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EFFECTS OF CHRONIC NITROGEN ADDITIONS ON UNDERSTORY SPECIES IN A RED PINE PLANTATION

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Abstract. Two plots in a red pine stand at the Harvard Forest, Massachusetts, have been fertilized for 7 yr with 5 $g \cdot m^{-2} \cdot yr^{-1}$ or 15 $g \cdot m^{-2} \cdot yr^{-1}$ of N and compared to an unfertilized control to study the effects of chronic N additions on nutrient cycling, plants, and soil. Movement of added N into soils and plant biomass was tracked using additions of an ^{15}N label to the 5 $g \cdot m^{-2} \cdot yr^{-1}$ and control plots for two of these years. We present data on changes in the understory plant community of these plots. We measured aboveground biomass, density, N and other elemental concentrations, and ^{15}N tracer recoveries to catalogue the effects of the N additions on this community. Nitrogen contents increased while biomass and nutrient cation concentrations decreased in some species. Percent recoveries of ^{15}N tracers were small but detectable. The natural abundances of ^{15}N also increased in a fertilized treatment without tracer additions. Though this forest has not yet reached N saturation by some definitions, it is possible that the understory is already saturated with N. Understory species may be useful indicators for N saturation through their increasing N content, decreasing nutrient concentrations, and increasing $\delta^{15}N$ in tissues.

Key words: ground flora; Harvard Forest; N cycle; N deposition; ^{15}N labeling; ^{15}N natural abundance; N saturation; Pinus resinosa; *red pine; temperate forests.*

INTRODUCTION

Forest ecosystems in the northeastern United States experience elevated nitrogen deposition rates compared to more remote areas (Galloway et al. 1984, Ollinger et al. 1993), and exhibit increased nitrogen cycling rates along corresponding gradients of increasing N deposition (McNulty et al. 1990). It has been hypothesized that prolonged N inputs could lead to ''N Saturation'' (sensu Aber et al. 1989), a condition where the availability of inorganic N in forest soil exceeds the biotic demands of microbes and plant roots, leading to increased N losses to drainage water and the atmosphere. Symptoms of N saturation include elevated N concentrations in plant tissues, NO_3 losses to ground and surface waters accompanied by base cation leaching, increased soil acidity, and eventual decreases in growth and live tree biomass (Aber et al. 1989, Stoddard 1994).

Few North American studies have reported on the effects of N deposition on forest understory vegetation, despite its role in biodiversity, its importance in nutrient cycling and retention (Zak et al. 1990), and its potential value as an indicator of pollution effects (Tappeiner and Alm 1975, Muller and Bormann 1976, Blank et al. 1980, Thimonier and Dupouey 1995). Therefore, we examined plant community and biogeochemical responses of understory vegetation in a 70-yr-old red pine (*Pinus resinosa*) plantation to chronic N additions. These plots were fertilized with NH_4NO_3 for 7 yr prior to our study. Responses of overall forest N cycling and trees after 3 and 6 yr of N additions have been reported by Aber et al. (1993, 1995) and Magill et al. (1997). N_2O fluxes were reported by Bowden et al. (1991). Movements of added N into tree tissues and soils as determined using ^{15}N tracer additions to plots are reported in Nadelhoffer et al. (1999). Here we report on the responses of understory plants to N additions. We hypothesized that understory species' responses could be used as early indicators of ecosystem N saturation, and might reflect processes that would later be observed in overstory trees. Specifically, we tested whether 7 yr of N fertilization affected understory species composition, stem densities, biomass, N content, and nutrient concentrations. We also assessed the role of understory plants in retaining N additions by following the movements of $^{15}N\text{-}NH_4$ and $^{15}N\text{-}NO_3$ tracers into understory plants in nonfertilized and fertilized plots. Finally, we used the natural abundance ^{15}N of understory species in a heavily fertilized, but nonlabeled plot to determine the sensitivity of stable N isotope techniques to ecosystem scale N cycling.

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METHODS

Fertilization and ^{15}N tracer additions

The experimental plots are located at the Harvard Forest in Petersham, Massachusetts, a National Science

PLATE 1. The edge of the High N treatment in the red pine plantation (Harvard Forest, Massachusetts) after 7 yr of fertilization with ammonium nitrate. Understory density is visibly reduced compared to the dense ferns in areas outside the treatment. Photo by Susan M. Rainey.

