

ECTOMYCORRHIZAL FUNGAL ABOVEGROUND COMMUNITY CHANGE OVER AN ATMOSPHERIC NITROGEN DEPOSITION GRADIENT

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Abstract. Atmospheric nitrogen deposition has been hypothesized as one of the causal factors in the decline of ectomycorrhizal fungal (EMF) sporocarps. We assessed the effects of N deposition on EMF of forests dominated by white spruce (*Picea glauca* (Moench) Voss) over a short, steep N deposition gradient in Alaska, USA. The study area had received high NH₃ inputs from an industrial ammonia production facility for almost 30 yr. Current N inputs varied 20-fold over the gradient. High N inputs have increased soil N availability, which has led to decreased soil pH and base cation availability; increased foliar N and decreased foliar P, Mg, and K; increased tree growth; and replacement of mosses by grasses. At the six lowest N sites, 144 species were encountered, whereas only 14 species were encountered at the six highest N sites. With increasing mineral N availability in the organic horizon, there were declines in both total species richness (1994 and 1995) and total sporocarp abundance (1994 only). Correlation analysis identified two groups of taxa that responded differently to the N inputs. One group (“nitrophobic” taxa: *Cortinarius*, *Russula*, *Tricholoma*, *Lactarius*, *Hebeloma*) declined in species richness or abundance with increasing organic horizon mineral N. In the second group (“nitrophilic” taxa: *Lactarius theiogalus*, *Laccaria*, *Paxillus involutus*, and *Hygrophorus olivaceoalbus*), sporocarp abundance was either not correlated or slightly positively correlated with organic horizon N availability. Redundancy analysis identified two axes of environmental variation that explained 62% and 7% of the variation in the EMF community and clearly distinguished the two groups of taxa. The environmental variables included in the final model were mineral soil base cations, organic horizon mineral N, and organic horizon net mineralization. These results support the hypothesis that long-term N inputs alone may lead to loss of EMF sporocarp diversity and indicate that EMF should be considered in the establishment of critical loads of N.

Key words: acidification; Alaska; *Cortinarius*; ectomycorrhizal sporocarps; *Laccaria bicolor*; *Lactarius theiogalus*; nitrification; nitrogen deposition; nitrogen mineralization; *Picea glauca*; redundancy analysis; species richness.

INTRODUCTION

Increased human N inputs into the atmosphere (Galoway et al. 1995, Vitousek et al. 1997) lead to eutrophication and acidification of forests, affecting tree health, ecosystem function, and biodiversity (Lovett and Lindberg 1993, Ulrich 1995, Vitousek et al. 1997). Arnolds (1991) described a dramatic decline in the diversity of ectomycorrhizal fungi (EMF) over large regions of Europe. One hypothesis he proposed to explain this decline was that increasing atmospheric N deposition causes a reduction in diversity of EMF.

Ectomycorrhizal fungi supply soil resources to their tree hosts in exchange for sugars (Smith and Read 1997). There are thousands of species of ectomycorrhizal fungi, with individual tree species capable of

forming relationships with hundreds of fungal species (Molina et al. 1992), and individual trees forming relationships with multiple species of fungi simultaneously (e.g., Gardes and Bruns 1996). Trees hosting EMF typically live in N-limited ecosystems (Read 1991). However, there is a great deal of variation in the physiology and life history strategies of EMF species (Smith and Read 1997), and potential for variation in response to anthropogenic N inputs.

Evidence for a nitrogen deposition effect on EMF comes from a number of sources (reviewed in Wallenda and Kottke 1998). Pollution gradient studies should more closely mimic the effects of atmospheric N deposition than do fertilization experiments (Johnson 1992), but multiple pollutants are often highly correlated (Termorshuizen and Schaffers 1987) and these gradients often occur over large spatial scales, where many other factors are also likely to vary.

We assessed the overall response of the EMF sporocarp community to N deposition in white spruce (*Picea glauca* (Moench) Voss)-dominated stands over a gradient in Alaska, USA, which avoids these problems

Manuscript received 9 September 1999; revised 4 January 2000; accepted 26 January 2000; final version received 28 February 2000.

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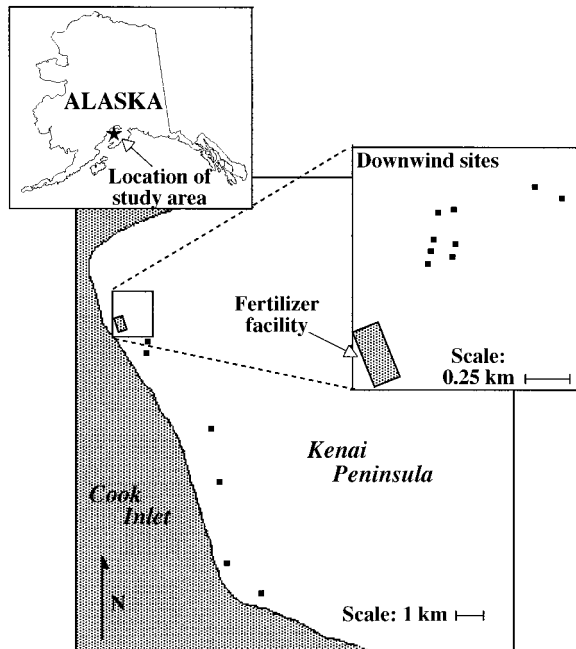


FIG. 1. Map of the study area north of Kenai, Alaska. Deposition is heaviest to the NNE of the fertilizer facility. Black squares indicate study sites, and the area of detail shows the downwind sites. Appendix D provides photographs of the study area, selected sites, and several dominant ectomycorrhizal fungi.

of multiple correlations and large scales. Our specific objectives were to determine the pattern of EMF species richness and abundance over the N gradient, and to evaluate the relationships of EMF species richness and abundance to various N-affected environmental factors. We hypothesized that EMF species richness and abundance would decline over the deposition gradient. Further, although EMF community composition could be affected by multiple environmental variables, we predicted that soil N availability was likely to be the best predictor of community effects because of its known direct effects on EMF growth (Wallander 1995), and its key effect on all other system variables (Aber et al. 1998).

METHODS

Study area

The study area is located near the town of Nikiski, on the Kenai Peninsula, in south-central Alaska, USA (60°40' N, 151°22' W; Fig. 1). The primary N source is an industrial ammonia production facility established in 1968, which uses natural gas from neighboring oil-fields to fix atmospheric N_2 . Gaseous ammonia leaks out of the facility and is deposited on the forest. Historic N inputs were considerably higher than present inputs, as control measures have been implemented since the mid-1980s, reducing emissions by ~80%

(Sullivan et al. 1990; D. Newbold, *personal communication*).

The prevailing onshore winds are from the south-southwest (Sullivan et al. 1990). Mean annual precipitation is 49 cm, with ~50% falling from May through September. Annual, January, and July mean temperatures are 1.1°C, -10.6°C, and 12.6°C, respectively (NOAA 1995).

