

# Effects of Silvicultural Practices on Soil Carbon and Nitrogen in a Nitrogen Saturated Central Appalachian (USA) Hardwood Forest Ecosystem

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**ABSTRACT** / Silvicultural treatments represent disturbances to forest ecosystems often resulting in transient increases in net nitrification and leaching of nitrate and base cations from the soil. Response of soil carbon (C) is more complex, decreasing from enhanced soil respiration and increasing from enhanced postharvest inputs of detritus. Because nitrogen (N) saturation can have similar effects on cation mobility, timber harvesting in N-saturated forests may contribute to a decline in both soil C and base cation fertility, decreasing tree growth. Although studies have addressed effects of either forest harvesting or N saturation separately, few data exist on their

combined effects. Our study examined the responses of soil C and N to several commercially used silvicultural treatments within the Fernow Experimental Forest, West Virginia, USA, a site with N-saturated soils. Soil analyses included soil organic matter (SOM), C, N, C/N ratios, pH, and net nitrification. We hypothesized the following gradient of disturbance intensity among silvicultural practices (from most to least intense): even-age with intensive harvesting (EA-I), even-age with extensive harvesting, even-age with commercial harvesting, diameter limit, and single-tree harvesting (ST). We anticipated that effects on soil C and N would be greatest for EA-I and least with ST. Tree species exhibited a response to the gradient of disturbance intensity, with early successional species more predominant in high-intensity treatments and late successional species more predominant in low-intensity treatments. Results for soil variables, however, generally did not support our predictions, with few significant differences among treatments and between treatments and their paired controls for any of the measured soil variables. Multiple regression indicated that the best predictors for net nitrification among samples were SOM (positive relationship) and pH (negative relationship). This finding confirms the challenge of sustainable management of N-saturated forests.

Atmospheric deposition of sulfur throughout much of eastern North America has declined over the past several years (Likens and others 1996, 2002), whereas deposition of nitrogen (N) has not (Lynch and others 1999). Holland and others (1999) reported median changes of  $-35\%$  and  $-26\%$  for sulfur dioxide emissions and sulfate concentrations in precipitation, respectively, for the eastern United States from 1989 to 1995, in contrast to only a  $-8\%$  median change for nitrate. Long-term precipitation chemistry data at Fernow Experimental Forest (FEF), West Virginia, USA, are consistent with this observation (Figure 1). Nitrogen in wetfall at FEF arises from measurable levels of

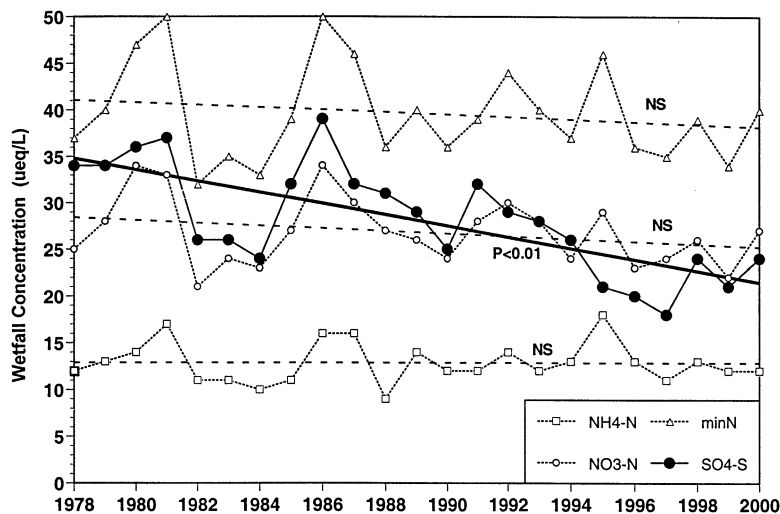
both nitrate and ammonium, neither of which exhibited significant change over the  $> 20$ -year period, from 1978 to 2000. Elevated inputs of N can disrupt the balance of N cycling such that forests that once were N-limited experience a supply of available N in excess of biological demand—a phenomenon called N saturation.

Another current trend of great interest is that of increasing demand for timber from forests of the eastern United States. For example, harvesting in West Virginia resulted in the removal of approximately  $3,100,000,000 \text{ m}^3$  of timber in 1996—twice the volume of wood removed in 1989 (Adams 1999). More intensive forest harvesting has been shown to exacerbate depletion of forest soil calcium (Federer and others 1989, Huntington and others 2000, Adams and others 2000), something that also occurs under conditions of N saturation via high mobility of base cations along with elevated pools of nitrate in N-saturated soils (Johnson and others 1991, Lawrence and others 1995, Likens and others 1996, Currie and others 1999). As a result, cation

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**Figure 1.** Volume-weighted mean annual concentrations of  $\text{SO}_4\text{-S}$ ,  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ , and total mineral N (sum of  $\text{NO}_3^-$  and  $\text{NH}_4\text{-N}$ ) in wetfall at the Fernow Experimental Forest, West Virginia. NS indicates a nonsignificant slope at  $P > 0.10$ .

depletion represents a serious challenge to sustainable management of some N-saturated forests (Fenn and others 1998, Gilliam and Adams 1999, Adams 1999, McLaughlin and Wimmer 1999, Adams and others 2000). Thus, forest harvesting operations have been shown to have at least short-term effects on nutrient cycling that are similar to the more long-term effects of N saturation (Parker and others 2001), especially responses of net nitrification, cation export via leaching of nitrate, and soil carbon (C) (Bormann and others 1968, Vitousek and Matson 1985, Johnson and others 1988, Currie 1999, Gilliam and Adams 1999, Herrmann and others 2001).

