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Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern USA

Erik A. Lilleskov, Philip M. Wargo, Kristiina A. Vogt, and Daniel J. Vogt

Abstract: Increased nitrogen (N) input has been found to alter ectomycorrhizal fungal communities over short deposition gradients and in fertilization experiments; however, its effects over larger spatial scales have not been determined. To address this gap, we reanalyzed data from a study originally designed to examine the effects of soil aluminum/calcium (Al/Ca) ratios on the vitality of red spruce fine roots over a regional acid and N deposition gradient in the northeastern USA. We used root N as an indicator of stand N availability and examined its relationship with the abundance of ectomycorrhizal morphotypes. The dominant morphotypes changed in relative abundance as a function of stand N availability. As root N concentrations increased, *Piloderma* spp. - like, *Cenococcum geophilum* Fr., and other unidentified mycorrhizal morphotypes declined in abundance, while other smooth-mantled morphotypes increased. Root N concentration in the 1–2 mm diameter class was the best predictor of the abundance of multiple morphotypes. The morphotype responses were consistent with those found in experimental and small-scale studies, suggesting that N availability is altering ectomycorrhizal communities over broad spatial scales in this region. This finding provides an impetus to conduct a more detailed characterization of mycorrhizal community responses to N deposition across large-scale gradients.

Résumé : Dans le cas de courts gradients de dépôts et d'expériences de fertilisation, il a été démontré qu'un apport d'azote (N) modifie les communautés de champignons ectomycorhiziens. Cependant, les effets à plus grande échelle n'ont pas été étudiés. Pour combler cette lacune, nous avons analysé à nouveau les données d'une étude conçue à l'origine pour étudier les effets de différents rapports entre l'aluminium et le calcium (Al/Ca) dans le sol sur la vitalité des racines fines de l'épinette rouge le long d'un gradient régional de dépôts acides et azotés dans le nord-est des É-U. Nous avons utilisé l'azote dans les racines à titre d'indicateur de la disponibilité de N dans un peuplement et nous avons étudié sa relation avec l'abondance des morphotypes ectomycorhiziens. L'abondance relative des morphotypes dominants a changé en fonction de la disponibilité de N dans le peuplement. À mesure que la concentration de N dans les racines augmentait, l'abondance d'un morphotype semblable à *Piloderma* spp., *Cenococcum geophilum* Fr., et d'autres morphotypes mycorhiziens non identifiés diminuaient tandis que d'autres morphotypes à manchon lisse augmentaient. La concentration racinaire de N dans la classe de diamètre de 1–2 mm était le meilleur prédicteur de l'abondance de plusieurs morphotypes. La réaction des morphotypes concordait avec les résultats obtenus dans les études expérimentales et les études à échelle réduite, ce qui indique que la disponibilité de N modifie les communautés ectomycorhiziennes à grande échelle dans cette région. Ces résultats procurent une motivation pour réaliser une caractérisation plus poussée des réactions des communautés mycorhiziennes aux dépôts azotés le long de gradients à grande échelle.

[Traduit par la Rédaction]

Introduction

Given the high functional diversity of mycorrhizal fungi, for example, in carbon (C) demand and types and quantities of nutrient molecules absorbed and transferred to hosts (Smith and Read 1997), factors that change mycorrhizal fungal community composition and structure have the potential to influence plant nutrition and element cycling. Controlled experiments and gradient studies over small spatial scales indicate that long-term N deposition can alter

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E.A. Lilleskov.[1] USDA Forest Service, Northern Research Station, Houghton, MI 49931, USA.
P.M. Wargo.[2] USDA Forest Service, Northern Research Station, Hamden, CT 06514, USA.
K.A. Vogt and D.J. Vogt. College of Forest Resources, University of Washington, Seattle, WA 98195, USA.

[1] Corresponding author (e-mail: elilleskov@fs.fed.us).
[2] Present address: Retired.

