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Impacts of elevated N inputs on north temperate forest soil C storage, C/N, and net N-mineralization

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ABSTRACT

Nitrogen (N) availability influences carbon (C) storage in forest soils through effects on plant growth, litter production, and soil C decomposition and stabilization. Soil C/N and net N-mineralization are commonly reported empirical measures of soil N availability, and changes in these variables due to N inputs may feed back to soil C storage through a variety of biotic and abiotic pathways. We conducted a meta-analysis of the responses of soil C storage, C/N, and net N-mineralization (N_{min}) to N inputs in north temperate forests. The modes of N addition we considered were the establishment of N-fixing vegetation (N_{fix}), N-fertilization (N_{fert}), and simulated chronic N deposition (N_{dep}). Overall, N inputs increased soil C (+7.7%) and N_{min} (+62%), while decreasing C/N (−4.9%). Soil C concentrations and C storage (pool sizes) responded similarly to N inputs, although increased soil C storage occurred only in the mineral soil (+12.2%). C/N shifts were restricted to the forest floor (−7.8%), whereas forest floor and mineral soil N_{min} responses to N inputs were very similar (+61% and +64%, respectively). Significant between-study variation in the effects of N inputs on soil parameters was related to the mode of N addition, biogeographic factors, and time. Temporal relationships between N inputs and soil response parameters suggested that increases in forest floor and mineral soil N_{min} were large but transient, and were followed by decadal-scale changes in forest floor C/N and mineral soil C storage. Temporal patterns present in the dataset could have been due to changes in soil organic matter decomposition and stabilization, or increased plant productivity and litter inputs. In either case, the results of this study quantitatively demonstrate that managing forest N supply affects N availability and soil C storage, and highlight the importance of long-term measurements for accurately assessing the effects of N inputs on forest soils.

1. Introduction

Nitrogen inputs in forests can affect soil C storage through effects on plant growth, litter production, and decomposition and stabilization of soil organic matter (SOM). Plant growth and litter production increase with the net rate of N supply by N-mineralization (N_{min}; Aber et al., 1985; Reich et al., 1997), which occurs when inorganic N is released from litter and SOM during decomposition (*sensu* Baldock and Skjemstad, 2000). In turn, substrate C/N ratios (i.e., litter and SOM) affect the processes involved in soil C decomposition, stabilization, and N-mineralization (Sollins et al., 1996; Vance and Chapin, 2001). Increasing forest N supply often affects N_{min} and soil C/N (Gundersen et al., 2006), so changes in these soil parameters may feed back to soil C storage through biotic and abiotic pathways.

Soil C storage is important because it affects forest productivity (Jurgensen et al., 1997; Grigal and Vance, 2000), and acts as a critical sink and source of atmospheric carbon (Kirschbaum, 1995). Soil C pools comprise the principal storehouse of energy for the nutrient-recycling activity of heterotrophic microbes, so maintaining soil C stocks is vital for sustaining forest productivity (Attiwill and Adams, 1993). Furthermore, SOM contains significant amounts of water, C, and N — all of which are exchanged between the biosphere and the atmosphere to affect Earth's atmospheric chemistry, energy and water budgets, and climate (Raich and Schlesinger, 1992; Conrad, 1996). Therefore, understanding how N supply affects forest soil C storage is fundamentally important for anticipating changes in ecosystem goods and services ranging from forest products, to water resources, to greenhouse gas mitigation.

The effects of N inputs on forest soil C and N dynamics have been studied through N-fertilization experiments, investigations of the biogeochemistry of N-fixing plants, and simulated chronic N

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deposition. Results from individual experiments are often highly variable, though some have demonstrated significant changes in soil C storage, C/N, and N_{min} in response to N inputs. However, this body of research has not been subject to quantitative synthesis since a meta-analysis by Johnson and Curtis (2001), who examined the effects of forest management, including fertilization and N-fixing plant establishment, on soil C and N storage. We collected data from north temperate forest sites exposed to experimentally elevated rates of N supply to address the following questions: 1) Do N inputs significantly affect soil C storage, C/N, or N_{min}? 2) Do soil responses to N inputs vary regionally, or according to species composition? 3) Do different modes of N addition (i.e., N-fertilization, N-fixing vegetation, and N deposition) induce different effects on soil C storage, C/N, and N_{min}? Meta-analysis is a powerful statistical tool for addressing these questions, because it can detect underlying patterns that are broadly consistent across studies, even when such patterns are obscured by variability within the individual studies.

2. Materials and methods

2.1. Literature searches and data extraction

We conducted this meta-analysis following the general methods of Curtis (1996) and Johnson and Curtis (2001). We searched the peer-reviewed literature using keyword searches within the online reference databases ISI Web of Science, BIOSIS, Agricola, and CAB Direct. Keyword search strings were combinations of terms such as: forest, soil C, soil N, fertilization, N-fix, N deposition, chronic N, soil amendment, and generic names of N-fixing plants commonly used in forestry. Our literature searches returned over 2600 references, but only 57 met our inclusion criteria of reporting control and treatment values for at least one response parameter of interest (soil C, C/N, or N_{min}) and being conducted in North American or European temperate forest (4–8 months of mean air temperature > 10 ° C; Köppen, 1931). We accepted soil C concentrations and pool sizes as metrics of soil C, and used meta-analysis to determine whether concentrations and pool sizes significantly differed in their responses to N inputs. Among publications that reported both concentrations and pool sizes, we chose pool sizes as the response parameter, and we calculated soil C pool sizes for publications that reported concentrations and bulk densities. The term 'soil C storage' as used in this study denotes soil C pool sizes only; we use the more general term 'soil C' when referring to soil C estimates that encompass both types of reporting units. N_{min} was measured in anaerobic and aerobic conditions, in lab and field incubations, and over variable temporal scales. Elevated N input treatments, which we refer to as modes of N addition, were N-fixing vegetation (N_{fix}), N-fertilization (N_{fert}; without additional nutrients; one or fewer applications per year), or simulated chronic N deposition (N_{dep}; 3–50 applications per year). We excluded N_{fert} experiments in which additional nutrients were added (e.g., P, K, and Ca) because additional elements are known to interact with N inputs and affect soil C and N cycling in complex ways (Thirukkumaran and Parkinson, 2000; Compton and Cole, 2001).

We extracted meta-data (potentially useful predictor variables) from each publication, including temporal, climatic, soil chemical and physical data, and descriptors of measurement units and analytical methods. One pertinent distinction in the soil physical data category was the soil layer sampled. We extracted data for organic and mineral soil components separately, and coded the data so that we could test for differences between soil layers defined as forest floor and mineral soil (ranging from 5 to 100 cm deep). Sample size limitations precluded analyzing topsoil and subsoil separately, which likely added variability to the mineral soil component due to different cycling rates commonly observed in upper and lower soils. We categorized experimental forest sites into three broadly defined biogeographic groups, including: 1) western conifers (WC), which were mostly Pacific Northwest sites, but also included cordilleran forests in California and the southwestern United States, 2) northeast hardwoods (NEH), which included sites in the eastern United States north and east of Illinois, and 3) northeast conifers (NEC), which combined northeast U.S. and northern European sites, which were found not to differ significantly in any analyses.

2.2. Meta-analysis

Meta-analysis estimates the magnitude of change in a parameter (i.e., the 'effect size') in response to an experimental treatment, which may be applied across a wide range of experimental systems and conditions. We used the ln-transformed response ratio R to estimate treatment effect size:

$$ln(R) = ln\left(\overline{X}^E / \overline{X}^C\right) \tag{1}$$

Where $\bar{X}^E$ is the mean value of treatment (elevated N) observations, and $\bar{X}^C$ is the mean value of control observations for a given set of experimental conditions, for soil C, C/N, or N_{min}. The number of response ratios (k) from a given publication depends on how many sets of experimental conditions are imposed. For example, one publication with soil C storage data from control soils and four different levels of N_{fert} would yield $k = 4$ response ratios, or 'studies'. Because it is unitless, the effect size R is a standardized metric that allows comparison of data between experiments reporting responses in different units (Hedges et al., 1999). After back transformation ($e^{\ln(R)}$), R can be conceptualized as the proportional change (%) in a parameter relative to its control value. When error terms and sample sizes are reported for each $\bar{X}^E$ and $\bar{X}^C$, a parametric, weighted meta-analysis is possible, but many publications we found did not report these data. Therefore, in order to include as many studies as possible, we used an unweighted meta-analysis, in which confidence intervals around mean effect sizes are generated with nonparametric resampling techniques (bootstrapping; Rosenberg et al., 1997). We performed analyses using MetaWin software (Sinauer Associates, Sunderland, MA USA).

One of our principal goals in this analysis was to identify categorical variables that had consistent impacts on soil C storage, C/N, and N_{min} responses to N inputs. Accomplishing this task with meta-analysis is similar to using analysis of variance to partition the total variance of a group of observations (Q_t, the total heterogeneity) into two components: within- and between-group heterogeneity (Q_w and Q_b, respectively; Hedges and Olkin, 1985). In such a Q_b analysis, a categorical variable that defines a group of response ratios with a large Q_b is a better predictor of variation than a categorical variable associated with small response-group Q_b. We examined the Q_b of all categorical variables within each of the three response parameters to identify those which consistently explained the most between-group heterogeneity in soil C, C/N, and N_{min} responses to N inputs. In Q_b analysis, and all other meta-analyses, we accepted tests with $P < .10$ as statistically significant.