The mature boreal forest at these sites is dominated by white spruce (*Picea glauca* (Moench) Voss). Kenai paper birch (*Betula kenaica* Evans) is subdominant, and lesser amounts of quaking aspen (*Populus tremuloides* Michx.) and balsam poplar (*P. balsamifera* L.) are present. The understory of the forest at the low-N sites is dominated by feather mosses, which are replaced by grasses, primarily *Calamagrostis canadensis* (Michx.) Beauv., at higher N sites. The fine sandy loam soils are typical cryorthods formed on well-drained glacial outwash of low relief (Rieger and Dement 1967, Rieger 1979).

Field sampling

Sampling was carried out in July–early August 1993, July–August 1994, and July–September 1995. To encounter a large range of N inputs over the shortest distance, we established sampling sites along a transect that led upwind (south) from a point downwind (northeast) of the source (Fig. 1). Density of sites was high in the downwind area, where variation in inputs was greatest. Nine sites were located in this area. Six sites were located upwind to receive minimal inputs. Some of the sites had been used in a previous study of N dynamics (Whytemare et al. 1997). All sites were dominated by white spruce, with some birch and aspen also present.

Bulk deposition.—To estimate the relative amounts of N deposited at the different sites, bulk deposition of N was estimated for all sites in late July–late September 1995. Samples were collected using open funnels plugged with polyester wool draining into foil-covered plastic containers, placed on wooden stakes in the center of clearings (~20 m minimum diameter) within 25 m of the sites. Within a day after precipitation events ended, precipitation volume was measured, and a subsample was taken for later chemical analysis. Precipitation samples were preserved with chloroform and refrigerated until NH_4^+ and NO_3^- analysis. Five bulk deposition samples were collected per site.

Focal tree selection.—Focal trees were used to minimize any effect of variation in basal area and tree species composition among sites. At each site, three mature, healthy white spruce trees 20–35 cm dbh (diameter at breast height) were randomly selected in 1993. This diameter range was typical of the canopy trees at these sites. These focal trees were used for growth rate sampling, foliar sampling, and as the center of sporocarp and soil sampling plots. In 1995, this number was expanded to five focal trees for all measures,

except for sporocarp sampling, for which 10 focal trees were used.

Foliage sampling.—In each year, foliage samples were collected at the beginning of August from the southern side of each tree. Subsamples were collected from three unshaded branches at a height of ~ 3 m using a pole pruner. Current-year foliage was pooled for each tree and air-dried for later analysis. Shoot length was determined for the main shoot axis for all three shoots, separately for current and second year shoots.

Tree cores.—To estimate aboveground growth rates, two tree cores were taken per focal tree. The initial core position was randomly chosen and the second core was taken at a 90° angle to the first. The cores were brought to the lab and annual radial growth was measured using a sliding stage micrometer and binocular dissecting microscope.

Plant community sampling.—Relative basal area of the different tree species was estimated for the focal tree plots using the Bitterlich variable radius method (Avery and Burkhart 1983). Within the 4-m² focal tree plots, the relative abundance of seedlings and saplings of ectomycorrhizal woody species was also estimated. Percent cover of four classes of ground cover was estimated in the plots: moss, grass, forbs, and unvegetated leaf litter. Mean height of grass (mostly *Calamagrostis canadensis* (Michx.) Beauv.) was also measured, and an index of grass abundance was calculated as the product of the grass height and cover estimates.

Soil sampling.—Soils were sampled in late August 1994 and in mid-September 1995, using a 1.9 cm diameter soil corer. Starting in a randomly chosen compass direction, we took, nine cores in a radial pattern around each tree, three at 1.5 m and six at 3 m from the trunk. Each core was 10 cm deep, and was divided into organic and mineral horizons and then bulked by horizon for each tree. Separation of organic and mineral horizons was usually obvious because of the sharp transition between the forest floor and the surface mineral horizon. All soils were refrigerated at 4°C until chemical analysis for extractable N within two weeks.

Ion exchange resins.—In early August 1994 and 1995, three replicate pairs of bags (each bag 35 cm² in area), one containing 7.4 cm³ of Dowex 1-X8 anion exchange resins (20–50 mesh, chloride form), the other 7.4 cm³ of Dowex 50W-X8 cation exchange resins (20–50 mesh, hydrogen form; Dow Chemical, Midland, Michigan, USA) (Giblin et al. 1994), were set out in the organic horizon at ~ 5 cm depth at 1.5 m from each tree. Bags were equally spaced around the tree, with the first bag placed at a random compass heading. The bags were collected after 28 d, frozen, and returned to the lab for analysis.

Sporocarp sampling.—Fungal sporocarps were sampled at 2–3 wk intervals during the sampling seasons: mid-July–early August 1993, July–August 1994, and July–mid-September 1995. In 1993, dry conditions led to negligible sporocarp production, despite our sam-

pling of 1200 m²/site (in belt transects) over the sampling period. In 1994 and 1995, sporocarps were sampled in circular plots centered on target spruce trees. In 1994, three trees per site were sampled and the plots had a 3 m radius (85 m²/site); in 1995, 10 trees per site were sampled and plots had a 4 m radius (503 m²/site).

Only ectomycorrhizal fungal taxa (based on Molina et al. 1992) were quantified. Sporocarps were identified based on macroscopic, microscopic, and chemical characteristics. Nomenclature follows Hansen and Knudsen (1992), except for a few taxa not present in that flora. Voucher specimens were placed in the herbarium of the University of Washington, Seattle, Washington, USA.

Lab analyses

Soil mineral N availability was assayed by three methods. First, field-moist soil samples were extracted with 2 mol/L KCl and extracts were analyzed for NH_4^+ and NO_3^- . Second, assays of laboratory potential net mineralization and nitrification were carried out, using 28-d incubations at 25°C (Hart et al. 1994). Third, ion exchange resins from the field were extracted as in Giblin et al. (1994). Analysis for solution concentration of NH_4^+ -N and NO_3^- -N in resin-bag extracts and soil extracts was carried out using standard colorimetric methods on a continuous-flow autoanalyzer (Orion Research, Beverly, Massachusetts, USA).

Soil pH was measured in a 1:10 slurry for organic horizon soils and a 1:3 slurry for mineral soils. The pH was measured in 0.01 mol/L CaCl_2 , which is supposed to give a more informative pH estimate in fertilized soils (Hendershot et al. 1993). Equivalent pH in H_2O was about 0.75 pH units higher. Soils for each site were bulked and analyzed for exchangeable cations and cation exchange capacity, using the ammonium chloride method at the Soil Analytical Laboratory, Department of Agronomy, Cornell University, Ithaca, New York, USA. Soil particle size analysis was carried out using the hydrometer method on soil samples pooled by site (Sheldrick and Wang 1993).

Leaf tissue nutrient content was determined via inductively coupled argon plasma atomic emissions spectrometer analysis, using the standard dry-ash method for all elements except N (Isaac and Johnson 1998). Foliar N was analyzed at the Cornell Laboratory for Stable Isotope Analysis (CLSLIA) by means of a Europa Scientific ANCA SL solid-liquid elemental analyzer (PDZ Europa, Crewe, Cheshire, UK) using the principles of the Dumas combustion.

