Plantation Management Intensity Affects Belowground Carbon and Nitrogen Storage in Northern California

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Belowground C and N storage is important in maintaining forest productivity and to CO_2 sequestration. How these pools respond to management is poorly understood. We investigated effects of repeated applications of complete fertilizer and competing vegetation control with herbicides on C and N storage in forest-floor, fine-root, and mineral-soil C and N pools to 1-m depth at three *Pinus ponderosa* P. Lawson & C. Lawson var. *ponderosa* plantations across a site quality gradient in northern California. Belowground C pools without treatment were 66, 153, and 199 Mg C ha^{-1} for the low-, intermediate-, and high-quality sites, respectively, and N pools were 5.1, 6.7, and 6.5 Mg N ha^{-1}, respectively. Treatments increased tree-bole volume at 20 yr as much as 400%, while changes in C and N pools belowground were less dramatic. Herbicide treatment increased forest-floor C pools 35% at the poorer quality site. Fertilization increased forest-floor C and N storage 46 to 106% at all sites. Fertilization decreased fine-root C pools at 0 to 0.3 m at the most productive site 43% and increased this N pool 43% at the least productive site, but did not influence fine-root pools to 1 m. Fertilization increased mineral-soil C pools on lower quality sites, resulting in 12 to 57% more belowground C storage. At the intermediate site, fertilization increased total belowground N storage 12%. Results of this study suggest that the major sequestration mechanism up to this point in stand development is through gains in tree biomass rather than storage in fine roots and soil belowground.

Abbreviations: SOM, soil organic matter.

Forests in the contiguous 48 states of the USA store approximately 71 Gt of C, more than half of which resides in soils (Heath et al., 2003). Another 16% of this C is stored in forest floor detrital material or in coarse woody debris (Heath et al., 2003). Consequently, factors influencing belowground C storage in forests draw increasing interest with respect to their role in sequestration of CO_2 and other greenhouse gases. Such factors include changes in climate, vegetation and soil type, N deposition, and forest management practices.

In addition, soil C and N are important in the context of sustainable forest management. Soil organic C can be used as a surrogate for soil organic matter (SOM) (Page-Dumroese et al., 2000; Ogle and Paustian, 2005). Soil organic matter is a key component in soil process and function as a C source for heterotrophic soil biota and through its influence on soil water dynamics, microclimate, and nutrient cycling (Amaranthus et al., 1989; Raison and Rab, 2001). Therefore, SOM protection has been identified as a major goal of sustainable management of forests of the western USA (Powers et al., 1990, 1998; Page-Dumroese et al., 2000).

Ponderosa pine is one of the most widely distributed tree species in western North America (Harlow et al., 1996). It is one of the leading conifers in sawtimber production in North America, second only to Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco), and is the most-planted tree species in California, often the tree of choice following stand-replacing wildfire (Jensen et al., 2002). Rotation lengths commonly are set at the culmination of mean annual volume increment (60–75 yr) or longer, depending on management objectives. Aboveground growth response to fertilization has been observed for a number of coniferous species (Baker et al., 1986; Gower et al., 1992; Haynes and Gower, 1995; Hangs et al., 2003; Adams et al., 2005; Will et al., 2006) including ponderosa pine (Powers et al., 1988). However, in California, growth response of ponderosa pine to fertilization varies with site-specific levels of shrub competition and soil moisture and can be improved when applied in combination with control of competing vegetation (Powers, 1983). On especially dry sites, ponderosa pine response to fertilization can be blocked if shrubs have not been controlled (Powers and Jackson, 1978). Success of planted or naturally regenerated conifers following timber harvest or stand-replacing fire may require control of

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competing vegetation on poorer sites (Conrad and Radosevich, 1982; Powers and Ferrell, 1996). Competition from shrubs and grasses can increase water deficits in soils, increasing water stress in trees (Shainsky and Radosevich, 1986; Petersen and Maxwell, 1987), as well as competition for nutrients (Hangs et al., 2003). For ponderosa pine, control of shrubs can increase water and nutrients available for trees, increasing tree growth and vigor, especially when trees are young (Lanini and Radosevich, 1986; Busse et al., 1996).

Silvicultural practices such as these may affect soil C and N storage, and increases in soil C and N pools following fertilization of forest stands have been reported in reviews (Johnson and Curtis, 2001; Johnson et al., 2002). However, results of individual studies are site- and experiment-specific (Prietzel et al., 2004; Jandl et al., 2007) and accurate investigation of these responses in field trials has been hindered by the inherently high spatial heterogeneity of forest soils (Homann et al., 2001a). For example, N fertilization of forest stands has increased (Nohrstedt et al., 2000; Jandl et al., 2003; Adams et al., 2005), decreased (Shan et al., 2001; Jandl et al., 2002), and had no effect (Harding and Jokela, 1994; Canary et al., 2000; Homann et al., 2001b; Giardina et al., 2004) on C storage in forest floors and mineral soils.

Similarly, fertilization has been reported to have variable influence over belowground biomass and litter inputs, which are primary sources of C to mineral soils (Giardina et al., 2004; King et al., 2002; Matamala et al., 2003; Yano et al., 2005). Fertilization decreased the amount of C entering mineral soil through roots and mycorrhizae in a tropical forest in Hawaii (Giardina et al., 2003, 2004) and decreased fine- and coarse-root production and turnover in conifers (Gower et al., 1992; Haynes and Gower, 1995). Contrasting evidence suggests that fine and coarse root production (Nadelhoffer et al., 1985), biomass (Haile-Mariam et al., 2000), turnover (King et al., 2002), and mortality rates (Haynes and Gower, 1995) are greater when N is more available, potentially increasing root C inputs to soil.

Competing vegetation control, a common silvicultural practice in western forests, improves seedling survival and can increase growth rates in conifers significantly (Busse et al., 1996; Powers and Ferrell, 1996; Hangs et al., 2003). There is evidence that competing vegetation control, particularly under conifers, may decrease soil quality through declines in C and N concentrations and content in soils (Busse et al., 1996; Shan et al., 2001; Echeverría et al., 2004) and forest floors (Will et al., 2006). Competing vegetation control may increase N losses early in stand development through increased NO_3^- leaching and erosion (Vitousek and Matson, 1985; Vitousek et al., 1992). Declines in soil quality such as these may result from reduced quantity or quality of litter inputs, particularly where competing vegetation control includes removal of N-fixing understory species that have been linked to increases in soil organic C and N content (Baker et al., 1986; Johnson, 1995).

We assessed effects of repeated fertilization and competing vegetation control with herbicides on belowground C and N pools at three ponderosa pine plantations along a gradient of site productivity in northern California. Specifically, we quantified amounts of C and N in the forest-floor, and in the fine-root and mineral-soil pools to 1-m depth and tested the effects of fertilization and vegetation control on (i) individual pools, (ii) total pools, and (iii) distribution of total belowground C and N amongst the individual pools. We hypothesized that fertilization would decrease forest-floor C/N ratios and increase forest-floor and total belowground N and C pools through increased litter production. We suspected that herbicide would decrease forest-floor mass and forest-floor and mineral-soil C and N pools in surface soils, especially at the higher quality sites where the role of shrub competition in reducing pine productivity was less than at the lowest-quality site (Powers and Ferrell, 1996). We suspected that increased nutrient and water availability following fertilizer and herbicide treatments might result in reduced fine-root biomass, especially at the more productive sites. We also expected these effects to differ in magnitude among sites as a result of differences in aboveground responses to treatment and differences in soil type.

METHODS

Site Descriptions

The three sites used for this study encompass the range in productivity and soil type found in the northern California westside ponderosa pine region (Fig. 1, Table 1). This area is characterized by a Mediterranean climate with dry summers and wet winters. These sites are part of a larger, long-term study that was initiated to assess effects of commonly applied forest management treatments (competing vegetation control, fertilization, and systemic insecticides) on ponderosa pine productivity (the Garden of Eden Study, see Powers and Ferrell, 1996; Powers and Reynolds, 1999). Sites for this study were selected to minimize within-site topographical variability by requiring slope variability <20% and aspects within 45° (Powers and Ferrell, 1996).

The least productive site is Elkhorn Ridge, which is located in the southern extreme of the Klamath Mountains. It is the westernmost, highest in elevation, and driest of the three sites. Elkhorn Ridge

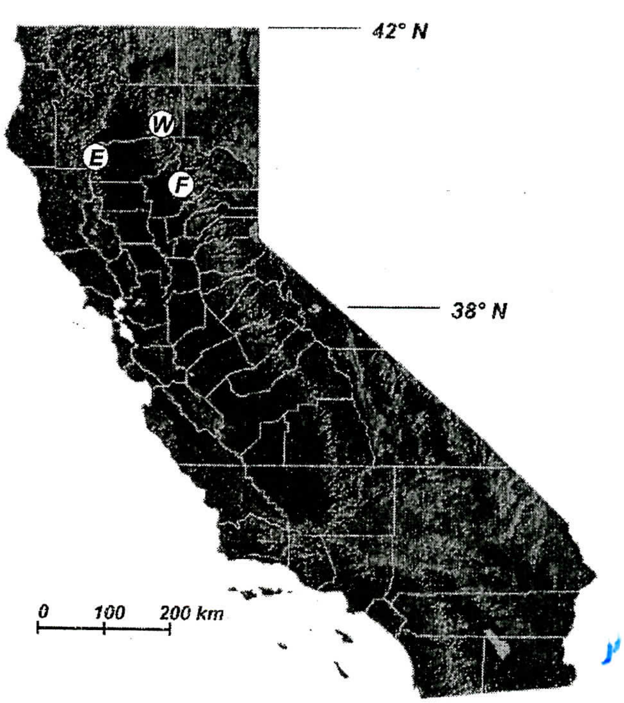

Fig. 1. Map of study site locations within the state of California. Sites: E = Elkhorn Ridge, W = Whitmore, F = Feather Falls. Base: California State Map Collection (http://geology.com/state-map/california.shtml).

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

Characteristic		Elkhorn Ridge	Whitmore	Feather Falls
Productivity		Low	Intermediate	High
SI_{50}, m†		17	23	30
Age at sampling, yr		18	19	18
Annual precipitation, mm		1015	1140	1780
Annual temperature, °C		9.4	14.5	12.0
Elevation, m		1490	730	1220
Soil great group		Dystroxerept	Haplohumult	Haploxeralf
Parent material		Metasediment	Volcanic	Volcanic
Fine Bulk Density, Mg m^{-3}	0–15 cm	0.86 ± 0.03‡	0.93 ± 0.15§	0.77 ± 0.19§
	15–30 cm	0.88 ± 0.03	1.00 ± 0.15	0.98 ± 0.19
	30–60 cm	0.85 ± 0.06	1.10 ± 0.15	1.13 ± 0.19
	60–100 cm	1.42 ± 0.07	1.16 ± 0.15	1.14 ± 0.19
Soil pH in water‡	0–15 cm	6.3 ± 0.1	6.2 ± 0.1	6.0 ± 0.1
	15–30 cm	5.9 ± 0.1	6.2 ± 0.1	5.8 ± 0.1
	30–60 cm	6.0 ± 0.1	6.3 ± 0.1	5.9 ± 0.1
	60–100 cm	6.1 ± 0.1	6.1 ± 0.1	5.9 ± 0.1

† Site index for ponderosa pine at 50 yr estimated from adjacent stands (Powers and Ferrell, 1996).

