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DIVISION S-7—FOREST & RANGE SOILS

Biotic and Abiotic Nitrogen Retention in a Variety of Forest Soils

D. W. Johnson,* W. Cheng, and I. C. Burke

ABSTRACT

Nitrogen (N) immobilization in sterilized (abiotic) and non-sterilized (biotic) O and A horizons was studied to determine the relative importance of biotic and abiotic processes in N retention in forest ecosystems. We collected samples from a variety of forest locations in Washington, Nevada, California, Tennessee, and North Carolina with differing soil types, vegetation, N status, and soil acidity. Included among these sites were adjacent stands of N₂-fixing and non-N₂-fixing species and sites of differing N status due to slope position at a given location. We treated O and A horizon samples from each site with (¹⁵NH₄)₂SO₄; sterilization was achieved by adding HgCl₂, which proved to be highly effective. We found significant levels of both abiotic and biotic N immobilization in all soils. Biotic N immobilization was much greater in the N-poor sites in California and Nevada than in the other sites and was inversely related to N concentration overall. Biotic immobilization was directly related to pH and base saturation among all sites, but we hypothesize that these correlations resulted from a correlation between those parameters and N concentration. Abiotic N immobilization varied less than biotic N immobilization across sites and was unrelated to N concentration or pH. The percentage of total N immobilization as abiotic N immobilization varied considerably (from 6–90%), and was positively correlated with N concentration. These results suggest that abiotic N immobilization can be a significant process in a variety of soil types. Across soil types with increasing N saturation, biotic N immobilization decreases and abiotic N immobilization accounts for a greater proportion of total N immobilization.

THE FACT that most N in soils is associated with organic matter has led many forest soil scientists and ecologists to assume that N retention in forest ecosystems is controlled almost exclusively by biological processes. It is commonly assumed that competition among plant roots, heterotrophs, and nitrifiers for NH₄⁺ dominates the fate of N in ecosystems (e.g., Vitousek et al., 1979; Johnson and Edwards, 1979; Riha et al., 1986; Johnson, 1992). Relatively little attention has been given to abiotic processes controlling N retention in forest soils (i.e., NH₄⁺ retention by 2:1 clays and chemical reactions between NH₄⁺ and organic matter), even though the latter have been known to exist since the 1940s (Mattson and Koulter-Andersson, 1942, 1943; Mortland and Wolcott, 1965; Nömmik, 1965; Nömmik and Vahtras, 1982; Paul and Clark, 1989). Abiotic N retention can result from physical condensation reactions of phenols (originating from partially degraded lignin and some fungal pigments) with either amino acids or NH₃, resulting in the formation of “brown, nitrogenous humates” (Mortland and Wolcott, 1965; Nömmik, 1965; Nömmik and Vahtras, 1982; Paul and Clark, 1989). These abiotic, autocatalytic reactions are important in the production of humus (Mortland and Wolcott, 1965; Paul and Clark, 1989). Abiotic incorporation of NH₃ into humus is enhanced by high pH (because NH₃ is the reactive form of N) and high NH₃ and/or NH₄⁺ concentrations (Nömmik and Vahtras, 1982). Both of these

D.W. Johnson, Desert Research Institute, 2215 Raggio Parkway, and Environmental and Resource Sciences, Univ. of Nevada, Reno, NV 89512; W. Cheng, Dep. of Environmental Studies, Univ. of California, Santa Cruz, CA 95064; I.C. Burke, Dep. of Forest Sciences and Natural Resource Ecology Lab., Colorado State Univ., Fort Collins, CO 80523.
*Corresponding author (dwj@dri.edu).

¹ The reader should recall that Oa horizons were either absent or too thin to be sampled in the ULVC and SB sites; thus, these sites are not included in any statistical analyses of patterns in Oa horizons.

Table 1. Vegetation, soils, soil parent material, elevation, mean annual temperature (MAT), mean annual precipitation (MAP, climatic, N deposition, N leaching, litter and soil C contents in the sites sampled.

Code	Major vegetation	Soils and parent material	Elev.	MAP	MAT	N Dep.	N Leach	Litter N	Soil N	Reference
			m	cm	°C	— kg ha ⁻¹ yr ⁻¹ —	— Mg ha ⁻¹ —			
Sagehen, CA										
SHF	<i>Abies magnifica</i>	Andic Xerochrept; andesitic lahar, tuff	2500	ND	ND	ND	ND	0.9	3.3	Johnson et al., 1996
SHP	<i>Pinus jeffreyi</i>	Ultic haploxeralf; andesite	1830	87	4.8	0.3	0.6	0.3	2.3	Johnson et al., 1997
Little Valley, NV										
ULVP	<i>Pinus jeffreyi</i>	Typic xeropsamment; granite	2380	ND	ND	ND	ND	0.8	2.2	Johnson, 1995
ULVC	<i>Ceanothus velutinus</i>	Typic xeropsamment; granite	2380	ND	ND	ND	ND	0.3	3.1	Johnson, 1995
MET	<i>Pinus contorta</i>	Aquic cryobrept; granite	2010	55	5	0.3	0.1	0.1	1.2	Johnson et al., 1997
Thompson, WA										
DF	<i>Pseudotsuga menziesii</i>	Entic durochrept; glacial till	220	114	9.8	5	<0.1	0.4	5.1	Johnson and Lindberg, 1992; Van Miegroet and Cole, 1984
RA	<i>Alnus rubra</i>	Entic durochrept; glacial till	220	114	9.8	5	39	1.6	7.1	Cole, 1984
Walker Branch, TN										
WB42	<i>Quercus prinus</i> , mixed deciduous	Typic paleult; ridgetop; dolomite	335	130	14.5	10	0.9	0.2	3.2	Johnson and Todd, 1990
WB98	<i>Lirodendron tulipifera</i>	Typic paleult; cove; dolomite	290	130	14.5	10	0.4	0.2	5.3	
Smoky Mountains, NC										
SB	<i>Fagus grandifolia</i>	Umbric dystrochrept; shale	1600	151	ND	ND	18	0.2	9.1	Johnson and Lindberg, 1992; Johnson et al., 1991
ST	<i>Picea rubens</i>	Umbric dystrochrept; sandstone	1740	203	6	27	21	2.2	9.0	

conditions occur following urea fertilization, which is known to cause abiotic NH₄⁺ retention (Foster et al., 1985). The importance of abiotic reactions under ambient pH conditions is unclear. Nömmik (1970) found

Table 2. Sign of slope (+ or -) and correlation coefficients (r²) for statistically significant regressions (linear) of various soil properties against N immobilization.†