The effects of forest harvesting on ecosystem nutrient cycling have been studied for a variety of forest types and harvesting practices. Such studies indicate that response of the biota (recovering vegetation) is largely responsible for regulating nutrient change as the forest recovers from the disturbance of the harvest regime (Tritton and others 1987, Reiners 1992). It also has been learned, however, that there is great variability in these responses among sites, precluding broad generalizations across forest ecosystems. Brais and others (2002) suggested that whole-tree harvesting could have long-term effects on N dynamics in conifer forests of Canada. Piirainen and others (2002) found increased net nitrification during a three-year period following clear-cutting in Finnish spruce forests. In a northern hardwoods forest, Johnson and others (1997) found that clear-cutting resulted in increased mobilization of exchangeable cations from the forest floor that accumulated in the spodic B-horizons following clear-cutting.

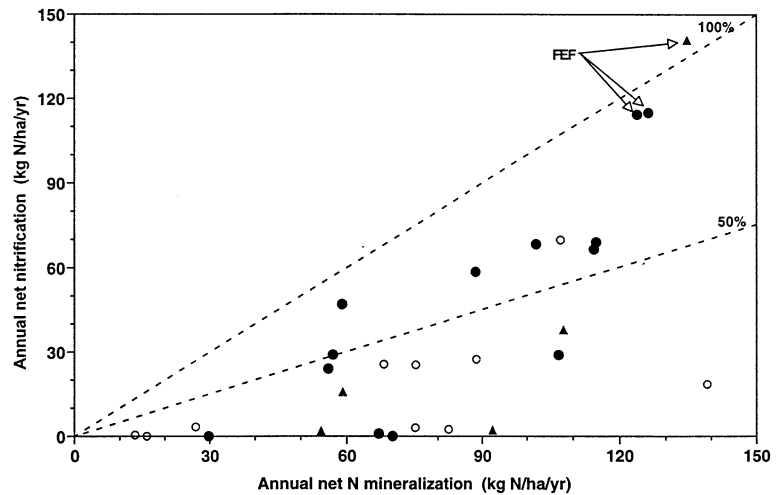
Because most N storage in forest ecosystems is in the form of organic N in mineral soil (Binkley 1986), it is

important also to consider effects of forest management on soil C and soil organic N. Tree harvesting has both direct and indirect effects on the biogeochemistry of forest ecosystems, including a reduction in pools of C in the forest floor (Parker and others 2001). Johnson and Curtis (2001) conducted a meta analysis of the effects of forest management on soil C and N storage. Although they concluded that harvesting in general had little or no effect on soil C and N, they found great variation among harvesting methods and stand types. Yanai and others (2003) demonstrated that the short- and long-term effects of harvesting on soil C can be quite complex with decreasing C from enhanced soil respiration and increasing C from enhanced postharvest inputs of detritus. Although harvesting effects have been studied in numerous other forest types, including hardwood and conifer forests, none has examined such effects in the context of N saturation, even though Fenn and others (1998) suggested that such an endeavor is a pressing research need.

#### Nitrogen Saturation Research at Fernow Experimental Forest

The experimental watersheds of the Fernow Experimental Forest (FEF) in north-central West Virginia have long been the focus of studies of hydrologic and nutrient cycling within the central Appalachian forest region (Aubertin and Patric 1974, Kochenderfer and Wendel 1983). The initiation of the Fernow Whole-Watershed Study in 1989 ushered in a new emphasis on experimental simulations of atmospheric deposition of acidity associated with inputs of S and N (Adams and others 1993, Adams and Kochenderfer 1999). Publications from this study have reported on the effects of

**Figure 2.** Annual net nitrification versus annual net N mineralization for various sites, based on literature values. Data for three watersheds at Fernow Experimental Forest are also indicated. Symbols are as follows: closed circles, hardwood-dominated stands; open circles, conifer-dominated stands; and triangles, stands with experimental N additions. Lines shown represent relative nitrification rates of 50% and 100%.



experimental acidification on stream chemistry (Adams and others 1997, Edwards and others 2002a), soil solution (Adams and others 1997, Edwards and others 2002b), herbaceous layer composition and cover (Gilliam and others 1994), and tree ring chemistry (DeWalle and others 1999).

Several published studies based on long-term data from FEF have included observations of increasing concentrations over time of stream nitrate in one of the undisturbed control watersheds (WS4) (Edwards and Helvey 1991, Stoddard 1994, Peterjohn and others 1996, Fernandez and Adams 2000). Considering that increased mobility and leaching loss of nitrate is one of several symptoms of N saturation (Aber and others 1998), additional research at FEF has focused on the possible effects of N saturation on plants (Gilliam and others 1996, Christ and others 2002) and soils (Peterjohn and others 1999, Gilliam and others 2001a) of these hardwood stands. These studies have provided compelling evidence to corroborate conclusions based on stream chemistry from WS4—soils of many forest stands of FEF have become N saturated. Notable among these published results is a combination of high rates of net nitrification (~115–140 kg nitrate N/ha/yr) and high relative rates of nitrification (i.e., net nitrification as a percent of net N mineralization) (Gilliam and others 2001a) (Figure 2).