‡ Measured in this study. Site means by depth are from analysis of variance followed by standard errors.

§ Estimated using data available from NRCS and in Zinke and Stangenberger (unpublished). Total bulk density values were estimated using polynomial equations. Coarse fraction contents measured in this study were used to calculate fine bulk densities. Estimates are followed by standard errors for the equations used.

is characterized by loamy-skeletal, mixed mineralogy Inceptisols of the Sheetiron series derived from metasedimentary mica-quartz schist (Soil Survey Staff, 2009). Whitmore is of intermediate site productivity and is located in the southern Cascades. Soils at Whitmore consist of fine, parasesquic Ultisols of the Aiken series weathered from basic volcanic rock (Soil Survey Staff, 2009). The most productive site is Feather Falls, which is located in the western Sierra Nevada. Soils at this site are fine-loamy, mixed mineralogy, super active Alfisols of the Cohasset series weathered from volcanic parent materials (Soil Survey Staff, 1997). Soils at all three sites contain charcoal, but are free of carbonates. A mixture of manzanita (*Arcostaphylos spp.*) species, woody shrubs ubiquitous to the ponderosa pine forest, occurs at all three sites, dominating at Elkhorn Ridge and Whitmore. *Ceanothus integerrimus*, a N-fixing deciduous shrub that is also common to the region, dominates at Feather Falls.

Table 2. Fertilizer treatments in the Garden of Eden Study by nutrient and application rate including total amount applied (Powers and Ferrell, 1996).

	Amount applied				
Nutrient	At planting	End of year 2	End of year 4	End of year 6	Total applied
	kg ha^{-1}				
N	15.6	46.6	213.7	798.7	1074.4
P	7.9	23.2	103.4	395.2	529.7
K	7.7	23.2	109.6	399.4	539.9
Ca	10.1	23.6	118.6	264.0	416.3
Mg	5.5	16.8	61.7	137.2	221.2
S	5.2	28.3	16.0	62.4	111.9
Zn	1.1	3.2	14.0	55.1	73.4
Cu	0.5	1.6	6.8	26.9	35.8
B	0.5	1.6	6.8	26.8	35.7

Field Experimental Design

The Garden of Eden experiment consists of a three-way, two-level factorial design. The current study assessed only the vegetation control and fertilization treatments, resulting in four treatment combinations: competing vegetation control only; fertilizer only; competing vegetation control plus fertilizer; and no applied treatments (control). Each treatment combination was replicated three times at each site so that treatment effects could be assessed at each location independently, as treatment × site interactions were expected.

All sites were cleared of existing vegetation before planting. Elkhorn Ridge previously supported a sparsely stocked ponderosa pine plantation, Whitmore was a brushfield of mixed manzanita, and Feather Falls was a natural stand of mixed-conifers and hardwoods. At each site 24 contiguous 0.04-ha (19.5 by 21.9 m) rectangular plots were marked and seedlings were planted in spring at a square spacing of 2.4 m (1680 trees ha^{-1}). Each site was planted with ponderosa pine seedlings representing high-performing families especially adapted for each seed zone and elevation. To ensure uniformity, seedlings were raised at a common nursery (the Institute of Forest Genetics at Placerville, CA). Whitmore was planted in 1986 and Elkhorn Ridge and Feather Falls were planted in 1988. The outer 4.8 m of each side of each plot was designated as a buffer strip, to minimize edge effects and influence of adjacent treatments. All samples and measurements were taken from within measurement plots excluding this buffer.

Treatments were applied at planting and repeatedly over the next 6 yr. The levels at which fertilizer and herbicide were applied were selected with the intention of alleviation of nutrient limitation and/or understory competition during establishment and early stand development for experimental purposes. Fertilization consisted of eight nutrients applied every 2 yr at an exponential rate, ending with a large fertilizer application at the end of Year 6 (Table 2). Spring fertilization, while appropriate in many regions, poses the risk in Mediterranean climates that an early dry season could leave dry salts unsolubilized. Thus, fertilizers were applied following the first fall rains so that dry salts could dissolve and infiltrate the soil profile as the wet season commenced. Foliar analyses reported in Powers and Reynolds (1999) suggest rapid nutrient uptake and incorporation into biomass by trees in fertilized plots, and studies elsewhere have shown that deep leaching of fertilizer elements is rare in the California climate (McColl and Powers, 1984; Miles and Powers, 1988). Competing vegetation control was accomplished by spraying understory plants with glyphosate each spring for the first 6 yr after planting. Additional information concerning the experimental design and early responses of aboveground tree growth are available in Powers and Ferrell (1996).

Pine Bole Volume and Canopy Cover

Aboveground stand characteristics were measured in each treatment plot at Whitmore in 2007 at a stand age of 21 yr and at Elkhorn Ridge and Feather Falls in 2008 at a stand age of 20 yr. Standing bole volume for pines was determined by measuring all plot trees for diameter at breast height with a diameter tape and tree height with a telescoping pole or, for exceptionally tall trees at Feather Falls, with a laser range finder. These data were used to estimate stem volumes for each tree using the equation developed by Oliver and Powers (1978).

Crown cover was determined by measuring the crown width of each individual tree in two right-angle directions using a metric tape. These measurements were rounded to the nearest centimeter and averaged. Crown area was estimated as πr^2, where r is one-half of crown width. For each plot, crown areas were summed, divided by the total ground area of each plot (118.912 m^2) and multiplied by 100 to give percent crown cover.

Sampling of Belowground Pools

For the Whitmore plantation, forest floor was sampled in June 2005, in the midst of the 20th growing season. For the Elkhorn Ridge and Feather Falls plantations, forest floor was sampled in June 2006, in the midst of the 19th growing season. For each treatment plot, the measurement plot was divided into a 3 by 4 cell grid, with each cell measuring 2.4 by 2.4 m. Five subsamples were taken from each plot, one from the approximate center cell and one from each of the corner cells. Forest floor samples were collected using a 0.5 by 0.5 m sampling frame and contained all material within the frame above the mineral soil surface, including foliage and woody components.

Whitmore mineral soil samples were collected in September 2005. At each plot, soil from each depth was collected using a soil auger from several points in the plot. One 0- to 15-cm soil sample was collected from the approximate center of each of the 12 cells. In eight cells, a 15- to 30-cm soil sample was collected. In three non-adjoining cells, soil samples were collected from the 30- to 60- and 60- to 100-cm depth increments. In each plot, cells were selected for deeper sampling with the intention to reduce disturbance within the plot and ensure that sampling locations were spread over the entire plot. This sampling scheme resulted in the collection of 26 cores from each plot. For each depth, soil was composited, mixed, and a subsample was placed in a plastic bag and transported to the laboratory for analysis.

Whitmore fine-root and bulk density cores were collected in August 2005. Fine-root and bulk density cores and mineral soil samples were collected at Elkhorn Ridge and Feather Falls in June 2006. For samples to 60-cm depth, cores were collected for fine-roots and bulk density using an Eijkelkamp bi-partite root auger (7.6-cm diameter and 15-cm length, Eijkelkamp, the Netherlands). Volumetric cores were taken in 0- to 15-, 15- to 30-, and 30- to 60-cm depth increments. When depth increments were longer than the sampler length, the sample was collected from approximately the middle of the depth increment (e.g., for the 30- to 60-cm increment a core sampled with the Eijkelkamp auger came from approximately 38–53 cm). Difficulties in volumetric sampling at 60- to 100-cm depth (rocks and high soil bulk densities) required that samples be collected using a soil auger. Volumes for these samples were estimated based on diameter and depth of the hole from which soil was taken. The same 3 by 4 cell grid was used for root sampling as was used for forest floor sampling. One 0- to 15-cm root core was collected from the approximate center of each of the 12 cells, at least 1 m from the nearest tree. At eight cells, a 15- to 30-cm root core was collected. At three non-adjoining cells, root cores were collected from the 30- to 60- and 60- to 100-cm depth increments. For every root core, depth to the top and bottom of the hole left by the sampler was measured to adjust core volumes when collected cores were not full.

Sample Analysis

Forest floor subsamples were dried to constant weight at 70°C and forest-floor mass (Mg ha^{-1}) for each plot was calculated. Samples were composited by plot and ground to 850 μm. Subsamples of ground composites were further ground to 250 μm and analyzed for total C and N using the Dumas combustion technique on a Fisons NA1500 NCS Elemental Analyzer (ThermoQuest Italia, Milan, Italy).

Soil and root samples were stored field-moist at 4°C until they were analyzed. Cores were composited by plot and depth, mixed, and weighed. A 10% subsample by weight was hand-picked for fine roots (<2 mm diam.). We did not attempt to separate fine roots by species. Roots were oven dried for at least 5 d at 60°C, weighed, ground to 250 μm, and analyzed for N and C in the same manner as the forest floor and soil samples. Root weights were corrected for ash-content and fine-root biomass to 1-m depth was calculated for every plot. Soil subsamples were sieved to 2 mm and ground to 250 μm. Ground samples were analyzed for total C and N in the same manner as the forest floor samples. Treatment effects on fine-root biomass and fine-root C and N pools were also conducted on the top 30 cm because, in general, most fine root biomass occurs in the top 30 cm in forests (Yanai et al., 2006), and we suspected that fine-root pools at this shallower depth might be more sensitive to treatments than those to 1 m.