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Table 1. Site information, root and soil N, and wet N deposition for 11 red spruce - dominated sites sampled across a regional N deposition gradient in the northeastern USA.

Location							
Site	State	Latitude (°N)	Longitude (°W)	Approx. elevation (m)	Sampling year(s)	C/N ratio in the Oa horizon (mass/mass)[a]	Estimated wet N deposition (kg N·ha^{-1}·year^{-1})[b]
Whiteface Mt.	New York	44.39	73.86	950	1993, 1994	21.7	7.9
Big Moose Lake	New York	43.83	74.85	550	1993, 1994	29.2	6.4
Groton	Vermont	44.21	72.20	520	1993, 1994	35.2	5.3
Hubbard Brook	New Hampshire	43.94	71.75	755	1994	25.2	6.0
Crawford Notch	New Hampsire	44.20	71.40	670	1993, 1994	28.7	5.5
Cone Pond	New Hampshire	43.90	71.60	610	1993, 1994	32.0	5.4
Bartlett	New Hampshire	44.11	71.29	525	1993, 1994	34.3	4.9
Bear Brook	Maine	44.87	68.11	400	1993, 1994	24.9	3.8
Bear Brook	Maine (fertilized)	44.87	68.11	400	1994	NA	3.8+25.2[c]
Howland	Maine	45.20	68.73	60	1993, 1994	43.7	3.1
Kossuth	Maine	45.40	67.90	100	1993, 1994	37.4	2.8

[a] Calculated using data from David and Lawrence (1996).

[b] Estimated using the equations of Ollinger et al. (1993).

[c] Nitrogen was applied bimonthly as 25.2 kg N·ha^{-1}·year^{-1} $(NH_4)_2SO_4$, starting in November 1989.

mycorrhizal fungal community composition and structure by both changing dominant species and reducing diversity (Wallenda and Kottke 1998; Lilleskov 2005 and references therein). However, it is not clear whether these results are generally applicable to larger-scale regional N deposition gradients. Taylor et al. (2000) found differences in spruce ectomycorrhizal communities across a north–south climate and N deposition gradient in Europe. However, no study has been carried out along a regional N gradient in which climate is held relatively constant.

In a study on the responses of red spruce (*Picea rubens* Sarg.) roots to soil acidification across an anthropogenic acid and N deposition gradient in the northeastern USA, Wargo et al. (2003) examined the response of a number of root traits, including ectomycorrhizal morphotypes, to elevated organic horizon Al/Ca ratios. They did not find strong relationships between organic horizon Al/Ca ratios and mycorrhizal morphotype frequency. As part of that study, fine root N concentrations (root %N) were recorded for different root diameter classes over this gradient. However, Wargo et al. (2003) did not examine the possible effect N availability may have on mycorrhizal morphotype abundances. In this paper, we use those data to examine whether root %N is a good predictor of the frequency of different morphotypes of ectomycorrhizal fungi. We hypothesized that root %N would be a good predictor of shifts in ectomycorrhizal fungal community structure, as fine root %N is strongly related to N input (Magill et al. 1997; Hendricks et al. 2000). We also hypothesized that the responses of mycorrhizal fungal communities to N fertilization or N deposition recorded at these large-scale gradients would parallel those found at smaller spatial scales in more controlled studies in temperate and boreal conifer-dominated ecosystems (Kårén 1997; Kårén and Nylund 1997; Peter et al. 2001; Lilleskov et al. 2002). To understand whether N deposition had altered N availability at the sites sampled, we were also interested in determining whether root %N and organic horizon C/N ratios were related to N deposition rates along this gradient.

Methods

Study sites and sampling methods are described in Wargo et al. (2003), and morphotyping methods are described in Wargo et al. (1993). Briefly, nine red spruce - dominated sites from New York to Maine were sampled in 1993, and these nine sites plus two additional high N sites (Hubbard Brook and Bear Brook fertilized watershed) were sampled in 1994 (Table 1). Soils at all of these sites were classified as Spodosols.