#### Silviculture Research at Fernow Experimental Forest

Experimental watershed studies represent one of two main areas for research at FEF. Elklick Run is a perennial stream that drains the entire experimental forest and divides it into two roughly even areas. As

early as the late 1940s and early 1950s forest stands on the side of Elklick Run opposite from the experimental watersheds were divided into compartments of varying size. These compartments were subjected to numerous silvicultural treatments used commercially in central Appalachian forests, including even-age silviculture (clear-cut harvesting), uneven-age silviculture (diameter limit harvesting), single-tree harvesting, group selection, and patch cuts (Trimble and Fridley 1963, Smith and Miller 1987, Miller and Smith 1993). These compartments generally range in size from ~2 to ~25 ha. Although they also vary in site quality, they are mostly of a medium to high site index.

By utilizing some of these timber management compartments, our study examined the responses of soil C and N to a variety of commercially used silvicultural treatments within the FEF, a site documented as being N saturated based on watershed studies. We addressed the following questions regarding potential biogeochemical responses to silvicultural practices of N-saturated stands of hardwood forests: (1) What is the effect of silvicultural practices on C and N stores in mineral soil? (2) How do rates of net N mineralization and nitrification vary with the various disturbances represented by contrasting silvicultural treatments? (3) What soil factors best predict spatial patterns of net nitrification among sites? We envisioned the following gradient of disturbance intensities among silvicultural practices (from most to least intense): even-age with intensive harvesting (EA-I), even-age with extensive harvesting, even-age with commercial harvesting, diameter limit, and single-tree harvesting (ST). Thus, we hypothesized that effects on soil C and N would be greatest for EA-I and least with ST.

Table 1. Importance values for important tree species in each of the silvicultural treatments: even-age intensive (EA-I), even-age extensive (EA-E), even-age commercial (EA-C), diameter limit (DL), and single-tree (ST)

Species	EA-I	EA-E	EA-C	DL	ST
<i>Acer saccharum</i>	4.1	12.2	19.0	33.7	36.6
<i>Betula lenta</i>			7.8		
<i>Fagus grandifolia</i>				5.7	
<i>Liriodendron tulipifera</i>	30.4	28.7	31.3	11.4	8.8
<i>Prunus serotina</i>	34.1	14.9	11.7		17.6
<i>Quercus rubra</i>				9.5	24.5
<i>Robinia pseudoacacia</i>	18.9	10.1			
<i>Tilia americana</i>		12.8	14.5	6.4	
Other	12.5	21.3	15.6	33.3	12.5
Total	100.0	100.0	100.0	100.0	100.0

It should be noted that we are considering differences among silvicultural treatments, if found, to be legacy effects, i.e., responses of the system long after the harvest disturbance (e.g., Arthur and others 1993). In doing so, we are assuming the conditions at the time of sampling to be typical of long-term status of the site as a result of forest management for the past 40–50 years. This does not consider the more transient responses of soil processes to the discrete events of timber harvesting, something that is proposed for future work.

## Methods

### Study Site

The Fernow Experimental Forest (FEF), a ~1900-ha area of largely montane hardwood forests in the Allegheny Mountain section of the unglaciated Allegheny Plateau, is located in Tucker County, north-central West Virginia, USA. Mean annual precipitation is approximately 1430 mm/yr, with most precipitation occurring during the growing season (Gilliam and Adams 1996). Topography is mountainous, ranging in elevation from 534 to 1113 m above mean sea level.

Most soils at FEF are relatively thin (< 1 m in depth), acidic, sandy-loam Inceptisols (Typic Dystrochrepts) of Berks and Calvin series (Gilliam and others 1994). However, some soils are Typic Normudalfs of the Belmont series, derived from limestone parent material (Madarish and Schuler 2002). Soils at FEF are generally acidic, but are high in organic matter, resulting in high cation exchange capacity.

Forest stands within the study compartments are dominated by mixed hardwood species. Two species, *Acer saccharum* and *Liriodendron tulipifera*, are found across all treatments (Table 1). Early-successional species, such as *Prunus serotina* and *Robinia pseudoacacia*, are dominant in more-intense treatments, whereas late-successional species, such as *Fagus grandifolia* and *Quercus*

*rubra* are dominant in less-intense treatments (Table 1). Dominant herbaceous layer species for other areas at FEF include *Laportea canadensis*, *Viola* spp., and several ferns, including *Dryopteris marginalis* and *Polystichum acrostichoides* (Gilliam and others 1995).

### Silvicultural Treatments

The following describes the five silvicultural treatments used in our study. These are presented in their hypothesized order of disturbance intensity, from highest to lowest.

1. Even-age silviculture, intensive management (EA-I): This silvicultural practice includes two precommercial operations: (a) a liberation cutting at three years where stems of advanced reproduction from the previous stand between 2.5 to 12.7 cm dbh were killed, and (b) a crop tree release harvest at seven years. Compartment establishment (clear-cut harvesting) was in 1960, with subsequent thinning harvests in 1964 and 1981.