N_{min} response ratios were considerably more variable than soil C and C/N response ratios. This is partly due to the fact that, while response ratios of soil C and C/N cannot be negative, N_{min} response ratios can, when either the control or elevated N plots exhibit net N-immobilization. In the N_{min} database, 15 of 190 response ratios involved negative N_{min} (i.e., net N-immobilization), which we felt represented a condition fundamentally different from the majority of response ratios, which showed significant (and quite large) increases in N_{min} following N inputs. Therefore, although data transformation would have allowed us to consider net N-immobilization and N_{min} together, we determined to consider separately the 15 response ratios exhibiting net N-immobilization.

2.3. Dataset information

Our dataset comprised 712 response ratios from 72 experimental forest sites subjected to N inputs. Information and references for these data are presented in Appendix A, and the full dataset is available through the USDA Forest Service Northern Research Station (http://www.nrs.fs.fed.us/niacs/tools/).

3. Results and discussion

3.1. Overview: effects of N inputs on soil parameters

Increasing forest N supply caused significant changes in soil C, C/N, and N_{min}. Overall results of the meta-analysis revealed that N inputs increased soil C (+7.7%) and N_{min} (+62%), while causing C/N to decline (−4.9%). However, changes in the response parameters varied between forest floors and mineral soils, and among modes of N addition (Table 1; Fig. 1). In addition to soil layer and mode of N addition, Q_b analysis indicated that time and biogeography were significant predictors of variation among soil responses to N inputs, at least for soil C and C/N (Table 1). Because there is strong conceptual basis for separating forest floor and mineral soil responses to N inputs, we performed Q_b analyses separately for these two soil layers, and the mode of N addition, biogeographic group, and time category generally remained significant predictors of variation, primarily among soil C and C/N (Table 2). Most other predictor variables we collected during data extraction were not statistically significant. Those predictors which were significant were either confounded with other variables, or explained less variation (lower Q_b) than soil layer, mode of N addition, biogeographic group, and time. Therefore, most of our Results and Discussion is framed in the context of these sources of variation. Additional sources of variation are considered in Section 3.6.

3.2. Forest floor vs. mineral soil responses to N inputs

When all modes of N addition were considered together, forest floor and mineral soil responses to N inputs differed significantly for two of the three response parameters (soil C and C/N; Table 1). While neither forest floor %C nor C storage changed with N inputs (Fig. 1A), mineral soils showed significant increases in %C (+11.0%) and C storage (+12.2%; Fig. 1D). In the forest floor, N inputs combined with unchanged soil C to decrease C/N by 7.8% (Fig. 1B), while mineral soil C/N did not change (Fig. 1E). Forest floors and mineral soils did not exhibit significantly different N_{min} responses to N inputs, as the two layers showed increases of 61% and 64%, respectively, with overlapping 95% confidence intervals (Fig. 1C,F).

Table 1
Sources of variation among overall soil responses to N inputs.

Response parameter	Predictor variable	*k*	Q_b	Q_t	*P*
Soil C	Soil layer[a]	302	1.5	27	<0.005
	Biogeographic group[b]	302	1.4	27	<0.005
	Mode of N addition[c]	302	1.5	27	<0.005
	Time category[d]	293	1.5	25	<0.005
Soil C/N	Soil layer	220	0.16	5.6	<0.05
	Biogeographic group	220	0.31	5.6	<0.005
	Mode of N addition	220	0.46	5.6	<0.005
	Time category	208	1.1	5.2	<0.005
Net N-min	Soil layer	175	<0.10	125	NS
	Biogeographic group	175	2.3	125	NS
	Mode of N addition	175	5.0	125	<0.05
	Time category	172	3.1	124	NS

Within each response parameter, the amounts of between-group (Q_b) and total (Q_t) heterogeneity associated with each predictor variable are shown. The statistical significance of Q_b for each predictor variable is shown in column (*P*), while column (k) is the number of response ratios tested in the groups defined by each predictor variable. Note that soil C statistics include both concentrations and pool sizes, which were not significantly different in the overall analysis.

[a] Forest floor or mineral soil.

[b] Northeast conifers, northeast hardwoods, or western conifers.

[c] N-fixing vegetation, N-fertilization, or simulated N deposition.

[d] Time since N inputs initiated: 0–10, 11–25, or >26 yr.

The observation that N inputs affected forest floor and mineral soil C and C/N differently suggests that multiple (though likely interdependent) processes are responsible for the responses of these soil layers to N inputs. The forest floor frequently is the strongest sink for N inputs to temperate forests (Buchmann et al., 1996; Tietema et al., 1998; Currie, 1999; Nadelhoffer et al., 1999; Templer et al., 2005), and the result that C/N declined significantly in this layer, but not in the mineral soil, supports this pattern. In comparison to C stored in the mineral soil, forest floor C substrates typically comprise a relatively small C pool with high C/N (~30–70), a relatively fast turnover time, and an inverse relationship between C/N and initial rates of decomposition and N_{min} (Sollins et al., 1984; Fog, 1988; Berg, 2000; Homann et al., 2001; Neff et al., 2002; Swanston et al., 2004). Accordingly, by lowering the C/N ratio, N inputs may accelerate forest floor C and N cycling by increasing decomposition and N_{min}. However, higher N_{min} is correlated with greater plant N uptake, productivity, and litterfall (Reich et al., 1997), which could offset potential C losses from faster forest floor decomposition with increased N inputs. In addition to lowering forest floor C/N and affecting plant and microbial processes, the retention of N inputs in the forest floor may elevate dissolved organic matter (DOM) and inorganic N export to the mineral soil below (Currie et al., 1996; Gundersen et al., 1998). Downward export of DOM from the forest floor may cause several significant changes in mineral soil C dynamics. First, adsorption of DOM molecules onto mineral particle surfaces may directly increase mineral soil C and N concentration and storage (Qualls and Haines, 1992; Kalbitz et al., 2000). Furthermore, accumulation of complex DOM molecules (such as polyphenols), as well as inorganic N, may reduce rates of microbial activity associated with SOM degradation (Hattenschwiler and Vitousek, 2000; Waldrop et al., 2004; Grandy et al., 2008). The decreasing C/N and increasing N_{min} in the forest floor suggest a sustained increase in N export to mineral soil, which maintains a balance between N and C as both accumulate in mineral soils in response to N inputs. This observation supports the idea that long-term ecosystem C accumulation is stoichiometrically limited by N (progressive N limitation; Luo et al., 2004; Johnson, 2006), and suggests a principal role of N redistributions between the forest floor and mineral soil, which have been studied by direct manipulation (Hart and Firestone, 1991) and ecosystem modeling (Currie et al., 2004).

3.3. Mode of N addition

The mode of N addition (N_{fix}, N_{fert}, and N_{dep}) was a highly significant predictor of variation in soil responses to N inputs in both layers (Table 2). While forest floor C storage did not change with N inputs, significant increases in mineral soil C storage occurred in response to N_{fix} (+11.8%) and N_{fert} (+23.5%), but not N_{dep} (Fig. 1A,D). In the forest floor, the three modes of N addition caused slightly different (but all negative) changes in C/N. The largest forest floor C/N decrease was due to N_{fix} (−13.5%), while N_{fert} (−9.3%) and N_{dep} (−4.1%) caused smaller declines (Fig. 1B). Mineral soil C/N changes varied significantly between modes of N addition, with N_{fix} and N_{dep} causing C/N changes of −6.5% and +4.0%, respectively, while N_{fert} had no significant effect (Fig. 1E). In the forest floor, the three modes of N addition affected N_{min} similarly (Fig. 1C), but this was not the case for mineral soils. Specifically, although N_{dep} did not change mineral soil N_{min}, N_{fix} and N_{fert} caused increases of 73% and 573%, respectively (Fig. 1F). The large effect of N_{fert} on N_{min} probably reflects high variability due to a limited sample size, though it is interesting to note that all 15 response ratios involving net N-immobilization were from N_{fert}, with most originating from mineral soils (data not shown).

While there were interesting trends in forest floor responses to N inputs, such as the tendency for the three modes of N addition to decrease forest floor C/N to varying degrees, the differences between modes of N addition generally were greater in the mineral soil. The effects of N inputs by N_{fix} and N_{dep} were in particularly marked contrast. Under N_{fix}, mineral soil C/N decreased, and C storage and N_{min} increased.