Soil Property	Horizon			
	Oi	Oe	Oa	A
Total N immobilization				
N Conc.	-0.26	-0.27*	-0.14	-0.23
C:N Ratio	+0.22	+0.22	+0.27	+0.65**
Lignin Conc.	+0.02	<0.01	-0.26	ND
Lignin:N	+0.26	+0.39**	+0.28	ND
pH	ND	ND	+0.28	+0.72***
% Base Sat.	ND	ND	ND	+0.72***
Biotic N immobilization				
N Conc.	-0.27	-0.35*	-0.21	-0.50**
C:N Ratio	+0.23	+0.45**	+0.24	+0.49**
Lignin Conc.	0.01	0.00	+0.37*	ND
Lignin:N	+0.28*	+0.45**	+0.16	ND
pH	ND	ND	+0.45*	+0.62***
% Base Sat.	ND	ND	ND	+0.79***
Abiotic N immobilization				
N Conc.	-0.16	-0.08	0.00	-0.16
C:N Ratio	+0.04	+0.09	+0.17	+0.11
Lignin Conc.	+0.08	+0.07	0.02	ND
Lignin:N	+0.09	+0.12	0.00	ND
pH	ND	ND	0.01	+0.06
% Base Sat.	ND	ND	ND	<0.01
Percent abiotic N immobilization				
Total N immob.	-0.41**	-0.55***	-0.07	-0.31*
N Conc.	+0.32*	+0.32*	+0.39*	+0.66***
C:N Ratio	-0.50**	-0.35**	-0.10	-0.22
Lignin Conc.	<0.01	+0.03	+0.27	ND
Lignin:N	-0.42**	-0.39**	-0.46**	ND
pH	ND	ND	-0.26	-0.36**
% Base Sat.	ND	ND	ND	-0.58***

†*, **, and *** refer to 0.1, 0.05, and 0.01 significance levels, respectively. ND = not determined.

little abiotic NH₄⁺ retention in acid Norway spruce humus unless pH was raised to neutrality or higher. On the other hand, Axelsson and Berg (1988) found that abiotic NH₄⁺ retention occurred at pH 4 on decomposing Scots pine (*Pinus sylvestris* L.) litter. They also noted an inverse relationship between N concentration and N retention capacity; thus, litter at later stages of decay retained less N because of its higher N concentration. Schimel and Firestone (1989a), using Nömmik's (1970) methods, found that non-biological reactions accounted for 20% of the N retained in an acid (pH 4.3–4.5) forest soil in Blodgett Forest, CA. In field studies at the same site, however, the same authors attributed the immobilization of ¹⁵N from applied NH₄⁺ entirely to microbial uptake (Schimel and Firestone, 1989b). Recently, Aber et al. (1998) have acknowledged that both microbial uptake and abiotic retention could be important in ecosystem N retention, but found that neither could account for the very high rate of ¹⁵N immobilization in soils (150 kg N ha⁻¹ yr⁻¹ for over 10 yr) observed in a field study at Harvard Forest. They posed a new hypothesis whereby mycorrhizae take up N and subsequently release it as extracellular enzymes which can then be stabilized by chemical reactions with organic matter.

The purpose of this paper is to report the results of a laboratory study on the biotic and abiotic incorporation of ¹⁵NH₄⁺ into O and A horizon soils from a variety of forest sites with differing vegetation, soils, climate, and N status. On the basis of the literature reviewed above, we hypothesized that (i) both biotic and abiotic N retention would be inversely correlated with N concentration, (ii) both biotic and abiotic N retention would be directly correlated with lignin concentration, and (iii) abiotic N retention would be positively correlated with Ph.

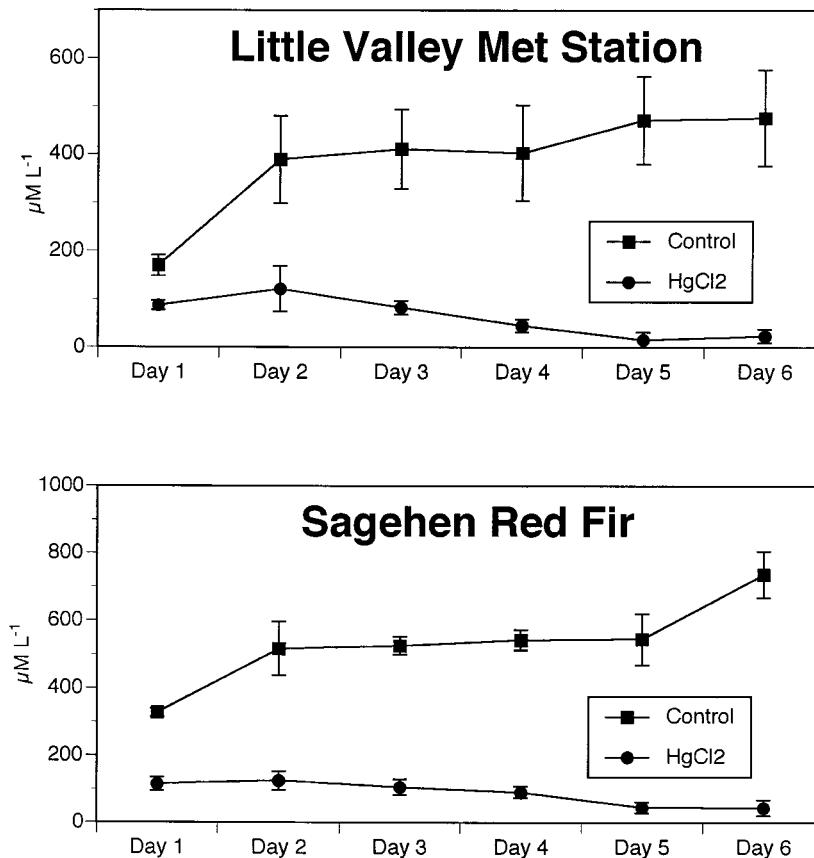


Fig. 1. Carbon dioxide concentration in the headspace of incubated soils with and without HgCl_2 .

MATERIALS AND METHODS

Sites

We samples soils from a set of sites located in Washington, California, Nevada, Tennessee, and North Carolina, representing a wide range of conditions in terms of vegetation, soils, climate, and N status (Table 1). Each site has a good background data set on N cycling from previous studies (Johnson and Lindberg, 1992; Johnson and Todd, 1990; Johnson et al., 1991, 1997; Van Miegroet and Cole, 1984). Nitrogen deposition ranged from 0.3 to 27.1 $\text{kg ha}^{-1} \text{yr}^{-1}$, and inputs via N fixation at the red alder (*Alnus rubra* Bong.) (RA) site at Thompson, WA, are estimated to have ranged from 100 to 300 $\text{kg ha}^{-1} \text{yr}^{-1}$ over the life of the stand (Van Miegroet and Cole, 1984). Nitrogen leaching ranged from 0.04 to 38.9 $\text{kg ha}^{-1} \text{yr}^{-1}$, indicating widely varying degrees of "N-saturation" (Aber et al., 1989). Forest floor N contents ranged from 0.1 to 2.2 mg ha^{-1} , and soil N contents ranged from 1.2 to 9.1 mg ha^{-1} .

Among the sites are two locations where symbiotic N_2 -fixing and non- N_2 -fixing vegetation occur adjacent to one another on the same soil: the red alder and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] sites at Thompson, WA, (RA and DF, respectively; Van Miegroet and Cole, 1984) and the jeffrey pine *Pinus jeffreyi* Grev. and Balf.) and *Ceanothus* (*Ceanothus velutinus* Dougl.) sites in Little Valley, NV, (ULVP and ULVC, respectively). We included the Sagehen sites (jeffrey pine, SHP, and red fir, SHF) because they provide a contrast in soil parent material and N status within the same climatic regime as the Little Valley sites (Johnson et al., 1997). In addition, there is some evidence of high soil solution NO_3^- in the SHF but not in the SHP site (Johnson et al., 1996). The

Walker Branch sites include an N-poor ridgetop plot (WB42) and an N-rich cove site (WB98) within the same basic climatic regime and soil parent material and classification. The Smokies red spruce (ST) and beech (*Fagus grandifolia* Ehrh.) (SB) sites provide contrasts in vegetation and soil parent material within the same climatic regime (within 3 km of one another) and with similar N status (both N-saturated) (Johnson et al., 1991).