2. Even-age silviculture, extensive management (EA-E): This silvicultural practice differs from even-age silviculture with intensive management in that it involves only one precommercial operation—a crop tree release harvest at seven years. Compartment establishment and subsequent thinning harvests are the same as with the previous treatment.

3. Even-age silviculture, commercial thinning (EA-C): The term “commercial” refers to an activity that it is associated with a timber sale. This compartment was established in 1960. Although there were no precommercial operations, there have been heavy, infrequent commercial thinning harvests in 1964 and 1981.

4. Diameter-limit harvesting (DL): This is a silvicultural practice wherein all trees above a set minimum diameter are harvested. The compartment was established in 1954. Harvests include all trees  $\geq 43$  cm dbh and have occurred in 1954, 1970, 1984, and 2001.

5. Single-tree selection (ST): As the name implies, single-tree silviculture involves harvesting of individual trees based on preestablished criteria. This compartment was established in 1952 and has been harvested with the following criteria: (a) maximum tree diameter at breast height (dbh) of 81.3 cm, (b) residual postharvest basal area of 14.9 m<sup>2</sup>/ha for trees > 27.9 cm dbh, and (c) a Q factor of 1.3. Q factors determine the change in density of stems across consecutive diameter classes, often to specify stand structural goals in uneven-aged management. The Q factor of 1.3 indicates that each consecutively smaller 5-cm-diameter class contains 1.3 times higher density than the preceding class for the range of 80 cm down to 30 cm. Single-tree harvests have taken place in 1968, 1973, 1977, and 1987.

For controls, all compartments have untreated areas adjacent to them that serve as controls. In the case of the ST and EA-I treatments, there was a single untreated area that served simultaneously as control for both treatments. Thus, in all, there was a total of nine areas for the establishment of plots and sampling. All sampled compartments were between 10 and 20 ha in area.

#### Field Sampling

We located five sample points within each of these areas, for a total of 45 sample points. These were located at random intervals along a 50-m transect that was parallel with the topographic contour to avoid confounding potential effects of elevation. At each point, mineral soil was taken to a 5-cm depth and divided into two sub-samples. The first sub-sample was placed into paper bag to allow for air-drying and analysis for total C and N (see below). The second subsample was placed in a polyethylene bag for organic matter analysis and net N mineralization and nitrification following laboratory incubation.

#### Laboratory Analyses

Soil samples brought back to the laboratory at Marshall University were extracted to determine preincubations levels of NH<sub>4</sub> and NO<sub>3</sub> and potential net N mineralization and nitrification. All soil samples were incubated under controlled conditions for 14 days at 25°C. Extraction and analysis for NH<sub>4</sub> and NO<sub>3</sub> followed methods described in Gilliam and others (2001b). Briefly, moist soils were extracted with 1 N KCl at an extract-soil ratio of 10:1 (v/w). Extracts were analyzed colorimetrically for NH<sub>4</sub> and NO<sub>3</sub> with a Bran + Luebbe TrAAcs 2000 automatic analysis system. Net N mineralization was calculated as postincubation (NH<sub>4</sub> plus NO<sub>3</sub>) minus preincubation (NH<sub>4</sub> plus NO<sub>3</sub>); net nitrification was calculated as postincubation NO<sub>3</sub>

minus preincubation NO<sub>3</sub>. Other analyses at the Marshall laboratory included organic matter (loss-on-ignition, 500°C for 5 hr) and pH (glass electrode).

Subsamples of soil originally placed in paper bags were taken to the USDA Forest Service Timber and Watershed Laboratory, Parsons, West Virginia. These samples were air dried and analyzed for C and N with a Leco CNS analyzer.

Importance values for tree species common among silvicultural treatments were determined as a percentage of total basal area. Personnel at the USDA Forest Service Timber and Watershed Laboratory provided data for tree basal area.

#### Statistical Analyses

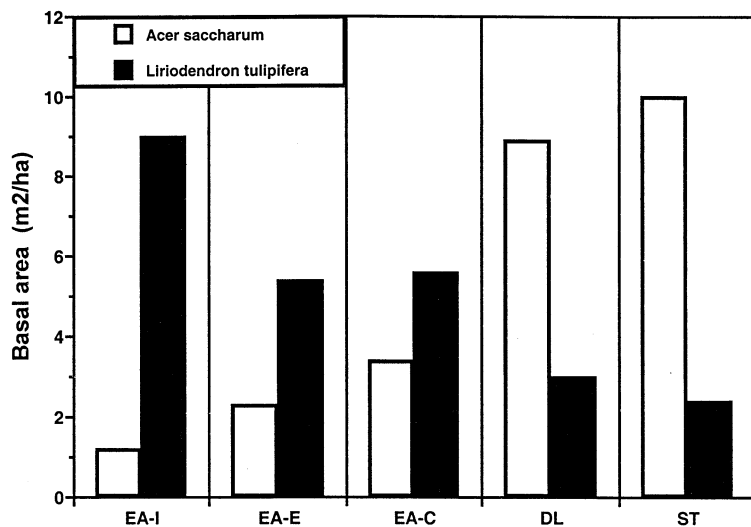
For each of the analyzed variables, we used analysis of variance and multiple range tests to determine significance of effects of silvicultural treatments (Zar 1996). We used linear regression to compare soil C versus soil N across all sample points, and to assess relative nitrification (i.e., the percent of net N mineralization that occurs as net nitrification) by comparing net nitrification versus net N mineralization.