Foundation Long Term Ecological Research (LTER) site (Aber et al. 1993). Treatments were started in 1988 in a 62-yr-old red pine (*Pinus resinosa*) plantation. Treatments included regular fertilization with 5 g $N \cdot m^{-2} \cdot yr^{-1}$ (''Low N'') or 15 g $N \cdot m^{-2} \cdot yr^{-1}$ (''High N'') on 30 × 30 m plots, divided into 36, 5 × 5 m quadrats for sampling purposes. A nonfertilized control plot (hereafter referred to as ''Ambient'') served as a reference for assessing effects of fertilizer additions on understory species abundance, biomass, and nutrient content. Six equal monthly applications of dissolved NH_4NO_3 were sprayed on the forest floor of fertilized plots. In 1988, only partial N applications were made (3 $g \cdot m^{-2} \cdot yr^{-1}$ in the Low N and 11.3 $g \cdot m^{-2} \cdot yr^{-1}$ in the High N plots) followed every subsequent year with full fertilization, through our June 1995 sampling (Aber et al. 1993).

Ammonium nitrate additions to the Low N plot in 1991 and 1992 were labeled with ^{15}N tracers as described by Nadelhoffer et al. (1999). Tracer masses added over these 2 yr were 17.9 mg $^{15}N \cdot m^{-2} \cdot yr^{-1}$ as NH_4 to one 15 × 30 m plot half, and 16.2 mg $^{15}N \cdot m^{-2} \cdot yr^{-1}$ as NO_3 to the other plot half. Equivalent masses of these tracers were added to halves of the Ambient plot (nonfertilized control) during the same years. Recoveries of these ^{15}N tracers in our 1995 sampling were expressed as percent recoveries of ^{15}N (''PR ^{15}N'') using mass balances as described in Nadelhoffer et al. (1999). The High N plot was not labeled with ^{15}N. Therefore, we used natural abundance units ($\delta^{15}N$ = [(atom % ^{15}N sample/0.3663) − 1] × 1000) to express the ^{15}N contents of materials from nonlabeled areas.

Sample collection and analysis

Plant samples were collected in June 1995 from eight randomly distributed 5 × 5 m quadrats, each within the larger 30 × 30 m treatment areas (n = 24). In the Ambient and Low N addition treatments, the quadrats were stratified such that four quadrats were randomly selected from each of the $^{15}NH_4$- and $^{15}NO_3$-labeled halves of the treatment plots. Within each quadrat, we randomly located subplots for sample collection; subplots in the Ambient treatment were 1 m^2, but were expanded to 2 m^2 (1 × 2 m) in the Low N and High N treatments to account for low stem densities and biomass of understory plants.

All plants were removed from each subplot, counted, separated by species, dried at 50°C, and weighed. Samples were bulked by species within each subplot for chemical analyses. Composite samples with adequate mass (>0.01 g) were ground in a Wiley Mill and analyzed for C and N on a Fisons CHN analyzer (CE Elantech, Incorporated, Lakewood, New Jersey, USA). Samples of *Maianthemum canadense* and *Trientalis borealis*, the two most abundant species that occurred in all three treatments, were selected from four subplots per treatment for chemical analyses. These samples were sent to the Chemical Analysis Laboratory at the University of Georgia, Athens, Georgia, for analysis. Samples were ashed and digested in HCl and HNO_3, and analyzed for Ca, Mg, K, Mn, Fe, Al, and P concentrations on a Jarrell-Ash 965 inductively coupled argon plasma emission spectrometer (Thermo Jarrell Ash Corporation, Franklin, Massachusetts, USA), (Jones 1988, USEPA methods number 6010). In addition, we selected tissues of *M. canadense* and *T. borealis* for ^{15}N analyses, from biomass samples from all eight subplots in the Ambient and Low N treatments, and from four subplots in the High N treatment. We bulked and analyzed a sample of each species taken from outside the treatments (no ^{15}N added) as reference material. Tissues were analyzed for ^{15}N content on a Finnigan MAT Delta S isotope ratio mass spectrometer (Finnigan Corporation, San Jose, California, USA), in the Stable Isotope Facility at The Ecosystems Center in Woods Hole, Massachusetts (Fry et al. 1992). Analytical error using this method is generally <0.2‰ $\delta^{15}N$.