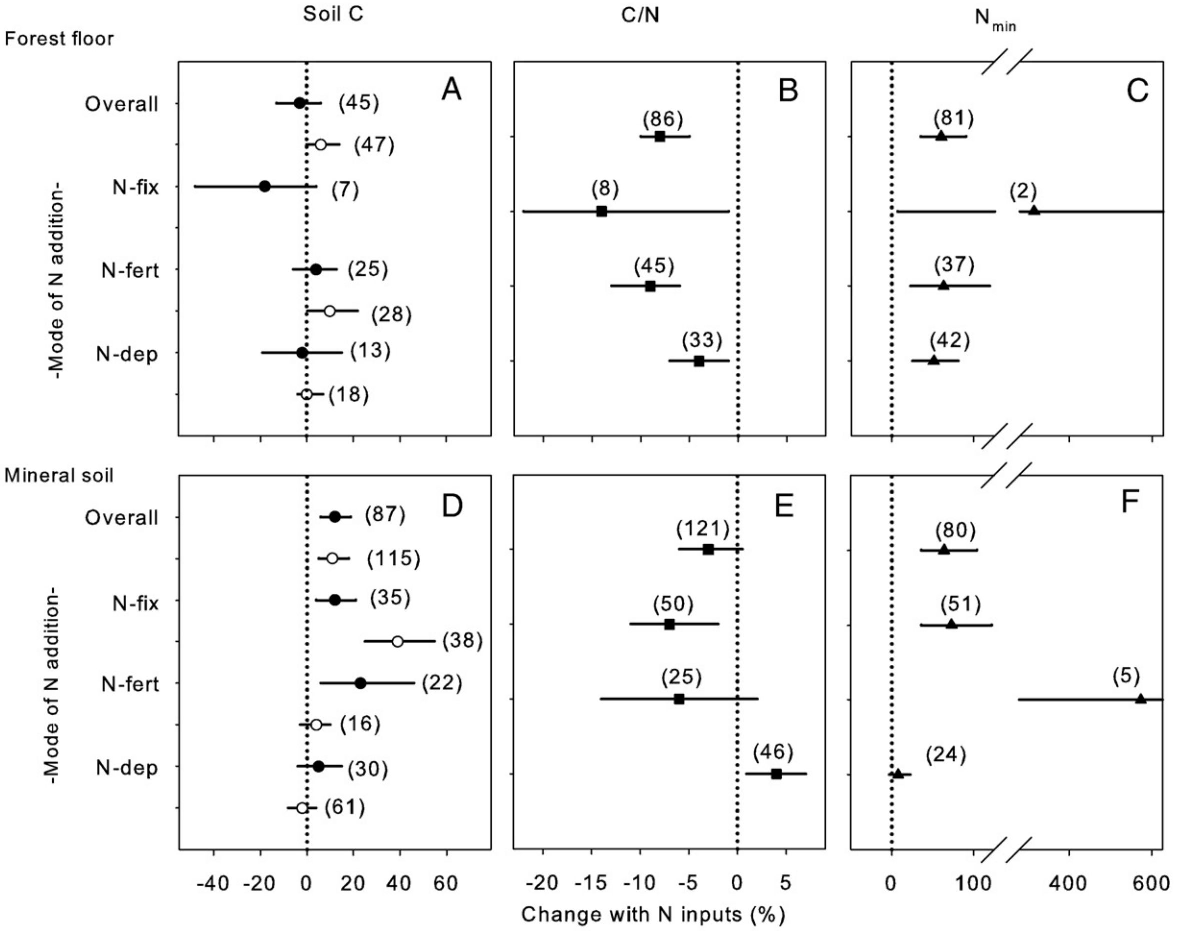

Fig. 1. The effects of N inputs on soil C, C/N, and N_{min} in forest floors (panels A–C) and mineral soils (panels D–F). Points are means ± bootstrapped 95% confidence intervals, with number of studies (*k*) in parentheses. Groups with confidence intervals overlapping the dotted reference line (0% change) show no significant effects of N addition. Soil C responses to N inputs are shown separately for pool sizes (filled symbols) and concentrations (open symbols). For each response parameter, the effects of N inputs are shown overall, and for individual modes of N addition, including the establishment of N-fixing vegetation (N-fix), large-dose N-fertilization (N-fert), and simulated chronic N deposition (N-dep). Note that points plotted in panels C and F have 95% CIs with upper bounds beyond the *x*-axis maximum (>600% increase in N_{min}).

Table 2
Sources of variation among soil responses to N inputs, shown separately for forest floors and surface mineral soils.

Response parameter	Predictor variable	Forest floor				Mineral soil			
		k	Q_b	Q_t	*P*	*k*	Q_b	Q_t	*P*
Soil C storage	Biogeographic group	45	0.20	5.1	NS	87	0.78	6.9	<.05
	Mode of N addition	45	0.74	5.1	<.05	87	0.34	6.9	NS
	Time category	44	0.23	4.5	NS	86	0.52	6.9	<.05
Soil C/N	Biogeographic group	86	0.11	1.4	<.05	121	0.27	3.8	<.05
	Mode of N addition	86	0.10	1.4	<.05	121	0.32	3.8	<.05
	Time category	84	0.23	1.3	<.005	111	0.87	3.4	<.005
Net N-min	Biogeographic group	81	0.69	52	NS	80	1.8	68	NS
	Mode of N addition	81	2.0	52	NS	80	14	68	<.005
	Time category	80	<0.10	52	NS	80	3.5	68	NS

Within each response parameter, the amounts of between-group (Q_b) and total (Q_t) heterogeneity associated with each predictor variable are shown. The level of statistical significance for each predictor variable is shown in column (*P*), while column (*k*) is the number of response ratios tested in the groups defined by each predictor variable. Note that soil C storage statistics include pool sizes only. See Table 1 notes for the categorical groups defined by each predictor variable.

Mineral soil N storage also increased significantly, at a rate nearly equal to that observed for C storage (+10.5%). Soil C and N storage increases were equal within the bounds of their confidence intervals, indicating that the decrease in C/N reflects a fine-scale shift in organic matter chemistry more than a bulk change in soil C and N storage. Thus, the decline in soil C/N reflects an improvement in organic matter quality that increased N_{min}, suggesting that the microbial activity responsible for N_{min} was N-limited in these study systems (Vance and Chapin, 2001). N_{dep}, on the other hand, increased mineral soil C/N, but did not significantly change C storage or N_{min}. Supplemental meta-analyses indicated that the increase in mineral soil C/N also did not involve any decrease in mineral soil N storage. However, mineral soil C and N storage showed nonsignificant tendencies that would tend to increase mineral soil C/N, including an effect size of +8.2% for C storage, and an effect size of −4.9% for N storage. Thus, the mineral soil C/N increase probably reflects an interaction of several processes that have been documented in N_{dep} studies, including increased soil C storage (Pregitzer et al., 2008) and N exports from mineral soil through NO_3^- leaching (Kjonaas et al., 1998; Aber et al., 2003) and vegetation N uptake (Magill et al., 2000; McNulty et al., 2005).

Taken together, mineral soil responses to N_{fix} and N_{dep} may represent points along an ecosystem trajectory from N limitation to N saturation. At the onset of N inputs, when N is limiting, highly efficient foliar N resorption results in the transfer of high C/N litterfall to the forest floor, where high C/N materials promote N retention (Vitousek, 1982; Johnson et al., 2000). Inputs of relatively high C/N root litter may also be important for retaining N (Stump and Binkley, 1993; Silver and Miya, 2001). Initially, retention of N inputs by the forest floor lowers its C/N and enhances N_{min}, as is observed for all modes of N addition. However, N may become less limiting as ongoing N inputs are immobilized, causing decreased vegetation and forest floor C/N and N retention capacity, and increases in nitrification, DOM, and N export from the forest floor to the mineral soil (Currie et al., 1996; Gundersen et al., 1998). As C and N accumulate in the mineral soil and its C/N decreases, these changes in C and N pool sizes and stoichiometry may accelerate N_{min}. This appears to be the N status of the N_{fix} studies in our database. Continuing N inputs could cause mineral soil C/N to drop even further, below the threshold value that limits NO_3^- leaching. By the time this stage has been reached, mineral soil N_{min} no longer increases in response to continued N inputs. Rather, lower rates of decomposition interact with elevated nitrification and N leaching and prevent mineral soil C/N from decreasing any further. This is the N status of the N_{dep} studies in our database, and the significant increase in mineral soil C/N among these studies may not represent a long-term trend, but rather a short-term periodic oscillation about some steady state value of mineral soil C/N. If different modes of N addition do, in fact, have comparable long-term effects on C and N biogeochemistry, then the forest floor and mineral soil may be expected to play sequential roles in N retention as ecosystem N status moves from N limitation to saturation.

In mineral soils, the effects of N_{fert} were distinct from those associated with N_{fix} and N_{dep}, in that C storage increased without any significant change in C/N. This suggests that mineral soil C and N accumulated at equal rates, perhaps due to elevated DOM and N exports from the forest floor (see Section 3.2). Mineral soil N_{min} responses to N_{fert} were somewhat variable, with N inputs causing very large N_{min} increases in some studies (Fig. 1F), and net N-immobilization in others. Ten of the 15 response ratios involving net N-immobilization were from mineral soils (the other 5 were forest floors), and all 15 came from experiments in which the most recent fertilizer application occurred within 1 yr of sampling (Aarnio and Martikainen, 1992; Matson et al., 1992; Vestgarden et al., 2003). The very large degree of variation among N_{min} responses to N_{fert} may exist because large N additions perturbed the balance between substrate and microbial biomass C/N, leading to shifts between net immobilization and mineralization (Vance and Chapin, 2001). Another possibility is that soils collected for incubation shortly after large N_{fert} doses were impacted by high spatial variability and N-rich microsites (Le Cadre et al., 2004). In any case, it is clear that N_{min} changes caused by N_{fert} were substantially less predictable than the changes associated with N_{fix} and N_{dep}, and that these changes occasionally had the counter-intuitive result of decreasing inorganic N supply.

3.4. Biogeographic groups

Biogeography was a significant source of variation among soil C storage and C/N responses to N inputs (Table 2, Figs. 2 and 3). Although sample sizes preclude making strong inferences about the full set of interactions between soil layers, modes of N addition, and biogeographic groups, several patterns emerge when all modes of N addition are considered collectively within each biogeographic group. First, forest floor C/N declines were greater among WC (−12.5%) than NEC (−6.3%), while NEH showed no significant change (Fig. 2). Second, significant increases in mineral soil C storage were restricted to WC (+25.6%), which also was the only group that exhibited a significant decline in C/N (−6.9%; Fig. 3). Finally, WC had greater N_{min} increases than NEC or NEH in both soil layers (Figs. 2 and 3).