A 300-g subsample by weight of the composited cores described above was sieved to 2 mm and coarse and fine fractions oven-dried at 105°C to estimate coarse fraction content, total bulk density, and fine bulk density. This method provided reasonable estimates for bulk density for the Elkhorn Ridge site, where our coring device cut through coarse fragments of soft schist and did not appear to cause compaction. However, bulk densities we calculated from our cores at the Whitmore and Feather Falls sites were appreciably higher than those previously reported (P.J. Zinke and A.G. Stangenberger, personal communication, 2008; Soil Survey Staff, 2008) for the soil series occurring at those sites. We suspect this discrepancy is due to compaction caused by our coring device in these finer-textured soils. Therefore, to err toward conservative estimates of C and N storage at the Whitmore and Feather Falls sites, we developed a polynomial function for total bulk density with depth from independent, whole-soil data for the series (P.J. Zinke and A.G. Stangenberger, personal communication, 2008; Soil Survey Staff, 2008). For the Aiken soil series at Whitmore, we used a polynomial where

$$\text{Total bulk density} = (3 \times 10^{-8} d^3) - (3 \times 10^{-5} d^2) + 0.0058d + 1.0214 \quad (R^2 = 0.41) \qquad [1]$$

where d is depth in centimeters. For the Cohassett soil series at Feather Falls, the best fit polynomial estimated total bulk density as

$$\text{Total bulk density} = (-3 \times 10^{-9} d^4) + (1 \times 10^{-6} d^3) - (2 \times 10^{-4} d^2) + 0.0173d + 0.8362 \quad (R^2 = 0.39) \qquad [2]$$

where d is depth in centimeters. We used these equations to estimate total bulk density at the middle of each depth increment, estimated fine fraction bulk densities by applying the coarse fraction content measured in our collections, and used these bulk density values to estimate soil C and N pools and total C and N storage for each plot at the Whitmore and Feather Falls sites.

Table 3. 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 20 yr.†

	Treatment	Elkhorn Ridge	Whitmore	Feather Falls
Standing bole volume (m^3 ha^{-1})	C	17 ± 6^{a}‡	40 ± 7^{a}	187 ± 20^{a}
	H	56 ± 6^{b}	118 ± 7^{b}	226 ± 20^{ab}
	F	33 ± 6^{ab}	93 ± 7^{b}	316 ± 20^{b}
	HF	90 ± 6^{c}	172 ± 7^{c}	296 ± 20^{b}
			p-value	
	H	**<0.01**	**< 0.01**	NS§
	F	**0.03**	**0.01**	**<0.01**
	H x F	NS	**0.05**	NS
Pine canopy (% cover)	C	46 ± 6^{a}	55 ± 5^{a}	118 ± 6^{a}
	H	81 ± 6^{b}	111 ± 5^{b}	125 ± 6^{a}
	F	55 ± 6^{c}	82 ± 5^{c}	166 ± 6^{b}
	HF	106 ± 6^{d}	115 ± 5^{b}	156 ± 6^{b}
			p-value	
	H	NS	NS	NS
	F	NS	NS	NS
	H x F	**<0.01**	**<0.01**	**<0.01**

† Means are followed by standard errors. P-values for treatment factors were determined from analysis of variance. Boldface p-values are significant, $\alpha = 0.1$. Treatments: C = control, H = herbicide only, F = fertilizer only, HF = herbicide and fertilizer.

‡ For each site, different letters denote statistically different treatments as assessed by multiple pair-wise comparisons with a Tukey adjustment, $\alpha = 0.1$.

§ NS, nonsignificant at the 0.1 α level.

Data Analysis

For each plot, forest-floor, fine-root, and mineral-soil C and N concentrations were extrapolated to pool values to 1-m depth (expressed in Mg C or N ha^{-1}). Values for each of the above components were summed to yield total belowground C and N pools for each plot, exclusive of coarse roots. To address changes in distribution, the proportion of the total pool for each of the forest-floor, fine-root, and mineral-soil pools was calculated (of 100% of the total pool).

Treatment differences were assessed using analysis of variance with the Mixed Procedure in SAS (SAS Institute, v. 9.1, Cary, NC). All data were analyzed with a completely randomized design for each site. Separate analyses were conducted for each site because of the occurrence of site-treatment interactions. Differences among sites were assessed by comparing control treatments using *t* tests. All statistical results significant at the 0.10 α level are discussed.

For each site, fine-root and mineral soil data including root mass density, root and soil chemistry, and soil bulk density were analyzed by depth with repeated-measures to account for correlation among depth increments in each plot. Changes in distribution of total C and N among individual pools (e.g., mineral soil or fine-root) were analyzed using a split–plot design where the total pool served as the whole-plot and individual pools served as subplots. When there was a significant treatment effect (fertilization or vegetation control main effect or an interaction of the two) differences among treatments were tested with multiple linear contrasts using a Tukey adjustment or a Dunnett's adjustment to compare controls to treatments. Both Tukey and Dunnett's tests were used because the combined effect of fertilizer and herbicide treatments compared with each treatment alone were of interest (Tukey) as well as differences between treatments and controls (Dunnett). When there was a significant depth × treatment interaction ($\alpha = 0.1$), differences among treatments by depth were identified and assessed by slicing and linear contrasts.

RESULTS

Pine Bole Volume and Canopy Cover

Standing bole volume increased dramatically with increasing site productivity and was 17.3, 39.9, and 186.7 m^3 ha^{-1} for controls at Elkhorn Ridge, Whitmore, and Feather Falls, respectively (Table 3). At Elkhorn Ridge fertilization or herbicide, applied alone, roughly doubled pine bole volume, whereas the combination of both treatments increased bole volume more than four times compared with the control. At Whitmore, compared with the control, bole volume increased by 32% following fertilization alone, nearly doubled following herbicide alone, and more than tripled when both treatments were applied together. At Feather Falls, herbicide applied alone had no effect on bole volume compared with the control, but fertilizer alone or with herbicide increased standing bole volume 60 to 70% compared with the control.

Pine productivity differences associated with site and treatment were reflected in degree of overstory canopy cover (Table 3). For controls, canopy cover was similar at Elkhorn Ridge (48%) and Whitmore (55%). However, canopy cover was appreciably higher at Feather Falls (118%), indicating a flattening in the trend analogous to leaf area saturation on this very productive site. At the less productive sites, canopy cover increased 26 to 49% with fertilization and 86 to 108% with herbicide. At Feather Falls, fertilizer increased canopy cover by 32%, while herbicide did not affect cover at the site.

Response of these aboveground stand characteristics to fertilizer and herbicide treatments suggests that the impact of understory competition on tree growth declines with increasing site quality. Competition with understory shrubs is a major factor in determining pine productivity at the lower quality sites, especially at Elkhorn Ridge where skeletal soil coupled with low precipitation produces low soil water storage. At the most productive site, however, shrub competition has less influence on pine growth.

Forest Floor

Forest floor characteristics varied by site quality. For controls, forest-floor mass at Elkhorn Ridge was one-third that at Whitmore and one-fourth that at Feather Falls (Table 4). Across sites, fertilization increased forest-floor mass, regardless of herbicide, by an average of 5.3 Mg ha^{-1} or 46%, but the magnitude of effect differed among sites (Table 4). Fertilization increased forest-floor mass by about one-third at the low- and high-quality sites and nearly doubled it at the intermediate-quality site. Herbicide treatment increased forest floor mass by 45% at Elkhorn Ridge, but had no influence elsewhere.

Elkhorn Ridge had appreciably lower N concentrations and higher C/N ratios in its forest floor material than the other two sites, and C concentrations there were increased slightly by all treatments (Table 4). Forest floor C concentrations were increased slightly by herbicide treatment at Whitmore, but

Feather Falls was unaffected. Fertilization increased forest-floor N concentrations by 0.9 g N kg soil^{-1} at Elkhorn Ridge and Whitmore and by 1.4 g N kg soil^{-1} at Feather Falls. Herbicide treatment decreased forest-floor N concentrations at Feather Falls by 1.2 g N kg soil^{-1} and raised C/N ratios by 16%, while the other sites were not affected. Forest-floor C/N ratios decreased with fertilization by 11 to 16% at all three sites.

Fertilization increased forest-floor C and N pools substantially at all sites (Table 4). Fertilization increased the forest-floor C pool by 46% and N pool by 62% at Elkhorn Ridge. At Whitmore, fertilization increased the C pool by 82% and the N pool was doubled. At Feather Falls, the C pool increased by 48% and the N pool by 75%. Herbicide treatment only affected forest-floor pools at Elkhorn Ridge, increasing forest-floor C mass by one third (Table 4).

Table 4. Forest-floor mass, C and N concentrations, C and N content, and C to N ratios by site and treatment for the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites.†

Treatment	Mass	C	N	C	N	C/N ratio
	Mg ha^{-1}	g kg soil^{-1}		Mg ha^{-1}		
			Elkhorn Ridge– Low			
C	6.0 ± 1.4 ^{a}‡	534 ± 1^{a}	4.6 ± 0.4^{a}	3.2 ± 0.8 ^{a}	0.03 ± 0.01^{a}	115 ± 9^{a}
H	10.7 ± 1.4^{b}	538 ± 1^{b}	4.4 ± 0.4^{a}	5.8 ± 0.8^{b}	0.04 ± 0.01^{a}	124 ± 9^{a}
F	10.0 ± 1.4^{c}	537 ± 1^{c}	5.9 ± 0.4^{b}	5.4 ± 0.8^{c}	0.06 ± 0.01^{b}	92 ± 9^{b}
HF	12.4 ± 1.4^{d}	542 ± 1^{d}	4.9 ± 0.4^{b}	6.7 ± 0.8^{d}	0.06 ± 0.01^{b}	111 ± 9^{b}
			p-value			
H	**0.04**	**< 0.01**	0.19	**0.03**	0.29	0.16
F	**0.08**	**0.03**	**0.07**	**0.07**	**0.05**	**0.09**
H x F	0.44	0.88	0.39	0.45	0.41	0.58
			Whitmore– Intermediate			
C	19.8 ± 2.8^{a}	519 ± 2^{a}	7.3 ± 0.5^{a}	10.3 ± 1.5^{a}	0.14 ± 0.03^{a}	71 ± 4^{a}
H	19.7 ± 2.8^{a}	534 ± 2^{c}	7.4 ± 0.5^{a}	10.5 ± 1.5^{a}	0.15 ± 0.03^{a}	73 ± 4^{a}
F	36.2 ± 2.8^{b}	523 ± 2^{ab}	8.0 ± 0.5^{b}	19.0 ± 1.5^{b}	0.29 ± 0.03^{b}	65 ± 4^{b}
HF	35.6 ± 2.8^{b}	529 ± 2^{bc}	8.5 ± 0.5^{b}	18.8 ± 1.5^{b}	0.31 ± 0.03^{b}	63 ± 4^{b}
			p-value			
H	0.90	**< 0.01**	0.55	0.96	0.74	0.91
F	**< 0.01**	0.91	**0.08**	**< 0.01**	**< 0.01**	**0.07**
H x F	0.93	**0.06**	0.63	0.90	0.82	0.61
			Feather Falls– High			
C	24.9 ± 2.7^{a}	536 ± 2	8.4 ± 0.6^{a}	13.3 ± 1.5^{a}	0.21 ± 0.03^{a}	65 ± 4^{a}
H	24.1 ± 2.7^{a}	541 ± 2	7.3 ± 0.6^{b}	13.0 ± 1.5^{a}	0.18 ± 0.03^{a}	74 ± 4^{b}
F	37.6 ± 2.7^{b}	540 ± 2	10.0 ± 0.6^{c}	20.3 ± 1.5^{b}	0.38 ± 0.03^{b}	54 ± 4^{c}
HF	34.3 ± 2.7^{b}	541 ± 2	8.6 ± 0.6^{d}	18.6 ± 1.5^{b}	0.30 ± 0.03^{b}	63 ± 4^{d}
			p-value			
H	**0.47**	0.20	**0.07**	0.52	0.11	**0.07**
F	< 0.01	0.25	**0.04**	**< 0.01**	**< 0.01**	**0.04**
H x F	0.66	0.34	0.76	0.64	0.42	0.95

† Means are followed by standard errors. P-values for treatment factors were determined from analysis of variance. Boldface p-values are significant, α = 0.1. Treatments: C = control, H = herbicide only, F = fertilizer only, HF = herbicide and fertilizer.