Statistical analyses

We used two approaches to examine quantitative relationships between the environmental variables and the fungal community at the site level: correlation analysis and redundancy analysis (RDA). Although results for total species richness and abundance were analyzed for both 1994 and 1995, the larger sample size in 1995

allowed for a more in-depth analysis of genus- or species-level patterns of relationship with environmental variables for that year's data.

For the correlation analysis, we examined both the correlation between the predictor variables and precipitation N and the correlation between predictor variables and EMF community measures, including both species richness and sporocarp abundance. Genus-level patterns were examined separately in order to determine whether individual genera were responding differently to the long-term N inputs. EMF sporocarp and species numbers were log-transformed, as were certain environmental variables (Neter et al. 1990). Correlation analyses were carried out on Minitab 10.5 (Minitab 1995).

The relationship among the various predictor variables was examined using principal components analysis (PCA). RDA was used to examine how the entire fungal community changed in relation to the N-affected environmental variables. RDA is a constrained canonical community ordination method used to describe the relationship between sets of species and environmental data, and can be thought of as a multivariate form of regression analysis (ter Braak 1994). The underlying model is linear (ter Braak 1994), making it appropriate for the community data of this study, which display monotonic relationships with the environmental variables.

The PCA and RDA analyses were conducted using Canoco 3.0 (ter Braak 1987–1992). We chose the best set of variables for the RDA using forward selection. The significance of added variables was tested using Monte Carlo permutation tests. We carried out RDA at two levels, the genus and species level.

RDA at the genus-level tests was carried out in three stages to determine whether the results were biased by a trend in basal area over the gradient. First, we carried out a full RDA using all environmental and community data. Next, we used two approaches to test for the effect of basal area on the outcome of the RDA. First, we used it as a covariate in a partial RDA. In partial RDA, the analysis is carried out on the residuals after an initial RDA using the covariate (basal area in this case) as the environmental variable (ter Braak 1988). Second, we performed the RDA using a subset of nine sites, eliminating the five lowest and one highest basal area sites. This eliminated a significant basal area effect from the RDA ($P = 0.40$ for basal area as the first variable in forward selection).

In order to examine the species-level EMF community patterns in relation to the environmental data, we performed an RDA using species data for species present at more than two sites. Environmental variables were the same as in the genus-level analysis.

RESULTS

N deposition and N-affected variables

There was a large range of bulk N deposition over short distances. At sites >2 km upwind from the

source, the bulk precipitation N inputs were as low as $0.1 \text{ kg} \cdot \text{ha}^{-1} \cdot 60 \text{ d}^{-1}$. Bulk N inputs near the source were at least one order of magnitude higher, up to $3 \text{ kg} \cdot \text{ha}^{-1} \cdot 60 \text{ d}^{-1}$. If we make the simplified assumption of uniform deposition rates through the year, this translates into a range of N inputs from <1 to $18 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. This agrees well with the $0.7\text{--}21.0 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ found in 1992 over the same gradient (Whytemare et al. 1997). Approximately 95% of the bulk deposition of N to the high-N sites was in the form of NH_4^+ , compared with approximately 75% at the low-N sites.

Bulk N deposition was highly correlated with many of the environmental variables measured, especially increased soil organic horizon N availability; decreased soil pH and base cations; decreased foliar P and cations; and decreased moss cover and increased grass abundance (Table 1). As might be expected, correlations among many of the predictor variables is also high, as can be seen from the PCA of the environmental variables (Fig. 2).

Measures of pooled EMF species richness

Our first approach was to pool sites based on their N status, in order to examine patterns of species richness above the site level. Pooling of sites was based on clear divisions among the sites in N inputs and N-affected variables (Table 1).

Sporocarp production was negligible in 1993, low in 1994, and very high in 1995. EMF species richness was much lower at the high-N sites in both 1994 and 1995 (Fig. 3). At the six lowest N sites in 1995, we found 144 species of ectomycorrhizal fungi, 122 of which were not found at any of the higher N sites. These 122 low-N species comprised one-fourth of the sporocarps at the low-N sites. In contrast, at the six highest N sites, only 14 species were observed in the plots, three of which were found only in these plots. These three species were quite rare (Fig. 3). Patterns were similar in 1994, except that the sample size was smaller and no unique taxa were found at high-N sites (Fig. 3).

There were two groups of species with differing relationships to site N status. For convenience, we use the terms nitrophilic and nitrophobic to describe these divergent groups, although the effect may be only indirectly attributed to nitrogen. Members of the nitrophilic group, consisting of only a few species that made up a large proportion of the sporocarps (Appendix A), fruited abundantly at high- and low-N sites. This group consisted of the following species (in descending order of abundance): *Lactarius theiogalus* (Bull.: Fr.) S.F. Gray; *Laccaria bicolor* (Maire) Orton; *Laccaria laccata* (Scop.: Fr.) Berk. & Br.; *Paxillus involutus* (Batsch: Fr.) Fr.; *Hygrophorus olivaceoalbus* (Fr.: Fr.) Fr.; *Lactarius olivaceo-umbrinus* (Smith); and *Russula betularum* (Hora). In the nitrophobic group, comprising the vast majority of species at the low-N sites, species

TABLE 1. A summary of the predictor variables measured (mean \pm SE) over a nitrogen deposition near Nikiski, Alaska, and their correlation with bulk N deposition.