Root samples were collected from nine red spruce trees per site by tracing lateral roots out from the three randomly sampled buttress roots. Only roots from the Oe and Oa horizons were sampled. Roots were returned to the laboratory on ice. In the laboratory, roots were placed in trays of water and gently washed with soft-bristled brushes and running water to clean debris from the root system.

Morphotype frequencies were determined using 270 nonwoody root branches (each with multiple tips) per site ((10 randomly selected nonwoody root branches per lateral root) × (3 lateral roots per tree) × (9 trees per site)). Each branch had an average of 37 live mycorrhizal root tips in 1993 and 57 in 1994, with no significant regression of root %N against live mycorrhizal tips per branch in either year. Presence or absence of all morphotypes was determined for each segment, and for each tree a morphotype percent frequency was calculated as the percentage of root branches in which that morphotype occurred. Mycorrhizal root tips were classified into eight mycorrhizal morphotypes in 1993 and nine in 1994 (Table 2). As more than one morphotype could be found on each branch, frequencies for all morphotypes can total >100%. Root %N was determined for three root-diameter classes: <1 mm, 1 to <2 mm, and 2 to <5 mm (Wargo et al. 1993).

Site N deposition was estimated using predictive equations for which the input variables were latitude, longitude, and elevation (Ollinger et al. 1993). We used the equations for wet deposition only to avoid uncertainties associated

Table 2. Descriptions of morphotypes found in red spruce stands across a regional N deposition gradient in the northeastern USA.

Morphotype	Description
1	Creamy tan (to tannish gray) with distinct mantle and no rhizomorphs
2	Light tannish brown with mantle and no rhizomorphs
3	Dark to reddish brown with mantle and no rhizomorphs
4	*Cenococcum geophilum*: black mantle with or without black emanating hyphae
5	Sulfur-yellow with yellow rhizomorphs
6	White mantle with many white rhizomorphs
7	White mantle with no rhizomorphs
8	Creamy tan translucent mantle (swollen, translucent with darker inner core)
9	Golden tan mantle (distinct with fuzzy surface)

with estimates of dry deposition rates. Therefore, calculated N deposition rates are an underestimate of total N deposition, but should be a good estimate of relative N deposition rates. C/N (mass/mass) ratios of the Oa horizon for each site were obtained for samples taken from the same stands, from data published in David and Lawrence (1996).

We performed linear and non-linear regression analyses of root %N in the three root-diameter classes versus the percent frequency of the nine mycorrhizal morphotypes for all data that met assumptions of independence of residuals, normality, and homogeneity of variance. Separate regression analyses were performed for each year. We performed Spearman rank correlation tests on data that violated regression assumptions.

We also performed regression analyses of estimated N deposition versus root %N and Oa C/N ratios, as well correlation analyses of root %N between size classes and years. Statistical analyses and curve fitting were performed using SPSS Version 14 (SPSS, Inc.) and Sigmaplot Version 9 (Systat Software, Inc.).

Results

Morphotype frequency and root %N

Frequencies of morphotypes 1, 2, and 3 were positively related to root %N for one or more root-diameter class during both years (Fig. 1*a*–1*c*, Table 3). The frequencies of morphotypes 4 (*Cenococcum geophilum* Fr.), 5 (putative *Piloderma* spp.), and 8 were negatively related to root %N for at least two root-diameter classes in one or both years (Fig. 1*d*–1*e*, 1*h*, Table 3). Frequencies of the other morphotypes (6, 7, and 9) were not significantly related to root %N, although the trends in the slopes were negative for morphotypes 6 and 7 and positive for morphotype 9 (Fig. 1*f*–1*g*, 1*i*, Table 3). Although the slopes and strengths of the relationships varied from year to year for some morphotypes, the sign of the relationships never reversed from year to year, suggesting broadly consistent interannual trends.