‡ For each column, different letters denote statistically different treatments as assessed by multiple pairwise comparisons with a Tukey adjustment, α = 0.1.

Fine Roots

Fine-root mass density (mg cm^{-3}) was related inversely to site quality (Fig. 2a). Root densities decreased with depth to 1 m from 2.13 to 0.66 mg cm^{-3} at Elkhorn Ridge, 2.94 to 0.59 mg cm^{-3} at Whitmore, and 3.84 to 0.91 mg cm^{-3} at Feather Falls ($p <$ 0.01). Within-site variability in root density was high, and no effect of treatment on root density was detectable at Elkhorn Ridge or Whitmore (Fig. 2a). At Feather Falls, however, fertilization decreased root density at the 0- to 15-cm depth increment by 63% ($p = 0.04$) and increased root density at the 30- to 60-cm depth increment by 70% ($p <$ 0.01) (Fig. 2a).

Fine root biomass also decreased with depth (Fig. 2b), with greater mass at Feather Falls and lesser but similar masses at Whitmore and Elkhorn Ridge (Table 5). Fine-root C concentrations averaged 540 g kg^{-1} across sites and depths and were not affected by fertilizer or herbicide at Elkhorn Ridge or Whitmore. At Feather Falls, however, herbicide decreased fine-root C concentrations from 544 to 504 g kg^{-1} C across depths ($p = 0.03$). Fine-root N concentrations averaged 7 g kg^{-1} across sites and depths. Fertilization increased fine-root N concentrations in the top 15 cm at Elkhorn Ridge (10.6 g kg^{-1} for fertilized vs. 6.2 g kg^{-1} N for unfertilized plots, $p < 0.01$). Fertilizer, regardless of herbicide application or depth, increased fine-root N concentrations from 6.3 to 7.6 g kg^{-1} at Whitmore ($p =$ 0.01) and from 7.1 to 8.3 g kg^{-1} at Feather Falls ($p = 0.03$). Herbicide treatment decreased fine-root N concentrations at Feather Falls from 8.3 to 7.0 g kg^{-1} across depths ($p = 0.03$).

Fertilization decreased the fine-root C pool to 30 cm at Feather Falls by 46% and increased the fine-root N pool within 0 to 30 cm at Elkhorn Ridge by 43% (Table 5). Treatments had no statistically significant effect on total fine-root biomass, fine-root C content, or fine-root N content to 1-m depth at any of the three sites (Table 5).

High within-site variability posed a challenge to detecting differences in the fine-root C and N pools to 1 m. Based on within-site variability, changes in fine-root C pools > 2.0, 3.0, and 3.8 Mg C ha^{-1} at Elkhorn Ridge, Whitmore, and Feather Falls, respectively, were required for detection of treatment effects. Changes in fine-root N pool of >0.04 Mg N ha^{-1} were necessary to detect any treatment effects at all three sites. We did not observe differences of this magnitude in the fine-root C or N pools among treatments.

Mineral Soil

Mineral-soil C concentrations, N concentrations, and C/N ratios decreased with depth across sites and treatments ($p < 0.01$, Fig. 3). Soil C pools to 1 m at Feather Falls averaged about 20 Mg C ha^{-1} more than those at Whitmore and approximately 105 Mg C ha^{-1} more than those at Elkhorn Ridge (Fig. 4). Soil N concentrations were also higher at Feather Falls than Elkhorn Ridge and Whitmore (Fig. 3b). Low concentrations and low fine-soil bulk densities (due to high coarse fragments) at Elkhorn Ridge resulted in much lower total C pools

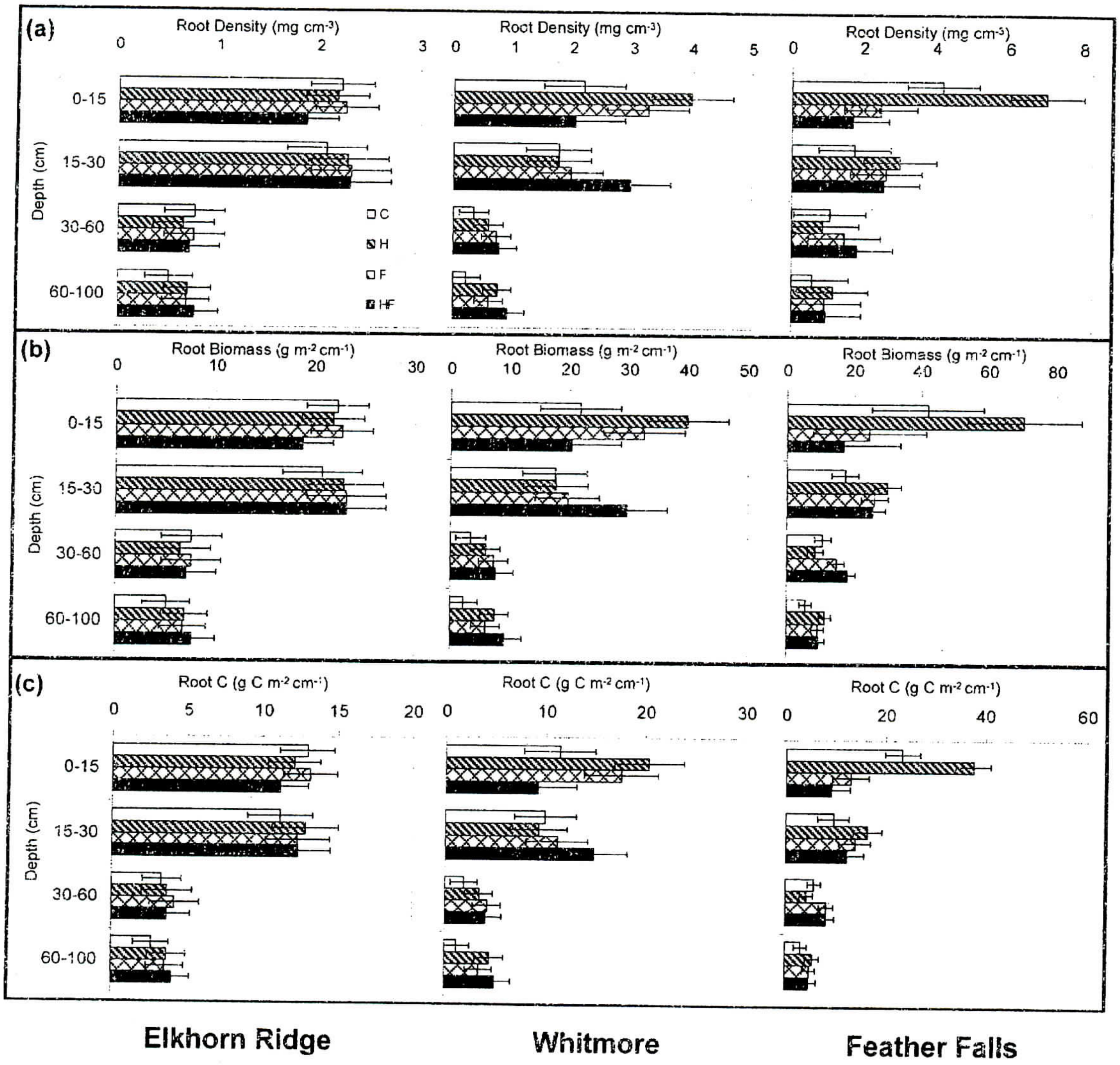

Fig. 2. Fine-root mass (a) density, (b) biomass, and (c) C storage by depth for each treatment at the Elkhorn Ridge (left), Whitmore (middle), and Feather Falls (right) Garden of Eden Study sites. Bars indicate standard errors. Note differences in scale for root density across sites. Data reflect all fine roots, regardless of species. Treatments: C = control, H = herbicide only, F = fertilizer only, HF = fertilizer and herbicide.

and detectably lower N pools there (83 Mg C ha^{-1} and 6 Mg N ha^{-1}) than Whitmore (177 Mg C ha^{-1} and 7 Mg N ha^{-1}) and Feather Falls (206 Mg C ha^{-1} and 7 Mg N ha^{-1}) (Fig. 4).

Fertilization affected mineral soil chemistry at specific depths at Elkhorn Ridge and Whitmore, but not at Feather Falls (Fig. 3). At Elkhorn Ridge, fertilizer increased 0- to 15-cm mineral-soil N concentrations (p = 0.09) by about 0.2 g N kg soil^{-1}, but had no effect on C concentrations or C/N ratios. At Whitmore, fertilized plots had higher mineral-soil C and N concentrations compared with control plots (p = 0.09 and 0.03, respectively). Also at Whitmore, fertilization, regardless of herbicide application, decreased mineral-soil C/N ratios for 0 to 15 cm slightly (p = 0.03), but had the opposite effect at 15- to 30-cm depth (p = 0.09). Herbicide did not affect mineral-soil C or N concentrations or C/N ratios at any site or any depth (Fig. 3).

Mineral-soil C and N pools to 1-m depth were highly variable across plots at each site (Fig. 4), resulting in high minimum detectable differences. Based on within-site variability, changes in mineral-soil C pools to 1-m depth, for example, needed to be >24 Mg C ha^{-1} at Elkhorn Ridge and Whitmore and >40 Mg C ha^{-1} at Feather Falls to detect main effects of fertilizer or herbicide at our sampling intensity. To detect differences between treatment combinations, changes >34 Mg C ha^{-1} at Elkhorn Ridge and Whitmore and >60 Mg C ha^{-1} at Feather Falls were necessary. The only case where a difference of this magnitude among treatment combinations occurred was at Elkhorn Ridge (H×F interaction, p = 0.05) where plots that received fertilizer alone had higher C pools than control plots by approximately 34 Mg C ha^{-1}, an increase of 60%. High variability occurred for mineral-soil N pools and the only statistically detectable treatment effect occurred at Whitmore, where fertilization increased mineral-soil N pools by about 13% or 0.7 Mg N ha^{-1} (p = 0.02) (Fig. 4).

