fraction; SOM, soil organic matter; SPT, sodium polytungstate; TDN, total dissolved nitrogen.

The sensitivity of SOM to forest management is important in the context of C sequestration and mitigation of anthropogenic CO₂ emissions at global, national, and regional scales (Dixon et al., 1994; Schimel, 1995; Jandl et al., 2007) and is relevant to ecosystem function and sustainable management of natural resources (Henderson, 1995; Jurgensen et al., 1997). Nearly 2500 Pg of C resides in terrestrial vegetation and soil to a 1-m depth, and forests account for approximately 46% of this pool (Watson et al., 2000). Of this, at least half exists belowground (Van Cleve and Powers, 1995). The Kyoto Protocol identified afforestation and reforestation as valid tools for mitigating greenhouse gas emissions, and it may be possible to manage existing forests, particularly timberlands, for enhanced sequestration of C (Dixon et al., 1994). Equally important, SOM is a key component in soil function through its influence on nutrient cycling and as a C source for heterotrophic soil biota (Amaranthus et al., 1989; Powers et al., 1990; Henderson, 1995). Therefore, conservation of SOM pools and maintenance of SOM dynamics are major goals of sustainable forest management (Powers et al., 1990; Jurgensen et al., 1997).

The processes involved in stabilization and destabilization of SOM are important mechanisms for soil C sequestration and loss (Jastrow et al., 1998; von Lützwow et al., 2006; Oades, 1988). Considerable effort has been invested in describing SOM characteristics (Stevenson and Elliott, 1989; Hassink, 1995) and identifying

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the factors controlling its dynamics, including litter and SOM decomposition, the chemistry of litter inputs and SOM, and protection of the organic matter within the soil matrix (Baldock and Skjemstad, 2000; von Lützow et al., 2006; Mikutta et al., 2006). Soil organic matter storage and dynamics are partly dependent on litter and SOM decomposition rates, which are controlled by different factors dependent on the stage of decay (Golchin et al., 1994a; von Lützow et al., 2006). Throughout the decay process, decomposition rates are regulated by moisture and O₂ availability, which may be influenced by climate and modified by the soil structure (Post et al., 1982; Schuur et al., 2001). The quantity and chemistry of litter inputs, however, appear to influence decomposition only during the early stages of litter decay when selective preservation of SOM with characteristics associated with chemical recalcitrance (such as aliphatics, polyphenols, and alkyl C groups) suggests a microbial preference for more labile C sources (such as sugars and proteins) (Berg, 2000; Krull et al., 2003). In contrast, as SOM becomes increasingly processed by microorganisms, the chemical composition of C sources appears to become less important, while mechanisms that reduce microbial accessibility to SOM become more relevant (Berg, 2000).

The protection of SOM from microbial decomposition represents a pathway for C stabilization in soils and may occur via the physical protection of SOM within soil aggregates or organo-mineral interactions. Soil properties including texture, mineralogy, and structure influence SOM stabilization. In general, soil C content tends to increase with increasing clay content (Baldock and Skjemstad, 2000; Oades, 1988; Schimel et al., 1994), resulting in part from high adsorption of dissolved organic matter (DOM) by clay-size particles (Silver et al., 2000). The capacity of soils to adsorb organic matter (OM) may be influenced more by soil mineralogy than texture, however (Kaiser and Zech, 2000; Kleber et al., 2005), with high levels of SOM retention, long SOM turnover times, and reduced rates of C mineralization coinciding with an abundance of poorly crystalline minerals, particularly those containing Fe and Al oxides (Torn et al., 1997; Percival et al., 2000). Soil structure also plays an important role in SOM dynamics, particularly considering the capacity of soil aggregates to physically protect OM from decomposition (Golchin et al., 1994b; Lehmann et al., 2007; Rasmussen et al., 2006).

Soil organic matter is complex and physical fractionation by density has been used to separate labile from recalcitrant SOM (Golchin et al., 1994b; Crow et al., 2007). Light-density fractions from SOM, which consist largely of identifiable plant materials such as root and leaf fragments and contain high amounts of plant- and litter-derived carbohydrates (Golchin et al., 1994b; Crow et al., 2007), can be used as surrogates for labile SOM pools. Light fractions (LFs) appear to be more sensitive to management disturbance than whole soils comprised of both mineral and organic fractions, potentially allowing the identification of subtle but ecologically important changes in labile SOM (Janzen et al., 1992; Alvarez and Alvarez, 2000; Echeverría et al., 2004).

Laboratory incubation experiments can provide indices for SOM dynamics including C mineralization or decomposi-

tion (Alvarez et al., 1998; Alvarez and Alvarez, 2000; Waldrop and Firestone, 2004), N mineralization (Powers, 1980, 1990), and the production of DOM (Magill and Aber, 2000; Neff and Hooper, 2002). Incubations have been used extensively to assess how such processes are affected by numerous factors including competing vegetation control (Echeverría et al., 2004) and nutrient manipulation (Haile-Mariam et al., 2000; Park et al., 2002; Swanston et al., 2004).

Field studies of the explicit effects of ecosystem productivity and environmental factors on SOM characteristics and dynamics are rare and anecdotal because natural gradients in productivity, temperature, or moisture often include changes in a vegetation community or soil characteristics. General trends for soil C storage include greater soil C storage with increasing precipitation, most pronounced in warm climates, and a decrease in those pools with increasing temperature when moisture is held constant (Post et al., 1982; Van Cleve and Powers, 1995; Alvarez and Lavado, 1998; Schuur et al., 2001). These trends have been explained primarily by limitations of temperature and moisture on decomposition (Post et al., 1982; Alvarez and Lavado, 1998), which seem to be more important in determining SOM storage than the rate of plant-derived C inputs in most terrestrial systems (Post et al., 1982; Yuste et al., 2007). Decomposition rates tend to increase with increasing temperature (Post et al., 1982) but may be constrained to a greater extent by moisture than by temperature under warm, dry conditions (Yuste et al., 2007) or in very wet environments (Alvarez and Lavado, 1998; Schuur et al., 2001). Soil C storage also tends to increase with soil development from young to intermediate-aged soils (Van Cleve and Powers, 1995; Torn et al., 1997; Lilienfein et al., 2003) and with increases in clay content (Oades, 1988; Schimel et al., 1994; Baldock and Skjemstad, 2000) and concentrations of poorly crystalline clay minerals (Torn et al., 1997; Percival et al., 2000; Kleber et al., 2005). Although these trends tend to be observed across large spatial scales, variability in factors such as soil type, topography, parent materials, and plant community limit their applicability at smaller scales. In addition, questions remain regarding how SOM is affected by management and how such effects vary with soil type, ecosystem productivity, and climate (Neff and Hooper, 2002; Waldrop and Firestone, 2004; Fissore et al., 2008).

Competing vegetation control and fertilization are commonly used to increase aboveground tree productivity in intensively managed forests (e.g., Busse et al., 1996; Powers and Reynolds, 1999; Hangs et al., 2003). In addition to improving tree growth, these practices can alter SOM dynamics through changes in the quantity and chemistry of litter inputs and nutrient availability for decomposers. Reductions in SOM pools following competing vegetation control with herbicides have been attributed to elevated decomposition resulting from increased soil temperature or moisture (Aust and Lea, 1991; Munson et al., 1993) or to declines in above- or belowground litter production (Shan et al., 2001; Echeverría et al., 2004). Declines in the N mineralization potential (Echeverría et al., 2004) and cation availability (Will et al., 2006) have also been observed following competing vegetation

control with herbicides, possibly caused by removal of above- or belowground inputs. Other studies have demonstrated reductions in microbial biomass and activity in response to herbicide application (Busse et al., 1996, 2006; Périé and Munson, 2000).

In contrast, fertilization often improves the soil characteristics associated with highly productive ecosystems, including elevated nutrient concentrations or lowered C/N ratios in surface soils that may be detected a decade or longer after fertilization (Harding and Jokela, 1994; Homann et al., 2001; Jandl et al., 2003). Contrasting effects of fertilization on SOM storage and dynamics, however, demonstrate the importance of multiple processes, including nutrient-C interactions, in affecting C storage (Neff et al., 2002). For example, numerous studies have observed increased C storage in litter layers following fertilization (Baker et al., 1986; Madeira et al., 2002; Giardina et al., 2004; McFarlane et al., 2009) resulting from increased litter production (Haynes and Gower, 1995; Haile-Mariam et al., 2000; Li et al., 2006) or a reduced decomposition rate (Magill and Aber, 1998; Franklin et al., 2003). On especially nutrient-poor sites, however, fertilizer additions can increase decomposition of forest-floor material, thereby releasing C, N, and cations previously bound in undecomposed litter (Jandl et al., 2002).