Root %N and N deposition

Estimated wet N deposition rates varied almost three-fold, from <3 $kg \cdot ha^{-1} \cdot year^{-1}$ in northern Maine to almost 8 $kg \cdot ha^{-1} \cdot year^{-1}$ on Whiteface Mountain in New York. There was a marginal to nonsignificant positive relationship between N deposition and root %N for all three root-diameter classes (1994 data: <1 mm, $r^2 = 0.39$, $p = 0.055$; ≥1 to <2 mm, $r^2 = 0.27$, $p = 0.12$; ≥2 to <5 mm, $r^2 = 0.22$, $p = 0.18$; Fig. 2*a*). Removal of a single outlier (the Bear Brook site) greatly improved this relationship (<1 mm, $r^2 = 0.58$, $p = 0.016$; ≥1 to <2 mm, $r^2 = 0.61$, $p = 0.013$; ≥2 to <5 mm, $r^2 = 0.46$, $p = 0.044$; Fig. 2*a*).

Similarly, C/N ratios of the Oa horizon were negatively related to N deposition across sites ($r^2 = 0.50$, $p = 0.02$; Fig. 2*b*), but the relationship was much stronger when the Bear Brook site was removed from the data set ($r^2 = 0.82$, $p = 0.0008$; Fig. 2*b*), again pointing to Bear Brook as an outlier. The Oa horizon in the sampled stand at Bear Brook has a C/N ratio of 24.9. This C/N ratio is intermediate between that recorded at Bear Brook for Oa + Oe in hardwood stands (C/N = 23) and mixedwood stands (C/N = 26), and well below that found in the softwood stands (C/N = 31) (Wang and Fernandez 1999). Inclusion of the Oe horizon with the Oa horizon typically raises the C/N ratio approximately 1 unit compared with the Oa horizon alone (E.A. Lilleskov, unpublished data), which is not enough to explain this difference. The low C/N ratio of the Oa horizon suggests that the plots may have had a high proportion of hardwood litter, leading to elevated soil N status in the Bear Brook plots relative to other sites. The sampled stand was dominated by red spruce, but was small and surrounded by hardwoods, so might easily have a significant hardwood litter input (G. Lawrence, personal communication).

Discussion

The parallel response to N among experimental studies, local gradients, and the present gradient all point to N availability as the most parsimonious causal explanation for much of the community variability observed. The almost three-fold increase in N deposition over the gradient spans a range of N deposition that has been demonstrated to alter the N status of forests across the region (McNulty et al. 1991; Aber et al. 2003). The strong link between N availability (as indicated by root %N) and mycorrhizal communities (as characterized by morphotypes) is consistent with results of other studies demonstrating community changes in response to N levels using both morphological and molecular methods (Wallenda and Kottke 1998; Lilleskov 2005 and references therein). For example, as in the present study, *Piloderma* spp. were present in both Alaska and Scandinavia at low N sites but absent at higher N sites (Kårén 1997; Lilleskov et al. 2002). While morphotype data must be interpreted with caution because both lumping and splitting of taxa can occur with this method, the consistency with other

Fig. 1. Linear and nonlinear regressions of the abundance of nine morphotypes found on red spruce roots against root N concentrations (root %N) in three root-diameter classes in red spruce stands across the northeastern USA. Open circles and broken lines, 1993; closed circles and solid lines, 1994. Regression lines are shown for fits with $p < 0.05$ in black, and $p \geq 0.05$ in grey. Data with no curve fit shown violated regression assumptions. r^2 and p values refer to the closest line.