The apparent biogeographic variation in forest floor C/N responses to N inputs may reflect the modes of N addition most commonly practiced in each biogeographic group, or relate to inherent differences in biogeochemistry between the three forest types. Unfortunately, all NEH forest floor C/N response ratios originated from N_{dep} studies, confounding biogeography with the mode of N addition for this response parameter. However, when biogeographic variation is considered simultaneously for all three response parameters and both soil layers, confounding relationships between biogeography and the mode of N addition are minimized. This is because, when taking such a 'big-picture' view, most comparisons between biogeographic groups have at least some response ratios from each mode of N addition. From this perspective, it becomes clear that WC generally were more responsive to N inputs than NEH or NEC, as evidenced by the greater number of significant responses to N inputs in the WC group. The result that N inputs were more likely to significantly affect WC than NEH and NEC soils may be due to geographic variation in long-term atmospheric deposition. Unlike WC sites, which receive comparatively little atmospheric pollution, NEH and NEC studies occurred in regions that have experienced decades of moderate-to-high atmospheric N deposition (Lovett, 1994; Galloway et al., 2003). Due to their history of N inputs, NEH and NEC systems may be less sensitive to further N inputs and perturbations of the N cycle. Indeed, in the northeast United States and Europe, some of the direct effects of N inputs on forest soils may have already occurred due to the atmospheric N load. Forest growth responses to N inputs that feed back to soil processes also may be less likely in NEH and NEC than

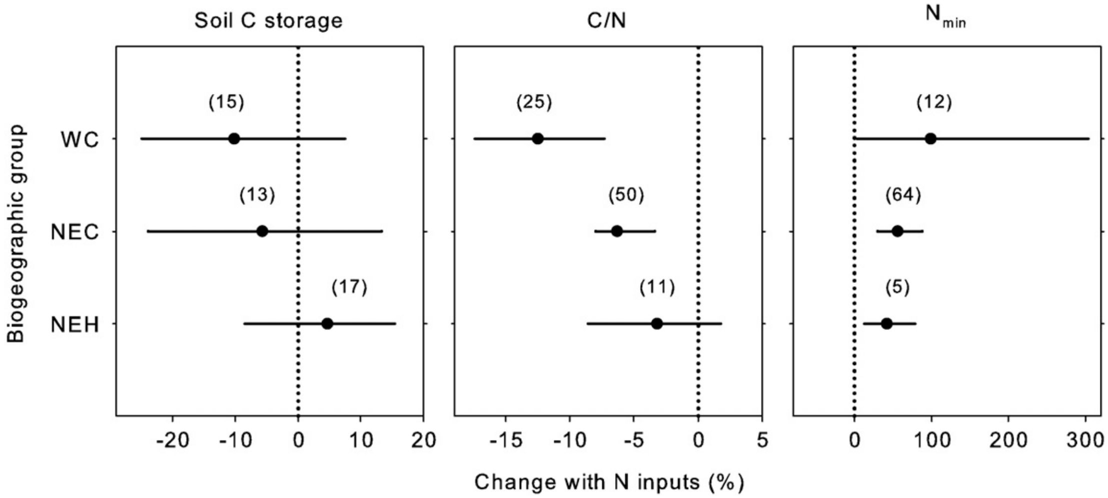

Fig. 2. The effects of N inputs on forest floor parameters, by biogeographic group. Points are means ± bootstrapped 95% confidence intervals, with number of studies (*k*) in parentheses. Soil C storage response ratios include pool sizes only. Biogeographic groups are western conifers (WC), northeast conifers (NEC), and northeast hardwoods (NEH).

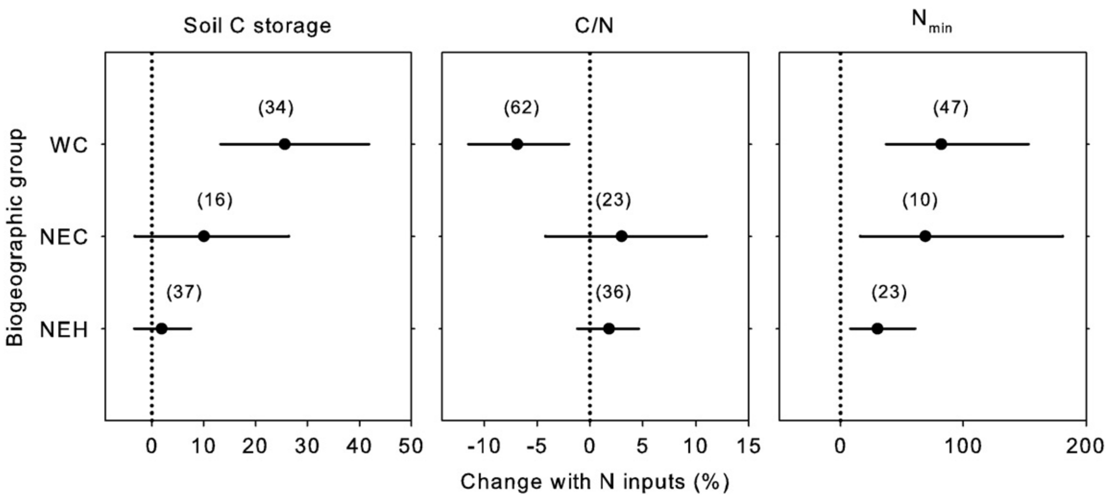

Fig. 3. The effects of N inputs on mineral soils, by biogeographic group. Points are means ± bootstrapped 95% confidence intervals, with number of studies (*k*) in parentheses. Soil C storage response ratios include pool sizes only. See Fig. 2 for biogeographic group abbreviations.

in regions with lower rates or a shorter history of atmospheric deposition, such as WC. In addition to the independent, direct role that initial ecosystem N status may have played in governing soil responses to N inputs, certain modes of N addition are more common in some locations than others. For example, N_{fix} and N_{fert} are more likely to be employed in systems of lower initial fertility (such as WC), while N_{dep} studies frequently occur in areas that have already been subjected to high atmospheric N inputs (e.g., NEH and NEC).

In addition to regional factors, site-specific causes probably contributed to biogeographic variation in soil responses to N inputs. These factors could include variation in: the chemical form of N inputs, management history (Goodale and Aber, 2001; Compton and Boone, 2002), microbial communities (Pennanen et al., 1999), and soil chemical/physical properties (Bergstrom et al., 2001). One particularly important source of variation in soil chemical and physical properties may be the distribution and abundance of labile and recalcitrant OM within the soil matrix, since these two SOM fractions may react differently to N inputs (Sollins et al., 1984; Fog, 1988; Neff et al., 2002; Swanston et al., 2004). Accordingly, geographic variation in pedogenesis and mineralogy are likely to play important roles in soil C responses to N inputs (Shaw et al., 2008). Ultimately, more primary research will be necessary to understand the sources of variation in soil responses to N inputs at even a regional scale. Considerably more effort will be required to determine the roles of site-specific factors.

3.5. Temporal patterns

There were significant temporal trends underlying soil responses to N inputs in the forest floor and mineral soil (Tables 1 and 2). In the forest floor, the time elapsed since initiation of N inputs explained a significant proportion of variation in C/N across all modes of N addition (Fig. 4). Declines in forest floor C/N were relatively consistent across biogeographic groups, though it appeared to take 15–20 yr of N inputs to significantly reduce C/N. Forest floor and mineral soil N_{min} responses to N inputs were not significantly different (Table 1), and pooling the data from both soil layers revealed a nonlinear temporal trend following N_{dep} and N_{fert} treatments (Fig. 5) However, the magnitude and duration of N_{min} increases differed between the two modes of N addition. Initiating relatively small, frequent N inputs (N_{dep}) induced a consistent, large (up to 300%), but short-lived increase in N_{min}, which declined back to control values within 4 yr. Larger, less frequent N inputs from N_{fert} were capable of causing larger short-term N_{min} increases than N_{dep}, but N_{min} declined more rapidly following fertilizer addition, and there were also numerous instances of net N-immobilization following N_{fert}. While there was no temporal component to forest floor C responses to N inputs, mineral soils accumulated C over time. Temporal trends in %C and C storage in mineral soils were similar, although significant increases were not detected until the second time interval evaluated (11–20 yr of N inputs, Fig. 6).

The temporal patterns underlying soil C, C/N, and N_{min} responses to N inputs have many possible explanations; two will be considered here. First, the long-term trajectories of all three response parameters support the idea (from Section 3.2) that N inputs have opposite effects on N cycling and C storage in two distinct SOM pools. Initially, N inputs may subsidize microbial degradation of labile, high C/N litter or SOM, increasing decomposition and N_{min} (see Section 3.2; also, Knorr et al., 2005). However, accelerated microbial activity may rapidly deplete the supply of labile SOM, causing N_{min} to decrease back towards pretreatment levels. Continued retention of N inputs decreases forest floor C/N, reducing the decomposability of recalcitrant SOM, but there is no further change in N_{min}. Instead, an increasing proportion of mineralized N may be nitrified and exported to the mineral soil, along with DOM leached from the forest floor. Over time, NO_3^- and DOM accumulation in the mineral soil increase C storage through a variety of mechanisms, including the inhibition of microbial enzyme production and consequent alteration of OM degradation (Waldrop et al., 2004; Waldrop and Zak, 2006). Enhanced

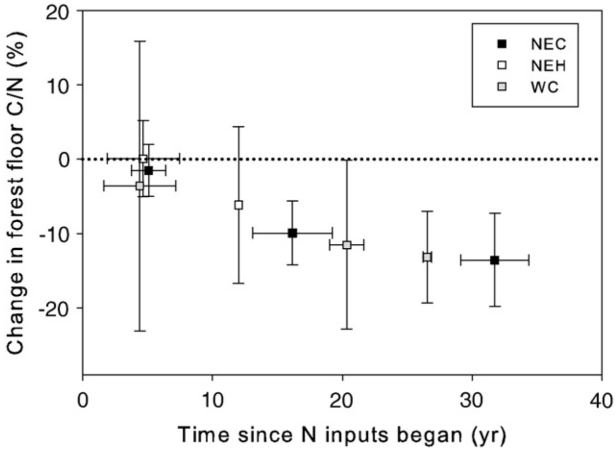

Fig. 4. Changes in forest floor C/N as a function of the time elapsed since N inputs began. Data from all modes of N addition are combined within each biogeographic group (see Fig. 2 for abbreviations). Points are means ± 95% confidence intervals within each time category (0–10, 11–25, and >26 yr).