Factors potentially influencing spatial patterns of soil N transformations were assessed with two multiple linear techniques, as described in Gilliam and others (2001a). First, multiple linear regression was used to examine the relationship between net nitrification rates and the following soil variables: C, N, C/N ratio, extractable pools of NH<sub>4</sub>, moisture, organic matter, and pH, following the approach taken by Koopmans and others (1995). Additionally, backward stepwise regression was used to identify further which of the independent variables may have been more significantly correlated with N transformations. This technique eliminates variables from the proposed model sequentially until all the variables remaining in the model produce F statistics significant at a given probability level, in this case  $P < 0.05$  (Zar 1996).

## Results and Discussion

#### Tree Species

Yellow poplar had a basal area of 8.5 m<sup>2</sup>/ha in the even-age management with intensive harvesting (EA-I) compartment and had successively lower basal area along our hypothesized disturbance gradient, with EA-I followed by even-age management with extensive harvesting (EA-E), even-age management with commercial harvesting (EA-C), diameter limit harvesting (DL), and a minimum basal area of 2.4 m<sup>2</sup>/ha for single-tree harvesting (ST). Sugar maple exhibited the opposite



**Figure 3.** Basal area for sugar maple (*Acer saccharum*) and yellow poplar (*Liriodendron tulipifera*) among silvicultural treatments: even-age with intensive harvesting (EA-I), even-age with extensive harvesting (EA-E), even-age with commercial harvesting (EA-C), diameter limit (DL), and single-tree harvesting (ST).

pattern, with minimum basal area of 1.2 m<sup>2</sup>/ha for EA-I and maximum basal area of 10.0 m<sup>2</sup>/ha for ST (Figure 3).

The most immediate and obvious effect of silvicultural treatments often is seen in forest vegetation. Forest managers in the eastern United States employ a variety of contrasting silvicultural approaches, depending on both the existing forest type and on the desired outcome, i.e., the structure and composition of the forest that will develop (Marquis and Johnson 1989, Crow and others 2002). Fast-growing, shade-intolerant tree species that are common early in secondary plant succession establish quickly in more intense silvicultural treatments, such as even-age management. By contrast, less intense techniques, such as single-tree harvesting, are likely to promote rapid growth among late-successional species already established in the stand.

Our data suggest that yellow poplar, an early successional species, increases with increasing intensity of disturbance, whereas sugar maple, a late successional species, decreases with increasing disturbance intensity (Figure 3). This is consistent with results of Gilliam and others (1995) from experimental watersheds of contrasting stand ages that early successional species for FEF included black locust, black cherry, and yellow poplar, and that late successional species included northern red oak, American beech, and sugar maple.

#### Soil Organic Matter, Carbon, and Nitrogen

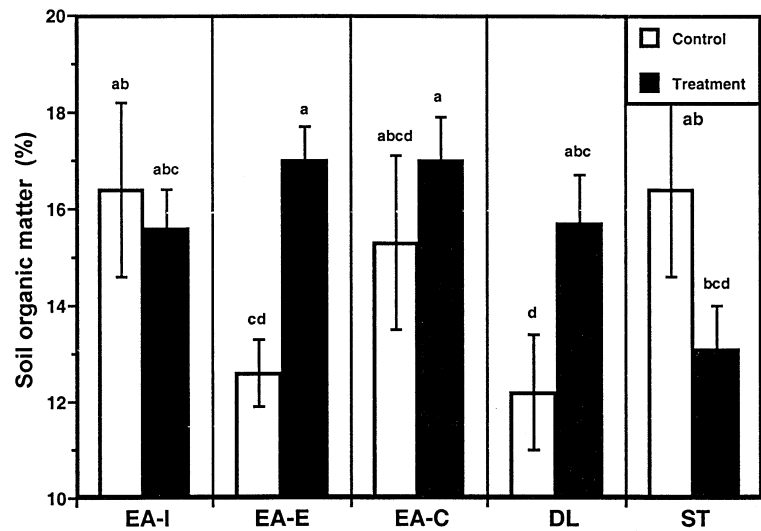
In contrast to the gradient response of tree species to the disturbance gradient of our silvicultural treatments, soil organic matter (SOM) did not exhibit any consistent pattern among the treatments; furthermore,

only EA-E and DL showed significant differences between the treatment compartment and their paired control areas, which had the lowest SOM of ~12% (Figure 4). Mean SOM was highest among EA-E and EA-C compartments at ~17%. These values are comparable to those reported for whole-tree harvesting and reference stands of Weymouth Point Watershed, Maine, of 11.6 and 18.9%, respectively (Parker and others 2001). Lack of a treatment effect in our study has implications for forest sustainability, considering that SOM has been shown to provide important mechanisms in conserving loss of essential base cations (Johnson and others 1997). In addition, the lack of consistent pattern in SOM along the disturbance gradient is further evidence of the complexities associated with evaluating SOM response to forest harvesting (Yanai and others 2000, 2003).