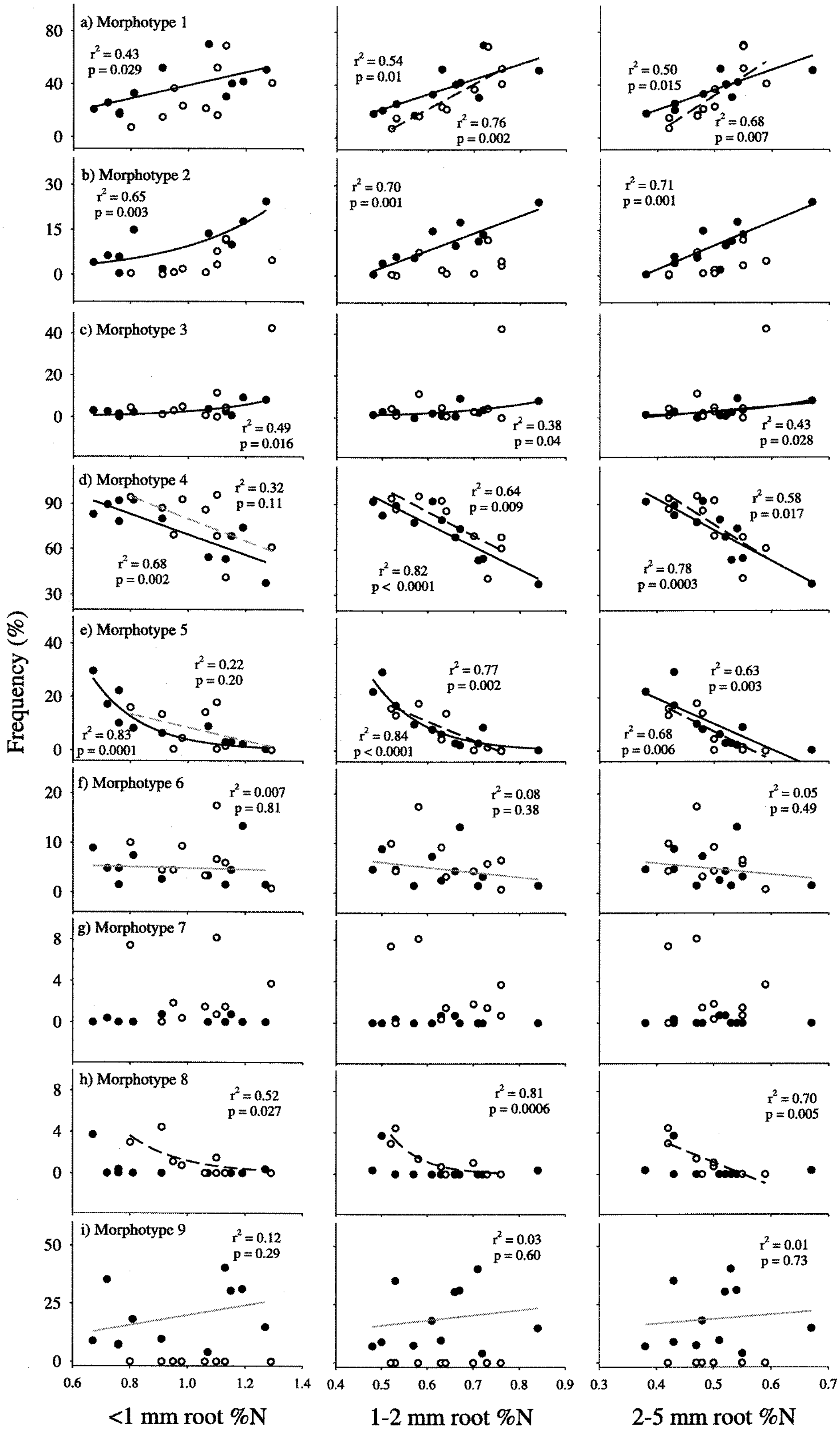


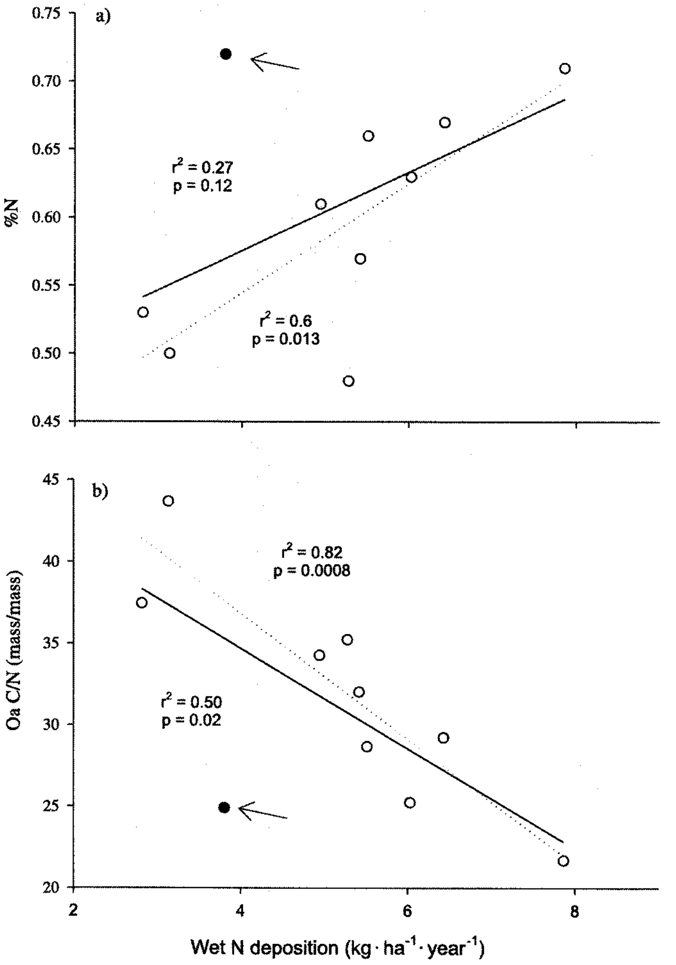
Table 3. Spearman rank correlations of root N concentration (root %N) with frequency of nine morphotypes, listed separately for three diameter classes and 2 years.

	<1 mm root %N		≥1–<2 mm root %N		≥2–<5 mm root %N	
Morphotype	1993	1994	1993	1994	1993	1994
1	**0.75 (0.02)**	**0.68 (0.02)**	**0.93 (<0.001)**	**0.77 (0.005)**	**0.94 (0.001)**	**0.80 (0.003)**
2	**0.89 (0.001)**	**0.72 (0.01)**	0.59 (0.10)	**0.77 (0.005)**	**0.67 (0.05)**	**0.79 (0.004)**
3	0.34 (0.38)	0.35 (0.29)	–0.07 (0.87)	0.47 (0.15)	0.17 (0.66)	0.51 (0.19)
4	–0.60 (0.09)	**-0.76 (0.007)**	**–0.86 (0.003)**	**–0.86 (0.001)**	**–0.82 (0.007)**	**–0.84 (0.001)**
5	–0.45 (0.23)	**–0.96 (<0.001)**	**–0.85 (0.004)**	**–0.84 (0.001)**	**–0.85 (0.004)**	**–0.85 (0.001)**
6	–0.25 (0.51)	–0.29 (0.38)	–0.50 (0.18)	–0.45 (0.16)	–0.40 (0.29)	–0.36 (0.28)
7	0.18 (0.65)	0.00 (1.00)	–0.08 (0.83)	–0.09 (0.80)	–0.06 (0.89)	–0.11 (0.74)
8	**–0.77 (0.01)**	–0.23 (0.49)	**–0.87 (0.003)**	–0.30 (0.37)	**–0.85 (0.004)**	–0.27 (0.43)
9[a]	—	0.31 (0.36)	—	0.22 (0.52)	—	0.17 (0.61)

Note: Values are Spearman's ρ followed by p values in parentheses. Values in boldfaced type are significant at $p < 0.05$.

[a] Morphotype 9 was not used until 1994.