METHODS

After considering and testing several methods for soil sterilization (including autoclaving, radiation, and other biocides), a 5% (w/v) HgCl_2 solution was selected because (i) it would remain in the samples and maintain its effectiveness throughout the experiments (whereas radiation may not) and (ii) its use would produce little change in the properties of organic matter, as autoclaving might (Wolf and Skipper, 1994). We tested the effectiveness of HgCl_2 as a biocide by measuring CO_2 evolution in laboratory incubations of selected soils and found the treatment to be completely effective in precluding soil respiration for periods much longer than needed for the completion of the ^{15}N experiments. In the biocide tests, we treated 1 g soil with 1 mL of either distilled water or 5% HgCl_2 and incubated the sample in Corning 15 mL centrifuge tubes (Corning Incorporated, Big Flats, NY) fitted with a septum. Each day for 6 d, CO_2 in the headspace was measured by extracting 100 μL of headspace gas with a Hamilton gas syringe and analyzing for CO_2 with a LI-COR 6250 CO_2 Analyzer (LI-COR, Inc., Lincoln, NE). We tested two Sierran soils which we considered to be potentially problematic because of their inherent hydrophobicity (Fig. 1); HgCl_2 was completely effective in preventing soil respiration.

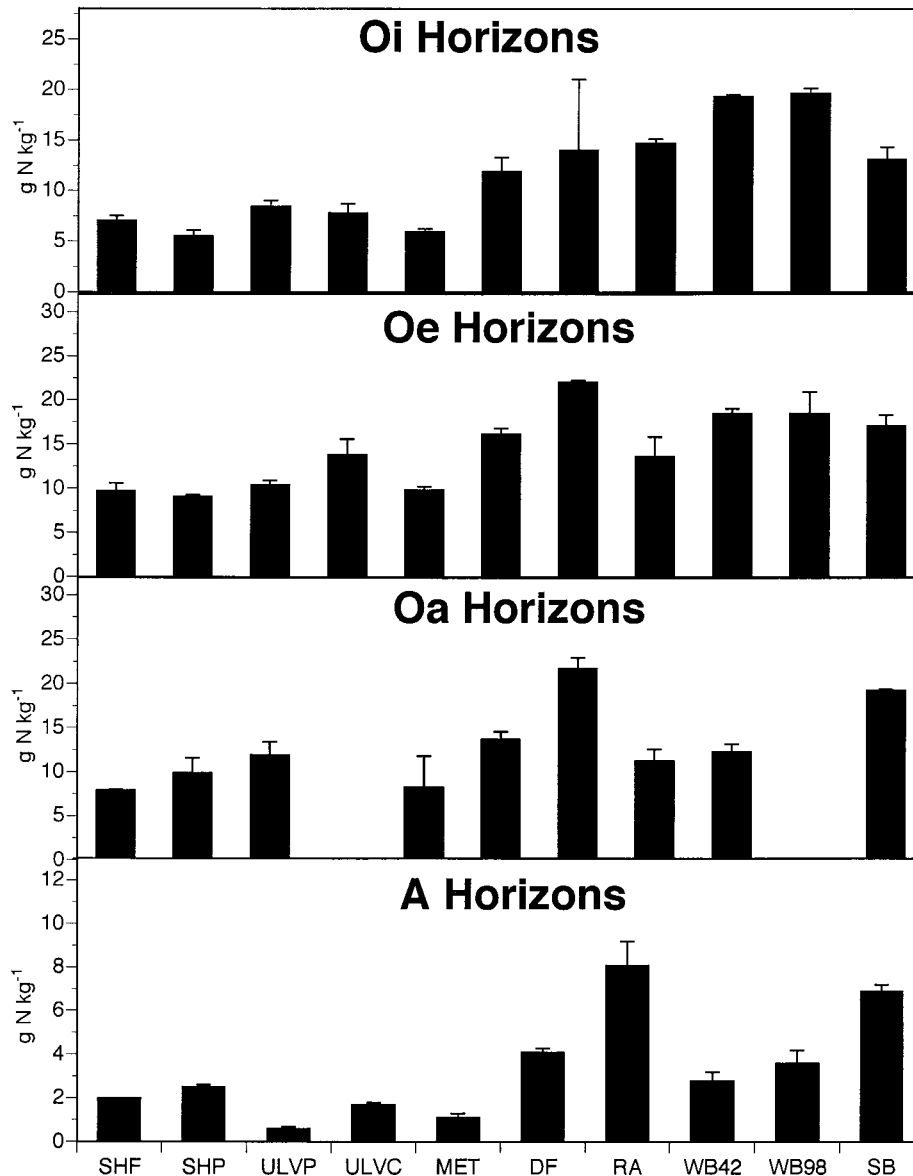


Fig. 2. Nitrogen concentration in samples from the study sites (see Table 1 for code). (Note that Oa horizons were either not present or too thin to be sampled at the ULVC and SB sites.)

O and A horizon samples from each site were oven dried them (65°C), and subsampled for total C and N analyses on a Perkin-Elmer 2400 CHN Analyzer (Perkin-Elmer, Norwalk, CT) at the Desert Research Institute. Bulk samples (no replicates) of Oi, Oe, and Oa horizons from each site were sent to the USDA Forest Products Laboratory at Madison, WI, for lignin analysis (performed by the sulfuric acid digest method; Efflund, 1977). Another set of subsamples was subjected to tests for biotic and abiotic immobilization. Triplicate subsamples of unground litter material or soil (2 g per replicate) were leached in a mechanical vacuum extractor (Centurion Corp.) over a 12-h period with 25 mL solution of $8 \times 10^{-5} M$ $(\text{NH}_4)_2\text{SO}_4$ containing 73.6% ^{15}N . At the end of this period, the subsamples were extracted with 25 mL of 2 M KCl over a period of 4 h to remove readily exchangeable NH_4^+ . Another set of subsamples was treated (in triplicate) with a $8 \times 10^{-5} M$ $(\text{NH}_4)_2\text{SO}_4$ solution containing 5% HgCl_2 (molarity adjusted for the presence of the HgCl_2) to preclude any biological N uptake. After treatment with ^{15}N , the extracts were

discarded and the solid samples were immediately recovered, oven dried at 60°C, and ground for ^{15}N analyses. The ^{15}N analyses were conducted at the University of California, Davis, by a Europa Scientific 'Integra' analyzer (Crewe, UK).