| Variable | High-N sites (n = 6) | Medium-N sites (n = 3) | Low-N sites (n = 6) | Correl. with bulk N dep. (r) [†] |
|--|-------------------------|---------------------------|------------------------|--|
| N inputs | | | | |
| Bulk N deposition (kg·ha ⁻¹ ·60 d ⁻¹) | 2.44 \pm 0.20 | 1.13 \pm 0.10 | 0.27 \pm 0.06 | |
| Organic horizon N availability | | | | |
| KCl extractable NO ₃ -N (mg/kg) | 49.7 \pm 4.0 | 26.9 \pm 4.9 | 18.1 \pm 1.15 | 0.90 |
| KCl extractable NH ₄ -N (mg/kg) | 134 \pm 6 | 104 \pm 9 | 29.0 \pm 4.3 | 0.89 |
| Net nitrification (mg·kg ⁻¹ ·28 d ⁻¹) | 128 \pm 10 | 83.8 \pm 17.7 | 10.3 \pm 5.0 | 0.87 |
| Net mineralization (mg·kg ⁻¹ ·28 d ⁻¹) | 143 \pm 9 | 154 \pm 21 | 74.2 \pm 13.4 | 0.54 |
| Anion exch. NO ₃ -N (mg·bag ⁻¹ ·28 d ⁻¹) | 3.88 \pm 0.49 | 3.10 \pm 0.81 | 0.07 \pm 0.01 | 0.89 |
| Cation exch. NH ₄ -N (mg·bag ⁻¹ ·d ⁻¹) | 5.24 \pm 0.30 | 4.59 \pm 0.52 | 2.35 \pm 0.17 | 0.83 |
| Organic soil pH and cations | | | | |
| pH (H ₂ O) | 4.62 \pm 0.02 | 4.69 \pm 0.03 | 4.96 \pm 0.03 | -0.90 |
| pH (CaCl ₂) | 3.37 \pm 0.02 | 3.38 \pm 0.03 | 3.73 \pm 0.03 | -0.83 |
| Exchangeable Ca (cmol/kg) | 7.69 \pm 0.69 | 8.84 \pm 0.78 | 11.82 \pm 0.91 | -0.67 [‡] |
| Exchangeable Mg (cmol/kg) | 2.04 \pm 0.22 | 2.67 \pm 0.19 | 3.55 \pm 0.54 | -0.58 [‡] |
| Exchangeable K (cmol/kg) | 0.66 \pm 0.05 | 0.58 \pm 0.04 | 0.78 \pm 0.07 | -0.31 [‡] |
| Exchangeable base cations (cmol/kg) | 10.7 \pm 0.9 | 12.3 \pm 1.0 | 16.4 \pm 1.5 | -0.64 [‡] |
| Mineral soil pH and cations | | | | |
| pH (H ₂ O) | 4.52 \pm 0.01 | 4.80 \pm 0.05 | 5.15 \pm 0.03 | -0.79 |
| pH (CaCl ₂) | 3.87 \pm 0.01 | 3.94 \pm 0.05 | 4.19 \pm 0.02 | -0.83 |
| Exchangeable Ca (cmol/kg) | 1.45 \pm 0.06 | 1.61 \pm 0.05 | 2.34 \pm 0.31 | -0.66 [‡] |
| Exchangeable Mg (cmol/kg) | 0.23 \pm 0.02 | 0.29 \pm 0.02 | 0.65 \pm 0.07 | -0.83 [‡] |
| Exchangeable K (cmol/kg) | 0.10 \pm 0.02 | 0.10 \pm 0.01 | 0.12 \pm 0.01 | -0.42 [‡] |
| Exchangeable base cations (cmol/kg) | 2.06 \pm 0.08 | 2.30 \pm 0.09 | 3.44 \pm 0.37 | -0.73 [‡] |
| Spruce foliar nutrients | | | | |
| N (g/kg) | 15.8 \pm 0.4 | 14.7 \pm 0.4 | 14.1 \pm 0.2 | 0.76 |
| K (g/kg) | 6.30 \pm 0.24 | 6.93 \pm 0.25 | 8.24 \pm 0.23 | -0.90 |
| P (g/kg) | 1.61 \pm 0.04 | 1.78 \pm 0.06 | 2.23 \pm 0.06 | -0.86 |
| Mg (g/kg) | 0.74 \pm 0.03 | 0.86 \pm 0.04 | 0.95 \pm 0.02 | -0.86 |
| Mn (mg/kg) | 449 \pm 30 | 483 \pm 37 | 266 \pm 18 | 0.61 |
| Al (mg/kg) | 32.0 \pm 2.7 | 24.9 \pm 1.3 | 25.1 \pm 1.3 | 0.59 |
| Tree growth and biomass | | | | |
| Mean radial growth 1993–1995 (mm/yr) | 1.89 \pm 0.03 | 1.96 \pm 0.03 | 1.13 \pm 0.02 | 0.61 |
| Total basal area (m ² /ha) | 21.7 \pm 1.6 | 27.9 \pm 2.6 | 34.0 \pm 1.6 | -0.75 |
| Plant community | | | | |
| Grass relative abundance (%) | 63.8 \pm 3.7 | 33.0 \pm 4.7 | 13.0 \pm 1.8 | 0.89 |
| Feathermoss cover (%) | 3.67 \pm 0.73 | 5.00 \pm 1.22 | 75.7 \pm 3.6 | -0.82 |

Note: Sites are grouped into high-N, medium-N, and low-N sites based on clear breaks in N inputs and site N status.

[†] Correlations with bulk N deposition are based on site means for all 15 sites.

[‡] Correlations for all soil cations were based on log-transformed values.

were present at low-N sites, but absent or rare at high-N sites. Most of these species were in the genera *Cortinarius* and *Russula*, but several other genera were represented in this group (Fig. 3). The most abundant species in this group were *Tricholoma inamoenum* (Fr.: Fr.) Gill.; *Cortinarius idahoensis* complex; *Cortinarius brunneus* (Pers.: Fr.) Kumm.; *Boletus subtomentosus* L.: Fr. var. *subtomentosus*; *Lactarius rufus* (Scop.: Fr.) Fr.; *Russula abietina* Peck; *Cortinarius* (Telamonia) sp. 12; *Hebeloma mesophaeum* (Pers.) Quel.; *Cortinarius umbilicatus* complex; and *Cortinarius obtusus* complex (Appendix A).

Correlation analyses

Despite the fact that the environmental variables are the predictors and that EMF species richness and sporocarp abundance are response variables, we present correlations in the text because the sign of the relationship remains intact, making interpretation easier for

the reader. Figures are presented with r^2 values in order to show the strength of the corresponding regression.

EMF species richness and environmental variables.—The highest correlations with EMF species richness in both years were measures of organic horizon N availability: organic horizon extractable NO₃-N ($r = -0.83$) in 1994, and organic horizon extractable mineral N in 1995 (Fig. 4a). Species richness was also highly negatively correlated with other N-affected environmental variables, especially measures of soil pH and base cations (Appendix B).

Within most genera, including all species-rich genera, species richness was highly negatively correlated with soil N availability. For example, correlation with organic horizon mineral N was strongly negative for *Cortinarius*, *Russula*, *Lactarius*, *Hebeloma*, and other nitrophobic genera (*Entoloma*, *Inocybe*, *Xerocomus*, *Leccinum*, and *Rozites*) pooled (Fig. 4b–f). Three genera, represented by only four species (*Laccaria laccata*,