We tested for treatment effects on response variables

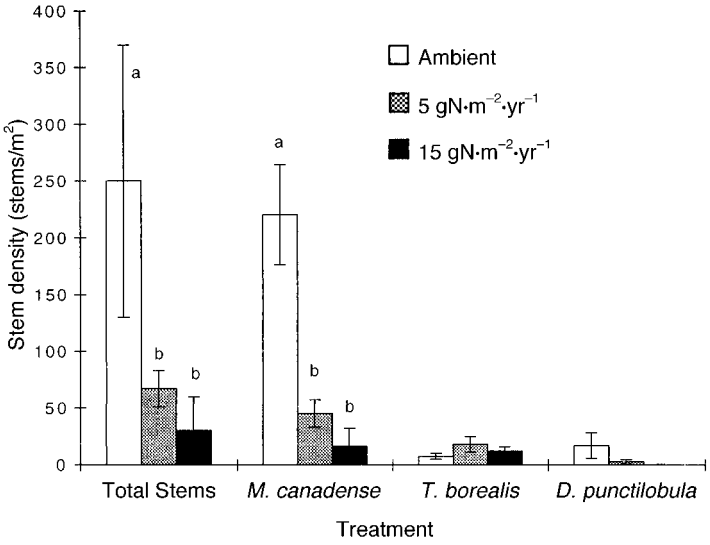

FIG. 1. Understory species stem density in a red pine plantation (Harvard Forest, Massachusetts) after 7 yr of fertilization with ammonium nitrate. Bars indicate means, and vertical lines are ±1 SE ($n = 8$). Within-species differences between treatments ($P < 0.05$) are indicated by different lowercase letters. No statistically significant differences were found for *T. borealis* or *D. punctilobula.*

using a one-way analysis of variance (ANOVA) in Systat version 5.03 (Wilkinson 1990). Data were log transformed when necessary to meet required assumptions. If ANOVA indicated treatment effects ($P < 0.05$), we then tested for differences among treatment means using the Least Significant Differences protocol. Patterns of $PR^{15}N$ in dominant species were examined using a *t* test. Statistics are not presented on measurements of $\delta^{15}N$ in nonlabeled plots since we used a single bulked sample for reference tissues.

RESULTS

Understory diversity, density, and biomass

M. canadense and *T. borealis* were the most abundant species in all treatments (Fig. 1). *Dennstaedtia punctilobula,* a fern, was abundant in the Ambient treatment, but was rare in the Low N treatment and was not present in the High N treatment (see Plate 1). The total number of species present varied from seven (Ambient) to nine (Low N), but did not differ significantly with treatment. Total stem density and stem density of *M. canadense* differed with N addition rates (Fig. 1). The total stem density decreased significantly by 73% under Low N addition and by 88% under High N addition relative to the Ambient treatment. *M. canadense* stem density decreased significantly in both the Low N and High N treatments. The density of *T. borealis* did not change significantly with N additions.

Treatment effects on total understory biomass and biomass of individual species were similar to those for stem density (Fig. 2). The N addition treatments had significantly less total biomass than the Ambient treatment. These reductions in biomass resulted from decreases in stem densities, as biomass per individual did not change within any species. Biomass of *M. canadense* was significantly lower in both the Low and the High N treatments than under Ambient conditions, while treatments did not significantly affect *T. borealis*