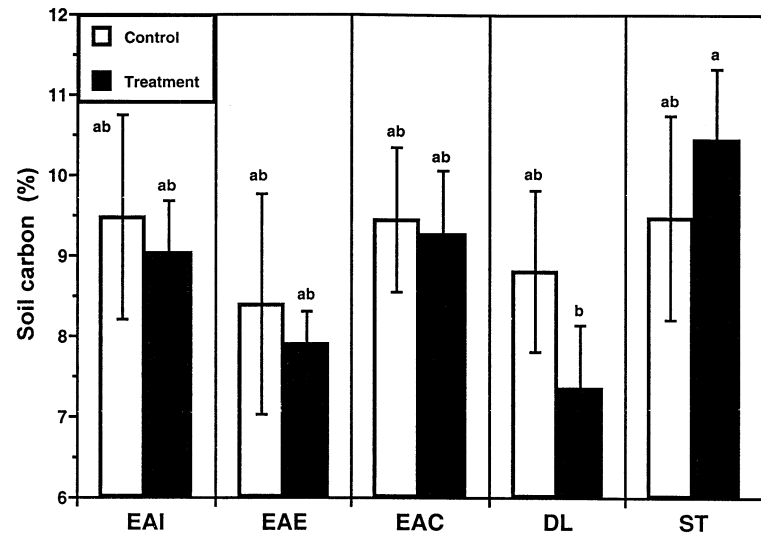
Neither soil C nor soil N varied significantly between any of the silvicultural treatments and paired controls. Mean soil C ranged from 7.4% for DL to 10.5% for ST (Figure 5), with mean soil N exhibiting a more limited range of variation—from 0.6% to just over 0.7% (Figure 6). As with SOM, neither soil C nor soil N displayed a gradient response to the treatments. These minimal effects of forest management on soil C and N stores are generally consistent with conclusions of Johnson and Curtis (2001), based on their meta-analysis of 26 studies. Despite this conclusion, they found great variation among harvesting methods and stand types. In particular, they found that whole-tree harvesting decreased soil C and N by 6% across all studies in the analysis (Johnson and Curtis 2001).

Because of the importance of soil C/N ratios in predicting and controlling numerous biogeochemical

**Figure 4.** Mean soil organic matter for each silvicultural practice (see Figure 3 for abbreviations) and its paired control. Errors bars are  $\pm 1$  standard error of the mean. Means with the same superscript are not significantly different at  $P < 0.05$ .



**Figure 5.** Mean soil carbon for each silvicultural practice (see Figure 3 for abbreviations) and its paired control. Errors bars are  $\pm 1$  standard error of the mean. Means with the same superscript are not significantly different at  $P < 0.05$ .

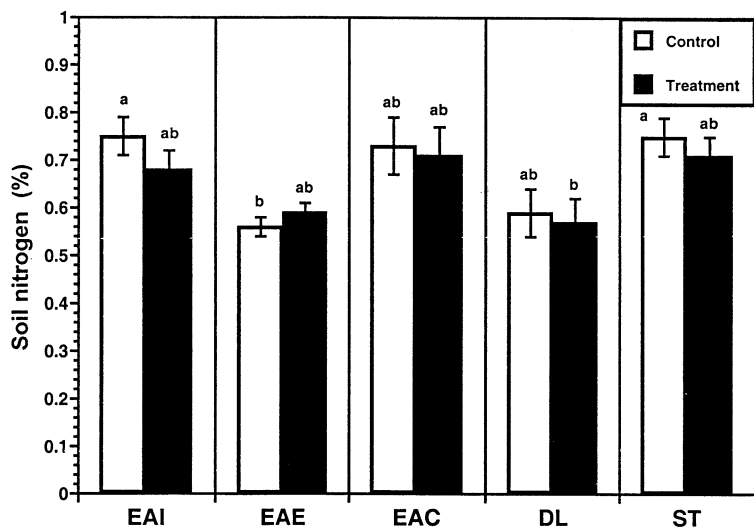


processes in forest ecosystems, in addition to assessing variation in soil C and N separately, it is also necessary to consider responses of the balance between these two components. Mean soil C/N ratios were  $< \sim 15$  for all treatments and controls in our study, and were  $< 13$  for several of these (Figure 7). Linear regression of soil C versus soil N across all sample points (all treatments and controls combined) revealed a highly significant ( $P < 0.001$ ,  $R^2 = 0.84$ ) relationship:  $C = 0.15 + 13.4N$  (Figure 8). This indicates that the C/N ratio was  $\sim 13$  across all sites, a value much lower than most found in the literature, e.g., 20–24 for Bear Brook Watershed, Maine (Parker and others 2001), 17–20 for White Mountain National Forest (Goodale and Aber 2001), 17–21 for boreal forest in Quebec (Brais and others