Total and abiotic N immobilization were calculated by subtracting natural abundance ^{15}N from measured ^{15}N in treated subsamples (termed "excess ^{15}N "), and dividing this value by 0.736, the fraction of the N in the added $(^{15}\text{NH}_4)_2\text{SO}_4$ solution that was ^{15}N . Biotic N immobilization was calculated as the difference in N immobilization between samples treated with $(^{15}\text{NH}_4)_2\text{SO}_4$ only and those treated with $(^{15}\text{NH}_4)_2\text{SO}_4$ plus HgCl_2 . We recognize that the separation of biotic and abiotic N immobilization in this study is somewhat artificial and arbitrary; such is invariably the case for soil fractionation schemes. The protocols we adopted could have been biased toward abiotic N immobilization, for example, if microbial competition for NH_4^+ in nonsterilized soils reduces abiotic immobilization. We see no way to resolve this issue with present techniques, however, and will proceed to utilize the scheme

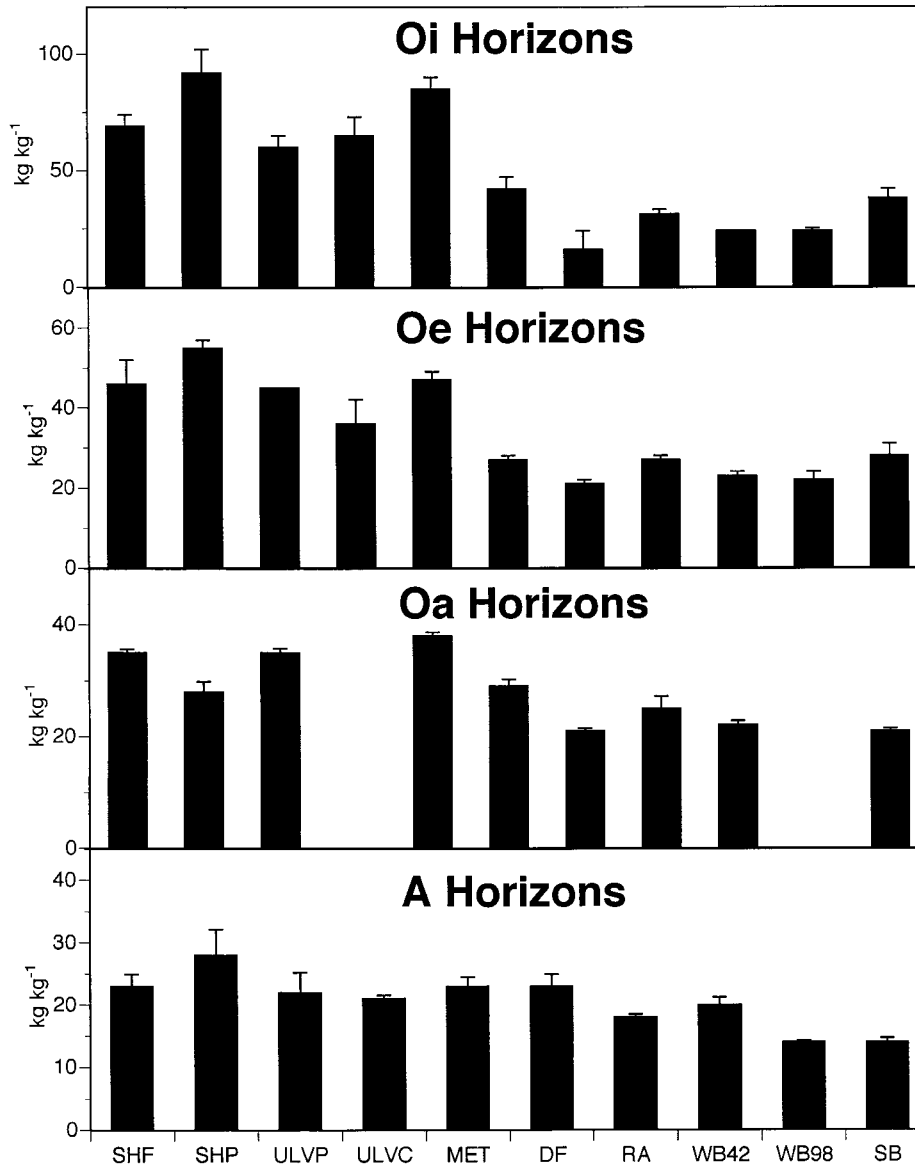


Fig. 3. C:N ratio in samples from the study sites (see Table 1 for code).

described above for separating biotic and abiotic N immobilization with the caveat that it, like many other soil analyses, should be regarded as an index to be used for comparisons among sites and treatments at a given site rather than as an absolute value.

Statistical analyses were performed by Microsoft Excel software. For comparisons across sites, regression analyses were used, accepting the significance level of $P < 0.10$. For comparisons between adjacent sites (N_2 -fixers vs. non- N_2 -fixers, ridgetop and cove sites), Student's t -tests were used, accepting the significance level of $P < 0.10$.

RESULTS AND DISCUSSION

Patterns in Nitrogen Concentration, Carbon:Nitrogen Ratios, Lignin, pH, Base Saturation and Natural Nitrogen-15 Abundance Among Sites

The N concentration and C:N ratio data from the study sites varied by more than twofold, reflecting the

many factors (species, soils, atmospheric deposition, N fixation) affecting the N status of each site (Fig. 2 and 3). The Sierran sites (SHF, SHP, ULVC, ULVP, and MET) fell on the low end of the scale, reflecting low N deposition rates and frequent N losses due to fire. The Smokies sites (SB and ST) fell on the high end of the scale, reflecting high N deposition rates and absence of fire. The positive effects of N_2 -fixers was evident in the higher N concentrations and lower C:N ratios in all horizons of the red alder (RA) site as compared to the adjacent Douglas-fir (DF) site at Thompson, WA. The effects of N_2 fixers was less apparent at the adjacent *Ceanothus* (ULVC) and Jeffrey pine (ULVP) sites at Upper Little Valley, NV, however. Oe horizon and A horizon N concentrations were greater in the *Ceanothus* than in the adjacent pine site ($P = 0.10$ and 0.001 , Student's t -test, respectively), but there were no significant differences in N concentration in the Oi horizon or in C:N ratio in any horizon (Fig. 2 and 3). The effect of