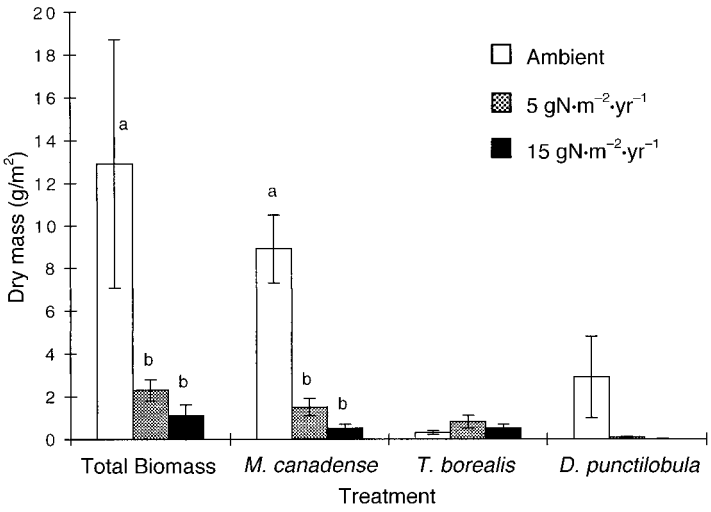

FIG. 2. Understory species biomass (dry mass) in a red pine plantation (Harvard Forest, Massachusetts) after 7 yr of fertilization with ammonium nitrate. Bars indicate means, and vertical lines are ±1 SE ($n = 8$). Within-species differences between treatments ($P < 0.05$) are indicated by different lowercase letters. No statistically significant differences were found for *T. borealis* or *D. punctilobula.*

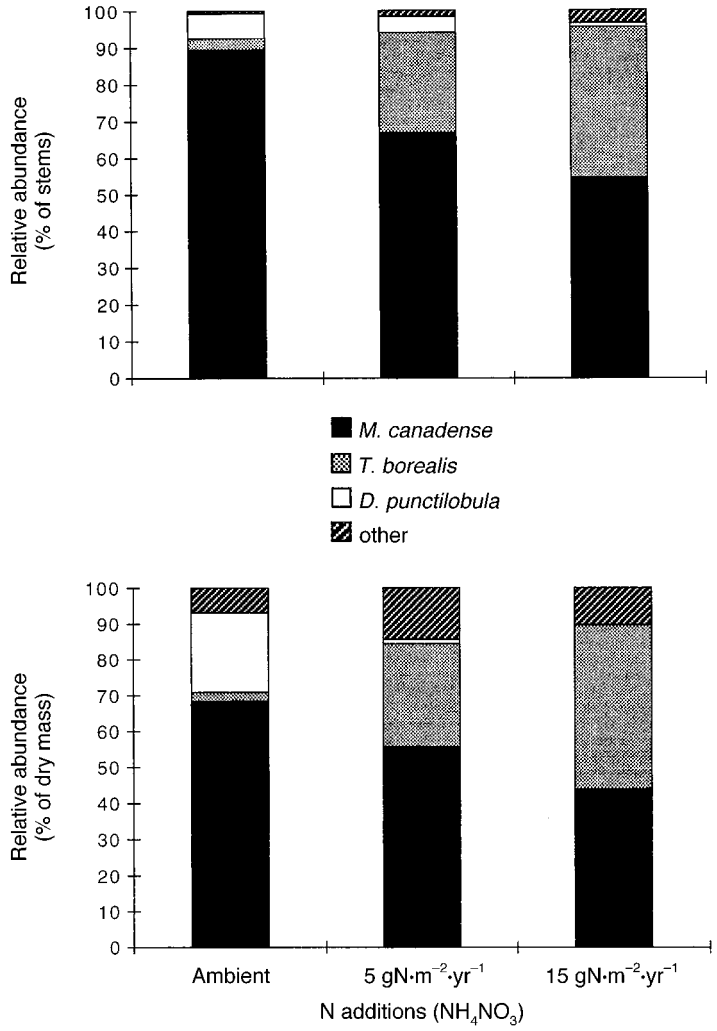

FIG. 3. Relative abundances of understory species stem density (top) and biomass (bottom) in a red pine plantation (Harvard Forest, Massachusetts) after 7 yr of fertilization with ammonium nitrate.

biomass. The relative abundance of stems and biomass of *T. borealis* increased with N additions, primarily as a result of decreased biomass and stem density of *M. canadense* and *D. punctilobula* (Fig. 3).

Tissue nitrogen and carbon

Tissue N concentrations increased significantly by 38 and 48% in the Low N and High N treatments respectively, relative to the Ambient treatment (Fig. 4). *T. borealis* had the lowest tissue N concentration in the Ambient treatment. Under low levels of N fertilization, tissue N concentrations were greater in *D. punctilobula* and *M. canadense* than in *T. borealis.* In the High N treatment, *M. canadense* and *T. borealis* had similar N concentrations.

The effects of N additions on the N content (g/m^2) of understory biomass differed by species (Fig. 5). *M. canadense* N content decreased significantly by 79% in the Low N treatment and by 93% in the High N treatment relative to the Ambient treatment, similar to the observed decrease in biomass for this species. *T. borealis* N content increased, though not significantly. Nitrogen additions had no significant effect on the percent C in tissues.