Total Belowground C and N Pools

Forest-floor, fine-root, and mineral-soil C and N pools were summed to provide estimates of total belowground C and N pools, exclusive of coarse roots, and these results followed similar patterns observed for mineral-soil pools which comprised 86 to 89% of the total C pool and 94–98% of the total N pool. Total belowground C pools were highest at Feather Falls where control plots contained 166 Mg C ha^{-1}, slightly lower at Whitmore (122 Mg C ha^{-1}), and lowest at Elkhorn Ridge where controls had 66 Mg C ha^{-1} (Fig. 4a). Total belowground N pools were similar at Elkhorn Ridge (5.1 Mg N ha^{-1}) and Whitmore (5.0 Mg N ha^{-1}) and slightly higher at Feather Falls (5.3 g N ha^{-1}, Fig. 4b).

Variability in total belowground C and N pools among replicate plots was high, as was the case with mineral-soil pools. Belowground C pools at Elkhorn Ridge were larger in plots treated with fertilizer alone, which had 37 Mg ha^{-1} more C than the control ($p = 0.09$, Dunnett's adjustment) (Fig. 4a). At Whitmore, fertilizer applications, regardless of herbicide, increased total belowground C and N pools by 16%, or 22 Mg C ha^{-1} ($p = 0.05$) (Fig. 4a) and by 16%, or 0.9 Mg N ha^{-1} ($p < 0.01$), respectively (Fig. 4b). Herbicide increased total belowground C and N pools compared with the control, but effects were not significant at the Whitmore site (Fig. 4a and 4b). Differences among treatment means at Feather Falls followed a similar trend but were not large enough to detect statistically significant differences for total belowground C (Fig. 4a) or N pools (Fig. 4b).

Table 5. Fine-root (<2-mm diam.) biomass, C pool, and N pool to 30-cm depth and to 1-m depth by site and treatment for the Elkhorn Ridge, Whitmore, and Feather Falls Garden of Eden Study sites.[†]

Treatment	0–30 cm Depth			0–1 m Depth		
	Root biomass	Root C Pool	Root N Pool	Root biomass	Root C Pool	Root N Pool
	Mg ha^{-1}					
			Elkhorn Ridge– Low			
C	6.4 ± 0.7	3.6 ± 0.5	0.04 ± 0.01	10.8 ± 1.9	5.8 ± 1.1	0.06 ± 0.02
H	6.7 ± 0.7	3.7 ± 0.5	0.05 ± 0.01	11.4 ± 1.9	6.3 ± 1.1	0.07 ± 0.02
F	6.9 ± 0.7	3.9 ± 0.5	0.07 ± 0.01	11.9 ± 1.9	6.5 ± 1.1	0.11 ± 0.02
HF	6.3 ± 0.7	3.5 ± 0.5	0.05 ± 0.01	11.6 ± 1.9	6.2 ± 1.1	0.08 ± 0.02
			p-value			
H	0.82	0.85	0.51	0.95	0.93	0.70
F	0.99	0.98	0.10	0.77	0.77	0.15
H x F	0.59	0.68	**0.09**[‡]	0.79	0.74	0.25
			Whitmore–Intermediate			
C	5.9 ± 1.5	3.2 ± 0.8	0.04 ± 0.01	7.8 ± 2.4	4.3 ± 1.3	0.05 ± 0.02
H	8.6 ± 1.5	4.5 ± 0.8	0.06 ± 0.01	13.4 ± 2.4	7.2 ± 1.3	0.09 ± 0.02
F	7.8 ± 1.5	4.3 ± 0.8	0.07 ± 0.01	12.4 ± 2.4	6.9 ± 1.3	0.10 ± 0.02
HF	6.5 ± 1.5	3.4 ± 0.8	0.05 ± 0.01	13.5 ± 2.4	6.7 ± 1.3	0.10 ± 0.02
			p-value			
H	0.66	0.82	0.67	0.28	0.41	0.38
F	0.95	0.98	0.42	0.43	0.50	0.22
H x F	0.26	0.24	0.22	0.43	0.34	0.50
			Feather Falls– High			
C	8.9 ± 2.5	5.0 ± 1.4^{a}[§]	0.08 ± 0.01	14.5 ± 3.1	8.0 ± 1.6	0.11 ± 0.02
H	15.1 ± 2.5	8.1 ± 1.4^{a}	0.08 ± 0.01	22.3 ± 3.1	11.6 ± 1.6	0.13 ± 0.02
F	7.6 ± 2.5	4.0 ± 1.4^{b}	0.08 ± 0.01	15.7 ± 3.1	8.5 ± 1.6	0.14 ± 0.02
HF	6.4 ± 2.5	3.1 ± 1.4^{b}	0.06 ± 0.01	15.6 ± 3.1	7.4 ± 1.6	0.11 ± 0.02
			p-value			
H	0.38	0.46	0.72	0.29	0.48	0.76
F	0.12	**0.09**	0.34	0.44	0.32	0.82
H x F	0.21	0.22	0.31	0.28	0.22	0.24

[†] Means are followed by standard errors. P-values for treatment factors were determined from analysis of variance. Boldface p-values are significant, $\alpha = 0.1$. C and N concentrations are shown in Fig. 2. Treatments: C = control, H = herbicide only, F = fertilizer only, HF = herbicide and fertilizer.

[‡] No pair-wise comparisons significant with a Tukey adjustment, $\alpha = 0.1$. F > C with Dunnett's adjustment to test treatments against control, $\alpha = 0.1$.

[§] For each column, different letters denote statistically different treatments as assessed by multiple pair-wise comparisons with a Tukey adjustment, $\alpha = 0.1$.

DISCUSSION

Forest-Floor Pools

The strongest effects of fertilizer and herbicide treatments on belowground C and N pools occurred in the forest floor. Fertilization increased mass, C content, and N content of the forest floor and decreased forest-floor C/N ratios at all sites, regardless of herbicide application. Fertilization increased forest-floor C and N pools on all sites with the largest effect at Whitmore, the intermediate-quality site. Herbicide treatment influenced forest floor pools only at Elkhorn Ridge, where mass and C content were increased substantially. Control of understory vegetation tripled tree crown cover at the site (Table 3) and litter production by pine more than compensated for litterfall in understory vegetation. This result likely reflects higher competition between pines and shrubs at the Elkhorn Ridge than the other sites, which may be due to low soil volume available for water storage and root exploration in this skeletal soil.

Forest-floor C/N ratios in this study were relatively high, much higher than 20, the conventional critical C/N ratio for organic matter above which decomposition by microbes requires the immobilization of inorganic soil N (Myrold, 2005). Fertilization decreased forest-floor C/N ratios at all sites, but not below 54. This decrease in forest-floor C/N ratios with fertilization may be the result of lowered plant N-use efficiency and reduced translocation of N from senescent foliage. Alternatively, fertilization may have resulted in an accumulation of partially decomposed forest floor material (i.e., Oa or H layer), which could also result in the observed decline in C/N ratios. Similar trends in forest-floor C/N ratios have been observed elsewhere in N fertilization studies of Douglas-fir (Prietzel et al., 2004).

In contrast, competing vegetation control with herbicides increased forest-floor C/N ratio at Feather Falls, suggesting a relatively higher retention of C than of N in the litter layer. Increased forest-floor C/N ratio following herbicide treatment may have been observed only at this site because a

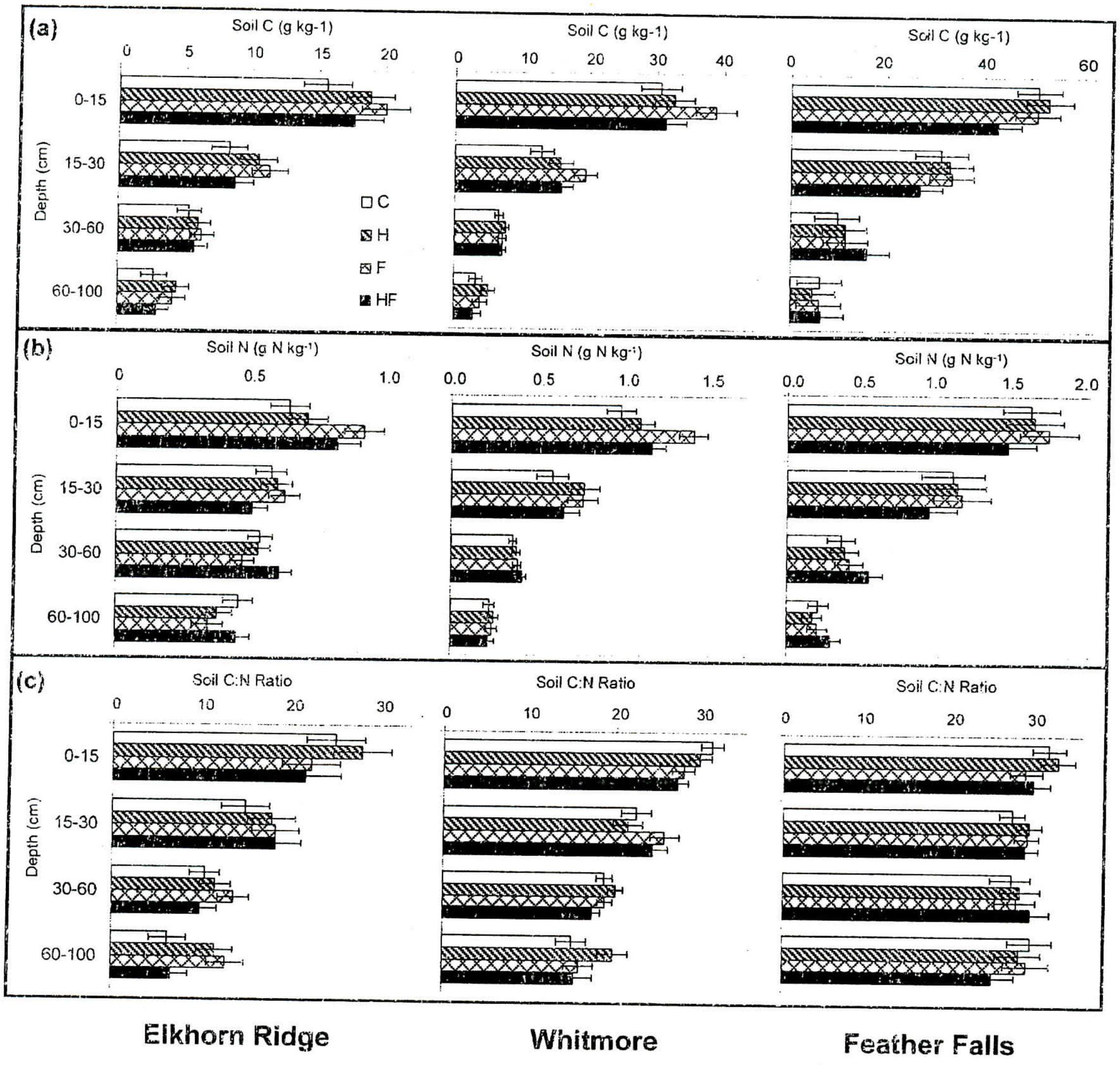

Fig. 3. Mineral-soil C (a) concentration, (b) N concentration, and (c) C/N ratio by depth for each treatment at Elkhorn Ridge (left), Whitmore (middle), and Feather Falls (right) Garden of Eden Study sites. Bars indicate standard errors. Note differences in scale for C and N concentrations across sites. Treatments: C = control, H = herbicide only, F = fertilizer only, HF = fertilizer and herbicide.