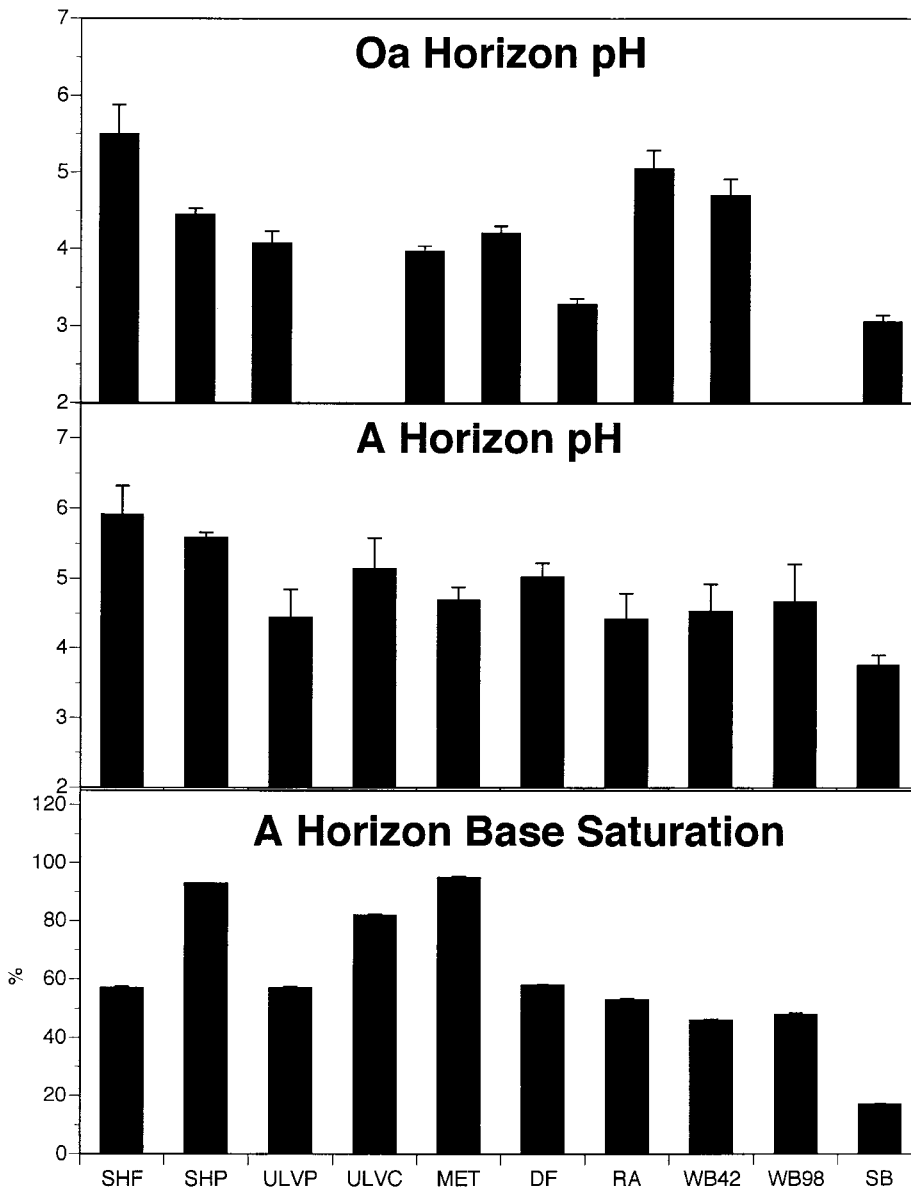


Fig. 4. Oa and A horizon pH and A horizon base saturation for samples taken from the study sites (see Table 1 for code).

slope position was reflected in N concentrations at Walker Branch, TN, where the cove (WB98) site had significantly higher N concentrations than in the ridgetop site (WB42) for in the Oi and Oe horizons ($P = 0.001$ and 0.07 , respectively, Student's *t*-test). There were no significant differences in N concentration in the Oa and A horizons at the two Walker Branch sites (Fig. 2 and 3). Lignin concentrations (not shown) varied little among sites.

Oa¹ and A horizon pH varied by two units among the study sites and followed a pattern opposite that of N concentration (Fig. 4). In the Oa horizons, pH varied from a low of 3.3 in the Smokies Red spruce site (ST) to a high of 5.5 in the Sagehen red fir (SHF) site. In the A horizons, pH varied from a low of 3.5 in the ST site to a high of 5.9 in the SHF site. A horizon base saturation followed the same pattern as pH and varied from a low of 9% in the ST site to a high of 95% in the

Sagehen pine (SHP) site. The pH and N concentration were significantly, negatively correlated ($r^2 = 0.61$, $P = 0.01$ for the Oa horizons and $r^2 = 0.31$, $P = 0.07$ for the A horizons). Base saturation was positively correlated with pH, as expected ($r^2 = 0.53$, $P = 0.01$).

Natural ¹⁵N abundance varied substantially among the sites but followed some of the patterns expected with respect to stage of decomposition and N-fixation. Natural ¹⁵N abundance normally increases during later stages of litter decomposition because of preferential losses of the lighter isotope (Nadelhoffer and Fry, 1988; Högberg, 1997), and this was reflected in the general increase in natural ¹⁵N abundance with from Oi to Oe, Oa, and A horizons (Fig. 5). Högberg (1997) concluded from a major review of the literature that comparatively low natural ¹⁵N abundance in surface soils usually indicates N limitation and low nitrification rates, whereas higher natural ¹⁵N abundance in surface than in subsurface soils

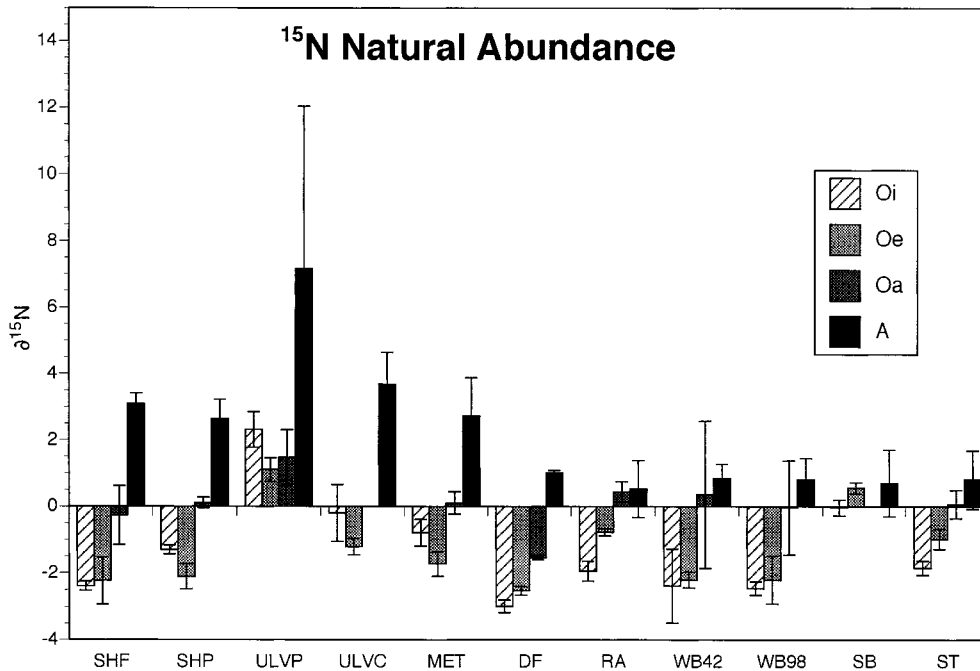


Fig. 5. ^{15}N natural abundance in samples from the study sites. (see Table 1 for code.)

indicates more abundant N and greater rates of nitrification. We did not sample deeper soil horizons in this study, but the natural ^{15}N abundance patterns among O and A horizons did not fit this pattern. The most positive natural ^{15}N abundance values in A horizons occurred in the most N-deficient systems, and there was a significant, negative correlation between natural ^{15}N abundance and N concentration in the A horizons ($r^2 = 0.54$, $P < 0.01$).

Natural ^{15}N abundance in litter and soils in the N_2 -fixing stands (RA and ULVC) was closer to atmospheric levels ($\delta^{15}\text{N} = 0$) than in adjacent non- N_2 -fixing stands (DF and ULVP), as was expected. The direction of the shifts, however, differed between sites; natural ^{15}N abundance in litter and soil was lower (less positive) in the N_2 -fixing (ULVC) than in the adjacent non- N_2 -fixing (ULVP) site in Little Valley, whereas the reverse was true at the Thompson RA and DF sites (natural ^{15}N abundance was less negative in RA than in DF). Garten (1993) found more positive natural ^{15}N abundance in foliage from trees in coves than in ridgetops at Walker Branch, TN, and attributed this to greater uptake from isotopically heavy pools in the cove sites. We saw no differences in natural ^{15}N abundance in the cove and ridgetop sites sampled in this study, however.

Patterns in Nitrogen Immobilization Among Sites

Biotic Immobilization

Biotic N immobilization in the O horizons varied by a factor of 10 or more among the sites, and was generally greater in the N-poor sites (especially SHF, and SHP, and ULVP) sites than in the others (Fig. 6). Simple linear regressions revealed statistically significant, nega-

tive correlations between biotic N immobilization and N concentration in the Oe and A horizons (Table 2). Simple linear regression gave a reasonable fit to the data in the A horizons. Linear regressions did not provide a good fit for biotic N immobilization versus N concentration in the O horizons, however; there appeared to be a threshold effect in which biotic N immobilization increased substantially as N concentration dropped below 10 g g^{-1} (Fig. 7). Power functions [of the form $y = a(x^b)$] improved the correlation coefficients for the O horizon regressions somewhat; however, the power function curve fit was poor and did not adequately describe the observed threshold effect (Fig. 7 and Table 2).