Plant cation and P concentrations

Nitrogen addition treatments influenced the concentrations of Ca, Mg, K, and Fe in *M. canadense* tissues, but had no significant effect on *T. borealis* (Table 1). In *M. canadense* tissues, Mg and K concentrations were significantly lower in fertilized treatments than under ambient conditions, and Ca and Fe concentrations were significantly lower in the High N treatment than in the Ambient treatment.

The ratios of elemental concentrations in tissues have been used to determine potential nutrient imbalances due to high nutrient inputs or potentially toxic conditions (Schulze 1989). The ratio of Ca:Al in understory tissues showed no statistically significant trends with treatment, although the Ca:Al ratio for *T. borealis* was consistently higher than *M. canadense* in all treatments (Table 2). The nutrient cation:N ratios decreased in *M.*

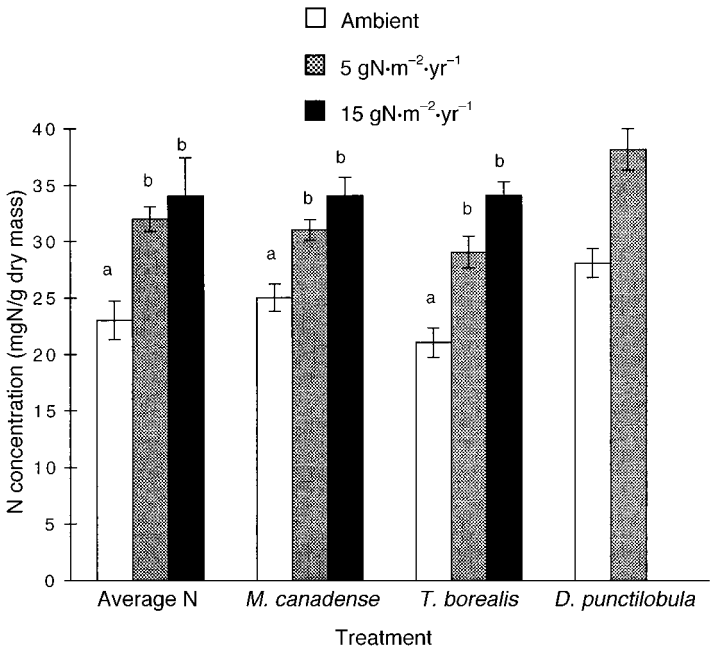

FIG. 4. Nitrogen concentrations (mg/g) in dominant understory species of a red pine plantation (Harvard Forest, Massachusetts) after 7 yr of fertilization with ammonium nitrate. Bars indicate means, and vertical lines are ±1 SE (n = 5–8). Within-species differences between treatments ($P < 0.05$) are indicated by different lowercase letters. Sample sizes for *D. punctilobula* were too small to perform statistical analyses.

canadense tissues in both fertilizer treatments relative to ambient conditions. The Ca:N and K:N ratios in *T. borealis* tissues decreased significantly under High N addition, and Mg:N ratios decreased with both levels of N addition (Table 2).

^{15}N tracers and natural abundance in understory plants

Samples of understory vegetation collected in June 1995 contained small but detectable amounts of the ^{15}N tracers added to the forest floor of the Ambient and Low N plots in the 1991 and 1992 growing seasons (Table 3). Percent recoveries of ^{15}N tracers were significantly greater in *M. canadense* in the Ambient $^{15}NO_3$ treatment than in the Low N $^{15}NO_3$ treatment (Table 3). Percent ^{15}N recoveries were slightly but not significantly higher in *T. borealis* in the Low N treatment than in the Ambient treatment.

Natural ^{15}N abundance in tissues of the two dominant species in the heavily fertilized, but nonlabeled, High N treatment (fertilizer δ^{15}N in the High N plot = 0‰) was approximately 6‰ higher than in tissues from nonlabeled reference areas (Fig. 6).