N-fixing deciduous shrub, *Ceanothus integerrimus*, dominated the understory vegetation at Feather Falls, whereas manzanita species dominated the understory at Elkhorn Ridge and Whitmore. A similar decrease in forest-floor N concentration was observed following herbicide applications in loblolly pine (*Pinus taeda*; Will et al., 2006).

There has been concern that competing vegetation control may decrease the quality of litter inputs and that this decrease could impair nutrient cycling (Busse et al., 1996, 2006; Munson et al., 1993). One source of concern is that pine litter is often nutrient-poor compared with litter of understory species. For example, manzanita leaves are particularly rich in Ca, averaging four-times the concentrations found in pine needles (Powers, 1981). High accumulations of Ca in manzanita litter might dilute fixed amounts of C, helping explain the apparent higher C concentrations in the forest floor of herbicide-treated plots at Elkhorn and Whitmore (Table 4). The elimination of N-inputs by N-fixing *Ceanothus*, may have caused the observed decrease in N concentration and increase in C/N ratio in the forest floor following understory control at Feather Falls. In contrast, increased forest-floor mass at Elkhorn Ridge with competing vegetation control using herbicides is probably a result of increased inputs associated with the tripling of aboveground pine productivity and a doubling of crown cover (Table 1), rather than depressed litter decomposition.

Fine-Root Pools

Fine roots in our study contributed 4 to 8% of the total belowground C pool, exclusive of coarse roots. Fine root initiation and turnover continues at variable rates throughout a year (Bowen, 1984). Our sampling occurred at a single interval during the growing season (August for Whitmore, June for Elkhorn Ridge and Feather Falls). Tingey et al. (1995) have shown that summer sampling such as done here marks both a peak and a period of relative stability in fine-root density for ponderosa pine, and this may be generally true for other species in the northern hemisphere (Ford and Deans, 1977). Thus, we believe that our sampling periods coincided with maximum fine-root density.

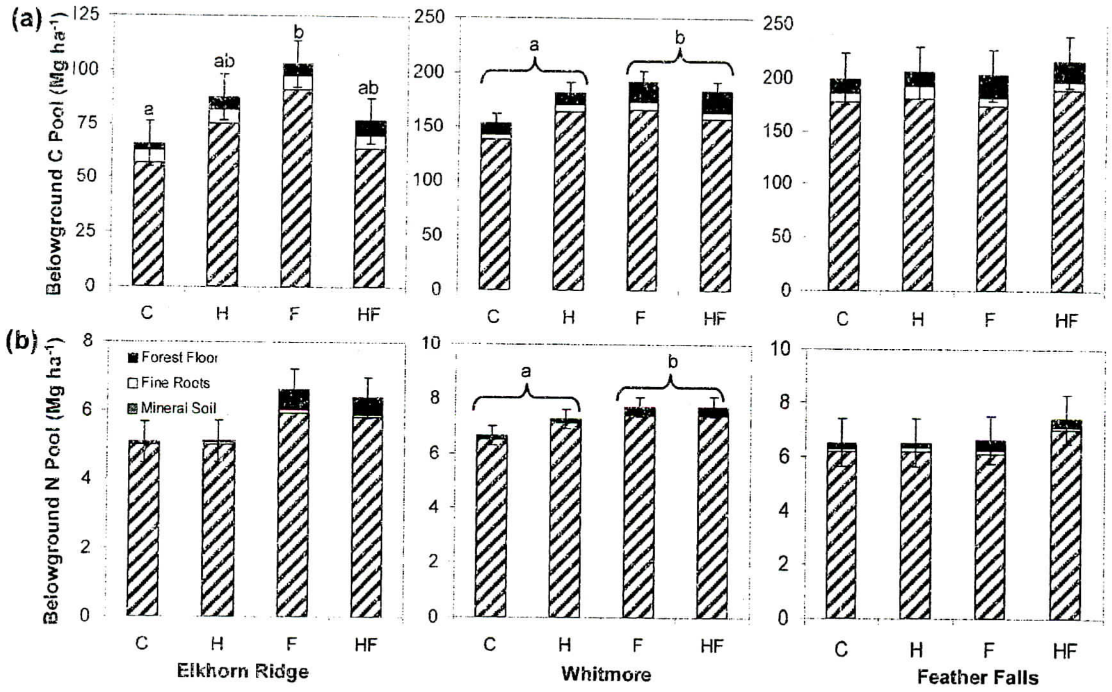

Fig. 4. (a) Total belowground C pools and (b) total belowground N pools for each treatment at Elkhorn Ridge (left), Whitmore (middle), and Feather Falls (right) Garden of Eden Study sites. Bars indicate standard errors for total pools. Note difference in scale for belowground C pool at Elkhorn Ridge. Treatments: C = control, H = herbicide only, F = fertilizer only, HF = fertilizer and herbicide. Different letters indicate statistically significant differences between treatment means, $\alpha = 0.1$. Brackets indicate main effects for fertilizer treatment. Specific *p* values are reported in the text.

Our estimates of fine-root C do not represent total fine-root C inputs as we did not quantify turnover occurring earlier and later in the year. It is possible that the major role of fine roots in belowground C storage and dynamics is through exudation and turnover (i.e., belowground litter production). Unfortunately, these processes, while known to be important, are not well understood. Nadelhoffer et al. (1985) proposed that while fine-root biomass tends to decrease with increasing soil N availability, fine-root production may increase. Evidence for this hypothesis includes patterns observed across gradients of nutrient availability and is reviewed in Nadelhoffer (2000). In contrast, Hendricks et al. (2006) observed decreased fine-root biomass with increasing soil N and water availability coincident with no change in fine-root production and mortality in longleaf pine (*Pinus palustris*). Similar inconsistencies in the literature include reports that fine-root production and turnover increased (King et al., 2002) or decreased (Haynes and Gower, 1995; Giardina et al., 2003, 2004) following fertilization.

Challenges to measuring changes in fine-root biomass or turnover and to comparing results across studies include differences in sampling methodology and differences in diameter classes and cutoffs. For example, in one study loblolly pine measurements recorded using minirhizotrons indicated increased production of fine roots < 1 mm in diameter (King et al., 2002), whereas sequential coring suggested decreased fine-root production (<2-mm diam.) (Albaugh et al., 1998) following fertilization. Fine-root biomass estimates from root coring were 27% greater than estimates from soil pits at Bartlett Experimental Forest, NH (Park et al., 2007). A study of slash pine (*Pinus elliotii*) observed decreased fine-root biomass (<2-mm diam.) following competing vegetation control, whereas fertilization decreased fine-root biomass only for roots < 0.5 mm (Shan et al., 2001).

Mineral-Soil Pools

Mineral-soil C pools in our study were not very responsive to silvicultural treatments, although high variability may have precluded detection of statistically significant treatment effects. Similar results were reported by Homann et al. (2001a) who observed large variability in soil C storage and no detectable effect of fertilization on soil C storage in Douglas-fir forests. In fact, a growing number of studies have reported no detectable change in soil C storage following fertilization of Douglas-fir (Canary et al., 2000), slash pine (Harding and Jokela, 1994; Shan et al., 2001), and loblolly pine (Sartori et al., 2007) stands. Similar results were reported for a red pine (*Pinus resinosa*)/mixed-hardwood forest (Parker et al., 2002) and for wet tropical forests (Giardina et al., 2004; Li et al., 2006). However, several of these studies did report increases in forest-floor C pools (Harding and Jokela, 1994; Canary et al., 2000; Parker et al., 2001; Sartori et al., 2007).

Fertilization increased mineral-soil N concentrations and the mineral-soil N pool to 1-m depth at Whitmore 12–13 yr after fertilizer applications ceased. The increase of 0.9 Mg N ha^{-1} at Whitmore was smaller than the total 1.1 Mg N ha^{-1} applied during the first 6 yr after tree establishment (Table 2). While fertilization had a profound effect on forest floor N concentrations and pools, high variability precluding detecting a residual effect in mineral soil at Elkhorn Ridge or Feather Falls. Some studies have reported residual elevation of mineral soil N a decade or longer following fertilizer applications (Homann et al., 2001b; Jandl et al., 2003). Other studies have reported no lasting effect of N additions on mineral soil (Harding and Jokela, 1994; Johnson et al., 2003; Adams et al., 2005).

Total Belowground Pools

Total belowground C pools, including forest floor, fine roots, and mineral soil, increased with increasing site productivity. Total N pools were less at Elkhorn Ridge than at the more productive sites, but appeared to be larger at Whitmore than at Feather Falls as a result of higher soil bulk densities at Whitmore. Competing vegetation control with herbicides did not appear to affect total C or N pools at any of the three sites. In contrast, fertilization increased total C pools at Elkhorn Ridge and increased total C and N pools at Whitmore. Despite California's droughty climate, high rates of N fertilization can lead to nitrate leaching on weakly developed, coarse-textured soils (McColl and Powers, 1984). However, deep leaching is unlikely on the fine-textured soils in our study (Miles and Powers, 1988). Fertilizers were applied at an incremental rate intended to meet anticipated demand, and soils at Whitmore and Feather Falls were fine-textured and well developed. Even at Elkhorn Ridge where skeletal soils are presumably more leachable, fertilization led to N gains in the forest floor, fine roots, and mineral soil equivalent to 84% of the N applied as fertilizer, and the remainder was probably retained in perennial biomass.

Mechanisms for Responses to Fertilization

Two mechanisms for increases in forest-floor- and mineral-soil C pools with fertilization have been proposed. The first is that increased tree productivity elevates litter production, which augments accumulation of organic matter and C belowground. Elevated litterfall following fertilization has been noted in many forests, ranging from cool, temperate red pine plantations (Haynes and Gower, 1995) to tropical wet forests (Li et al., 2006). This explanation for fertilizer-induced increases in forest-floor or mineral-soil C pools has been proposed in a number of additional studies where fertilization or other forest management treatments resulted in improved aboveground productivity and increased forest-floor mass or C pool (Baker et al., 1986; Harding and Jokela, 1994) or mineral-soil C pool (Adams et al., 2005).