Fig. 2. Regressions of wet N deposition versus (*a*) 1–2 mm root %N (1994) and (*b*) C/N ratio of the Oa horizon in red spruce stands across the northeastern USA. Solid lines are regression fits with all data included; broken lines are fits with the Bear Brook outlier (closed circle, arrow) excluded. r^2 and p values refer to nearest line.



results suggests that N effects may be powerful enough to be detected over large spatial scales.

In a gradient study one cannot rule out the possibility that factors other than N that vary over the regional gradient have generated the patterns observed. However, the regional environmental gradient held latitude almost constant (Table 1), so we do not expect any strong environmental trends. Soil type, host species, and stand maturity were also held constant. Biogeographic studies that detail the trends in soil communities over environmental gradients in which N availability is held constant are lacking, so we have little baseline data with which to compare this gradient. The fact that the two morphotypes that were identified sufficiently to determine taxonomic identity (*C. geophilum* and *Piloderma fallax* Erikss. & Hjortst.) both have wide host and geographic ranges in the absence of N deposition (see below) suggests that they should be found across the region in mature mesic spruce forests on Spodosols. Given the above, we believe that these results lend support to the hypothesis that N availability affects fungal communities across this region. However, biogeographic studies with more definitive molecular identification methods spanning a diversity of resource gradients of natural and anthropogenic origin are required in order to both test this hypothesis more rigorously and elucidate how N availability interacts with other controls on species distribution (Lilleskov and Parrent 2007).

Morphotype and ectomycorrhizal species response to N

Morphotype descriptions in Wargo et al. (2003) were not detailed enough to permit identification of the mycorrhizal fungi to the genus or species level, except for morphotypes 4 and 5. However, in some cases we can compare morphotype responses with responses in other study systems of species resembling those morphotypes, with the caveat that we cannot be certain of identities without more detailed morphological or molecular analysis. Unfortunately, the root tips from this study are not available for that purpose.

The two morphotypes that increased most dramatically with N availability (morphotypes 1 and 2) are similar to each other and likely represent several species. Although there is not enough information to assign these morphotypes to any species, their description is consistent with several spruce ectomycorrhizal species that have been found to respond positively to long-term N inputs in other studies (e.g., *Lactarius theiogalus* (Bull.: Fr.) S.F. Gray, *Tomentella sublilacina* (Ellis & Holw.) Wakef., and *Thelephora terrestris* Fr.) (Kårén and Nylund 1997; Lilleskov et al. 2002).

The responses to N deposition of species likely included in morphotype 3 are less certain. In other studies, some species that fit this description declined in response to N deposition (e.g., dark red brown *Tomentella* spp.), whereas others increased or were unchanged in response to N deposition (e.g., *Paxillus involutus* (Batsch: Fr.) Fr., unidentified corticioid fungi, and *Tylospora fibrillosa* (Burt) Donk) (Lilleskov 2005 and references therein).

Morphotype 4 was identified as *C. geophilum*. *Cenococcum geophilum* has a very broad host range and distribution (Trappe 1964) and is one of the most frequently encountered mycorrhizal species (Lilleskov et al. 2004), so we would a priori expect to find it equally abundant over the entire gradient. Given its frequency and wide distribution, understanding its response to N deposition is of particular importance. The negative response to N availability seen in *C. geophilum* in the present study has been corroborated in other studies in spruce stands (Kårén and Nylund 1997; Lilleskov et al. 2002), but not in all other ecosystem types (e.g., Avis et al. 2003). Caution must be taken with this identification because ectomycorrhizas formed by dark-mantled species such as some *Tomentella* spp. and *Meliniomyces bicolor* Hambleton & Sigler (Hambleton and Sigler 2005) can be erroneously identified as *C. geophilum*, and both of these taxa have been reported to respond negatively to N input (Kårén and Nylund 1997; Lilleskov et al. 2002). In addition, *C. geophilum* has been found to be a species complex (Douhan and Rizzo 2005), so species in the complex might differ in response to N inputs, explaining the differences between this and other studies.