DISCUSSION

Seven years of N additions to the chronically fertilized plots influenced the composition of the understory in this red pine forest. Although no measurements of ground flora were made prior to the start of fertilizer additions in 1988, the effects of fertilizer additions on

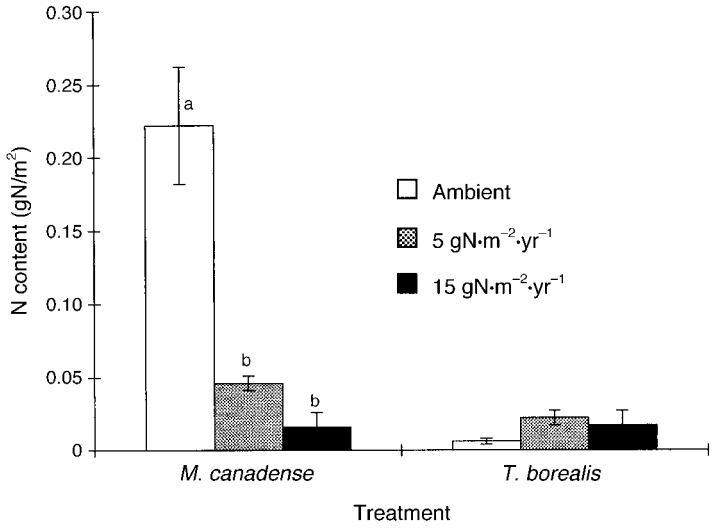

FIG. 5. Nitrogen content (g/m^2) in dominant understory species of a red pine plantation (Harvard Forest, Massachusetts) after 7 yr of fertilization with ammonium nitrate. Bars indicate means, and vertical lines are ±1 SE (n = 5–8). Within-species differences between treatments ($P < 0.05$) are indicated by different lowercase letters.

TABLE 1. Tissue element concentrations (percentages) in dominant understory species in N fertilizer addition and control plots in a red pine stand at the Harvest Forest, Massachusetts.

Element	Ambient	Low N addition (5 $gN \cdot m^{-2} \cdot yr^{-1}$)	High N addition (15 $gN \cdot m^{-2} \cdot yr^{-1}$)
Ca			
M. canadense	0.64 (0.03)[a]	0.55 (0.03)[a]	0.42 (0.04)[b]
T. borealis	0.53 (0.01)	0.53 (0.02)	0.58 (0.02)
Mg			
M. canadense	0.18 (0.01)[a]	0.15 (0.01)[b]	0.14 (0.01)[b]
T. borealis	0.20 (0.01)	0.17 (0.01)	0.17 (0.01)
K			
M. canadense	3.75 (0.21)[a]	3.00 (0.19)[b]	2.29 (0.16)[b]
T. borealis	1.72 (0.10)	2.06 (0.25)	1.79 (0.06)
P			
M. canadense	0.32 (0.02)	0.34 (0.02)	0.36 (0.03)
T. borealis	0.23 (0.02)	0.26 (0.02)	0.25 (0.04)
Fe			
M. canadense	0.009 (0.001)[a]	0.008 (0.001)[ab]	0.006 (0.001)[b]
T. borealis	0.009 (0.001)	0.009 (0.001)	0.008 (0.001)
Al			
M. canadense	0.004 (0.001)	0.005 (0.001)	0.003 (0.001)
T. borealis	0.003 (0.001)	0.003 (0.001)	0.003 (0.001)
Mn			
M. canadense	0.17 (0.01)	0.18 (0.01)	0.17 (0.02)
T. borealis	0.10 (0.01)	0.11 (0.02)	0.08 (0.02)

Notes: Values are treatment means (n = 5–8) with one standard error in parentheses. Lowercase letters indicate statistically significant differences ($P < 0.05$) among treatments within each species and element.

ground flora species abundances and composition immediately within fertilized plot boundaries are visually striking, particularly for *D. punctilobula* and *M. canadense*. Moreover, *D. punctilobula* was abundant in both the Low N and High N plots before treatment (K.J. Nadelhoffer, *personal observation*), but were rare after 7 yr of N additions. Therefore, N additions most likely led to lower stem density and biomass of *M. canadense* and *D. punctilobula* (Figs. 1 and 2), but did not affect biomass and stem density of *T. borealis*. These changes resulted in greater relative abundance of *T. borealis* (Fig. 3) as the previously important species, *M. canadense* and *D. punctilobula*, decreased. The change in relative abundance of *T. borealis* on treated plots may have resulted from reduced competition, greater N availability, increased nutrient uptake, or a combination of these factors.