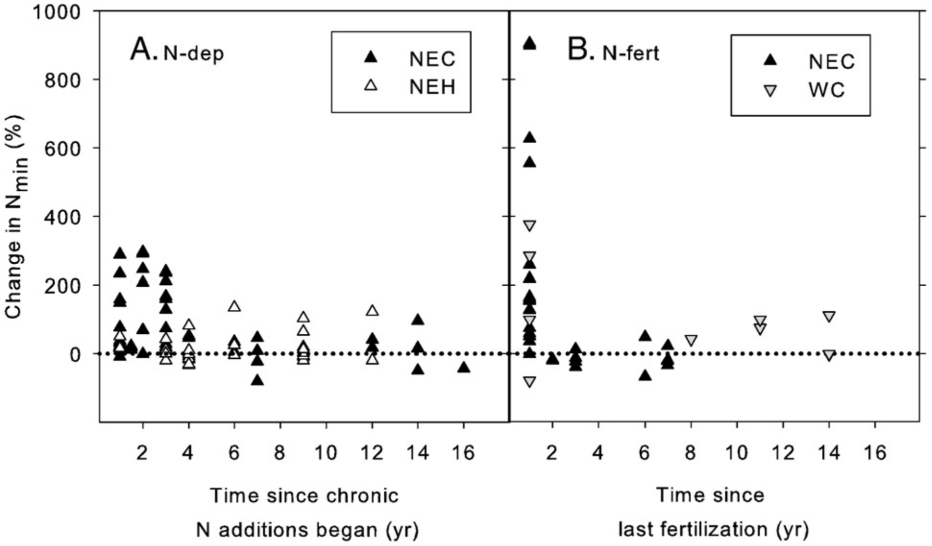

Fig. 5. Changes in N_{min} over time in response to simulated chronic N deposition (panel A) and large-dose N-fertilization (panel B). Forest floor and mineral soil data are pooled in this figure, and each point is one response ratio. Note that three response ratios corresponding to immediate N_{min} increases of over 1000% are not shown in B.

stabilization of SOM might also occur due to greater biogeochemical recalcitrance of degraded, N-rich litter (Berg, 2000). Nitrogenous compounds may also foster more biogeochemically stable organo-mineral associations (Sollins et al., 2006; Kleber et al., 2007). These chemical and physical changes in SOM affect not only soil C storage, but also are important drivers of the attenuation of N_{min} after its initial increase in response to N inputs (Aber et al., 1998). Therefore, the N_{min} increase following N inputs may represent a short-term indicator of increased microbial activity within a small and rapidly depleted labile SOM pool. The long-term effect of N inputs may be to increase soil C storage by lowering forest floor C/N, causing leaching of compounds into the mineral soil that stabilizes SOM. However, since our analysis did not specifically investigate two distinct SOM pools, we cannot definitively conclude that the two-pool explanation is the mechanism responsible for temporal patterns in soil C and N.

A second, but not mutually exclusive, explanation for the temporal patterns of soil C storage, C/N, and N_{min} is that N inputs increased N availability, resulting in greater plant growth and plant litter inputs to soil. In addition to the direct, immediate effects of N inputs on plant growth, N inputs also have a longer-term, indirect effect on plant productivity by increasing N_{min}. N_{min} is positively correlated with plant N uptake and leaf, wood, and fine root production (Nadelhoffer et al., 1985; Reich et al., 1997), suggesting that even short-term increases in N_{min} may enhance growth and subsequent C inputs to soil by litterfall. If some of the litterfall C inputs that follow a forest growth increase become stabilized within the soil, then this could also increase soil C storage. In the long-term, forest trees mine deeper layers of the mineral soil to acquire N (Currie et al., 2004), and root and mycorrhizal litter inputs to these deep soil layers could be the basis for increased mineral soil C storage (Langley and Hungate, 2003; Bird et al., 2008).

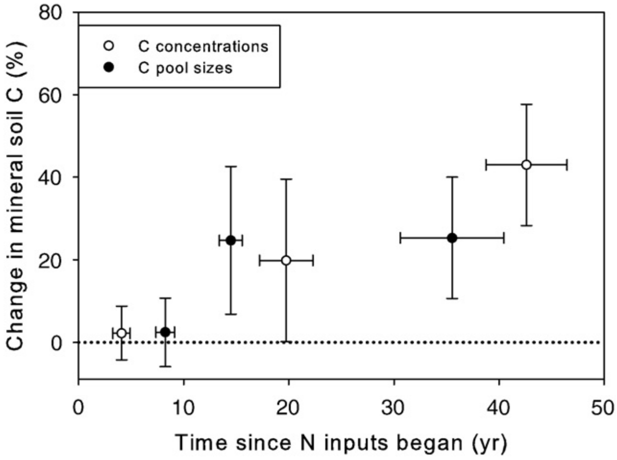

Fig. 6. Changes in mineral soil C as a function of the time elapsed since N inputs began. Data are plotted separately for soil C concentrations (open symbols) and pool sizes (filled symbols), and include response ratios from all modes of N addition and biogeographic groups. Points are means ± 95% confidence intervals within each time category (0–10, 11–25, and >26 yr).

3.6. Other sources of variation

Variation among soil responses to N inputs was most affected by temporal factors and the mode of N addition, but also by biogeographic factors and differences between the forest floor and mineral soil, when Q_b was examined at the response variable level (Table 1). We tested other variables for their predictive capability, such as the chemical form of N inputs, soil texture, and mean annual precipitation, but these and other variables did not have as strong a statistical basis (as determined by Q_b values) for explaining variation simultaneously across the three response parameters we analyzed. We devoted particular attention to testing the effects of data collection and analysis methods on the results reported across different studies, and found little evidence for methodological variation among soil C and C/N response ratios. However, N_{min} increases in response to N inputs appeared to be greatest for *in situ* core (ISC) incubations, slightly less for buried bag (BB) measurements, and least for lab incubations (LI). Qualitatively, it is interesting to note that the degree of physical disturbance (ISC<BB<LI) was negatively correlated with the apparent increase in N_{min} under N inputs. Differences among methods are consistent with findings from studies comparing multiple methods of estimating N_{min} (Binkley et al., 1986, 1992a), but are not likely to have confounded the results of our analysis since categorical groups defined by time, mode of N addition, soil layer, and biogeography included response ratios from each N_{min} method.

4. Conclusions

Using meta-analysis to test a database of over 700 response ratios, we detected statistically significant changes in soils subjected to N inputs at 72 north temperate experimental forest sites. Our analysis identified the mode of N addition (N_{fix}, N_{fert}, and N_{dep}) and time elapsed since N inputs began as the strongest predictors of variation in soil C, C/N and N_{min} responses to N inputs. Although biogeographic factors contributed to variation among soil responses to N inputs, our results demonstrate broadly consistent effects of N inputs on soil C (+7.7%), C/N (−4.9%), and N_{min} (+62%). Temporal patterns and relationships between forest floor and mineral soil C and N properties suggest that these results may have been due to a combination of N-induced shifts in SOM decomposition/stabilization, and increased plant growth and litter inputs to soil. Further primary research into the effects of N supply on forest C and N cycling will add to the already large body of work in this area, making more powerful cumulative meta-analyses possible. The present meta-analysis identifies the need for more targeted research into the mechanisms by which N inputs increase soil C storage, especially across sites with diverse characteristics and management practices.