The second possible mechanism for accumulation of forest-floor- and surface-soil C following fertilization is reduced decomposition of partially decomposed organic matter (Berg, 2000; Neff et al., 2002; Franklin et al., 2003). In forest floors, depressed long-term decomposition increases C accumulation as humified organic matter, particularly in O_e horizons (Nohrstedt et al., 1989). In fact, decreased decomposition following fertilization was more important than litter production in increasing forest-floor C in one study of Scots pine (*Pinus sylvestris*) in Sweden (Franklin et al., 2003). Fertilization has also resulted in decreased soil respiration measured in the field (Haynes and Gower, 1995) and during laboratory incubations of whole-soils and soil fractions (Swanston et al., 2004).

This longer-term reduction in decomposition following fertilization, particularly with N, may be due to suppression of the microbial community (Nohrstedt et al., 1989; Bååth et al., 1995), more rapid decline in organic matter quality during decomposition (Berg, 2000; Ågren et al., 2001), or increases in decomposer efficiency (Ågren et al., 2001). Several studies have shown changes in the microbial community following fertilization in Scandinavian forests. Nitrogen fertilization increased forest-floor mass coincident with decreases in soil respiration, microbial biomass, ATP content (Nohrstedt et al., 1989) and changed species composition of the fungal community (Arnebrant et al., 1990). Fertilization with wood-ash decreased microbial biomass and had a larger effect on the fungal community than on bacteria (Bååth et al., 1995). In contrast, fertilization increased microbial biomass in a wet tropical forest (Li et al., 2006).

Of these two mechanisms, we believe that increased litter production associated with increased aboveground productivity following fertilization is primarily responsible for the greater forest floor mass on fertilized plots in this study. Although forest-floor N concentrations were significantly higher on fertilized plots (Table 4), we suspect that C/N ratios were sufficiently high to preclude rapid decomposition, especially in a summer-dry climate. However, we did not measure litterfall or litter decomposition or separate forest floor material into Oi/Oe/Oa (L/F/H) horizons and such data may have provided additional insight into the mechanisms behind our observations.

CONCLUSIONS

We expected to observe increased total belowground C and N pools following fertilization and decreased C and N pools following herbicide applications. Fertilization increased forest-floor C and N pools at all sites, and the magnitude of effect decreased with increasing site productivity. Total belowground pools were not as strongly affected by fertilization, however. Herbicide had no effect on total belowground pools, and only affected forest-floor C pools at Elkhorn Ridge where competing vegetation control resulted in an unexpected increase in C storage, either as a result of slower decomposition of pine litter relative to mixed litter or increased litterfall associated with increased pine productivity.

Herbicide did not reduce forest-floor- or total belowground C and N pools, but we did observe some evidence for changes in litter quality in the presence of competing vegetation control. Decreased N concentration and higher C/N ratios in the forest floor at Feather Falls are one indication of reduced litter quality following shrub removal that eliminated N-rich *Ceanothus* litter. Elevated forest-floor C concentrations at Elkhorn Ridge and Whitmore following herbicide application reflect inputs of pine litter with lower nutrient status. In addition, we saw evidence for reduced SOM quality through density fractionation and laboratory incubation of soils from these sites when treated with competing vegetation control (McFarlane, 2007). It remains possible that over the longer period of multiple rotations declines in soil quality could occur in association with competing vegetation control, but any suggestions that this might affect site productivity are speculative.

Our results suggest that the largest increases in C sequestration with forest management occur in the aboveground biomass with smaller, but potentially significant, responses occurring in forest floors. In forests managed for timber production, it is especially important to consider the longevity of management-enhanced C sequestration. Increases in C storage in forest floors and, to a lesser extent, in mineral soils resulting from nutrient additions or competing vegetation control may not amount to long-term C storage if stands are subjected to fire or harvested before organic matter is stabilized. Selection of forest stands to be managed for C storage will require consideration of site characteristics, other management objectives, and plans for future harvest and thinning operations. While it may be possible to increase C sequestration by forests with management practices such as these, our results suggest that the major mechanism for increases in stored C will be through increased incorporation of C in tree biomass with storage of C in forest-floor, fine-root, or mineral soil C pools, a lesser, but still important mechanism.

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REFERENCES

Adams, A.B., R.B. Harrison, R.S. Sletten, B.D. Strahm, E.C. Turnblom, and C.M. Jensen. 2005. Nitrogen-fertilization impacts on carbon sequestration and flux in managed coastal Douglas-fir stands of the Pacific Northwest. For. Ecol. Manage. 220:313–325.

Ågren, G.I., E. Bosatta, and A.H. Magill. 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. Oecologia 128:94–98.

Albaugh, T.J., H.L. Allen, P.M. Dougherty, L.W. Kress, and J.S. King. 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. For. Sci. 44:317–328.

Amaranthus, M.P., J.M. Trappe, and R.J. Molina. 1989. Long-term forest productivity and the living soil. p. 36–52. *In* D.A. Perry et al. (ed.) Maintaining the long-term productivity of Pacific Northwest forest systems. Timber Press, Portland, OR.

Arnebrant, K., E. Bååth, and B. Söderström. 1990. Changes in microfungal community structure after fertilization of Scots pine forest soil with ammonium nitrate or urea. Soil Biol. Biochem. 22:309–312.

Bååth, E., A. Frostegård, T. Pennanen, and H. Fritze. 1995. Microbial community structure and pH response in relation to soil organic matter quality in wood-ash fertilized, clear-cut or burned coniferous forest soils. Soil Biol. Biochem. 27:229–240.

Baker, T.G., G.R. Oliver, and P.D. Hodgkiss. 1986. Distribution and cycling of nutrients in *Pinus radiata* as affected by past lupin growth and fertiliser. For. Ecol. Manage. 17:169–187.

Berg, B. 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manage. 133:13–22.

Bowen, G.D. 1984. Tree roots and the use of soil nutrients. p. 147–149. *In* G.D. Bowen and E. K. Nambiar (ed.) Nutrition of plantation forests. Academic Press, London.

Busse, M.D., P.H. Cochran, and J.W. Barrett. 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. Soil Sci. Soc. Am. J. 60:1614–1621.

Busse, M.D., S.E. Beattie, R.F. Powers, F.G. Sanchez, and A.E. Tiarks. 2006. Microbial community responses in forest mineral soil to compaction, organic matter removal, and vegetation control. Can. J. For. Res. 36:577–588.

Canary, J.D., R.B. Harrison, J.E. Compton, and H.N. Chappell. 2000. Additional carbon sequestration following repeated urea fertilization of second-growth Douglas-fir stands in western Washington. For. Ecol. Manage. 138:225–232.

Conrad, S.G., and S.R. Radosevich. 1982. Growth responses of white fir to decreased shading and root competition by montane chapparral shrubs. For. Sci. 28:309–320.

Echeverría, M.E., D. Markewitz, L.A. Morris, and R.L. Hendrick. 2004. Soil organic matter fractions under managed pine plantations of the southeastern USA. Soil Sci. Soc. Am. J. 68:950–958.

Ford, E.D., and J.D. Deans. 1977. Growth of a Stika spruce plantation: Spatial distribution and seasonal fluctuations of lengths, weights, and carbohydrate concentrations of fine roots. Plant Soil 47:463–485.

Franklin, O., P. Högberg, A. Ekblad, and G.I. Ågren. 2003. Pine forest floor carbon accumulations in response to N and PK additions: Bomb ^{14}C modelling and respiration studies. Ecosystems 6:644–658.

Giardina, C.P., K.C. Ryan, D. Binkley, and J.H. Fownes. 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Glob. Change Biol. 9:1438–1450.

Giardina, C.P., D. Binkley, M.G. Ryan, J.H. Fownes, and R.S. Senock. 2004. Belowground carbon cycling in a humid tropical forest decreases with fertilization. Oecologia 139:545–550.

Gower, S.T., K.A. Vogt, and C.C. Grier. 1992. Carbon dynamics of rocky mountain Douglas-fir: Influence of water and nutrient availability. Ecol. Monogr. 62:43–65.

Haile-Mariam, S., W. cheng, D.W. Johnson, J.T. Ball, and E.A. Paul. 2000. Use of carbon-13 and carbon-14 to measure the effects of carbon dioxide and nitrogen fertilization on carbon dynamics in ponderosa pine. Soil Sci. Soc. Am. J. 64:1984–1993.

Hangs, R.D., J.D. Knight, and K.C.J. Van Rees. 2003. Nitrogen accumulation by conifer seedlings and competitor species from ^{15}nitrogen-labeled controlled-release fertilizer. Soil Sci. Soc. Am. J. 67:300–308.

Harlow, W.M., E.S. Harrar, J.W. Hardin, and F.M. White. 1996. Textbook of dendrology. McGraw-Hill Series in Forest Resources. McGraw-Hill, New York.

Harding, R.B., and E.J. Jokela. 1994. Long-term effects of forest fertilization on site organic matter and nutrients. Soil Sci. Soc. Am. J. 58:216–221.

Haynes, B.E., and S.T. Gower. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. 15:317–325.

Heath, L.S., J.E. Smith, and R.A. Birdsey. 2003. Carbon trends in U.S. forestlands: A context for the role of soils in forest carbon sequestration. p. 35–45. *In* J.M. Kimble et al (ed.) The Potential for U.S. forest soils to sequester carbon and mitigate the greenhouse effect. CRC Press, New York.

Hendricks, J.J., R.L. Hendrick, C.A. Wilson, R.J. Mitchell, S.D. Pecot, and D. Guo. 2006. Assessing the patterns and controls of fine root dynamics: An empirical test and methodological review. J. Ecol. 94:40–57.

Homann, P., B.T. Bormann, and J.R. Boyle. 2001a. Detecting differences in soil carbon and nitrogen resulting from forest manipulations. Soil Sci. Soc. Am. J. 65:643–469.

Homann, P.S., B.A. Caldwell, H.N. Chappell, P. Sollins, and C.W. Swanston. 2001b. Douglas-fir soil C and N properties a decade after termination of urea fertilization. Can. J. For. Res. 31:2225–2236.

Jandl, R., H. Kopeszki, A. Bruckner, and H. Hager. 2003. Forest soil chemistry and mesofauna 20 years after an amelioration fertilization. Restor. Ecol. 11:239–246.

Jandl, R., F. Starlinger, M. Englisch, E. Herzberger, and E. Johann. 2002. Long-term effects of a forest amelioration experiment. Can. J. For. Res. 32:120–128.