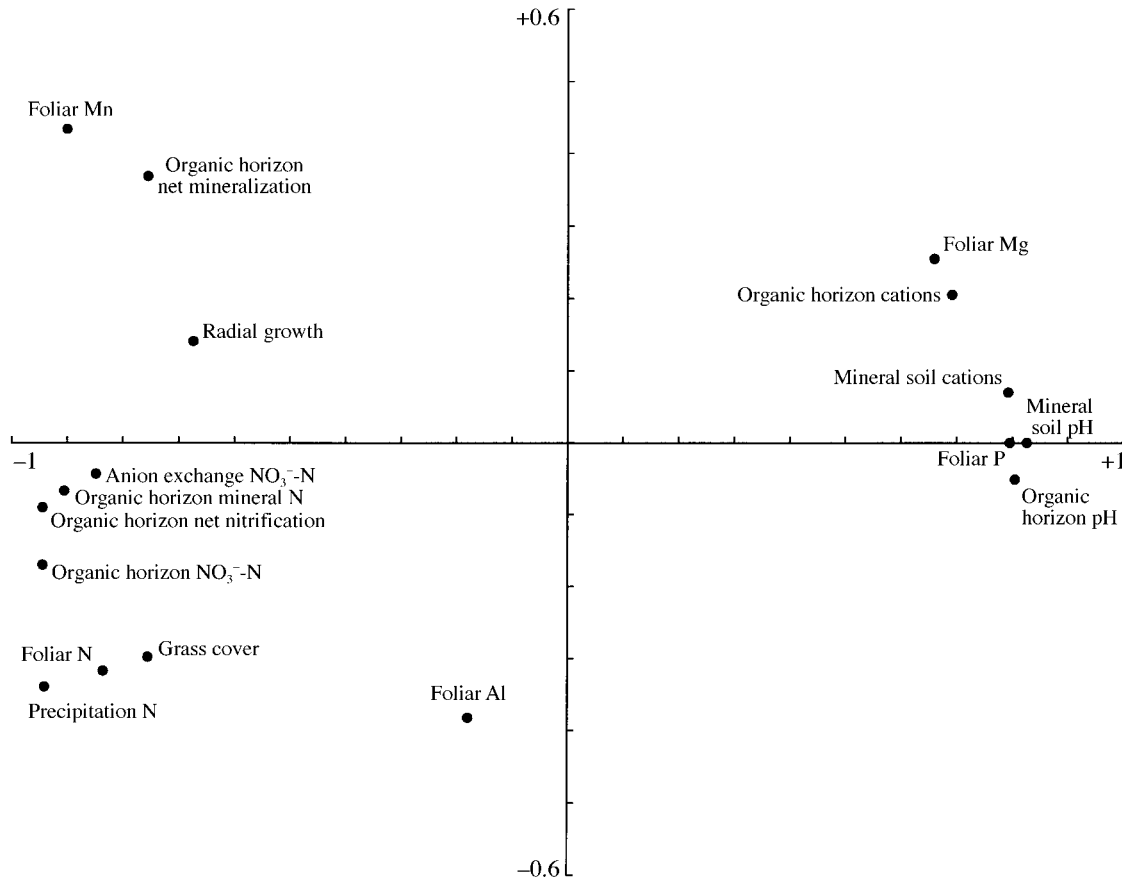


FIG. 2. Plot of the first and second axes of the PCA for representative N-affected environmental variables measured across an atmospheric N deposition gradient near Kenai, Alaska. The first and second axes explain 85% and 14% of the variance in the environmental data, respectively.

L. bicolor, *Paxillus involutus*, and *Hygrophorus olivaceoalbus*), remained unchanged in species richness over the gradient (Fig. 5g, nitrophilic genera).

EMF sporocarp abundance and environmental variables.—In 1994, sporocarp abundance was most strongly, and negatively, correlated with organic horizon NO_3^- -N ($r = 0.85$). In 1995, total sporocarp abundance was not strongly correlated with any of the environmental variables (Fig. 5a).

In both years, but more strongly in 1995, there were divergent fruiting responses among taxa. Most genera fell into the nitrophobic group, which declined dramatically across the gradient. In 1994, although sample sizes were too small to analyze the response of individual genera, the sporocarp abundance of the nitrophobic genera pooled was negatively correlated with organic horizon mineral N availability ($r = -0.83$). In 1995, the abundance of many of the nitrophobic genera was also most highly, and negatively, correlated with organic horizon N availability (Fig. 5b–e, i, l). *Tricholoma* and *Hebeloma* abundance was also highly correlated with organic horizon pH ($r = 0.92$ and 0.81 , respectively).

In contrast with the consistent, strong negative relationship with N availability shown by sporocarp abundance of nitrophobic taxa from year to year, a small set of dominant fruiters (the nitrophilic taxa) displayed weak negative (1994) or weak positive (1995) relationships with measures of N availability. For example, the correlation of *L. theiogalus* and *Laccaria* spp. with organic horizon mineral N was not significant in 1995 (Fig. 5h, j), and was weakly negative in 1994 ($r = -0.46$ for both; data not shown). In 1995, abundance of the dominant nitrophilic taxa (*L. theiogalus*, *Laccaria* spp., and *P. involutus*) was most strongly, and positively correlated with organic horizon net N mineralization ($r = 0.62$, 0.68 , and 0.67 , respectively) and foliar Mn ($r = 0.72$, 0.58 , and 0.67 , respectively).

Redundancy analysis (RDA)

The best RDA model accounted for 71% of the variation in the generic abundance data, and included three soil variables: organic horizon mineral N, organic horizon net mineralization, and mineral soil base cations (Fig. 6; see the legend for interpretation of the correlation biplots). The first (x) axis can be interpreted as

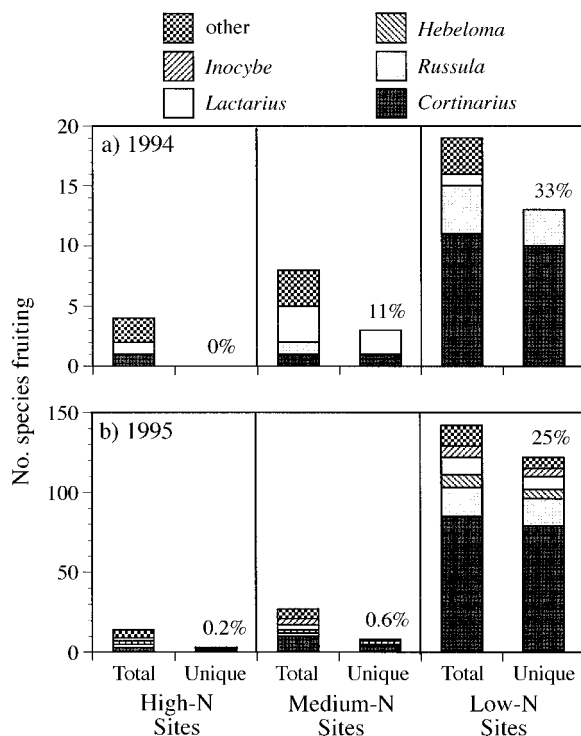


FIG. 3. Ectomycorrhizal fungal species richness across an N deposition gradient pooled by site N status into three deposition classes: high ($n = 6$ sites), medium ($n = 3$ sites), and low ($n = 6$ sites), presented for both (a) 1994 and (b) 1995. See Table 1 for environmental variables. Species richness is presented for all species found at the sites (total) and for species found only in that deposition class (unique). Numbers above the bars represent the percentage of total sporocarps in a site class consisting of unique species, indicating that there are almost no species unique to the high-N sites, and when they are present, they fruit quite rarely.

the “organic horizon mineral N/mineral soil base cation” axis, with taxa to the left positively correlated with organic horizon mineral N and negatively correlated with mineral soil base cations, and vice versa (Fig. 6). The second (y) axis can be interpreted as the “organic horizon net mineralization” axis. The community separated out into two groups of genera on these axes (Fig. 6). Abundance of the dominant nitrophobic taxa was positively correlated with the first axis, consistent with their negative relationship with organic horizon N availability and positive relationship with mineral soil base cations (Appendix C). The nitrophilic taxa clustered negative on the first axis and positive on the second axis, consistent with their positive relationship with measures of soil N availability, especially organic horizon net mineralization (Fig. 6; Appendix C).