Other measured parameters that were significantly correlated with biotic N immobilization included C:N ratio in the Oe and A horizons (positive correlations), lignin concentration in the Oa horizons (positive), lignin:N ratio in the Oi and Oe horizons (positive), pH in the Oa and A horizons (positive), and base saturation in the A horizons. We hypothesize that the positive correlation between pH and biotic immobilization was spurious: pH and N concentration were negatively correlated, as noted above, and base saturation was positively correlated with pH.

The effects of N fixers and slope position on biotic immobilization at any one location were mixed. At Upper Little Valley, biotic immobilization was significantly lower in the *Ceanothus* (ULVC) than in the adjacent jeffrey pine (ULVP) sites in the O horizons ($P = 0.03$ and 0.06 , respectively for the Oi and Oe horizons; Student's t -test) (Fig. 6). (Note that the Oa horizon was too thin and indistinct to sample in the ULVC site.) In the A horizons, however, the differences reversed: biotic immobilization was significantly greater in the *Ceano-*

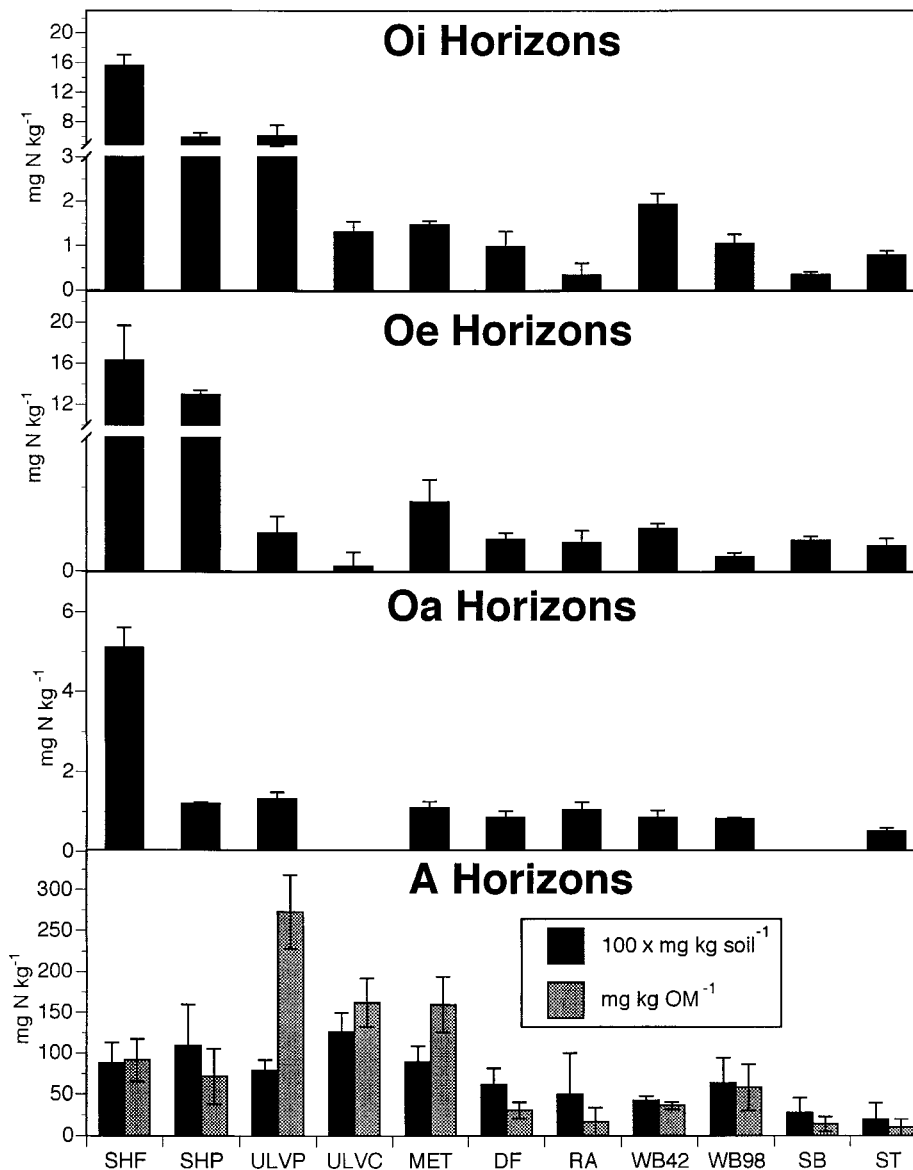


Fig. 6. Biotic N immobilization samples from the study sites (see Table 1 for code). In the A horizons, values are plotted on the basis of soil weight ($100 \times \text{mg N kg soil}^{-1}$) and on the basis of organic matter weight in soil (mg N kg OM^{-1}). Values on the soil weight basis are multiplied by 100 for scale.

thus than in the pine soil ($P = 0.02$). Biotic immobilization was lower in the Oi horizon of red alder (RA) than in the Oi horizon of the adjacent Douglas-fir (DF) site at the Thompson, WA, site ($P = 0.09$); however, the differences in the other horizons were not significant (Fig. 6). Biotic immobilization was significantly lower in the Oi ($P = 0.01$) and Oe ($P = 0.06$) horizons of the N-rich cove site (WB98) than in the N-poor ridgetop site (WB42) at Walker Branch, TN (Fig. 6). Differences in the other horizons at the Walker Branch site were not significant.

There were no consistent patterns of biotic N immobilization with stage of litter decomposition. At some sites (ULVP, WB42, ST), biotic N immobilization decreased from Oi to Oe horizons, whereas in other sites the re-

verse was true (SHP, SB), and in others there was no significant difference (Fig. 6). Similarly, biotic immobilization was lower in Oa than in Oe horizons in some sites (SHF, SHP, ULVP, MET) but not significantly different in others (DF, RA, WB42, WB98, ST). Biotic N immobilization in the A horizons was generally equal to or lower than that in the Oa horizons when expressed on the basis of soil weight. However, when, biotic N immobilization in the A horizons was expressed on the basis of weight of organic matter, it far exceeded that in the O horizons in all sites, and soils with low organic matter (i.e., ULVP and MET) showed the highest values (Fig. 6). Thus, while comparisons among the O horizons suggest that biotic N immobilization decreases during later stages of litter decomposition at some sites (SHF,