Jandl, R., M. Lindner, L. Versterdal, B. Bauwens, R. Baritz, F. Hagedorn, D.W. Johnson, K. Minkkinen, and K.A. Byrne. 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137:253–268.

Jensen, E.C., W.R. Randall, R.F. Keniston, and D.N. Bever. 2002. Manual of Oregon trees and shrubs. John Bell and Associates, Corvallis, OR.

Johnson, D.W. 1995. Soil properties beneath ceanothus and pine stands in the eastern Sierra Nevada. Soil Sci. Soc. Am. J. 59:918–924.

Johnson, D.W., and P.S. Curtis. 2001. Effects of forest management on soil C and N storage: Meta analysis. For. Ecol. Manage. 140:227–238.

Johnson, D.W., D.E. Todd, and V.R. Tolbert. 2003. Changes in ecosystem carbon and nitrogen in a loblolly pine plantation. Soil Sci. Soc. Am. J.

67:1594–1601.

Johnson, D.W., J.D. Knoepp, W.T. Swank, J. Shan, L.A. Morris, D.H. Van Lear, and P.R. Kapeluck. 2002. Effects of forest management on soil carbon: Results of some long-term resampling studies. Environ. Pollut. 116:S201–S208.

King, J.S., T.J. Albough, H.L. Allen, M. Buford, B.R. Strain, and P. Dougherty. 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. New Phytol. 154:389–398.

Lanini, W.T., and S.R. Radosevich. 1986. Response of three conifer species to site preparation and shrub control. For. Sci. 32:61–77.

Li, Y., M. Xu, and X. Zou. 2006. Effects of nutrient additions on ecosystem carbon cycle in a Puerto Rican tropical wet forest. Glob. Change Biol. 12:284–293.

Matamala, R., M.A. Gonzales-Meler, J.D. Jastrow, R.J. Norby, and W.H. Schlesinger. 2003. Impacts of fine root turnover on forest NPP and Soil C sequestration potential Science 302:1385–1387.

McColl, J.G., and R.F. Powers. 1984. Consequences of forest management on soil-tree relationships. p. 379–412. *In* G.D. Bowen and E.K. Nambiar (ed.) Nutrition of plantation forests. Academic Press, London.

Miles, S.R., and R.F. Powers. 1988. Ten-year results of forest fertilization in California. Earth Resour. Monogr. 15. USDA Forest Service Region 5, San Francisco, CA.

McFarlane, K.J. 2007. Belowground carbon storage and dynamics in fertilized and herbicide-treated ponderosa pine plantations along a site quality gradient in Northern California. Dissertation, Oregon State Univ., Corvallis.

Munson, A.D., H.A. Margolis, and D.G. Brand. 1993. Intensive silvicultural treatment: Impacts on soil fertility and planted conifer response. Soil Sci. Soc. Am. J. 57:246–255.

Myrold, D. 2005. Transformations of nitrogen. P. 333–373. *In* D.M. Sylvia et al (ed.) Principles and applications of soil microbiology. 2nd ed. Pearson-Prentice Hall, Upper Saddle River, NJ.

Nadelhoffer, K.J. 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. New Phytol. 147:151–159.

Nadelhoffer, K.J., J.D. Aber, and J.M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: A new hypothesis. Ecology 66:1377–1390.

Neff, J.C., A.R. Townsend, G. Gleixner, S.J. Lehman, J. Turnbull, and W.D. Bowman. 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. Nature 419:915–917.

Nohrstedt, H.Ö., S. Jacobson, and U. Sikström. 2000. Effects of repeated urea doses on soil chemistry and nutrient pools in a Norway spruce stand. For. Ecol. Manage. 130:47–56.

Nohrstedt, H.Ö., K. Arnebrant, E. Bååth, and B. Söderström. 1989. Changes in carbon content, respiration rate, ATP content, and microbial biomass in nitrogen-fertilized pine forest soils in Sweden. Can. J. For. Res. 19:323–328.

Ogle, S.M., and K. Paustian. 2005. Soil organic carbon as an indicator of environmental quality at the national scale: Inventory monitoring methods and policy relevence. Can. J. Soil Sci. 85:531–540.

Oliver, W.W., and R.F. Powers. 1978. Growth models for ponderosa pine: I. Yield of unthinned plantations in northern California. Res. Pap. 133. USDA Forest Service Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Page-Dumroese, D., M. Jurgensen, W. Elliott, T. Rice, J. Nesser, T. Collins, and R. Meurisse. 2000. Soil quality standards and guidelines for forest sustainability in northwestern North America. For. Ecol. Manage. 138:445–462.

Park, B.B., R.D. Yanai, M.A. Vadeboncoeur, and S.P. Hamburg. 2007. Estimating root biomass in rocky soils using pits, cores, and allometric equations. Soil Sci. Soc. Am. J. 71:206–213.

Parker, J.L., I.J. Fernandez, L.E. Rustad, and S.A. Norton. 2001. Effects of nitrogen enrichment, wildfire, and harvesting on forest-soil carbon and nitrogen. Soil Sci. Soc. Am. J. 65:1248–1255.

Parker, J.L., I.J. Fernandez, L.E. Rustad, and S.A. Norton. 2002. Soil organic matter fractions in experimental forested watersheds. Water Air Soil Pollut. 138:101–121.

Petersen, T.D., and B.D. Maxwell. 1987. Water stress of *Pinus ponderosa* in relation to foliage density of neighboring plants. Can. J. For. Res. 17:1620–1622.

Powers, R.F. 1981. Nutritional ecology of ponderosa pine (*Pinus ponderosa* Laws.) and associated species. Ph.D., Univ. of California, Berkeley.

Powers, R.F. 1983. Forest fertilization research in California. p. 388–397. *In* R. Ballard and S.P. Gessel (ed.) IUFRO symposium on forest site and continuous productivity. USDA Forest Service Gen. Tech. Rep. PNW-163, Portland, OR.

Powers, R.F., and G.T. Ferrell. 1996. Moisture, nutrient, and insect constraints on plantation growth: The "Garden of Eden" study. N. Z. J. Sci. 26:126–144.

Powers, R.F., and G.D. Jackson. 1978. Ponderosa pine response to fertilization: Influence of brush removal and soil type. Res. Pap. PSW-RP-128. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Powers, R.F., and P.E. Reynolds. 1999. Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. Can. J. For. Res. 29:1027–1038.

Powers, R.F., A.E. Tiarks, and J.R. Boyle. 1998. Assessing soil quality: Practical standards for sustainable forest productivity in the United States. p. 53–80. *In* M. B. Adams et al (ed.) The contribution of soil science to the development of and implementation of criteria and indicators of sustainable forest management. SSSA. Madison, WI.

Powers, R.F., D.H. Alban, R.E. Miller, A.E. Tiarks, C.G. Wells, P.E. Avers, R. Cline, O. Fitzgerald, and N.S. Loftus, Jr. 1990. Sustaining site productivity in North American forests: Problems and prospects.p. 49–79. *In* S.P. Gessel et al (ed.) 7th North American Forest Soils Conference. Univ. of British Columbia, Faculty of Forestry, Vancouver, BC, Canada.

Powers, R.F., S.R. Webster, and P.H. Cochran. 1988. Estimating the response of ponderosa pine forests to fertilization. p. 219–225. *In* W.C. Schmidt (ed.) Future forests of the mountain west: A stand culture symposium. USDA Forest Service, Logan UT, Intermountain Research Station, Missoula, MT.

Prietzel, J., G.L. Wagoner, and R.B. Harrison. 2004. Long-term effects of repeated urea fertilization in Douglas-fir stands on forest floor nitrogen pools and nitrogen mineralization. For. Ecol. Manage. 193:413–426.

Raison, R.J., and M.A. Rab. 2001. Guiding concepts for the application of indicators to interpret change in soil properties and processes in forests. p. 215–258. *In* R.J. Raison et al (ed.) Criteria and indicators for sustainable forest management, Vol. 7. CAB International in association with the International Union of Forestry Research Organizations, Wallington, UK.

Sartori, F., D. Markewitz, and B.E. Borders. 2007. Soil carbon storage and nitrogen and phosphorus availability in loblolly pine plantations over 4 to 16 years of herbicide and fertilizer treatments. Biogeochemistry 84:13–30.

Shan, J., L.A. Morris, and R.L. Hendrick. 2001. The effects of management on soil and plant carbon sequestration in slash pine stands. J. Appl. Ecol. 38:932–941.

Shainsky, L.J., and S.R. Radosevich. 1986. Growth and water relations of *Pinus ponderosa* seedlings in competive regimes with *Arcostaphylos patula* seedlings. J. Appl. Ecol. 23:957–966.

Soil Survey Staff. 2009. National Soil Survey Characterization Data [Online].Soil Survey Laboratory. National Soil Survey Center. USDA-NRCS- Lincoln, NE. Available at http://ssldata.nrcs.usda.gov/ (verified 3 Mar. 2009).

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. 2009. Official Soil Series Descriptions [Online]. Available at http://soils.usda.gov/technical/classification/osd/index.html (verified 3 Mar. 2009).

Swanston, C.W., P.S. Homann, B.A. Caldwell, D.A. Myrold, L. Ganio, and P. Sollins. 2004. Long-term effects of elevated nitrogen on forest soil organic matter stability. Biogeochemistry 70:227–250.

Tingey, D.T., D.L. Phillips, M.G. Johnson, M.J. Storm, and J.T. Ball. 1995. Effects of elevated CO2 and N fertilization on fine root dynamics and fungal growth in seedling *Pinus ponderosa*. J. Biogeography 22:281–287.

Vitousek, P.M., and P.A. Matson. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology 66:1360–1376.

Vitousek, P.M., S.W. Andariese, P.A. Matson, L.A. Morris, and R.L. Sanford. 1992. Effects of harvest intensity, site preparation, and herbicide use on soil nitrogen transformations in a young loblolly pine plantation. For. Ecol. Manage. 49:277–292.

Will, R.E., D. Markewitz, R.L. Hendrick, D.F. Meason, T.R. Crocker, and B.E. Borders. 2006. Nitrogen and phosphorus dynamics for 13-year-old loblolly pine stands recieving complete vegetation control and annual N fertilizer. For. Ecol. Manage. 227:155–168.

Yanai, R.D., B.B. Park, and S.P. Hamburg. 2006. The vertical and horizontal distribution of roots in northern hardwood stands of varying age. Can. J. For. Res. 36:450–459.

Yano, Y., Kk. Lajtha, P. Sollins, and B.A. Caldwell. 2005. Chemistry and dynamics of dissolved organic matter in a temperate coniferous forest on Andic soils: Effects of litter quality. Ecosystems 8:286–300.