When the effect of basal area was removed from the analysis, using both partial RDA and a subset of the sites, results differed little from the original RDA. When we used the same three predictors as in the full RDA, the first three axes explained 52%, 9%, and 1%

of the residuals after we accounted for basal area. Similarly, when we used a subset of sites, the first three axes explained 60%, 12%, and 3% of the variation. In both cases, the dominant taxa had essentially the same relationship to the axes.

RDA of the EMF species data showed that within individual genera, the range of correlations with the first axis of the RDA (the pH–organic horizon N axis) increased in breadth in the following order (Fig. 7): *Cortinarius* (0.32 to 0.72) < *Hebeloma* (0.16 to 0.82) < *Russula* (0.08 to 0.80) < *Laccaria* (–0.58 to 0.22) < *Lactarius* (–0.42 to 0.80). This suggests that some genera (e.g., *Cortinarius*) consistently responded negatively to higher N, whereas others (e.g., *Lactarius*) showed a great deal of interspecific variation in response to the gradient.

DISCUSSION

The relationship between site N status and species richness strongly suggests that high N availability caused a decline in species richness of EMF fruiting. The most parsimonious interpretation of these results is that long-term N deposition caused this decline.

Comparison with fertilization experiments

The contrasting fruiting patterns among taxa suggest that different EMF taxa have divergent responses to long-term N inputs. Our results closely parallel those of fertilization experiments (summarized in Brandrud 1995, Wallenda and Kottke 1998). In all of those studies, N fertilization had a more positive effect on taxa that we have classified as nitrophilic than on those classified as nitrophobic. Some experiments show a decline in all taxa, others show an increase in the nitrophilic taxa and a decline in nitrophobic taxa, and others show an initial increase in nitrophilic taxa followed by decline. This variation may be, in part, a function how quickly fertilization shifts the site into a eutrophied state, depending on the natural N status of the site, land use history, tree species, tree age, the amount of anthropogenic N deposited on the site, and the size of the initial fertilization. In early forest fertilization experiments (e.g., Hora 1959), and in regions with low background deposition, such as Finland (Laiho 1970, Ohenoja 1978, Salo 1979), high fertilization rates led to increased fruiting of nitrophilic taxa *Lactarius rufus* and *Paxillus involutus*. However, in sites that had experienced long-term high N deposition, such as the Netherlands and southern Sweden, high N fertilization led to immediate declines of all taxa (e.g., Rühling and Tyler 1991, Termorshuizen 1993, Wiklund et al. 1995). When the N treatment was lower, however, the initial response was an increase in nitrophiles (Brandrud 1995), but then a decline after several years (Brandrud and Timmermann 1998). An exception is the study of Wåsterlund (1982), in which fertilization for 12 yr, while negatively affecting nitrophobes, still had a positive effect on *P. involutus* and *L. rufus*. This may be

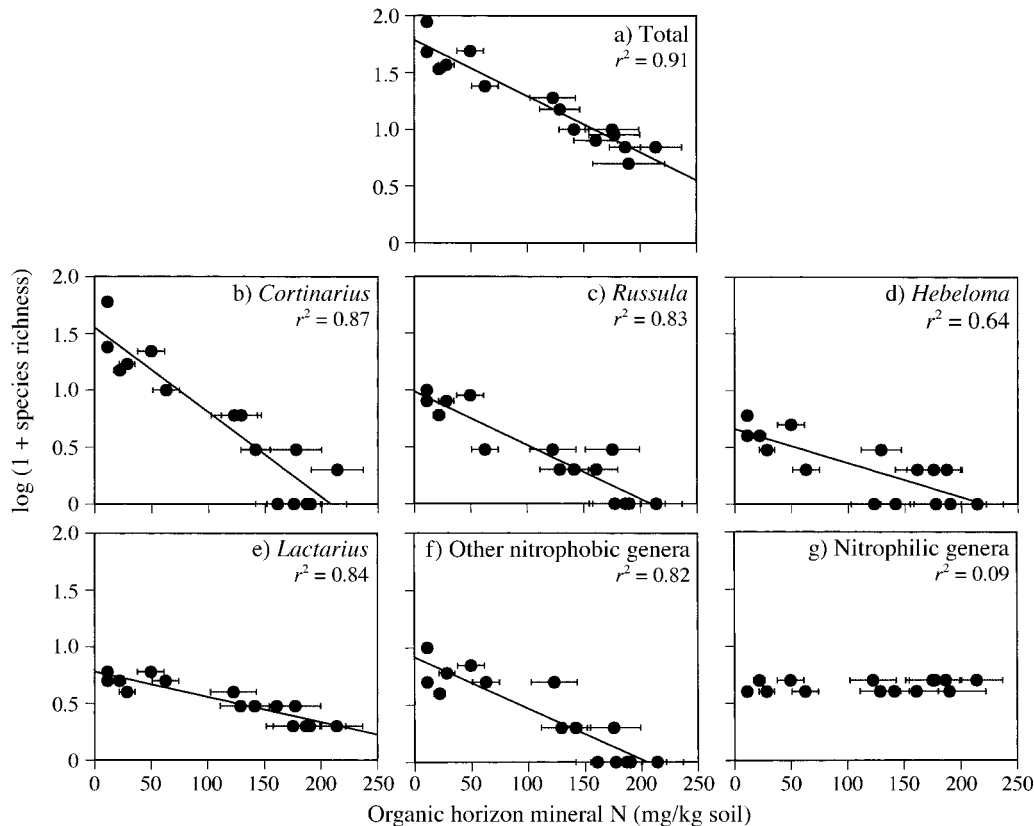


FIG. 4. The relationship between organic horizon mineral N and species richness of ectomycorrhizal fungi, based on sporocarp samples over a nitrogen deposition gradient near Kenai, Alaska, 1995. "Other nitrophobic genera" are the genera represented by few species that appear to be declining at the high-N sites: *Inocybe*, *Entoloma*, *Tricholoma*, *Boletus*, *Rozites*, and *Leccinum*. "Nitrophilic genera" are the genera that are found across the gradient but do not appear to be declining in species richness across the gradient: *Hygrophorus*, *Laccaria*, and *Paxillus* ($n = 4$ spp.).

an effect of fertilizing a young pine stand, which can be less sensitive to N additions than older stands, perhaps because of soil disturbance during site preparation, lower N deposition rates, and higher N uptake by growing trees (Termorshuizen and Schaffers 1987). Hence, long-term atmospheric N inputs and fertilization experiments result in similar relative effects on nitrophilic and nitrophobic taxa, but the absolute response of the community may depend on a variety of site and environmental factors.

Comparison with European patterns of sporocarp decline

One of the striking features of the community response to N inputs is how closely it parallels the pattern of decline in Europe. *Cortinarius*, *Tricholoma*, and *Russula* declined steeply in the present study, and are also declining in Europe (Arnolds 1991). Of the genera that declined somewhat less steeply in this study (*Lactarius*, *Hebeloma*, and *Inocybe*), all have some declining species in Europe, but are considered less critical, with *Hebeloma* being the least affected (Arnolds 1991, Arnolds and de Vries 1993). Of the species common

at the high-N sites, all are described as "uncritical" (Arnolds 1991, i.e., fruiting where other taxa have disappeared). This parallel supports the hypothesis that N deposition is sufficient to explain the decline in EMF sporocarp diversity in Europe.