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Appendix A. Study information for the references included in the meta-analysis

Reference	Mode of N addition	BG group	Dominant canopy genera	Location
Aarnio and Martikainen (1992)	N-fert	NEC	*Pinus*, *Picea*	Southern Finland
Aarnio and Martikainen (1995)	N-fert	NEC	*Pinus*, *Picea*	Southern Finland
Aber et al. (1993)	N-dep	NEC, NEH	*Pinus*, *Quercus*, *Acer*	Massachusetts, USA
Adams et al. (2005)	N-fert	WC	*Pseudotsuga*	Washington, USA
Binkley and Husted (1983)	N-fix	WC	*Pseudotsuga*	British Columbia
Binkley et al. (1982)	N-fix	WC	*Pseudotsuga*	Oregon, USA
Binkley et al. (1992a)	N-fix	WC	*Pseudotsuga*	Washington and Oregon, USA
Binkley et al. (1992b)	N-fix	WC	*Pseudotsuga*	Washington and Oregon, USA
Binkley (1983)	N-fix	WC	*Pseudotsuga*	Washington, USA and British Columbia
Bormann and Debell (1981)	N-fix	WC	*Pseudotsuga*	Washington, USA
Cole et al. (1990)	N-fix	WC	*Pseudotsuga*	Washington, USA
Emmett et al. (1995)	N-dep	NEC	*Picea*	Scotland
Erickson et al. (2005)	N-fix	WC	*Abies*, *Calocedrus*, *Pinus*	California, USA
Fox (2004)	N-fert	WC	*Pseudotsuga*	Washington, USA
Frey et al. (2004)	N-dep	NEC, NEH	*Pinus*, *Quercus*, *Acer*	Massachusetts, USA
Gallo et al. (2005)	N-dep	NEH	*Acer*, *Quercus*, *Tilia*	Michigan, USA
Gilliam et al. (1996)	N-dep	NEH	*Acer*, *Betula*, *Liriodendron*	West Virginia, USA
Gilliam et al. (2001)	N-dep	NEH	*Acer*, *Betula*, *Liriodendron*	West Virginia, USA
Griffiths et al. (1998)	N-fix	WC	*Pseudotsuga*	Washington, USA
Gundersen et al. (1998)	N-dep	NEC	*Picea*	Southern Sweden, Denmark, Scotland
Hart et al. (1997)	N-fix	WC	*Pseudotsuga*	Washington and Oregon, USA
Hungate et al. (2007)	N-fert	WC	*Pinus*	Arizona, USA
Jefts et al. (2004)	N-dep	NEC, NEH	*Picea*, *Abies*, *Fagus*, *Acer*	Maine, USA
Johnson (1995)	N-fix	WC	*Pinus*	California, USA
Kjonaas et al. (1998)	N-dep	NEC	*Picea*, *Pinus*	Southern Sweden
Landgraf et al. (2005)	N-fix	NEC	*Pinus*, *Robinia*	Germany
Lavery et al. (2004)	N-fix	NEC, NEH	*Abies*, *Pinus*, *Tsuga*	British Columbia
Magill et al. (1996)	N-dep	NEC, NEH	*Picea*, *Abies*, *Fagus*, *Acer*	Maine, USA
Magill et al. (2000)	N-dep	NEC, NEH	*Pinus*, *Quercus*, *Acer*	Massachusetts, USA
Matson et al. (1992)	N-fert	WC	*Pseudotsuga*	New Mexico, USA
McNulty and Aber (1993)	N-dep	NEC	*Picea*, *Abies*	Vermont, USA
McNulty et al. (1996)	N-dep	NEC	*Picea*, *Abies*	Vermont, USA
McNulty et al. (2005)	N-dep	NEC	*Picea*, *Abies*	Vermont, USA
Moldan et al. (2006)	N-dep	NEC	*Picea*, *Pinus*	Southern Sweden
Nohrstedt et al. (1988)	N-fert	NEC	*Picea*	Southern Sweden
Nohrstedt (2002)	N-fert	NEC	*Picea*	Southern Sweden
Oakley et al. (2003)	N-fix	WC	*Abies*	California, USA
Oakley et al. (2006)	N-fix	WC	*Abies*	California, USA
Parker et al. (2001)	N-dep	NEC	*Picea*, *Abies*, *Fagus*, *Acer*	Maine, USA
Paschke et al. (1989)	N-fix	NEH	*Juglans*	Illinois, USA
Pregitzer et al. (2008)	N-dep	NEH	*Acer*, *Fagus*	Michigan, USA
Prietzel et al. (2004)	N-fert	WC	*Pseudotsuga*	Washington, USA
Prietzel et al. (2008)	N-fix	NEC	*Pinus*	Germany
Ring et al. (2003)	N-fert	NEC	*Picea*	Southern Sweden
Rothe et al. (2002)	N-fix	WC	*Pseudotsuga*	Oregon, USA
Sjoberg et al. (2003)	N-fert	NEC	*Picea*	Southern Sweden
Smolander et al. (1995)	N-fert	NEC	*Picea*	Southern Finland
Smolander et al. (2005)	N-fert	NEC	*Picea*	Southern Finland
Stanturf and Stone (1994)	N-fert	NEH	*Acer*, *Fraxinus*, *Prunus*	New York, USA
Swanston et al. (2004)	N-fert	WC	*Pseudotsuga*	Washington and Oregon, USA
Tiedemann et al. (1998)	N-fert	WC	*Abies*	Oregon, USA
Vesterdal and Raulund-Rasmussen (2002)	N-fert	NEC	*Picea*	Denmark
Vestgarden and Kjonaas (2003)	N-dep	NEC	*Pinus*, *Picea*	Southern Sweden
Vestgarden et al. (2003)	N-fert	NEC	*Pinus*	Southern Norway
Vestgarden et al. (2004)	N-fert	NEC	*Pinus*	Southern Norway
Waldrop et al. (2004)	N-dep	NEH	*Acer*, *Quercus*, *Tilia*	Michigan, USA
Wallenstein et al. (2006)	N-dep	NEC, NEH	*Picea*, *Abies*, *Pinus*, *Quercus*	Maine, Vermont, Massachusetts, USA
Zak et al. (2006)	N-dep	NEH	*Acer*, *Fagus*	Michigan, USA

See Table 1 for mode of N addition and biogeographic group abbreviations.

References

Aarnio, T., Martikainen, P.J., 1992. Nitrification in forest soil after refertilization with urea or urea and dicyandiamide. Soil Biology & Biochemistry 24 (10), 951–954.

Aarnio, T., Martikainen, P.J., 1995. Mineralization of C and N and nitrification in Scots pine forest soil treated with nitrogen fertilizers containing different proportions of urea and its slow-releasing derivative, ureaformaldehyde. Soil Biology & Biochemistry 27 (10), 1325–1331.

Aber, J.D., Magill, A., Boone, R., Melillo, J.M., Steudler, P., Bowden, R., 1993. Plant and soil responses to chronic nitrogen additions at the Harvard Forest, Massachusetts. Ecological Applications 3 (1), 156–166.

Aber, J., McDowell, W., Nadelhoffer, K., Magill, A., Berntson, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L., Fernandez, I., 1998. Nitrogen saturation in temperate forest ecosystems — hypotheses revisited. Bioscience 48 (11), 921–934.

Aber, J.D., Goodale, C.L., Ollinger, S.V., Smith, M.L., Magill, A.H., Martin, M.E., Hallett, R.A., Stoddard, J.L., 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? Bioscience 53 (4), 375–389.

Adams, A.B., Harrison, R.B., Sletten, R.S., Strahm, B.D., Turnblom, E.C., Jensen, C.M., 2005. Nitrogen-fertilization impacts on carbon sequestration and flux in managed coastal

Douglas-fir stands of the Pacific Northwest. Forest Ecology and Management 220 (1–3), 313–325.

Attiwill, P.M., Adams, M.A., 1993. Nutrient cycling in forests. New Phytologist 124 (4), 561–582.

Baldock, J.M., Skjemstad, J.O., 2000. The role of the soil matrix and minerals in protecting natural organic materials against biological attack. Organic Geochemistry 31, 697–710.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecology and Management 133 (1–2), 13–22.

Bergstrom, D.W., Monreal, C.M., St Jacques, E., 2001. Spatial dependence of soil organic carbon mass and its relationship to soil series and topography. Canadian Journal of Soil Science 81 (1), 53–62.

Binkley, D., 1983. Ecosystem production in Douglas-fir plantations: interactions of red alder and site fertility. Forest Ecology and Management 5, 215–227.

Binkley, D., Husted, L., 1983. Nitrogen accretion, soil fertility, and Douglas-fir nutrition in association with redstem ceanothus. Canadian Journal of Forest Research 13 (1), 122–125.

Binkley, D., Cromack, K., Fredriksen, R., 1982. Nitrogen accretion and availability in some snowbrush ecosystems. Forest Science 28 (4), 720–724.

Binkley, D., Bell, R., Sollins, P., 1992a. Comparison of methods for estimating soil–nitrogen transformations in adjacent conifer and alder–conifer forests. Canadian Journal of Forest Research 22 (6), 858–863.

Binkley, D., Sollins, P., Bell, R., Sachs, D, Myrold, D., 1992b. Biogeochemistry of adjacent conifer and alder–conifer stands. Ecology 73, 2022–2033.

Bird, J.A., Kleber, M., Torn, M.S., 2008. C-13 and N-15 stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. Organic Geochemistry 39, 465–477.

Bormann, B.T., Debell, D.S., 1981. Nitrogen-content and other soil properties related to age of red alder stands. Soil Science Society of America Journal 45 (2), 428–432.

Buchmann, N., Gebauer, G., Schulze, E-D., 1996. Partitioning of 15-N labeled ammonium and nitrate among soil, litter, below- and above-ground biomass of trees and understory in a 15-year-old *Picea abies* plantation. Biogeochemistry 33, 1–23.

Cole, D.W., Compton, J., Vanmiegroet, H., Homann, P., 1990. Changes in soil properties and site productivity caused by red alder. Water Air and Soil Pollution 54, 231–246.

Compton, J.E., Cole, D.W., 2001. Fate and effects of phosphorus additions in soils under N-2-fixing red alder. Biogeochemistry 53, 225–247.

Compton, J.E., Boone, R.D., 2002. Soil nitrogen transformations and the role of light fraction organic matter in forest soils. Soil Biology and Biochemistry 34, 933–943.

Conrad, R., 1996. Soil microorganisms as controllers of atmospheric trace gases (H-2, CO, CH4, OCS, N2O, and NO). Microbiological Reviews 60 (4), 609–640.

Currie, W.S., 1999. The response C and N biogeochemistry of the temperate forest floor. Trends in Ecology and Evolution 14, 316–320.