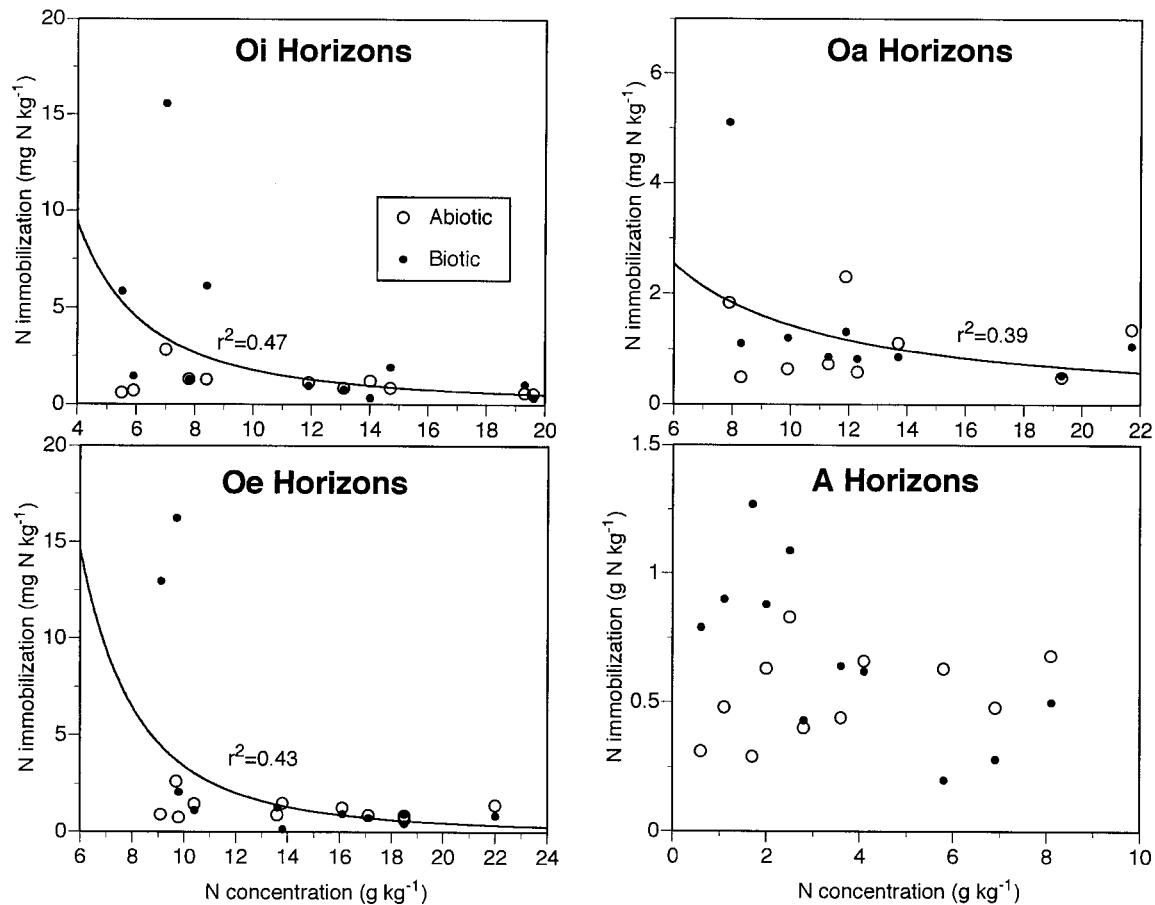


Fig. 7. Plots of biotic and Abiotic N immobilization against N concentration. Correlation coefficients (r^2) are shown for power function regressions of the form $y = a(x^b)$ of biotic N immobilization and N concentration in the O horizons.

SHF, ULVP, WB42), the opposite seems to hold true as litter transforms into soil organic matter.

Abiotic Immobilization

We found significant levels of abiotic immobilization in nearly all samples. Abiotic N immobilization in the O horizons varied by a factor of two to three among the sites, but showed only a weak and non-significant downward trend with increasing site N status (Fig. 8). Abiotic N immobilization in the Oi and Oe horizons was greatest in the Sagehen red fir (SHF), but there was no particular trend among the other sites. In the Oa horizons, the SHF and ULVP sites had greater values but there were no particular trends among the other sites. There were no statistically significant correlations between abiotic N immobilization and N concentration, C:N ratio, lignin concentration, lignin:N ratio, pH, or base saturation within any horizon (Table 2). There were no statistically significant differences in abiotic immobilization between the N₂-fixing and non-N₂-fixing sites at Upper Little Valley, NV, (ULVC and ULVP), or Thompson, WA, (RA and DF). Abiotic N immobilization was lower in the Oi horizon of the cove site (WB98) than in the ridgetop site (WB42) at Walker

Branch, TN ($P = 0.01$, Student's t -test), but differences were not significant in other horizons.

Contrary to what was found by Axelsson and Berg (1988), we found no consistent relationship between abiotic N immobilization and stage of litter decomposition. In some cases (SHF, MET, and ST), abiotic N immobilization decreased with stage of litter decomposition, and in other cases (ULVP, WB98), the reverse was true. In most cases, however, there was no clear pattern of abiotic N immobilization with stage of litter decomposition. Abiotic N immobilization in the A horizons varied much less than and was generally lower than abiotic N immobilization in the O horizons when expressed on the basis of soil weight. However, as was the case for biotic immobilization, abiotic immobilization in the A horizons exceeded that in the O horizons in all sites when expressed on the basis of organic matter weight (Fig. 8). This does not necessarily imply that abiotic N immobilization increases as litter transforms into soil organic matter, however, because an unknown but potentially significant proportion of abiotic N immobilization in A horizons is likely due to clay fixation of NH₄⁺. We are in the process of investigating the role of clay fixation of NH₄⁺ in these sites at this time.