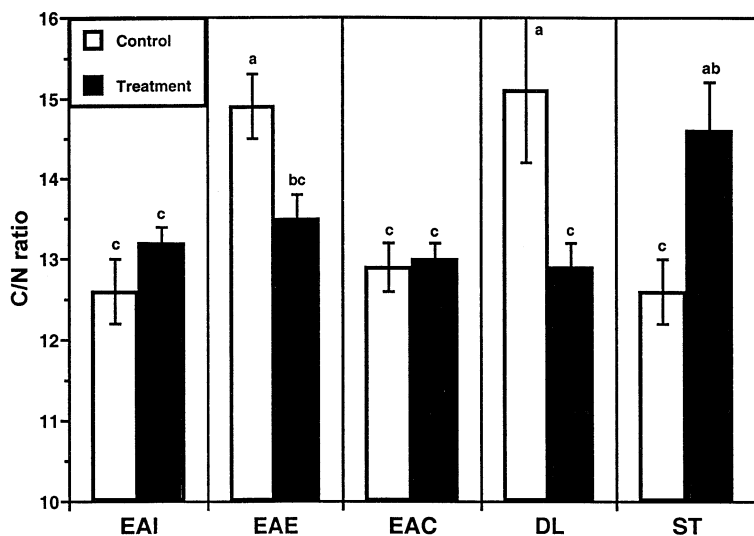
2002). Low soil C/N ratios are among several lines of evidence indicative of N saturation (Aber and others 1998).

#### Net Nitrification

Other indicators of N saturation include high absolute and relative rates of net nitrification (Aber and others 1991). Accordingly, a major emphasis of this study is on the potential effects of forest management on nitrification in mineral soil. Similar to results for the other soil variables in our study, mean rates of net nitrification neither exhibited a gradient pattern among treatments, nor differed significantly between treatments and paired controls (Figure 9). It should be noted that because they are the result of laboratory



**Figure 6.** Mean soil nitrogen for each silvicultural practice (see Figure 3 for abbreviations) and its paired control. Errors bars are  $\pm 1$  standard error of the mean. Means with the same superscript are not significantly different at  $P < 0.05$ .



**Figure 7.** Mean soil C/N ratio for each silvicultural practice (see Figure 3 for abbreviations) and its paired control. Errors bars are  $\pm 1$  standard error of the mean. Means with the same superscript are not significantly different at  $P < 0.05$ .

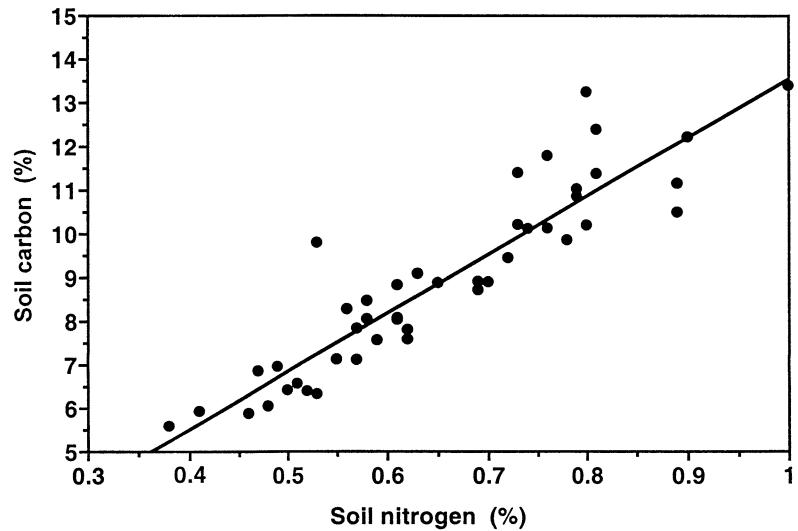
incubations under controlled conditions, these data reflect potential net nitrification, rather than actual field values. Despite this possible limitation, the daily rates of net nitrification found in this study are comparable to daily rates based on monthly in situ incubations in a three-year study across three experimental watersheds at FEF (Gilliam and others 2001b).

Linear regression of net nitrification versus net N mineralization across all sample points (all treatments and controls combined) produced a highly significant ( $P < 0.001$ ,  $R^2 = 0.85$ ) relationship:  $\text{Nit} = 0.21 + 0.89\text{Nmin}$  (Figure 10). The slope of 0.89 indicates that, for all treatment and control soils combined, nitrification is as nearly 90% of N mineralization. Most points were on or near the 100%, indicating that nitrification

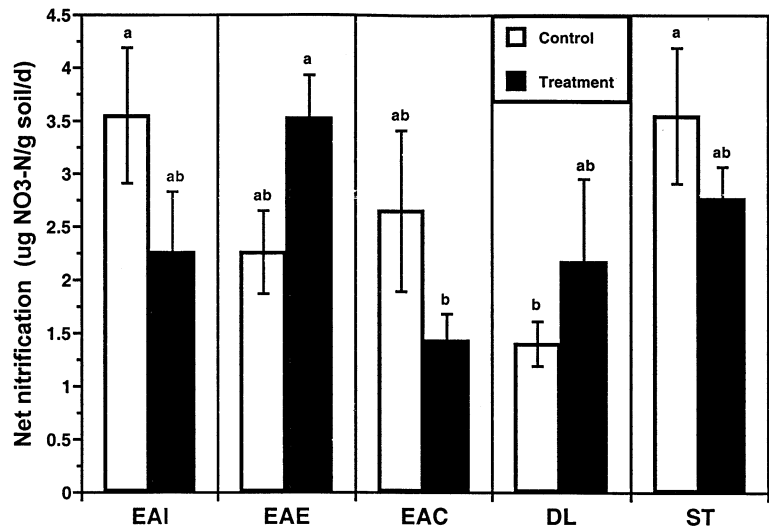
was essentially 100% of N mineralization for a majority of the soils of the study. These high values for relative nitrification are consistent with results for experimental watersheds at FEF (Figure 2, Gilliam and others 2001a).