We used density fractionation and laboratory incubations to study the SOM characteristics and dynamics at three ponderosa pine plantations of varying productivity and soil type in northern California. In addition, we investigated how fertilization and competing vegetation control through application of an herbicide, applied alone and in combination, affect the surface SOM at our three sites. Specifically, we hypothesized that: (i) the amount of SOM increases with increasing site productivity resulting from increased litter inputs and differences in soil type across sites; (ii) fertilization increases the amount of available N, but the effects of fertilization on labile SOM differ at sites with varying nutrient availability; (iii) competing vegetation control with herbicides decreases the amount of labile SOM and available N through reduced litter inputs; and (iv) the effects of individual and combined treatments vary across sites with changes in productivity and soil characteristics.

MATERIALS AND METHODS

Study Sites

Our three plantations span the range in productivity and soil type found in the ponderosa pine region of northern California west of the crest of the Cascades and Sierra Nevada mountains (Fig. 1; Table 1). The productivity gradient also correlates with a gradient in mean annual precipitation (MAP), which ranges from 1015 to 1780 mm, and a gradient in surface soil C and N concentrations (Table 1). The study region is characterized by a Mediterranean climate with warm, dry summers and cold, wet winters. These plantations are part of a larger, long-term experiment to assess effects of competing vegetation control and fertilization on ponderosa pine productivity (the Garden of Eden

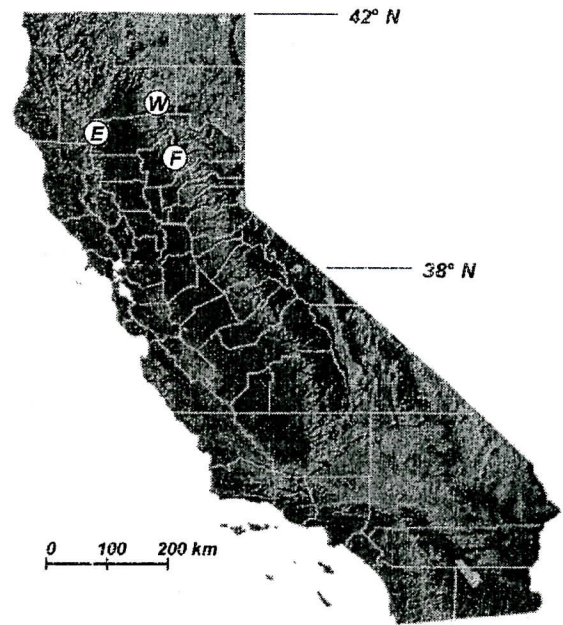


Fig. 1. Map of study site locations within the state of California. Sites: E = Elkhorn Ridge, W = Whitmore, F = Feather Falls. Base: California state map collection.

Eden Study; see Powers and Ferrell, 1996; Powers and Reynolds, 1999). Competing vegetation control is a topic of interest in this region because competition from shrubs and grasses can increase water deficits in soils, increasing water stress in trees (Petersen and Maxwell, 1987; Shainsky and Radosevich, 1986) to the extent that the success of planted or naturally regenerated conifers following stand-replacing disturbance may require control of competing vegetation on poorer sites (Conrad and Radosevich, 1982; Powers and Ferrell, 1996).

The least productive site is Elkhorn Ridge located in the Klamath Mountains. Soils at the site are mapped as loamy-skeletal, mixed, active, mesic Typic Dystrochrepts of the Sheetiron series derived from metasedimentary mica-quartz schist (www2.ftw.nrcs.usda.gov/osd/dat/S/SHEETIRON.html; verified 3 Mar. 2010). Elkhorn Ridge has the lowest soil water-holding capacity (J. Zhang, personal communication, 2009) in addition to the lowest MAP (Table 1), making it the driest of

Table 1. Summary of selected characteristics for the Elkhorn Ridge, Whitmore, and Feather Falls study sites selected from the Garden of Eden Study.

	Elkhorn Ridge	Whitmore	Feather Falls
Productivity	low	intermediate	high
Age at sampling, yr	16	18	16
Soil Great Group	Dystrochrept	Haplohumult	Haploxeralf
Parent material	metasediment (mica-quartz schist)	volcanic (andesite)	volcanic (basalt)
Mean annual precipitation, mm	1015	1140	1780
Mean annual temperature, °C	9	15	12
Elevation, m	1490	730	1220
0–20-cm soil pH†	5.8	5.6	5.4
0–20-cm clay content, %‡	18	31	27
0–20-cm sand content, %‡	50	42	41
0–20-cm organic C, g kg soil ⁻¹ †	18	26	48
0–20-cm total N, g kg soil ⁻¹ †	0.9	1.1	1.7

† Data from the initiation of the Garden of Eden Study (from R.F. Powers, personal communication, 2007); pH analyzed with a 1:1 soil/water paste, organic C concentration determined by the Walkley-Black method, and total N concentration determined by the Kjeldahl method.

‡ Measured in this study using soil collected from control and herbicide-plus-fertilizer treatment plots and the hydrometer method for soil particle-size distribution.

the three sites. This site also has the lowest organic C and total N concentrations in the surface soils (Table 1).

The Whitmore site is of intermediate site productivity (Table 1) and is located in the southern Cascades. Soils at Whitmore are classified as fine, parasequic, mesic Xeric Haplohumults of the Aiken series weathered from an andesitic mudflow (www2.ftw.nrcs.usda.gov/osd/dat/A/AIKEN.html; verified 3 Mar. 2010).

The most productive site is Feather Falls, which is located on the western slope of the Sierra Nevada. The soil there is described as a fine-loamy, mixed, superactive, mesic Ultic Haploxeralf of the Cohasset series weathered from basalt (www2.ftw.nrcs.usda.gov/osd/dat/C/COHASSET.html; verified 3 Mar. 2010). Feather Falls receives the most precipitation and has the highest surface soil C and N concentrations of the three sites (Table 1).

The sites were planted at a 2.4-m square spacing with ponderosa pine known to be superior for each seed zone and elevation. Before clearing and planting, Elkhorn Ridge supported a young, poorly stocked ponderosa pine plantation, Whitmore was a brush field of mixed manzanita (*Arctostaphylos* sp.) that established following a 1967 wildfire, and Feather Falls was a natural mixed conifer and hardwood stand of tan-oak [*Lithocarpus densiflorus* (Hook. & Arn.) Rehder] and California black oak (*Quercus kelloggii* Newb.). Whitmore was planted in spring 1986 and Elkhorn Ridge and Feather Falls were planted in spring 1988. Manzanita is a prominent understory evergreen shrub at all three sites and is the dominant shrub at Elkhorn Ridge and Whitmore. In contrast, deerbrush ceanothus (*Ceanothus integerrimus* Hook. & Arn.), a deciduous N₂-fixing species, is the dominant shrub at Feather Falls.

Field Experimental Design

Treatments were applied in each plantation to 12 randomized, 0.04-ha plots in a two-way factorial design with two levels of herbicide application for competing vegetation control and two levels of fertilization, resulting in four treatment combinations: herbicide only, fertilizer only, herbicide plus

Table 2. Standing bole volume and pine canopy cover by site and treatment for the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites at 15 yr.

Treatment† or vegetation type	Elkhorn Ridge	Whitmore	Feather Falls
Standing bole volume, m ³ ha ⁻¹			
C	7 ± 3 a‡	15 ± 5 a	109 ± 14 a
H	26 ± 3 b	64 ± 5 b	141 ± 14 ac
F	14 ± 3 c	39 ± 5 c	206 ± 14 b
HF	43 ± 3 d	92 ± 5 d	183 ± 14 bc
ANOVA P value			
H	<0.01**	<0.01**	0.78
F	<0.01**	<0.01**	<0.01**
H × F	0.15	0.47	0.08**
Understory vegetation on control plots, % cover§			
<i>Arctostaphylos</i> spp.	40.8 ± 5.6	73.2 ± 7.9	4.0 ± 2.5
<i>Ceanothus</i> spp.	0.2 ± 0.2	3.6 ± 1.6	55.1 ± 7.9
Other deciduous species	3.7 ± 2.6	6.0 ± 3.2	10.2 ± 3.2

** Significant at $\alpha = 0.1$.

† Treatments: C = control, H = herbicide only, F = fertilizer only, HF = herbicide plus fertilizer.

‡ Means ± standard errors. Values followed by different letters denote statistically different treatments as assessed by multiple pairwise comparisons with a Tukey adjustment, $\alpha = 0.1$.