Nitrogen additions also resulted in an increase in

TABLE 2. Selected element ratios in dominant understory species in fertilized red pine plots at the Harvard Forest, Massachusetts.

Element ratio	Ambient	Low N addition (5 $g \cdot m^{-2} \cdot yr^{-1}$)	High N addition (15 $g \cdot m^{-2} \cdot yr^{-1}$)
Ca:Al			
M. canadense	150 (10)	122 (4.8)	135 (21)
T. borealis	187 (18)	185 (8.7)	223 (12)
Ca:N			
M. canadense	0.26 (0.02)[a]	0.18 (0.01)[b]	0.13 (0.02)[c]
T. borealis	0.26 (0.03)[a]	0.19 (0.01)[ab]	0.17 (0.01)[b]
K:N			
M. canadense	1.53 (0.13)[a]	0.99 (0.05)[b]	0.69 (0.06)[c]
T. borealis	0.84 (0.09)[a]	0.66 (0.03)[ab]	0.54 (0.02)[b]
Mg:N			
M. canadense	0.07 (0.01)[a]	0.05 (0.01)[b]	0.04 (0.01)[b]
T. borealis	0.10 (0.01)[a]	0.06 (0.01)[b]	0.05 (0.01)[c]

Notes: Values are treatment means (n = 4) of mass ratios with one standard error in parentheses. Significant differences are indicated by different superscript lowercase letters within a row.

TABLE 3. Percent recoveries of ^{15}N tracers (PR ^{15}N) in dominant understory species on plots with ambient N deposition and chronic fertilization (5 g $N \cdot m^{-2} \cdot yr^{-1}$) at the Harvard Forest, Massachusetts.

Treatment	^{15}N tracer recovered	
	$^{15}NH_4$ label	$^{15}NO_3$ label
Ambient		
M. canadense	0.114 (0.039)	0.269 (0.052)[a]
T. borealis	0.008 (0.004)	0.005 (0.002)
Low N addition		
M. canadense	0.041 (0.016)	0.052 (0.026)[b]
T. borealis	0.010 (0.006)	0.015 (0.008)

Notes: Both plots were labeled with similar amounts of ^{15}N in 1991 and 1992, and understory vegetation was sampled in 1995. Values are means (one standard error in parentheses; $n = 4$). Significant differences are indicated by different superscript lowercase letters.

foliar N concentrations (Fig. 4). Similar increases in foliar N of tree species have been shown in the red pine trees in this study plot (Aber et al. 1995, Magill et al.1997), as well as for beech (Christ et al. 1995), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*; McNulty and Aber 1993) along gradients of N deposition. Nitrogen concentrations differed among species. *T. borealis* showed the largest increase in tissue N concentration with treatment, although *M. canadense* also exhibited significantly higher tissue N concentrations relative to ambient conditions. Under higher levels of fertilization, no differences in tissue N concentrations occurred between the two dominant species.

Cation concentrations of *M. canadense* were influenced by the 7 yr of chronic N additions to this forest (Table 1). Concentrations of Ca, Mg, K, and Fe in tissues of this species decreased in the High N plot, while *T. borealis* tissues showed no significant treatment effects. Aber et al. (1989) hypothesized that chronically elevated N inputs to forests can lead to increased nitrification in soils and that nutrient cations such as Ca, Mg, and K, would accompany losses of excess NO_3 in leachate. Zero-tension lysimeters installed in the O_a horizon showed increasing concentrations of nutrient cations in leachate with increasing levels of N fertilization (W. Currie, *personal communication*). Even if these cations were retained in the mineral soil below the O_a horizon, they could be less available to the shallow roots of the understory species.

Ratios of nutrient cations:N decreased in the High N plot in both species. Our results are consistent with other studies that have reported changes in cation:N ratios or lower concentrations of base cations in tree foliage with N deposition. For example, Aber et al. (1995) reported declining foliar Mg:N ratios for the red pine trees in this stand. Decreased foliar Mg concentrations have been reported with increasing N deposition in tree species in spruce–fir forests across New England, and may implicate nutrient imbalances as a possible cause of forest decline in this region (McNulty et al. 1991).