Contrary to what was hypothesized and what has been

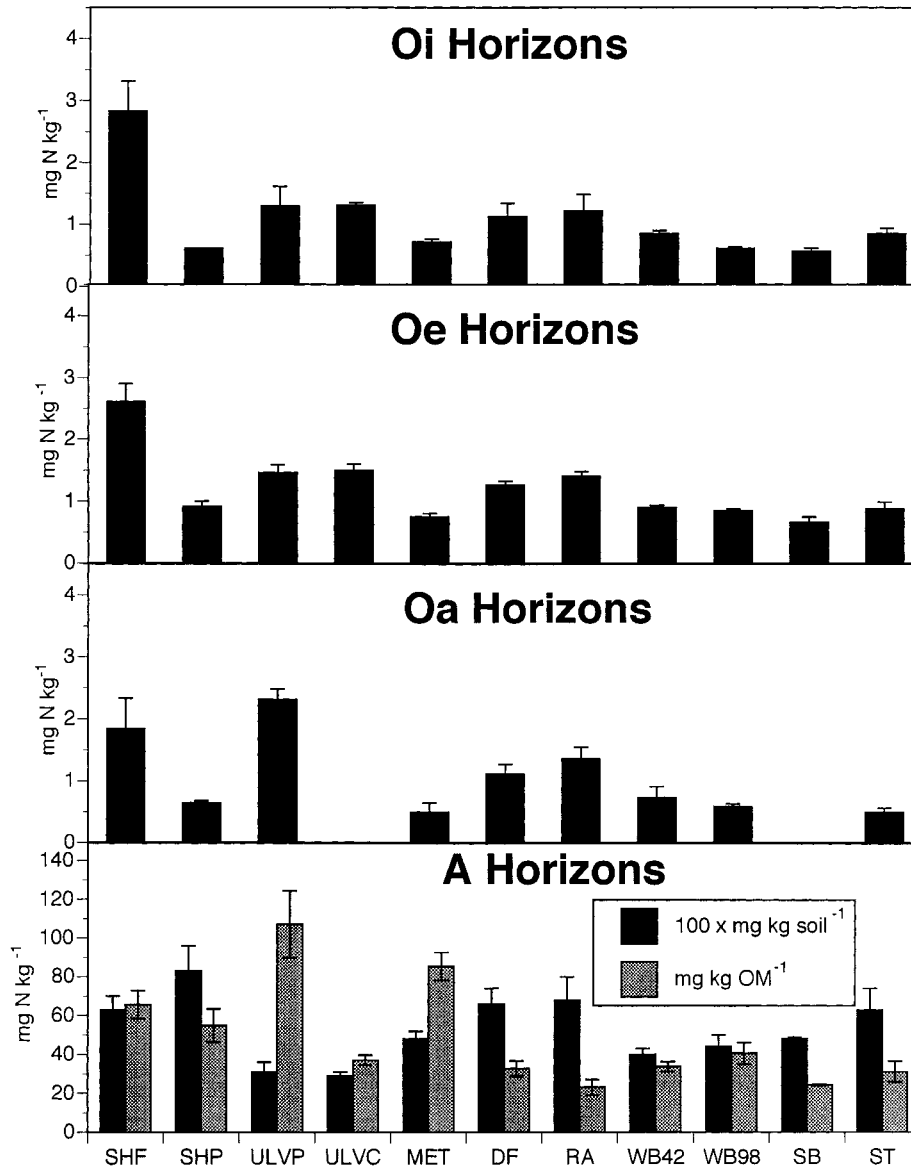


Fig. 8. Abiotic N immobilization samples from the study sites (see Table 1 for code). In the A horizons, values are plotted on the basis of soil weight ($100 \times \text{mg N kg soil}^{-1}$) and on the basis of organic matter weight in soil (mg N kg OM^{-1}). Values on the soil weight basis are multiplied by for scale.

found previously in the literature, we found no relationship between either N status or pH and abiotic immobilization among these samples. The lack of correlation between pH and abiotic immobilization does not imply that changing pH on an individual sample would have no effect on abiotic N immobilization; indeed, the opposite has been shown in detailed laboratory studies in which pH was manipulated (Nömmik, 1970; Nömmik and Vahtras, 1982). Experiments involving pH manipulations of pH and abiotic immobilization on these samples are underway at this time.

The percentage of total N immobilization accounted for abiotic immobilization varied considerably. Among the Oi horizons, this percentage ranged from a low of 9% in SHP to a high of 78% in RA (Fig. 9). Among the

Oe horizons, it ranged from 9 (SHP) to 90% (ULVC); in the Oa horizons it ranged from 26 (SHF) to 63% (ULVP); and in the A horizons it ranged from 18 (ULVC) to 76% (ST). We note that our values for percentage abiotic N immobilization in jeffrey pine O horizons in this laboratory study (6–63%) well encompass the value of 20% reported by Schimel and Firestone (1989a) in a field study of N immobilization in the O horizon of a ponderosa pine forest.

Total Nitrogen Immobilization

Because of the widely varying contributions of biotic and abiotic components, the factors correlated with total N immobilization differed from those correlated with

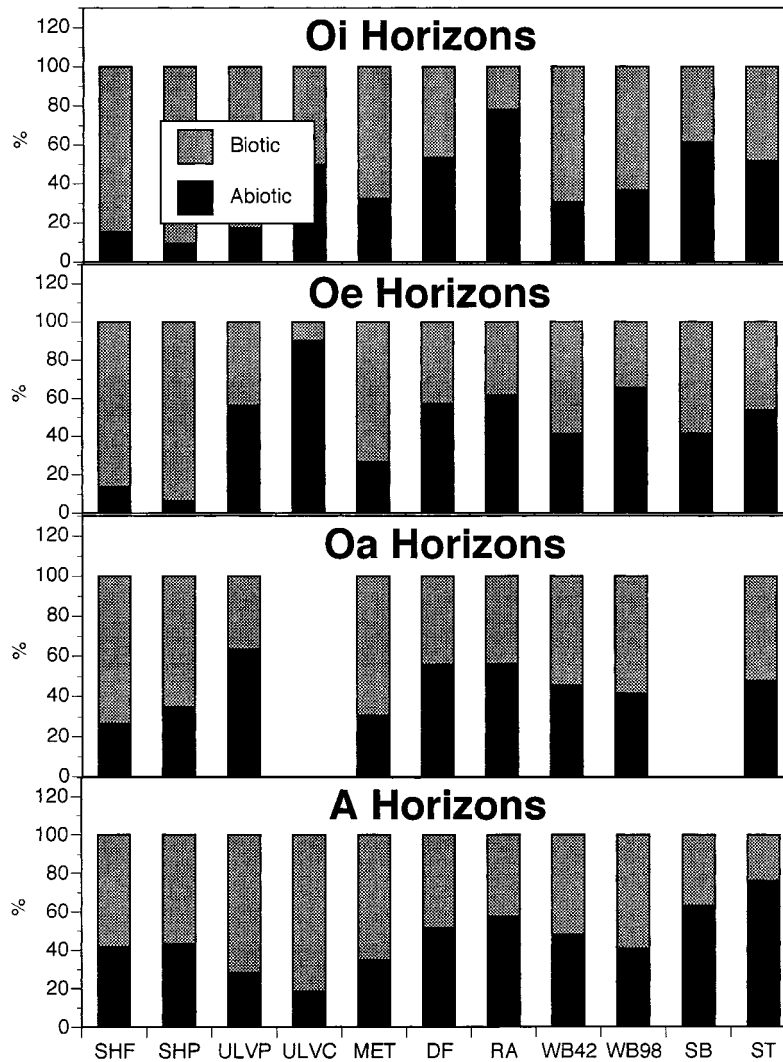


Fig. 9. Percentage abiotic and biotic N immobilization in O and A horizons from the study sites (see Table 1 for code).

biotic and abiotic N immobilization separately. Total N immobilization was not significantly correlated with N, lignin, or lignin:N ratio in any horizon (Table 2). Total N immobilization was positively correlated with C:N ratio in the A horizons only and positively correlated with pH and base saturation in the A horizons only. The percentage of total immobilization as abiotic was significantly, positively correlated with N concentration in all horizons and negatively correlated with total N immobilization for all but the Oa horizon (Table 2). Biotic and total immobilization were greatest in the N-poor soils, but the percentage of total immobilization as abiotic was greater in the N-rich soils. Thus, this study suggests that the relative importance of abiotic N immobilization increases as soils become enriched in N.

SUMMARY AND CONCLUSIONS

Our study demonstrates that abiotic N immobilization occurs in a wide variety of soil types, and that the levels could be significant for ecosystem processes. Our results

indicated that biotic N immobilization in the laboratory was greatly reduced in sites with greater N availability (because of N fixation, slope position, or atmospheric deposition). Abiotic N immobilization, on the other hand, tended to remain more constant and was not significantly related to N status. In contrast to previous laboratory studies, we found little evidence that either pH or lignin were important factors affecting either biotic or abiotic N immobilization among these sites. This does not necessarily imply that pH is unimportant for abiotic N immobilization; it merely implies that no overall correlation between pH and abiotic N immobilization across the sites we studied was found. We hypothesize that manipulating pH of individual samples from this study would result in changes in abiotic N immobilization, as has been found in the past.

Laboratory studies of this nature cannot provide a complete picture of soil N cycling processes because laboratory conditions differ substantially from field conditions (especially with respect to the presence of plants). Laboratory studies of this kind can, however,

provide comparisons of selected processes among a number of sites that would be prohibitively expensive in a field setting. The results of this study suggest the hypothesis that abiotic N immobilization is much less affected by N status than biotic immobilization is, and that abiotic immobilization may therefore become relatively more important in sites that are “N saturated” due to atmospheric deposition, fertilization, or natural processes. Field studies are needed to test this hypothesis.

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