Interannual variation in the relationship between sporocarp abundance and N inputs

Although the effect on EMF species richness at high-N sites was consistent from year to year, the pattern of sporocarp abundance was somewhat more complex. We found decreased sporocarp numbers at the high-N sites in 1994 but not 1995, perhaps as a result of climatic variation. During the growing season (May–September), precipitation was 70% of the average in 1994 and 164% of the average in 1995 (NOAA 1994, 1995).

We measured numbers of EMF sporocarps rather than biomass. It is possible that as soil N increased, there would have been a declining trend in sporocarp biomass in 1995, if nitrophiles were consistently smaller than nitrophobes. Using average mass for taxa from our sporocarp collections, we estimated sporocarp biomass at the sites and regressed it against organic ho-

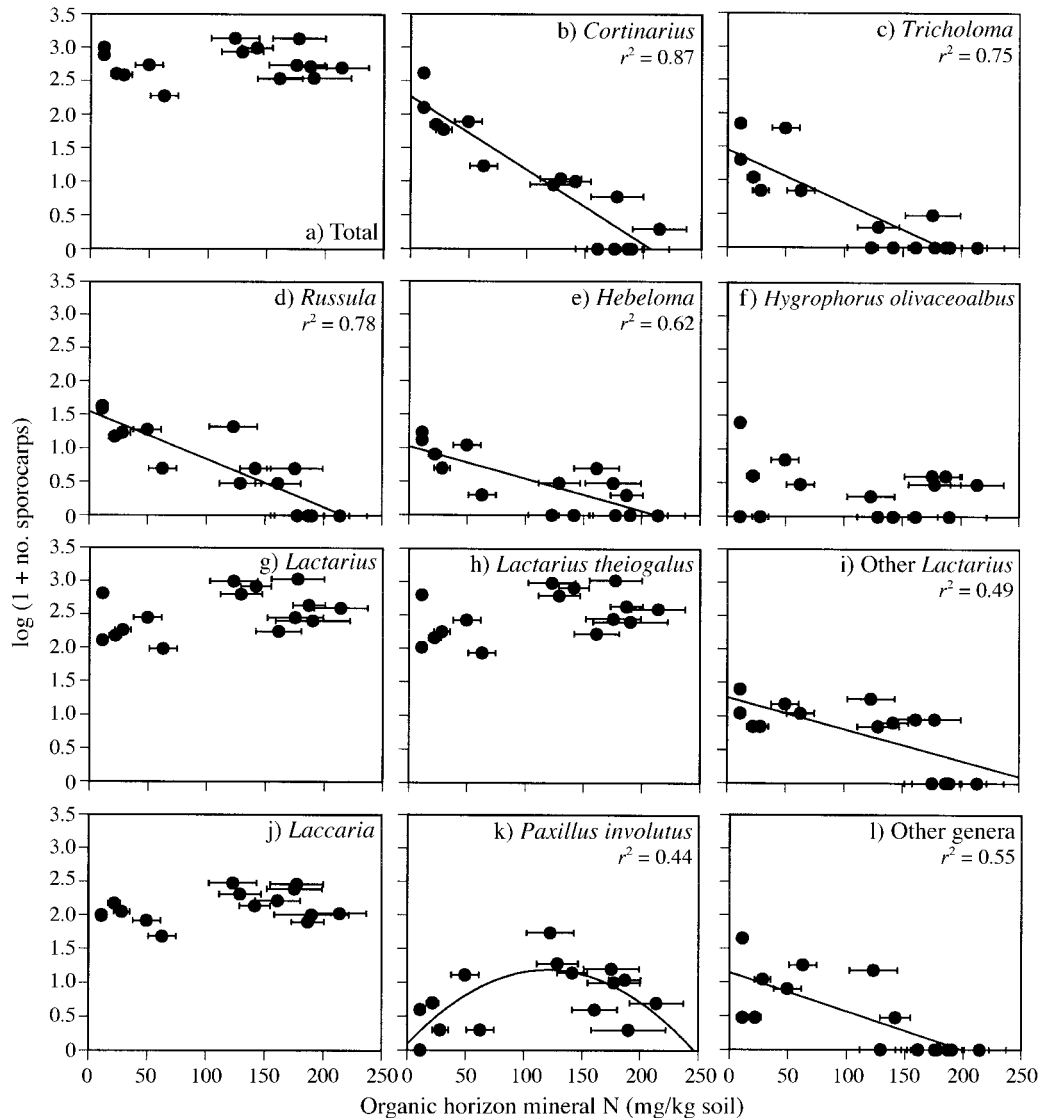


FIG. 5. The relationship between organic horizon mineral N and sporocarp abundance for ectomycorrhizal fungi over a nitrogen deposition gradient near Kenai, Alaska, 1995. Abundance of *Lactarius* is divided into *L. theiogalus* and other *Lactarius*. "Other genera" includes *Inocybe*, *Entoloma*, *Boletus*, *Rozites*, and *Leccinum*. Regression fits for *Paxillus* are based on a quadratic regression; all others are based on simple linear regression.

zation mineral N. It revealed no trend in sporocarp biomass ($r^2 = 0.02$, $P = 0.64$). Even if we assume that our estimates of sporocarp biomass were low for nitrophobic taxa only, and recalculate biomass using double our average biomass for those taxa, we still find no significant trend ($r^2 = 0.13$, $P = 0.18$). These estimates, which are admittedly crude, nevertheless suggest that sporocarp biomass did not decline significantly with increasing N inputs in 1995.

Although the relationship of sporocarp abundance to the N-affected environmental variables changed from year to year, the N effect was consistently more negative for the nitrophobic taxa than for the nitrophilic taxa in both years, suggesting that relative ranking of

response to N additions may be more consistent from year to year (e.g., the effect of N additions on *Cortinarius* should always be more negative than their effect on *L. theiogalus*).

EMF decline and N-affected environmental factors

Our results are consistent with the hypothesis that nitrogen is a causal factor in the decline of ectomycorrhizal sporocarp diversity, but they do not clearly distinguish among possible alternative causal mechanisms. Assuming that N deposition is causal in the decline, the strong correlation of diversity and abundance with soil nitrogen could be especially high because (1) soil nitrogen availability itself affects EMF

community structure; (2) soil N availability directly influences one or more other environmental factors (e.g., soil pH, plant nutrition, plant community) that act to alter community structure; or (3) some combination of these.

Can we separate the effects of changing soil N from those of other variables? Diversity and abundance of *Cortinarius* and *Russula* were best predicted by measures of soil N availability, whereas diversity and abundance of *Tricholoma inamoenum*, *Hebeloma*, and "other *Lactarius*" were slightly better predicted by measures of soil base cation availability or plant community factors. It is possible that the groups of taxa are actually responding to different sets of environmental factors, one of which is changed rapidly after soil fertilization (N availability), whereas the other changes more gradually after fertilization begins (e.g., soil base status and pH, plant nutritional status, or plant community factors).