§ Understory composition at 15 yr based on line intercepts along four 10-m transects in each control plot.

fertilizer, and no applied treatments (control). Each treatment combination was randomly replicated three times at each site so that treatment effects could be assessed at each location independently. Treatments were applied at planting and repeatedly through 6 yr, ending 10 to 12 yr before our sampling. Fertilized plots received eight nutrients applied at an exponential rate during the dormant season, commencing at planting and continuing every 2 yr through Year 6. Cumulative loadings were as follows: 1074 kg N ha⁻¹, 530 kg P ha⁻¹, 540 kg K ha⁻¹, 416 kg Ca ha⁻¹, 221 kg Mg ha⁻¹, 112 kg S ha⁻¹, 73 kg Zn ha⁻¹, 36 kg Cu ha⁻¹, and 36 kg B ha⁻¹. Details on periodic rates of application and uptake are found in Powers and Ferrell (1996) and Powers and Reynolds (1999). Competing vegetation was controlled by spraying understory plants directly with glyphosate [N-(phosphonomethyl)glycine] each spring for the first 6 yr (Busse et al., 2001).

Vegetation Measurements

Measurement plots consisted of the innermost 20 trees separated from the treatment plot boundary by two rows of buffer trees. Trees were measured regularly (every second year through Year 10 and at 5-yr intervals thereafter) for several characteristics, including height and diameter at breast height, and bole volumes were estimated using standard procedures (Oliver and Powers, 1978). All understory vegetation was measured at the same interval for height and cover percentage by species, using four parallel, 10-m, line intercept transects between tree rows. Cover was estimated by the line intercept method (Kaiser, 1983). Because layering occurs in a diverse understory, crowns of each species intercepting 4 m of a transect were measured independently, and the sum of their coverages defined the total understory ground cover. The data collected in Year 15 are shown in Table 2.

Soil Sample Collection and Analysis

In August 2004, 16 yr after planting of the Elkhorn Ridge and Feather Falls plantations and 18 yr after planting of the Whitmore plantation, the mineral soil was collected in each measurement plot from the surface 20 cm at five locations (each of the four corners and the approximate center) within the sampling area and ≥ 0.5 m away from the closest tree. Samples were collected with an 8-cm-diameter soil auger, combined into one composite sample per plot, and stored field moist at 4°C until analysis. Subsamples from the composites were sieved to 2 mm and the SOM quality was assessed in two ways: (i) the soil was fractionated by density, and density fractions and the whole soil were analyzed for total C and N; and (ii) the soil C and N mobilization potentials were investigated by laboratory incubation.

Density Fractionation

Soil was separated into light and dense fractions by dispersion in a high-density (1.65 g mL⁻¹) sodium polytungstate (SPT, Na₆[H₂W₁₂O₄₀], Sometu-USA, Van Nuys, CA) solution. In this method, the LF is collected by aspirating the floating material following dispersion, while the dense fraction (DF), also referred to as the heavy fraction, settles as sediment (Strickland and Sollins, 1987). Approximately 45 g (dry-mass equivalent) of field-moist, sieved soil was placed in a 175-mL, polystyrene, conical-bottom centrifuge bottle and 100 mL of premixed 1.65 g mL⁻¹ solid SPT powder was added to correct the solution density for soil water content. Samples were shaken on a shaker table for

1 h to disperse weakly bound soil aggregates and left to separate overnight. The next day, the floating material was aspirated. Additional SPT solution was added to the remaining sediment, which was shaken for another hour and then centrifuged at 1480 rpm in a swinging-bucket rotor for 15 min. The samples were left to settle 5 min and then the floating material was aspirated and added to the previously collected LF. The samples were shaken again and allowed to separate overnight. The procedure was repeated the following day.

Light and dense fractions were rinsed thoroughly with deionized water to remove residual SPT. The LFs were rinsed five times on a Whatman GF/F filter (ashed, 0.7- μ m pore size). Dense fractions also were rinsed five times, but the samples were left in the centrifuge bottles. For each rinse, the supernatant (SPT and water) was decanted and deionized water was added. The samples were shaken vigorously to suspend all the sediment in water and then centrifuged. The rinsed LF and DF were dried at 60°C for 6 d or until a constant weight was reached.

Whole soils, LFs, and DFs were dried at 65°C and analyzed for total C and N using the Dumas combustion technique on a Fisons NA1500 NCS Elemental Analyzer (ThermoQuest Italia, Milan, Italy). The moisture contents of the whole soils and DFs were determined (2 d at 105°C) and C and N concentrations were converted to an oven-dry basis. The LFs were not dried at 105°C because of the small amount of sample and because of a high potential for loss of C (and mass) following drying at temperatures >65°C. Moisture contents for the DF were used to adjust LF C and N concentrations to oven-dry equivalents.

Long- and Short-Term Laboratory Incubations

The potential for C and N to be mobilized via leaching of dissolved organic C (DOC) and dissolved N was investigated in two laboratory incubations of whole soils, one for 225 d (long) and one for 16 d (short). During the short incubation, C mineralization via soil respiration was also measured.

For both incubations, whole soils were incubated at 25°C, ambient humidity, and with moisture held at -22 kPa (roughly 50% water-holding capacity). Approximately 30 g (dry-weight equivalent) of field-moist soil was mixed with 30 g of oven-dry quartz sand (VWR International, West Chester, PA) that had been acid washed and autoclaved. The soil-sand mixtures were incubated in microlysimeters constructed of bench-top filtration units (Falcon Filter, Becton Dickinson Labware, Franklin Lakes, NJ) modified as described by Nadelhoffer (1990). One subsample was incubated for each treatment plot at each site. At the start of the incubations, the soil-sand mixtures were rewetted by adding 100 mL of deionized water and allowing the substrate and water to equilibrate for 1 h before extracting excess solution with a -22 kPa vacuum. Moisture contents were monitored weekly by weight and deionized water was added as needed to maintain moisture at -22 kPa.

Microlysimeters were leached periodically during the long incubation (on Days 16, 36, 55, 78, 136, 171, and 225) and at the end of the short incubation (Day 16). At each leaching, 100 mL of deionized water was added to the top of the microlysimeter, allowed to permeate and equilibrate with the soil-sand mixture for 1 h, and extracted from the microlysimeter using a -22 kPa vacuum. The leachate was analyzed for DOC and total dissolved N (TDN) within 72 h (total organic C analyzer TOC-VCSH, total N measuring unit TNM-1, Shimadzu, Kyoto,

Japan) and for NH_4^+ -N and NO_3^- -N within 48 h (Lachat QuickChem FIA+ 8000 series autoanalyzer, Loveland, CO). Dissolved inorganic N (DIN) was calculated as the sum of NH_4^+ -N and NO_3^- -N. Dissolved organic N (DON) was calculated as the difference between TDN and DIN. Concentrations were multiplied by the volume extracted to yield C and N in milligrams. Individual and cumulative losses of DOC, TDN, NH_4^+ -N, NO_3^- -N, and DON are expressed per gram of initial C or initial N because we were primarily interested in the lability of the SOM present rather than the absolute amount of C or N released.

For the short incubation, CO_2 evolution was measured on Days 4, 10, and 16 by sealing the microlysimeters and measuring CO_2 accumulation during a 4-hr period. Headspace gas was sampled initially and after 4 h with a 0.5-mL syringe. Immediately after sampling, the gas was injected into a calibrated gas chromatograph (5700 A series Hewlett-Packard, Palo Alto, CA, fitted with a Poropak R 80/100 packed column and a thermal conductivity detector). Respiration rates were calculated from the amount of CO_2 accumulated during the 4-h period, and cumulative respiration was estimated by calculating the area under the curve of respiration rate over time using the trapezoidal method in PROC EXPAND in SAS version 9.1 (SAS Inst., Cary, NC). Cumulative respiration is expressed on a per-gram-of-initial-C basis.

Data Analysis

Data were analyzed for treatment effects and means or medians (back-transformed data) were calculated using PROC MIXED in SAS. Tests for statistically significant differences were conducted at $\alpha = 0.1$. Pine bole volume and whole-soil data were analyzed by site with a 2×2 factorial design. Density fractions were analyzed using a split-plot design, where field plot served as the whole plot and density fraction served as the subplot, to account for correlation between fractions derived from a single field plot. Model assumptions of normality and constant variance were checked using PROC UNIVARIATE and residual plots. Differences among sites were assessed using *t*-tests comparing controls at each site.

Incubation data were analyzed by site using a repeated-measures analysis of variance to test for treatment effects during each of the two incubations. Initial (Day 0) leaching data and final cumulative DOC and TDN loss for the long incubation were also analyzed separately to determine if the treatment affected the initial water-extractable C and N or the total C and N losses during the 225 d. Only the initial DON data were analyzed because during subsequent leachings, relatively high levels of inorganic N generated from N mineralization precluded the detection of DON for many samples. The DOC/DON ratios were also calculated for the initial leaching data.

To maintain a normal data distribution and constant variance, the data analyzed with repeated measures were logarithmically transformed before analysis. In cases without split plots or repeated measures (i.e., whole-soil or final cumulative flux data), treatment effects were assessed as follows. When the fertilizer and herbicide interaction was not significant, it was left in the model and the main effects of each factor were tested. When the treatment was significant, linear contrasts were used to test the differences between treatment combinations using a Tukey adjustment.