Currie, W.S., Aber, J.D., McDowell, W.H., Boone, R.D., Magill, A.H., 1996. Vertical transport of dissolved organic C and N under long-term N amendments in pine and hardwood forests. Biogeochemistry 35, 471–505.

Currie, W.S., Nadelhoffer, K.J, Aber, J.D., 2004. Redistributions of ^{15}N highlight turnover and replenishment of mineral soil organic N as a long-term control on forest C balance. Forest Ecology and Management 196, 109–127.

Curtis, P.S., 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. Plant, Cell, and Environment 19, 127–137.

Emmett, B.A., Brittain, S.A., Hughes, S., Kennedy, V., 1995. Nitrogen additions (Nano3 and Nh4no3) at Aber Forest, Wales.2. Response of trees and soil–nitrogen transformations. Forest Ecology and Management 71 (1–2), 61–73.

Erickson, H.E., Soto, P., Johnson, D.W., Roath, B., Hunsaker, C., 2005. Effects of vegetation patches on soil nutrient pools and fluxes within a mixed-conifer forest. Forest Science 51 (3), 211–220.

Fog, K., 1988. The Effect of Added Nitrogen on the Rate of Decomposition of Organic-Matter. Biological Reviews of the Cambridge Philosophical Society 63 (3), 433–462.

Fox, T.R., 2004. Nitrogen mineralization following fertilization of Douglas-fir forests with urea in western Washington. Soil Science Society of America Journal 68 (5), 1720–1728.

Frey, S.D., Knorr, M., Parrent, J.L., Simpson, R.T., 2004. Chronic nitrogen enrichment affects the structure and function of the soil microbial community in temperate hardwood and pine forests. Forest Ecology and Management 196 (1), 159–171.

Gallo, M.E., Lauber, C.L., Cabaniss, S.E., Waldrop, M.P., Sinsabaugh, R.L., Zak, D.R., 2005. Soil organic matter and litter chemistry response to experimental N deposition in northern temperate deciduous forest ecosystems. Global Change Biology 11 (9), 1514–1521.

Galloway, J, Aber, J, Erisman, J, Seitzinger, S, Howarth, R, Cowling, E, Cosby, B, 2003. The nitrogen cascade. Bioscience 53, 341–356.

Gilliam, F.S., Adams, M.B., Yurish, B.M., 1996. Ecosystem nutrient responses to chronic nitrogen inputs at Fernow Experimental Forest, West Virginia. Canadian Journal of Forest Research 26 (2), 196–205.

Gilliam, F.S., Yurish, B.M., Adams, M.B., 2001. Temporal and Spatial Variation of Nitrogen Transformations in Nitrogen-Saturated Soils of a Central Appalachian Hardwood Forest, pp. 1768–1785.

Goodale, C., Aber, J., 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. Ecological Applications 11, 253–267.

Grandy, A.S., Sinsabaugh, R.L., Neff, J.C., Stursova, M., Zak, D.R., 2008. Nitrogen deposition effects on soil organic matter chemistry are linked to variations in enzymes, ecosystems, and size fractions. Biogeochemistry 91, 37–49.

Griffiths, R.P., Homann, P.S., Riley, R., 1998. Denitrification enzyme activity of Douglas-fir and red alder forest soils of the Pacific Northwest. Soil Biology & Biochemistry 30 (8–9), 1147–1157.

Grigal, D.F., Vance, E.D., 2000. Influence of soil organic matter on forest productivity. New Zealand Journal of Forestry Science 30, 169–205.

Gundersen, P., Emmett, B.A., Kjonaas, O.J., Koopmans, C.J., Tietema, A., 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. Forest Ecology and Management 101 (1–3), 37–55.

Gundersen, P., Schmidt, I.K., Raulund-Rasmussen, K., 2006. Leaching of nitrate from temperate forests — effects of air pollution and forest management. Environmental Reviews 14 (1), 1–57.

Hart, S.C., Firestone, M.K., 1991. Forest floor–mineral soil interactions in the internal nitrogen cycle of an old-growth forest. Biogeochemistry 12, 103–127.

Hart, S.C., Binkley, D., Perry, D.A., 1997. Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. Soil Biology & Biochemistry 29 (7), 1111–1123.

Hattenschwiler, S., Vitousek, P.M., 2000. The role of polyphenols in terrestrial nitrogen cycling. Trends in Ecology and Evolution 15, 238–243.

Hedges, L.V., Olkin, I., 1985. Statistical Methods for Meta-Analysis. Academic Press, New York.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80 (4), 1150–1156.

Homann, P.S., Caldwell, B.A., Chappell, H.N., Sollins, P., Swanston, C.W., 2001. Douglas-fir soil C and N properties a decade after termination of urea fertilization. Canadian Journal of Forest Research 31, 2225–2236.

Hungate, B.A., Hart, S.C., Selmants, P.C., Boyle, S.I., Gehring, C.A., 2007. Soil responses to management, increased precipitation, and added nitrogen in ponderosa pine forests. Ecological Applications 17 (5), 1352–1365.

Jefts, S., Fernandez, I.J., Rustad, L.E., Dail, D.B., 2004. Decadal responses in soil N dynamics at the Bear Brook Watershed in Maine, USA. Forest Ecology and Management 189 (1–3), 189–205.

Johnson, D.W., 1995. Soil properties beneath ceanothus and pine stands in the Eastern Sierra-Nevada. Soil Science Society of America Journal 59 (3), 918–924.

Johnson, D.W., 2006. Progressive N limitation in forests: review and implications for long-term responses to elevated CO2. Ecology 87, 64–75.

Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta-analysis. Forest Ecology and Management 140, 227–238.

Johnson, D.W., Cheng, W., Burke, I.C., 2000. Biotic and abiotic nitrogen retention in a variety of forest soils. Soil Science Society of America Journal 64, 1503–1514.

Jurgensen, M.F., Harvey, A.E., Graham, R.T., PageDumroese, D.S., Tonn, J.R., Larsen, M.J., Jain, T.B., 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. Forest Science 43 (2), 234–251.

Kalbitz, K., Solinger, S., Park, J.H., Michalzik, B., Matzner, E., 2000. Controls on the dynamics of dissolved organic matter in soils: a review. Soil Science 165, 277–304.

Kirschbaum, M.U.F., 1995. The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic-C storage. Soil Biology & Biochemistry 27 (6), 753–760.

Kjonaas, O.J., Stuanes, A.O., Huse, M., 1998. Effects of weekly nitrogen additions on N cycling in a coniferous forest catchment, Gardsjon, Sweden. Forest Ecology and Management 101 (1–3), 227–249.

Kleber, M., Sollins, P., Sutton, R., 2007. A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. Biogeochemistry 85, 9–24.

Knorr, M., Frey, S.D., Curtis, P.S., 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86, 3252–3257.

Köppen, W., 1931. Grundrisse der Klimakunde. Walter de Gruyter Co., Berlin.

Landgraf, D., Wedig, S., Klose, S., 2005. Medium- and short-term available organic matter, microbial biomass, and enzyme activities in soils under *Pinus sylvestris* L. and *Robinia pseudoacacia* L. in a sandy soil in NE Saxony, Germany. Journal of Plant Nutrition and Soil Science 168 (2), 193–201.

Langley, J.A., Hungate, B.A., 2003. Mycorrhizal controls on belowground litter quality. Ecology 84, 2302–2312.

Lavery, J.M., Comeau, P.G., Prescott, C.E., 2004. The influence of red alder patches on light, litterfall, and soil nutrients in adjacent conifer stands. Canadian Journal of Forest Research 34 (1), 56–64.

Le Cadre, E., Genermont, S., Azam, F., Recous, S., 2004. The SAHGA model to calculate the spatial ammoniacal heterogeneity at the soil surface after fertilizer granule application. Biology and Fertility of Soils 40 (3), 178–180.

Lovett, G, 1994. Atmospheric deposition of nutrients and pollutants in North America: an ecological perspective. Ecological Applications 4, 629–650.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R., Field, D.B., 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience 54, 731–739.

Magill, A.H., Downs, M.R., Nadelhoffer, K.J., Hallett, R.A., Aber, J.D., 1996. Forest ecosystem response to four years of chronic nitrate and sulfate additions at Bear Brooks Watershed, Maine, USA. Forest Ecology and Management 84 (1–3), 29–37.

Magill, A.H., Aber, J.D., Berntson, G.M., McDowell, W.H., Nadelhoffer, K.J., Melillo, J.M., Steudler, P., 2000. Long-term nitrogen additions and nitrogen saturation in two temperate forests. Ecosystems 3 (3), 238–253.

Matson, P.A., Gower, S.T., Volkmann, C., Billow, C., Grier, C.C., 1992. Soil nitrogen cycling and nitrous oxide flux in a Rocky Mountain Douglas-fir forest — effects of fertilization irrigation, and carbon addition. Biogeochemistry 18, 101–117.

McNulty, S.G., Aber, J.D., 1993. Effects of chronic nitrogen additions on nitrogen cycling in a high-elevation spruce-fir stand. Canadian Journal of Forest Research 23 (7), 1252–1263.

McNulty, S.G., Aber, J.D., Newman, S.D., 1996. Nitrogen saturation in a high elevation New England spruce-fir stand. Forest Ecology and Management 84 (1–3), 109–121.

McNulty, S.G., Boggs, J., Aber, J.D., Rustad, L., Magill, A., 2005. Red spruce ecosystem level changes following 14 years of chronic N fertilization. Forest Ecology and Management 219 (2–3), 279–291.