Factors that potentially influence spatial patterns of net nitrification among our sites were examined with multiple linear regression. This was highly significant ( $R^2 = 0.52$ ,  $P < 0.001$ ) for a model of net nitrification versus soil C, N, C/N ratios, OM, pH,  $\text{NH}_4$  pools, and soil moisture. Of these factors, however, only SOM and pH accounted significantly ( $R^2 = 0.49$ ,  $P < 0.005$ ) for variability in the final stepwise model (Table 2). The coefficient for SOM (0.32) indicates a positive relationship between SOM and net nitrification, whereas the coefficient for pH ( $-2.30$ ) indicates a negative relation-





**Figure 8.** Soil carbon (C) versus soil nitrogen (N) for all plots and treatments combined. Line shown is the following:  $C = 0.15 + 13.4N$ ,  $R^2 = 0.84$ ,  $P < 0.001$ .

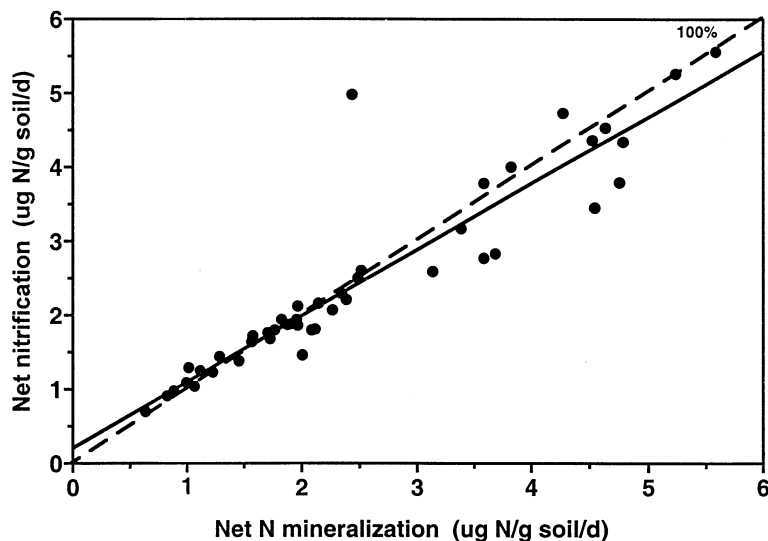


**Figure 9.** Mean rates of net nitrification for each silvicultural practice (see Figure 3 for abbreviations) and its paired control. Error bars are  $\pm 1$  standard error of the mean. Means with the same superscript are not significantly different at  $P < 0.05$ .

ship. The lack of a relationship for C/N ratio is in contrast to published results of studies suggesting that soil C/N ratios exert a significant control on nitrification (Goodale and Aber 2001, Ollinger and others 2002).

Aber and others (1991) used the VEGIE model to predict the effects of timber harvesting on N mineralization and the time required for a northern hardwood stand to reach N saturation, using a net N mineralization rate of 95 kg/ha/yr as the level indicating N saturation. They found that harvesting had a transient effect on mineralization, which increased abruptly following harvesting, then returned close to preharvest levels within  $\sim 50$  years. They also concluded that harvesting hastened the onset of N saturation (Aber and

others, 1991). Similarities between results of this study and previous work on experimental watersheds at FEF (Gilliam and others 2001a,b) suggest that soils of these silvicultural treatments and their paired controls are already well above the threshold level used by Aber and others (1991) as an indicator of N saturation. In addition, low C/N ratios (Figure 7) and high relative net nitrification (Figure 10) are further evidence of N saturation for our sites. Finally, the relationship between SOM and net nitrification confirms the challenge of sustainable management of N-saturated forests. That is, it is possible that management practices designed to improve levels of SOM could further exacerbate base cation loss by increasing nitrification and soil nitrate leaching.



**Figure 10.** Net nitrification (Nit) versus net N mineralization (Nmin) for all plots and treatments combined. Line shown is the following:  $\text{Nit} = 0.21 + 0.89\text{Nmin}$ ,  $R^2 = 0.85$ ,  $P < 0.001$ . Dashed line indicates net nitrification as 100% of net N mineralization.

Table 2. Summary of regression analyses of potential controlling factors of mineral soil for net nitrification across all silvicultural treatments and controls<sup>a</sup>

Source	Degrees of freedom	SS	MS	<i>F</i>	<i>P</i>	<i>R</i> <sup>2</sup>
A. Multiple regression						
Regression	7	38.4	5.48	5.89	0.001	0.52
Residual	37	34.4	0.93			
Total	44	72.8				
B. Multiple regression with backward stepwise procedure						
Final model						
Net nitrification = $6.59 + 0.32\text{OM} - 2.30\text{pH}$ , $P < 0.005$ , $R^2 = 0.49$						

<sup>a</sup>(A) Multiple linear regression (see model below); (B) Multiple regression using backward stepwise procedure, wherein variables significantly accounting for variability in the model at  $P < 0.05$  are listed with their coefficients. See Methods for further details.

Multiple regression model and original model for backward stepwise procedure: Net nitrification =  $C + N + C/N + \text{OM} + \text{pH} + \text{NH}_4 \text{ pool} + \text{Moisture}$

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