In cases where a repeated-measures or split-plot design provided a third treatment factor (e.g., density in the fractionation data), treatment

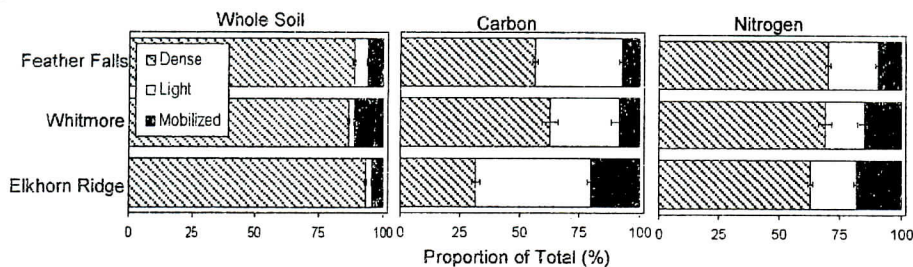


Fig. 2. Mass balance of total recovered and mobilized fractions of the whole soil, total C, and total N for the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites. Mobilized fractions were calculated as the difference between the whole soil (unfractionated) and the recovered dense and light fractions. Values are means across treatments with ± 1 standard error for dense and light fractions.

effects were analyzed as follows. When there was a treatment interaction with density, for example, the effect of treatment (herbicide or fertilizer) was assessed first by slicing by density. If a treatment effect was detected in one density fraction, multiple pairwise comparisons were conducted to compare treatments within that density fraction, with *P* values adjusted using the Bonferroni adjustment.

Table 3. Treatment means for the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites for whole-soil C and N concentrations and C/N ratios in the upper 20 cm of mineral soil.

Treatment or factor†	C	N	C/N ratio
	g kg soil ⁻¹		
<u>Elkhorn Ridge, low productivity</u>			
C	18.7 ± 2.4‡	0.9 ± 0.1 a§	21.0 ± 1.7
H	21.2 ± 2.4	1.0 ± 0.1 ab	22.2 ± 1.7
F	26.3 ± 2.4	1.1 ± 0.1 b	23.6 ± 1.7
HF	20.2 ± 2.4	0.9 ± 0.1 a	21.9 ± 1.7
	ANOVA <i>P</i> value		
H	0.20	0.17	0.90
F	0.45	0.09**	0.51
H × F	0.11	0.02**	0.41
<u>Whitmore, intermediate productivity</u>			
C	30.7 ± 3.4	1.0 ± 0.1 a	29.3 ± 1.1 a
H	26.4 ± 3.4	1.0 ± 0.1 a	26.4 ± 1.1 a
F	32.6 ± 3.4	1.2 ± 0.1 b	26.0 ± 1.1 b
HF	29.6 ± 3.4	1.2 ± 0.1 b	25.3 ± 1.1 b
	ANOVA <i>P</i> value		
H	0.31	0.50	0.12
F	0.47	0.07**	0.07**
H × F	0.86	0.81	0.34
<u>Feather Falls, high productivity</u>			
C	60.8 ± 6.8	2.0 ± 0.2	30.8 ± 1.9
H	58.5 ± 6.8	1.9 ± 0.2	30.5 ± 1.9
F	60.4 ± 6.8	2.1 ± 0.2	28.2 ± 1.9
HF	59.8 ± 6.8	1.9 ± 0.2	31.5 ± 1.9
	ANOVA <i>P</i> value		
H	0.83	0.42	0.45
F	0.95	0.65	0.72
H × F	0.91	0.60	0.39

** Significant at $\alpha = 0.1$.

† Treatments: C = control, H = herbicide only, F = fertilizer only, HF = fertilizer and herbicide.

‡ Means \pm standard errors.

§ Values followed by different letters denote statistically different treatments as assessed by multiple pairwise comparisons with a Tukey adjustment, $\alpha = 0.1$.

RESULTS

Aboveground Response

Vegetation measurements made nearest to the soil sampling dates are shown in Table 2. As witnessed by standing bole volumes on plots that received an herbicide treatment, our three plantations differed substantially in fundamental pine productivity, with each successively productive site having roughly a doubling of standing volume, ranging from a low of 26 m³ ha⁻¹ at Elkhorn to a high of 141 m³ ha⁻¹ at Feather Falls. Treatments increased pine growth at all three sites. Competing vegetation control had a strong effect on the droughty Elkhorn Ridge and Whitmore sites, roughly tripling the 15-yr bole volumes. Fertilization alone had a strong but less-pronounced effect, more than doubling bole volumes relative to controls. Combining vegetation control with fertilization on these droughty sites had at least an additive effect, boosting standing bole volumes by more than five times those of the controls. At Feather Falls, the standing bole volume was nearly doubled by fertilization. Combining vegetation control with fertilization at Feather Falls produced gains that were no greater than those from fertilization alone. Understory vegetation at 15 yr was dominated by woody shrubs on all sites, with the least total ground coverage found at Elkhorn Ridge (43%) and the most coverage at Whitmore (84%).

Density Fractionation

Mobilization

Soil mass recovery was $\geq 89\%$ for soils from all three sites (Fig. 2), with the highest losses from the Whitmore soils, which had the highest clay content of the soils studied. This mobilized fraction consists of SPT-soluble or colloidal fractions lost during fractionation and rinsing. Total C and N recoveries were $\geq 80\%$ for soils from all three sites, with the largest mobilized C and N fractions from the Elkhorn soil. Silvicultural treatment did not affect the amounts of total soil C or N mobilized during fractionation ($P > 0.1$, data not shown).

Whole-Soil Properties

Whole-soil C and N concentrations increased with site quality (Table 3). A comparison of the soil C and N concentrations measured in this study with C and N concentrations measured at plantation establishment (Table 1) suggest that soil C and N may have accumulated slightly since plantation establishment at some sites and for some treatments. The initial concentration values shown in Table 1 are from pooled samples analyzed by different methods than those used in this study, however, and may not be directly comparable. Whole-soil C/N ratios also followed the site quality gradient and ranged from 21 at Elkhorn Ridge to 31 at Feather Falls (Table 3) in control plots. Fertilizer and herbicide treatments had a limited effect on the

soil C concentration at any of the sites (Table 3). At Elkhorn Ridge, fertilization without herbicide application increased the soil N concentration relative to the control and to the combination of both treatments by about 0.2 g N kg⁻¹ soil ($P = 0.04$ and 0.07 , respectively). At Whitmore, fertilization increased the soil N concentration by 0.18 g N kg⁻¹ soil and decreased the C/N ratio by 8% regardless of herbicide application. Fertilization had no effect on soil N or the C/N ratio at Feather Falls (Table 3).

Light and Dense Fractions

Across sites and treatments, the LF represented $\leq 6\%$ of the recovered soil mass in the surface 20 cm of mineral soil. Carbon concentrations in the LF were 12- to 50-fold higher than in the DF, and N concentrations were 6- to 12-fold higher in the LF than in the DF (Table 4). Light-fraction C/N ratios ranged from two to five times higher than C/N ratios of the DF (Table 4). Light fractions also contained a smaller portion (21–24%) of the total N recovered than the DF at all sites. The distribution of soil C and N among fractions was not affected by treatment. In soils from Elkhorn Ridge, the LF contained $>60\%$ of the total recovered C, whereas 34 and 41% of the recovered C was in the LF for Whitmore and Feather Falls, respectively. Consequently, the amount of recovered C in the DF increased with increasing clay content (Table 1). Light-fraction C concentrations decreased with increasing clay content from 381 g C kg⁻¹ fraction for the control plots at Elkhorn Ridge ($P < 0.01$) (Table 4), where clay comprised 18% of the soil fraction (Table 1), to 364 g C kg⁻¹ fraction for the control plots at Whitmore (Table 4), where clay comprised 31% of the soil fraction (Table 1).

Dense-fraction chemistry was not affected by treatment at any site, nor did treatment impact the LF chemistry at Feather Falls; however, fertilization and competing vegetation control affected the LF chemistry at Elkhorn Ridge and Whitmore (Table 4). At Elkhorn Ridge, competing vegetation control increased the LF C concentrations by 5% ($P = 0.02$) (Table 4). Fertilization increased the LF N concentrations and decreased the C/N ratios relative to the control ($P < 0.05$); however, competing vegetation control decreased the LF N concentrations in fertilized plots by 10% (Table 4). At Whitmore, fertilization increased the LF N concentrations by 1.3 g N kg⁻¹ fraction and decreased the C/N ratios by 21% ($P < 0.01$). Competing vegetation control decreased the LF C/N ratios by 2% ($P = 0.01$) and the combination of both treatments had an additive effect such that the lowest LF C/N ratios were in plots that received both treatments (Table 4).

Table 4. Treatment means for the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites for light- and dense-fraction C and N concentrations and C/N ratios in the upper 20 cm of mineral soil.