Morphotype 5, which also declined with root %N, is distinct enough that we can be fairly certain that it represents *P. fallax*, which has been found (along with closely related European *Piloderma croceum* Erikss. & Hjortst.) to respond negatively to elevated N in other studies (Kårén 1997; Lilleskov et al. 2002). However, since common *Piloderma* spp. can exhibit color variation from yellow to white within the same individual, this morphotype likely represents only a subset of the *Piloderma* spp. tips. *Piloderma fallax* and *P. croceum* are widely distributed in mature coniferous forests with organic soil horizons in a diversity of climates, soils, and hosts (Smith et al. 2000 and references therein).

Morphotype 6, which showed no significant response to root %N, likely includes highly rhizomorphic *Cortinarius* spp., *Piloderma* spp., and *Hebeloma* spp., taxa commonly present on red spruce roots that vary in their responses to elevated ecosystem N. *Cortinarius* spp. and *Piloderma* spp. frequencies generally decline with increased N, while some *Hebeloma* spp. may respond positively to increasing N (e.g., Sagara 1992; Lilleskov et al. 2002). It is unclear what species are likely to be encompassed by morphotypes 7 through 9.

Root %N as a predictor

In general, regressions of morphotype frequency with larger diameter root N explained more of the variance than those with the smallest diameter root N, probably because the smallest diameter class had noisier values that diverged from the larger diameter classes. Correlations between root %N of the two larger root diameter classes were stronger (r = 0.96 (1993) and 0.98 (1994)) than correlations between root %N of the <1 mm diameter class with those of the 1–2 mm (r = 0.46 (1993) and 0.90 (1994)) and 2–5 mm (r = 0.63 (1993) and 0.87 (1994)) diameter classes. In addition, the correlation of root %N values between years within diameter classes was very weak in the <1 mm root diameter class (r = 0.11) whereas it was quite strong in the 1–2 mm and 2–5 mm classes (r = 0.96 and 0.89, respectively).

One possible reason for the divergence of the smallest diameter class from the others is that root %N in the smallest diameter class is a function of both plant and ectomycorrhizal fungal tissue N status. Fungal tissue has a higher N concentration. N fertilization has often been shown to reduce fungal percent colonization (Wallenda and Kottke 1998 and references therein) and fungal biomass on roots (e.g., Wallander and Nylund 1991; Wallenda et al. 1996). If fungal biomass in ectomycorrhizas declines as a function of host or soil N status, then root %N in the smallest diameter class might decline, leading to a poor relationship between root %N and N availability. In addition, the smallest root diameter class is more likely to have soil adhering to the roots, which would increase variability in root %N among samples. Given the high predictive ability for morphotype frequency and year-to-year stability, root %N in the 1–2 mm diameter class seems like a potentially useful predictor of ectomycorrhizal fungal community structure. Another advantage is that tissue samples can be derived from the same soil cores used for characterization of the ectomycorrhizal fungal community, minimizing both sampling effort and the effects of spatial heterogeneity.

Conclusions

Although factors besides N deposition can affect soil N availability and ultimately what is detected in plant root tissues, the results of the present study suggest a link between N deposition and ecosystem N status, and other studies have shown that N deposition is altering the N status of forests across the northeastern USA (McNulty et al. 1991; Aber et al. 2003). Therefore, if we accept that N deposition affects ecosystem N status in the region, and ecosystem N status affects mycorrhizal fungal communities across the northeastern USA, it follows that N deposition affects mycorrhizal fungal community structure across this region. Detailed molecular analyses and more extensive sampling will be needed to resolve the exact nature of this community response and to test for the presence of confounding factors that covary with N. Ectomycorrhizal fungal community changes have potential implications for ecosystem function — including nutrient and C cycling, plant nutrition, and buffering of environmental change — across large regions affected by N deposition, so it is critical that we determine community responses to changing N availability more fully over these scales.

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