Fertilization vs. acidification effects.—What is known about the ecology and short-term response to fertilization of the EMF in the present study lends support to a significant N fertilization effect on the fungal community. In fertilization experiments, changes in community structure in response to fertilization typically occurred during the early stages of fertilization, before soil pH had been much reduced, also pointing to a dominant nitrogen rather than pH effect. One of the dominant nitrophilic species in this study (*Laccaria bicolor*) is often found fruiting on physically disturbed soils under mature trees (Sagara 1992, Baar and Kuyper 1993) or early in secondary succession (Dighton et al. 1986), where nitrogen availability and pH should be relatively high. It also increases in sporocarp production after N addition to small patches of forest soils (Sagara 1992). In contrast, many of the nitrophobic taxa (e.g., *Cortinarius*, *Russula*, and *Tricholoma*) are typically associated with later successional stages (e.g., Visser 1995) in which soil humus has accumulated, soil pH has declined, and decomposition and nutrient mineralization rates have decreased (e.g., Van Cleve and Viereck 1981). Given the increase in acidity with stand development, one would expect greater acid tolerance in the late-stage species, yet these are the species that decline under N deposition, suggesting that forest acidification is not a major factor driving the community changes.

Despite these observations, there is some inconsistency in the response of taxa in the present study with what we know about their relationship with soil N. In the present study, the abundance of *Hebeloma* in general, and *Hebeloma mesophaeum* in particular, was positively associated with soil base cations and negatively associated with soil N. This is surprising, considering that this genus, and particularly *H. mesophaeum*, is commonly found in greenhouses and fertile field soils (Ingleby et al. 1990). Many other *Hebeloma* species commonly fruit in response to microsite N fertilization

(Sagara 1992, Sagara et al. 1993, Fukiharu and Hongo 1995). Liming of an acidified forest in Germany led to an increase in sporocarp production of two *Hebeloma* species (Kraepelin and Michaelis 1997), suggesting that the decline of *Hebeloma* may have more to do with soil pH and base status than with N availability per se, although the authors attributed the increase to higher N mineralization rates after liming.

As soils become acidified, Al and Mn can both become more available. Foliar Mn was one of the best predictors for abundance of the nitrophilic EMF taxa. Soil Mn availability increases as soils become acidified, and then can decrease as prolonged acidification leaches Mn from the soil (Ulrich 1995). High foliar Mn can be toxic to trees, but even the highest levels in the present study were below toxic levels (Ulrich 1995), and high foliar Mn was not associated with decreased tree growth. It is possible that high soil Mn could be directly toxic to certain nitrophobic fungi, but pure culture studies have found very high Mn tolerance in several ectomycorrhizal fungi in pure culture (Thompson and Medve 1984, Hintikka 1987).

Aluminum is toxic to fungi at lower concentrations than Mn (Thompson and Medve 1984). However, foliar Al concentrations in this study (Table 1) were not strongly correlated with the abundance of any taxa, and the soil pH indicates that even the highest N soils were above the Al buffering range of pH (H₂O) < 4.2 (Ulrich 1995), so we should not expect strong Al effects on the EMF community in the present study.

An alternative is that the positive relationship between fruiting in these taxa and foliar Mn could be the result of an optimum sporocarp production at moderate N inputs; i.e., Mn could be an indicator of moderate N availability. Foliar Mn, organic horizon net mineralization, and tree growth were positively correlated (Fig. 3), and all were highest at the intermediate N deposition sites (Table 1). Jansen and de Vries (1988) found the highest sporocarp production at sites with intermediate N deposition in the Netherlands. This would be consistent with pot experiments in which the highest frequency of fruiting of the nitrophilic *Laccaria bicolor* was at intermediate N fertilization levels (Godbout and Fortin 1992), and with the effect that high N inputs have on the fungal C cost of N assimilation (Wallander 1995), reducing the carbon available for sporocarp production.

Plant community changes.—The dramatic decrease in moss and the increase in grass across the gradient raise the possibility that some of the community effects are mediated by changes in ground vegetation. However, the results of an RDA analysis that controlled for grass abundance suggest that the major changes in the EMF community can occur in the absence of grass effects (data not shown). This is supported by Tyler et al. (1992), who found, in a fertilization experiment examining sporocarp production, that the EMF community changed before changes in ground vegetation.

Thus, it is unlikely that the change from moss to grass dominance is a major cause of community change.

Predicting EMF community response to site N status

The indicators of site N status measured in the present study are likely to be better predictors of EMF community status than N inputs, because sites vary in the effect that equal N inputs have on internal N cycling (Aber et al. 1998), and it is the internal N cycling that is likely to be the critical driver of EMF community change. We hypothesize that this occurs primarily via alteration of soil N availability. Simple measures such as laboratory potential net nitrification rates, which are easily comparable among sites, should be evaluated as indicators of the status of the EMF community at larger spatial scales. Furthermore, we should carry out experimental studies that can separate plant nutrition from soil factors as drivers of community change.

Determining critical loads of N from the EMF perspective must be done rapidly, given increasing N deposition (Galloway et al. 1994, Galloway 1995, Vitousek et al. 1997), and regional declines and extinctions in areas of heavy N deposition (Arnolds and de Vries 1993, Arnolds 1997). Although N deposition is certainly not the sole cause of these declines, multiple lines of evidence, including the present study, indicate that it has a major negative impact, at least on sporocarp production. What is unknown is the degree to which these changes in sporocarp production reflect below-ground EMF community shifts. In a subsequent paper, we will present results on belowground EMF community structure over this gradient.

ACKNOWLEDGMENTS

We thank T. Dawson, K. Mudge, M. Fisk, and anonymous reviewers for critical evaluation of the manuscript. Both J. Ammirati and R. Fatto provided invaluable help with identification of fungi, for which we are especially grateful. We also thank all the Fahey lab assistants who helped on this project. This research was supported an NSF Dissertation Improvement Grant DEB-9520760, a graduate research assistantship from the Andrew W. Mellon Foundation, and research grants from the Andrew W. Mellon Foundation, the Kieckhefer Foundation, and Sigma Xi.

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APPENDIX A

A table presenting sporocarp abundance of ectomycorrhizal fungal species across an atmospheric N deposition gradient near Kenai, Alaska, is available in ESA's Electronic Data Archive: *Ecological Archives* A011-007-A1.

APPENDIX B

A table presenting correlations between environmental variables across an atmospheric N deposition gradient and ectomycorrhizal fungal species, richness, community wide and for species-rich genera, is available in ESA's Electronic Data Archive: *Ecological Archives* A011-007-A2.

APPENDIX C

A table presenting correlations between environmental variables across an atmospheric N deposition gradient and abundance of ectomycorrhizal fruit bodies, community wide and for abundant genera, is available in ESA's Electronic Data Archive: *Ecological Archives* A011-007-A3.

APPENDIX D

Photographs of the Kenai, Alaska study area, selected study sites, and several dominant ectomycorrhizal fungi are available in ESA's Electronic Data Archive: *Ecological Archives* A011-007-A4.