Treatment†	Light fraction			Dense fraction		
	C	N	C/N ratio	C	N	C/N ratio
	— g kg ⁻¹ fraction —			— g kg ⁻¹ fraction —		
	<u>Elkhorn Ridge, low productivity</u>					
C	381 ± 6 a‡	6.3 ± 0.1 a	61 ± 2 a	6.0 ± 6.3	0.6 ± 0.1	11 ± 2
H	400 ± 6 b	6.7 ± 0.1 ac	60 ± 2 a	6.6 ± 6.3	0.6 ± 0.1	11 ± 2
F	381 ± 6 a	7.7 ± 0.1 b	49 ± 2 b	8.3 ± 6.3	0.7 ± 0.1	12 ± 2
HF	399 ± 6 b	7.0 ± 0.1 c	57 ± 2 ab	7.1 ± 6.3	0.6 ± 0.1	11 ± 2
	<u>Whitmore, intermediate productivity</u>					
C	364 ± 9	6.5 ± 0.3 a	56 ± 1 a	18.1 ± 8.6	0.7 ± 0.3	26 ± 1
H	350 ± 9	6.9 ± 0.3 b	51 ± 1 b	15.8 ± 8.6	0.7 ± 0.3	24 ± 1
F	350 ± 9	8.0 ± 0.3 a	44 ± 1 c	17.7 ± 8.6	0.8 ± 0.3	23 ± 1
HF	326 ± 9	8.0 ± 0.3 b	41 ± 1 d	20.9 ± 8.6	0.9 ± 0.3	24 ± 1
	<u>Feather Falls, high productivity</u>					
C	369 ± 13	7.1 ± 0.3	52 ± 3	32.6 ± 13.4	1.3 ± 0.3	25 ± 3
H	375 ± 13	6.5 ± 0.3	58 ± 3	31.2 ± 13.4	1.2 ± 0.3	25 ± 3
F	360 ± 13	7.4 ± 0.3	49 ± 3	31.7 ± 13.4	1.4 ± 0.3	23 ± 3
HF	370 ± 13	6.6 ± 0.3	56 ± 3	28.9 ± 13.4	1.2 ± 0.3	24 ± 3

† Treatments: C = control, H = herbicide only, F = fertilizer only, HF = fertilizer and herbicide.

‡ Means ± standard errors. Treatment effects were assessed using a split-plot analysis of variance. Different letters within a column denote statistically different treatments as assessed by multiple pairwise comparisons with a Bonferroni adjustment, $\alpha = 0.1$.

Whole-Soil Laboratory Incubations Long-Term Incubation

Initial leachates (extracted on Day 0) from Elkhorn Ridge soils contained three and five times as much DOC per gram of initial C as soils from Whitmore and Feather Falls, respectively (Table 5). The trend of decreasing DOC release with increasing site productivity continued during the 225-d incubation, with soils from Elkhorn Ridge producing two to three times more DOC than soils from the other sites (Table 6; Fig. 3). Elkhorn Ridge soils also initially released three to five times more DON per gram of initial N than the other sites (Table 5). Soils from Whitmore initially released nearly twice as much DON than soils from Feather Falls (Table 5). The initial release of DOC was positively correlated with the initial release of DON across all sites and treatments ($r^2 = 0.7$). The initial leachate DOC/DON ratio followed the trends in the whole-soil C/N ratio and was lower for Elkhorn Ridge (34) than for Whitmore (51) and Feather Falls (55) but was unaffected by treatment at any site (Table 5). The initial and cumulative leachate DOC concentrations varied little across treatments (Tables 5 and 6).

More than half of the TDN in the initial leachates from the Elkhorn Ridge and Whitmore soils was DON, whereas the majority of N released from the soils initially and throughout the incubation from Feather Falls was NO₃⁻-N (Fig. 4). During the 225-d incubation, the dominant form of N loss shifted to NO₃⁻-N for both Elkhorn Ridge and Whitmore, with Whitmore soils also producing the greatest proportion of TDN as NH₄⁺-N (5% of cumulative TDN, on average).

The soils from Feather Falls produced more NO₃⁻-N than the other sites initially but lost less during the incubation (Tables 5 and 6). Fertilization at Feather Falls increased the NO₃⁻-N (and TDN) extracted during the first leaching (Table 5). For this

Table 5. Initial releases of dissolved organic C (DOC), dissolved organic N (DON), NO₃⁻-N, NH₄⁺-N, and DOC/DON ratio of leachates for each treatment at the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites at the start of the 225-d incubation.

Treatment or factor†	DOC g kg ⁻¹ initial C	DON g kg ⁻¹ initial N	NO ₃ ⁻ -N g kg ⁻¹ initial N	NH ₄ ⁺ -N g kg ⁻¹ initial N	DOC/DON ratio
<u>Elkhorn Ridge, low productivity</u>					
C	2.11 ± 0.37‡	1.25 ± 0.26	0.11 ± 0.03	0.21 ± 0.13	34 ± 7
H	1.94 ± 0.37	1.62 ± 0.26	0.10 ± 0.03	0.21 ± 0.13	28 ± 7
F	1.69 ± 0.37	1.36 ± 0.26	0.13 ± 0.03	0.44 ± 0.13	36 ± 7
HF	2.01 ± 0.37	1.34 ± 0.26	0.09 ± 0.03	0.19 ± 0.13	31 ± 7
<u>ANOVA P value</u>					
H	0.84	0.51	0.53	0.33	0.57
F	0.64	0.75	0.89	0.40	0.89
H × F	0.53	0.47	0.72	0.36	0.47
<u>Whitmore, intermediate productivity</u>					
C	0.69 ± 0.06	0.42 ± 0.07	0.21 ± 0.04	0.19 ± 0.02	51 ± 6
H	0.70 ± 0.06	0.45 ± 0.07	0.24 ± 0.04	0.13 ± 0.02	43 ± 6
F	0.81 ± 0.06	0.58 ± 0.07	0.21 ± 0.04	0.13 ± 0.02	38 ± 6
HF	0.80 ± 0.06	0.49 ± 0.07	0.13 ± 0.04	0.15 ± 0.02	41 ± 6
<u>ANOVA P value</u>					
H	0.70	0.79	0.56	0.30	0.98
F	0.78	0.84	0.22	0.48	0.33
H × F	0.37	0.32	0.25	0.11	0.49
<u>Feather Falls, high productivity</u>					
C	0.40 ± 0.06	0.24 ± 0.08	0.38 ± 0.23 a§	0.13 ± 0.02	55 ± 22
H	0.32 ± 0.06	0.18 ± 0.08	0.34 ± 0.23 b	0.08 ± 0.02	57 ± 22
F	0.36 ± 0.06	0.17 ± 0.08	1.27 ± 0.23 c	0.08 ± 0.02	69 ± 22
HF	0.39 ± 0.06	0.28 ± 0.08	0.38 ± 0.23 a	0.11 ± 0.02	78 ± 22
<u>ANOVA P value</u>					
H	0.93	0.63	0.08**	0.53	0.79
F	0.11	0.18	0.08**	0.56	0.98
H × F	0.82	0.42	0.25	0.04***¶	0.59

** Significant at $\alpha = 0.1$.

† Treatments: C = control, H = herbicide only, F = fertilizer only, HF = fertilizer and herbicide.

‡ Means ± standard errors.

§ Values followed by different letters denote statistically different treatments as assessed by multiple pairwise comparisons with a Tukey adjustment, $\alpha = 0.1$.

¶ No significant contrasts between treatments, $\alpha = 0.1$.

site, control of competing vegetation decreased NO₃⁻-N (and TDN) release initially and during the incubation by about one-third (Tables 5 and 6; Fig. 5).

Short-Term Incubation

As in the long-term incubation, soil respiration (g CO₂ kg⁻¹ initial C) and DOC release during the short-term incubation were inversely related to site quality (Table 7). Soils from controls at Elkhorn Ridge mobilized the most C as CO₂ and DOC after 16 d of incubation (0.8 and 4.2 g kg⁻¹ initial C, respectively, Table 7). Feather Falls mobilized the least C (0.3 and 1.2 g kg⁻¹ initial C for C as CO₂ and DOC, respectively; Table 7). The site means for CO₂/DOC ratios ranged from 0.19 to 0.26. Cumulative fluxes of CO₂ and DOC during the short-term incubation were not correlated with one another ($P > 0.1$, Pearson and Spearman coefficients <0.1).

Similar to the 225-d incubation, fertilizer and herbicide treatments did not affect DOC release during the short-term incubation; however, they did influence the CO₂ fluxes and thus altered the CO₂/DOC ratios. The effects varied by site. Fertilizer,

regardless of the presence or absence of competing vegetation control, increased CO₂ production substantially for the soils from Whitmore, but decreased respiration by 42% for the soils from Feather Falls (Table 7). The CO₂/DOC ratios for the soils from Elkhorn Ridge were 40% higher with competing vegetation control and 32% lower with fertilizer. A similar effect of fertilizer occurred at Feather Falls, where soils from the fertilized plots had 48% lower CO₂/DOC ratios, but the opposite was true at Whitmore, where fertilizer increased the CO₂/DOC ratios by 30% (Table 7).