Moldan, F., Kjonaas, O.J., Stuanes, A.O., Wright, R.F., 2006. Increased nitrogen in runoff and soil following 13 years of experimentally increased nitrogen deposition to a coniferous-forested catchment at Gardsjon. Sweden. Environmental Pollution 144 (2), 610–620.

Nadelhoffer, K.J., Aber, J.D., Melillo, J.M., 1985. Fine roots, net primary production, and soil–nitrogen availability — a new hypothesis. Ecology 66 (4), 1377–1390.

Nadelhoffer, K.J., Downs, M.R., Fry, B., 1999. Sinks for 15N-enriched additions to an oak forest and a red pine plantation. Ecological Applications 9, 72–86.

Neff, J.C., Townsend, A.R., Gleixner, G., Lehman, S.J., Turnbull, J., Bowman, W.D., 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. Nature 419 (6910), 915–917.

Nohrstedt, H.O., 2002. Effects of liming and fertilization (N, PK) on chemistry and nitrogen turnover in acidic forest soils in SW Sweden. Water Air and Soil Pollution 139 (1–4), 343–354.

Nohrstedt, H., Arnebrant, K, Baath, E, Soderstrom, B., 1988. Changes in carbon content, respiration rate, ATP content, and microbial biomass in nitrogen-fertilized pine forest soils in Sweden. Canadian Journal of Forest Research 19, 323–328.

Oakley, B.B., North, M.P., Franklin, J.F., 2003. The effects of fire on soil nitrogen associated with patches of the actinorhizal shrub *Ceanothus cordulatus*. Plant and Soil 254 (1), 35–46.

Oakley, B.B., North, M.P., Franklin, J.F., 2006. Facilitative and competitive effects of a N-fixing shrub on white fir saplings. Forest Ecology and Management 233 (1), 100–107.

Parker, J.L., Fernandez, J., Rustad, L.E., Norton, S.A., 2001. Effects of nitrogen enrichment, wildfire, and harvesting on forest–soil carbon and nitrogen. Soil Science Society of America Journal 65 (4), 1248–1255.

Paschke, M., Dawson, JO, David, MB., 1989. Soil nitrogen mineralization in plantations of Juglans nigra interplanted with actinorhizal *Elaegnus umbellata* of *Alnus glutinosa*. Plant and Soil 118, 33–42.

Pennanen, T., Liski, J., Baath, E., Kitunen, V., Uotila, J., Westman, C.J., Fritze, H., 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. Microbial Ecology 38 (2), 168–179.

Pregitzer, K.S., Burton, A.J., Zak, D.R., Talhelm, A.F., 2008. Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests. Global Change Biology 14 (1), 142–153.

Prietzel, J., Wagoner, G.L., Harrison, R.B., 2004. Long-term effects of repeated urea fertilization in Douglas-fir stands on forest floor nitrogen pools and nitrogen mineralization. Forest Ecology and Management 193 (3), 413–426.

Prietzel, J., Rehfuess, K.E., Stetter, U., Pretzsch, H., 2008. Changes of soil chemistry, stand nutrition, and stand growth at two Scots pine (*Pinus sylvestris* L.) sites in Central Europe during 40 years after fertilization, liming, and lupine introduction. European Journal of Forest Research 127 (1), 43–61.

Qualls, R.G., Haines, B.L., 1992. Biodegradability of dissolved organic-matter in forest throughfall, soil solution, and stream water. Soil Science Society of America Journal 56, 578–586.

Raich, J.W., Schlesinger, W.H., 1992. The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus Series B-Chemical and Physical Meteorology 44 (2), 81–99.

Reich, P.B., Grigal, D.F., Aber, J.D., Gower, S.T., 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology 78 (2), 335–347.

Ring, E., Bergholm, J., Olsson, B.A., Jansson, G., 2003. Urea fertilizations of a Norway spruce stand: effects on nitrogen in soil water and field-layer vegetation after final felling. Canadian Journal of Forest Research 33 (2), 375–384.

Rothe, A., Cromack, K., Resh, S.C., Makineci, E., Son, Y., 2002. Soil carbon and nitrogen changes under Douglas-fir with and without red alder. Soil Science Society of America Journal 66 (6), 1988–1995.

Rosenberg, M.S., Adams, D.C., Gurevitch, J., 1997. Meta Win—Statistical Software for Meta-Analysis with Resampling Tests. Sinauer Associates Publishing, Sunderland, MA.

Silver, W.L., Miya, R.K., 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129 (3), 407–419.

Sjoberg, G., Bergkvist, B., Berggren, D., Nilsson, S.I., 2003. Long-term N addition effects on the C mineralization and DOC production in mor humus under spruce. Soil Biology & Biochemistry 35 (10), 1305–1315.

Smolander, A., Kitunen, V., Priha, O., Malkonen, E., 1995. Nitrogen transformations in limed and nitrogen-fertilized soil in Norway spruce stands. Plant and Soil 172 (1), 107–115.

Smolander, A., Barnette, L., Kitunen, V., Lumme, I., 2005. N and C transformations in long-term N-fertilized forest soils in response to seasonal drought. Applied Soil Ecology 29 (3), 225–235.

Sollins, P., Spycher, G., Glassman, C.A., 1984. Net nitrogen mineralization from light-fraction and heavy- fraction forest soil organic-matter. Soil Biology and Biochemistry 16, 31–37.

Sollins, P., Homann, P., Caldwell, B.A., 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74 (1–2), 65–105.

Sollins, P., Swanston, C., Kleber, M., Filley, T., Kramer, M., Crow, S., Caldwell, B.A., Lajtha, K., Bowden, R., 2006. Organic C and N stabilization in a forest soil: evidence from sequential density fractionation. Soil Biology and Biochemistry 38, 3313–3324.

Shaw, C.H., Banfield, E., Kurz, W.A., 2008. Stratifying soils into pedogenically similar categories for modeling forest soil carbon. Canadian Journal of Soil Science 88, 501–516.

Stanturf, J.A., Stone, E.L., 1994. Loss of Nitrogen and Bases after Fertilization of 2nd-Growth hardwood forest soils. Forest Ecology and Management 65 (2–3), 265–277.

Stump, L.M., Binkley, D., 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Canadian Journal of Forest Research 23, 492–502.

Swanston, C., Homann, P.S., Caldwell, B.A., Myrold, D.D., Ganio, L., Sollins, P., 2004. Long-term effects of elevated nitrogen on forest soil organic matter stability. Biogeochemistry 70 (2), 227–250.

Templer, P.H., Lovett, G.M., Weathers, K.C., Findlay, S.E., Dawson, T.E., 2005. Influence of tree species on forest nitrogen retention in the Catskill Mountains, New York, USA. Ecosystems 8, 1–16.

Tiedemann, A.R., Mason, R.R., Wickman, B.E., 1998. Forest floor and soil nutrients five years after urea fertilization in a grand fir forest. Northwest Science 72 (2), 88–95.

Tietema, A, Emmett, B, Gundersen, P, Kjonaas, O, Koopmans, C., 1998. The fate of N-15 labelled nitrogen deposition in coniferous ecosystems. Forest Ecology and Management 101, 19–27.

Thirukkumaran, C.M., Parkinson, D., 2000. Microbial respiration, biomass, metabolic quotient and litter decomposition in a lodgepole pine forest floor amended with nitrogen and phosphorous fertilizers. Soil Biology and Biochemistry 32, 59–66.

Vance, E.D., Chapin, F.S., 2001. Substrate limitations to microbial activity in taiga forest floors. Soil Biology & Biochemistry 33 (2), 173–188.

Vesterdal, L., Raulund-Rasmussen, K., 2002. Availability of nitrogen and phosphorus in Norway spruce forest floors fertilized with nitrogen and other essential nutrients. Soil Biology & Biochemistry 34 (9), 1243–1251.

Vestgarden, L.S., Kjonaas, O.J., 2003. Potential nitrogen transformations in mineral soils of two coniferous forests exposed to different N inputs. Forest Ecology and Management 174 (1–3), 191–202.

Vestgarden, L.S., Selle, L.T., Stuanes, A.O., 2003. *In Situ* Soil Nitrogen Mineralisation in a Scots Pine (*Pinus sylvestris* L.) Stand: Effects of Increased Nitrogen Input, pp. 205–216.

Vestgarden, L.S., Nilsen, P., Abrahamsen, G., 2004. Nitrogen cycling in *Pinus sylvestris* stands exposed to different nitrogen inputs. Scandinavian Journal of Forest Research 19 (1), 38–47.

Vitousek, P.M., 1982. Nutrient cycling and nutrient use efficiency. The American Naturalist 119, 553–572.

Waldrop, M.P., Zak, D.R., 2006. Response of oxidative enzyme activities to nitrogen deposition affects soil concentrations of dissolved organic carbon. Ecosystems 9, 921–933.

Waldrop, M.P., Zak, D.R., Sinsabaugh, R.L., Gallo, M., Lauber, C., 2004. Nitrogen deposition modifies soil carbon storage through changes in microbial enzymatic activity. Ecological Applications 14 (4), 1172–1177.

Wallenstein, M.D., McNulty, S., Fernandez, I.J., Boggs, J., Schlesinger, W.H., 2006. Nitrogen fertilization decreases forest soil fungal and bacterial biomass in three long-term experiments. Forest Ecology and Management 222 (1–3), 459–468.

Zak, D.R., Holmes, W.E., Tomlinson, M.J., Pregitzer, K.S., Burton, A.J., 2006. Microbial cycling of C and N in northern hardwood forests receiving chronic atmospheric NO3- deposition. Ecosystems 9 (2), 242–253.