DISCUSSION

Responses across the Productivity Gradient Vegetation

The responses of pine productivity to treatment at our sites complement previous studies in this region that have shown a varied response of ponderosa pine to nutrient additions dependent on site-specific levels of shrub competition (Powers, 1983). On sites drier than Elkhorn Ridge, ponderosa pine response to fertilization can be nonexistent where shrubs have not been controlled (Powers and Jackson, 1978). For ponderosa pine, the control of shrubs can increase water and nutrients available for trees, increasing tree growth and vigor, especially when trees are young

(Busse et al., 1996; Lanini and Radosevich, 1986).

Low soil C and N concentrations suggest low soil fertility at the Elkhorn Ridge and Whitmore sites. Previous work showed that by the fifth year following planting, foliar N concentrations in the control treatments at these sites were at or below levels critical for growth (Powers, 1983; Powers et al., 1988; Powers and Ferrell, 1996), suggesting that N limits tree productivity at these sites. Understory vegetation control resulted in much greater tree growth than fertilization alone, however, suggesting that water stress limits productivity on these sites. The response to fertilization was considerably greater when the understory vegetation was eliminated, an effect that was more evident earlier in plantation development (Powers and Ferrell, 1996; Powers and Reynolds, 1999). Competing vegetation control reduced water stress in trees at Whitmore, as demonstrated by higher summer leaf water potentials (Powers and Ferrell, 1996) and reduced August stomatal conductance rates (Powers and Reynolds, 1999) earlier in plantation development. Unfortunately, similar measurements were not taken at Elkhorn Ridge. Because Elkhorn Ridge is an even droughtier site than Whitmore, however, we

suspect that similar physiological responses to herbicide application probably occurred at Elkhorn Ridge.

In contrast, higher annual precipitation, lower vapor pressure deficits, and greater water use efficiency (Powers and Reynolds, 1999) at Feather Falls permitted a strong, positive response to fertilization regardless of vegetation control. Powers and Reynolds (1999) reported that foliage N concentrations of 1-yr-old needles from unfertilized plots at Feather Falls were below the critical level for growth (Powers, 1983; Powers and Reynolds, 1999), indicating that trees are N limited at the site. The increase in pine growth caused by fertilization was so pronounced that productivity on fertilized plots at Feather Falls exceeds any reported previously for ponderosa pine plantations in California (Oliver and Powers, 1978). Rapid canopy development even in untreated plots led to a rapid decline in understory vegetation that had averaged 111% ground cover only 5 yr previously (Powers and Reynolds, 1999).

Density Fractions

We recovered a greater proportion of whole-soil C in the LF for soils from Elkhorn Ridge and in the DF for the finer textured soils of Whitmore and Feather Falls. Similarly, Echeverría et al. (2004) recovered more whole-soil C in the LF of coarser textured soils and more in the DF ($>2 \text{ g cm}^{-3}$) of finer textured soils from a study of pine plantations in the southeastern United States.

Light-fraction C/N ratios observed for these soils (41–61) are higher than those from most of the 29 soils reviewed by Sollins et al. (2006), which ranged from 10 to 40. In that study, however, they observed a much higher LF C/N ratio (66) for the Pacific Northwest forest soils (Sollins et al., 2006). They attributed the relatively high C/N ratio in their soil LF to a high charcoal content. It is possible that the somewhat high C/N ratios observed in our study were also elevated as a result of charcoal content, a theory supported by the observation of charcoal in these soils and the relatively high LF C concentrations (350–400 g C kg⁻¹ fraction) observed in these soils compared with the 150 to 360 g C kg⁻¹ fraction range reported by Sollins et al. (2006).

Density fractionation has been used in attempts to physically separate the most biologically active fraction of the SOM from the rest of the soil matrix. Unfortunately, success in isolating such a fraction in the laboratory has been limited because operationally defined SOM pools only approximate conceptual pools (Crow et al., 2007). One of the limitations of the density fractionation method is the loss of soil mineral and organic materials during the fractionation process. Suspended material can be lost during the rinsing of the fractions (Crow et al., 2007). The mobilized fractions of C and N were lower in this study (7–20%) than the mobilized fractions reported by Crow et al. (2007) for the top 5 cm of an Andisol and an Alfisol, which ranged from 21 to 27% of the total soil C and N (Crow et al., 2007). Mobilized fractions could contain DOM from different sources, including SOM soluble in SPT solution or SOM associated with colloidal soil particles. The SPT-soluble component could be similar to a water-soluble fraction (comparable to DOM from the initial leachates from our

Table 6. Cumulative releases of dissolved organic C (DOC), NO₃⁻-N, and NH₄⁺-N of leachates for each treatment at the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites during the 225-d incubation.

Treatment†	DOC		NO ₃ ⁻ -N		NH ₄ ⁺ -N	
	g kg ⁻¹ initial C		g kg ⁻¹ initial N		g kg ⁻¹ initial N	
<u>Elkhorn Ridge, low productivity</u>						
C	8.6 ± 0.8‡	55.9 ± 7.6	1.3 ± 0.3			
H	8.1 ± 0.8	72.8 ± 7.6	1.1 ± 0.3			
F	6.2 ± 0.8	78.9 ± 7.6	1.2 ± 0.3			
HF	9.2 ± 0.8	67.7 ± 7.6	1.1 ± 0.3			
<u>ANOVA P value</u>						
H	0.17	0.72	0.41			
F	0.47	0.27	0.89			
H × F	0.06**§	0.10	0.70			
<u>Whitmore, intermediate productivity</u>						
C	4.5 ± 0.3	49.6 ± 6.6	2.2 ± 2.3			
H	4.9 ± 0.3	74.0 ± 6.6	3.9 ± 2.3			
F	4.6 ± 0.3	72.2 ± 6.6	4.6 ± 2.3			
HF	5.1 ± 0.3	69.2 ± 6.6	5.5 ± 2.3			
<u>ANOVA P value</u>						
H	0.79	0.49	0.78			
F	0.70	0.54	0.80			
H × F	0.69	0.29	0.27			
<u>Feather Falls, high productivity</u>						
C	2.6 ± 0.3	46.5 ± 5.8 a¶	0.7 ± 0.2			
H	2.8 ± 0.3	31.8 ± 5.8 b	0.8 ± 0.2			
F	2.9 ± 0.3	48.2 ± 5.8 a	0.5 ± 0.2			
HF	2.9 ± 0.3	38.3 ± 5.8 b	0.8 ± 0.2			
<u>ANOVA P value</u>						
H	0.25	0.07**	0.31			
F	0.72	0.50	0.95			
H × F	0.86	0.69	0.82			

** Significant at $\alpha = 0.1$.

† Treatments: C = control, H = herbicide only, F = fertilizer only, HF = fertilizer and herbicide.

‡ Means ± standard errors.

§ No significant contrasts between treatments, $\alpha = 0.1$.

¶ Values followed by different letters denote statistically different treatments as assessed by multiple pairwise comparisons with a Tukey adjustment, $\alpha = 0.1$.

incubations) and is probably a highly labile SOM pool. Organic matter associated with colloidal clays, however, is likely to be part of a much more stable SOM pool that cycles more slowly. Crow et al. (2007) found large discrepancies in radiocarbon-based mean residence times for mobilized fractions at their eastern deciduous forest and western coniferous forest, suggesting that the composition of the mobilized fraction is soil specific.

Laboratory Incubations

Whitmore soils produced small but measureable portions of TDN as NH₄⁺-N, which we suspect was caused by inhibited nitrification during leaching because filters gradually clogged with clay particles during the 226-d incubation. A decline in the DOC/TDN ratio of leachates with time results primarily from increased N mineralization during the incubation, resulting in a higher N release. In addition, extractions occurring early in the incubation process probably contained relatively high amounts of C-rich DOM, including compounds such as carbohydrates and phospholipids (Yano et al., 2004). These compounds tend

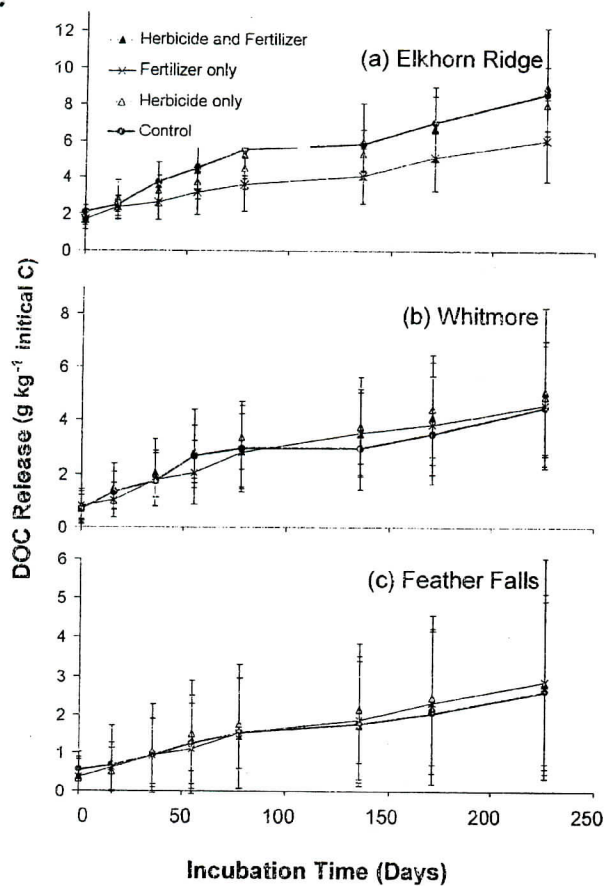


Fig. 3. Cumulative releases of dissolved organic C (DOC) in leachates for each treatment from the (a) Elkhorn Ridge, (b) Whitmore, and (c) Feather Falls Garden of Eden Study sites during the 225-d incubation. Error bars are back-transformed 95% confidence intervals.

to have a high potential for translocation in the soil profile as DOM and for utilization as a C source for microbiota (Lajtha et al., 2005).

The ratios of cumulative CO_2 /DOC fluxes observed during the 16-d incubation reported in this study were low (0.2) relative to those reported by Neff and Hooper (2002), who observed CO_2 /DOC ratios of about 10 during a 1-yr incubation of tundra soils. If not a result of ecosystem differences, the ratios we observed may have been low because we did not inoculate the soils at the beginning of the incubation. Storage before incubation may have resulted in a relatively low microbial biomass, depressing CO_2 production during the 16-d period, and a longer term incubation, such as the one reported by Neff and Hooper (2002), would probably have resulted in higher CO_2 /DOC ratios.

Soil Organic Matter Stability

Our results suggest that the SOM at Elkhorn Ridge may be less stable, that is, less protected against decomposition, than the SOM at the more productive Whitmore and Feather Falls sites. During density fractionation, more than half of the soil C recovered from the Elkhorn Ridge soils was in the LF. In addition, a larger fraction of soil C was lost during density fractionation at the Elkhorn Ridge site, indicating that the surface soil C at Elkhorn Ridge is more labile or less protected than the C

at Whitmore and Feather Falls. The Elkhorn Ridge soils lost a higher portion of total soil C during the first leaching in both incubations and respired more (cumulative grams C per kilogram initial C) during the 16-d incubation than those from the Whitmore and Feather Falls sites.

In contrast, the SOM at Feather Falls appears to be relatively stable. Despite having the largest portion of soil material recovered in the LF, the soils from Feather Falls retained more C and N (grams C per kilogram initial C or grams N per kilogram initial N) during incubation than the soils from Elkhorn Ridge or Whitmore. The soils from Feather Falls also had the highest whole-soil C and N, but relatively small portions were extractable as DOM. These results suggest that the SOM at Feather Falls is more protected than the SOM at Elkhorn Ridge and Whitmore.

The differences in apparent SOM protection across sites may be partially explained by differences in soil texture and parent materials. The significance of SOM protection by soil colloids has become increasingly evident (Oades, 1988). For example, Spaccini et al. (2002) analyzed the ^{13}C signatures of the SOM from several soils and concluded that coarser soil fractions provide little protection from microbial activity and favor extensive mineralization of SOM, whereas SOM interactions with silt and clay particles provide a physical environment that is less accessible to soil microbes. Torn et al. (1997) reported that volcanic soils rich in the noncrystalline minerals allophane, imogolite, and ferrihydrite are particularly effective in forming stable organic-mineral bonds, and they concluded that models aiming to characterize fast- and slow-cycling soil C pools should include soil mineralogy as well as texture in determining storage and turnover rates.

The soils and climatic conditions at Elkhorn Ridge differ substantially from those at Whitmore or Feather Falls. The conditions at Elkhorn Ridge are favorable for the accumulation of fresh organic matter because of low-nutrient-status litter and low soil moisture in the summer (McFarlane et al., 2009). Compared with the finer textured volcanic soils at Whitmore and Feather Falls, the sandy mica-quartz soils at Elkhorn Ridge are less conducive to organic matter stabilization. Thus, accumulated organic matter from the site may have a relatively high potential for mobilization through leaching or soil respiration when favorable conditions for such processes occur in the field.

Responses of Soil Organic Matter to Silvicultural Treatments

Fertilization Effects

As expected, nutrient additions early in stand development tended to increase N storage and availability, but the effects on the SOM quality varied across sites. Whole-soil and LF total N concentrations and C/N ratios suggested that fertilization increased N availability at Elkhorn Ridge and Whitmore. In contrast, the soils from Feather Falls contained twice as much total N without fertilization as the other sites, possibly reflecting the abundance of N_2 -fixing *Ceanothus* at Feather Falls on control or fertilizer treatment plots that did not have competing vegetation

controlled. On plots that did not receive an herbicide treatment, the presence of a predominantly *Ceanothus* understory may have accounted for roughly an 8% increase in whole-soil N during 16 yr (Table 3). We observed weak and inconsistent effects of fertilization on DOC production; however, N mineralization increased at all three of our sites following fertilization (McFarlane, 2007). These results are consistent with other studies that have reported varied responses of DOC and CO₂ production to nutrient additions but have often shown elevated release of DON and DIN following N fertilization (e.g., Park et al., 2002; Magill and Aber, 2000; Adams et al., 2005).

Nitrogen additions often increase decomposition and CO₂ release from fresh fine litter and coarse woody debris (Homann et al., 2001; Vestgarden, 2001; Jandl et al., 2002, 2003; Li et al., 2006). Substantial evidence suggests, however, that decomposition of older, more humified material decreases following fertilization in boreal and temperate systems (Berg, 2000; Berg and Matzner, 1997; Magill and Aber, 1998; Neff et al., 2002). In contrast, tropical soils have demonstrated increased utilization of old C pools following fertilization (Waldrop and Firestone, 2004). Nitrogen fertilization in a tropical forest where N limited plant growth decreased SOM turnover rates, but P inputs increased turnover rates, suggesting that there may be asynchrony among nutrients limiting plant growth and SOM decomposition (Torn et al., 2005). Our observation of increased CO₂ production at Whitmore following fertilization and decreased respiration at Feather Falls coincident with increased aboveground pine productivity supports the hypothesis that plants and microbes may be limited by different nutrients and illustrates the importance of interactions between C and nutrient dynamics.

Competing Vegetation Control Effects

We hypothesized that competing vegetation control through repeated application of herbicides during the first 6 yr following stand establishment would reduce the labile SOM pool including reduced N availability. Competing vegetation control did not affect whole-soil C or total N concentrations detectable at $\alpha = 0.10$ but did influence the density fractionation results at Elkhorn

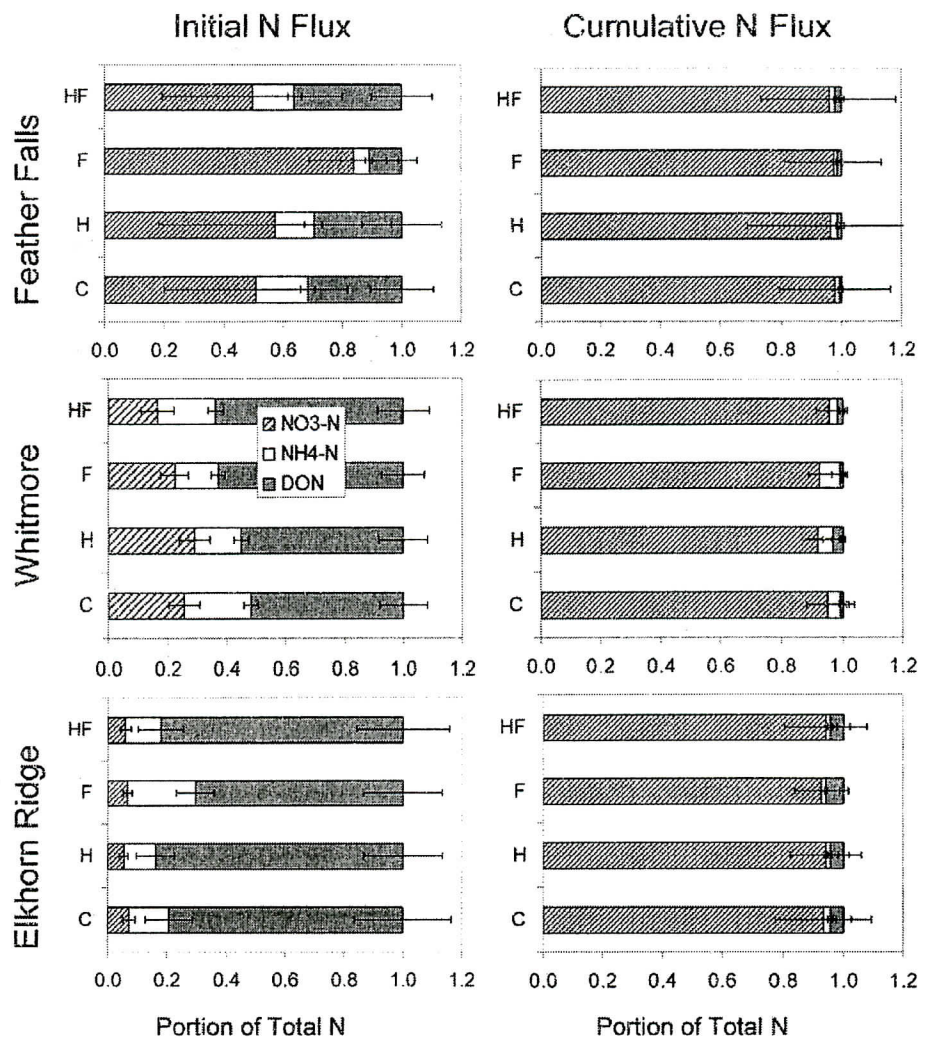


Fig. 4. Forms of N as a proportion of total dissolved N (TDN) in the initial leachate and total cumulative leachate after 225 d of laboratory incubation by site and treatment for the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites. Treatments are: HF = herbicide and fertilizer, F = fertilizer only, H = herbicide only, C = no treatment control. Values are means determined by analysis of variance at Day 0 or Day 225 \pm 1 standard error.

Ridge and Whitmore. At Elkhorn Ridge, where the understory was dominated by whiteleaf manzanita (*Arctostaphylos viscidula* Parry), removal of shrub litter inputs through the application of herbicides may have reduced the SOM decomposability as suggested by increasing C concentrations and decreasing N concentrations in the LF. The opposite occurred at Whitmore, where competing vegetation control decreased the LF C/N ratios despite having no effect on N concentrations.

Few studies have investigated the role of understory vegetation or competing vegetation control on SOM dynamics through laboratory incubation. A decline in TDN and NO₃⁻-N release during the incubation of soils from Feather Falls with competing vegetation control suggests that the presence of understory vegetation may enhance potential N availability. This hypothesis is supported by the work of Echeverría et al. (2004), who observed lower N mineralization potential in southern pine soils where competing vegetation had been controlled. A reduction

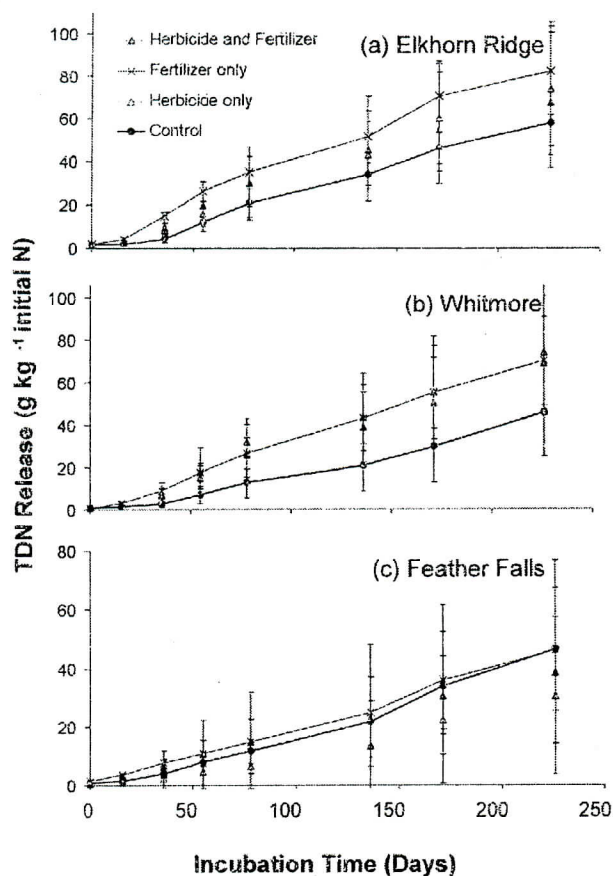


Fig. 5. Cumulative releases of total dissolved N (TDN) in leachates for each treatment at the (a) Elkhorn Ridge, (b) Whitmore, and (c) Feather Falls Garden of Eden Study sites during the 225-d incubation. Error bars are back-transformed 95% confidence intervals.

in N mineralization following competing vegetation control may have occurred at Feather Falls but not at the other sites, because Feather Falls was the only site where a N_2 -fixing deciduous shrub, *Ceanothus integerrimus*, was abundant.

Competing vegetation control increased the CO_2/DOC ratio of the C released during incubation at Elkhorn Ridge, indicating that more of the mobilized C was lost as respiration and less was lost as DOC. This suggests that competing vegetation control reduces the retention of C in soils at Elkhorn Ridge because proportionally less of the C released during decay has the potential to be translocated as DOC and retained deeper in the soil profile.

CONCLUSIONS

Our hypothesis of greater accumulation of SOM with increasing site productivity was supported by our observations. The influences of fertilization and competing vegetation control on SOM storage and dynamics assessed 10 to 12 yr following these treatments differed among sites, as was also expected. We found evidence that fertilization increased SOM cycling and accumulation at our poorer quality sites. In contrast, fertilization did not increase SOM accumulation at our highest quality site and may have inhibited C cycling, as suggested by depressed C mineralization. Our hypothesis that herbicide application would diminish SOM accumulation and cycling was also substantiated

Table 7. Cumulative CO_2 and dissolved organic C (DOC) release treatment means for the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites during the 16-d incubation.

Treatment†	CO_2 flux	DOC	CO_2/DOC
	g kg ⁻¹ initial C		
<u>Elkhorn Ridge, low productivity</u>			
C	0.8 ± 0.2‡	4.2 ± 0.9	0.19 ± 0.03 a§
H	1.1 ± 0.2	3.6 ± 0.9	0.31 ± 0.03 b
F	0.7 ± 0.2	4.3 ± 0.9	0.16 ± 0.03 a
HF	0.8 ± 0.2	4.7 ± 0.9	0.18 ± 0.03 a
<u>ANOVA P value</u>			
H	0.19	0.88	0.05**
F	0.20	0.51	0.03**
H × F	0.65	0.61	0.14
<u>Whitmore, intermediate productivity</u>			
C	0.4 ± 0.1 a	2.3 ± 0.4	0.20 ± 0.04 a
H	0.4 ± 0.1 a	2.8 ± 0.4	0.17 ± 0.04 a
F	0.6 ± 0.1 b	1.9 ± 0.4	0.31 ± 0.04 b
HF	0.5 ± 0.1 b	1.9 ± 0.4	0.25 ± 0.04 b
<u>ANOVA P value</u>			
H	0.22	0.59	0.27
F	0.08**	0.19	0.06**
H × F	0.54	0.51	0.79
<u>Feather Falls, high productivity</u>			
C	0.3 ± 0.1 a	1.2 ± 0.2	0.26 ± 0.04 a
H	0.4 ± 0.1 a	1.2 ± 0.2	0.32 ± 0.04 a
F	0.2 ± 0.1 b	1.2 ± 0.2	0.13 ± 0.04 b
HF	0.2 ± 0.1 b	1.4 ± 0.2	0.17 ± 0.04 b
<u>ANOVA P value</u>			
H	0.40	0.96	0.28
F	0.01**	0.68	0.01**
H × F	0.93	0.63	0.79

** Significant at $\alpha = 0.1$.

† Treatments: C = control, H = herbicide only, F = fertilizer only, HF = fertilizer and herbicide.

‡ Means ± standard errors.

§ Values followed by different letters denote statistically different treatments as assessed by multiple pairwise comparisons with a Tukey adjustment, $\alpha = 0.1$.

by our observations, suggesting decreased in situ decomposition at less productive sites and reduced N mineralization at the most productive site in response to the control of competing understory vegetation.

Consequently, our results emphasize the importance of using multiple methods to assess SOM stability and highlight the potential for SOM to respond differently to experimental manipulations at different sites. Soil organic matter dynamics are complex and we believe that progress in understanding these processes in response to management will only be made by incorporating factors reflecting ecosystem productivity, nutrient cycling, plant community composition, climate, and soil characteristics. Our study demonstrates the importance of site characteristics in determining the effects of forest management practices on SOM characteristics and dynamics. Future research of mechanisms controlling SOM stabilization and of the long-term impacts of changes in SOM distribution and stability on ecosystem function will benefit management strategies aimed at conservation of SOM storage and the dynamics and maintenance of long-term site productivity.

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