Recoveries of ^{15}N tracers in the understory were low but detectable (Table 3), with recovery in *M. canadense* in the Ambient treatment higher than in the Low N treatment. Slightly greater recoveries were found in *T. borealis* in the Low N treatment than in the Ambient treatment. Of the two dominant species, *T. borealis* retained a smaller percentage of the added ^{15}N label than did *M. canadense* in both the Ambient and Low N treatments. Recovery of tracers in *T. borealis* tissues was similar to the results of Nadelhoffer et al. (1999) who found greater recoveries of tracers in trees in fertilized treatments than in the Ambient treatment in both this red pine stand and a nearby oak forest. The increase in recovery in *T. borealis* may be explained by the increase in N content of that species in the Low N plot. The lower tracer recovery in *M. canadense* may be explained by the decrease in N content (resulting from a significant decline in biomass) under low N additions. It is also possible that applications of nonlabeled fertilizers to the Low N treatment from 1992 to 1995 served to dilute the tracer.

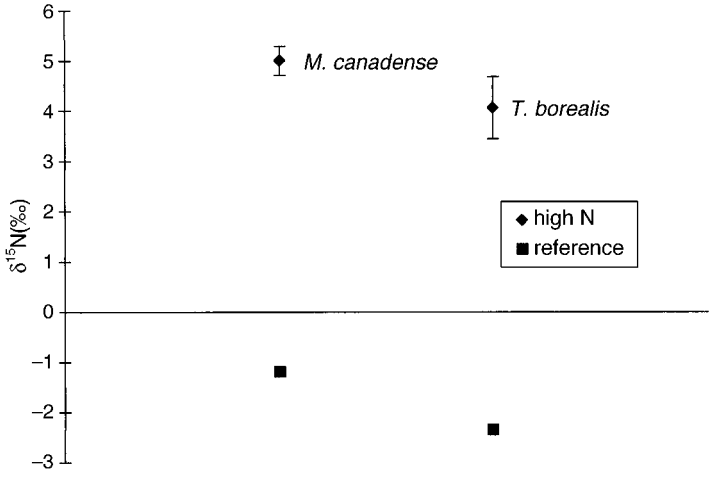

FIG. 6. ^{15}N abundance of understory plant tissues in High N-fertilized plot and reference tissues in a red pine plantation at the Harvard Forest, Massachusetts. Symbols show mean $\delta^{15}N$ values (♦ = high N fertilization, ■ = reference tissues), and vertical lines indicate ±1 SE (n = 4–5 for treated samples, 1 for reference).

The natural ^{15}N abundance in *M. canadense* and *T. borealis* tissues from the nonlabeled High N treatment was greater than in tissues from nonlabeled reference areas (Fig. 6). Average $\delta^{15}N$ values of these species were elevated by at least 5‰ in the High N treatment relative to overstory foliar tissues from nonfertilized, nonlabeled plots at Harvard Forest (Nadelhoffer et al. 1999), or tissues from other forests (Nadelhoffer and Fry 1994). The increase in natural abundance of ^{15}N in plant tissues in nonlabeled, but highly fertilized plots, is consistent with another study that found increased $\delta^{15}N$ in an understory grass in a Swedish forest after chronic N additions (Högberg 1990). Such a pattern would occur if increases in nitrification resulting from the elevated N inputs (reported by Magill et al. 1997 for the High N treatment) led to the production of ^{15}N-depleted NO_3 that was translocated downward in the soil profile (Högberg and Johannisson 1993, Nadelhoffer and Fry 1994). Gaseous loss of N (reported by Magill et al. 1997 for the High N treatment) may be another process depleting the ^{14}N in this plot. These losses would then result in a higher ^{15}N content of the N cycling within the rooting zone of the understory species.

Our results suggest that $\delta^{15}N$ of understory plants could be used as an indicator of N saturation in forest ecosystems. If losses of ^{15}N-depleted NO_3 from N-saturated sites do occur and serve to increase the $\delta^{15}N$ of residual N available to plant roots, then increased $\delta^{15}N$ of understory tissues may serve as an indicator of NO_3 losses and N saturation.

Conclusions

Should this system be labeled ''N-saturated''? Many of the conditions of an N-saturated plant community as hypothesized by Aber et al. (1989) are apparent in this study. These include increased tissue N content, decreased tissue cation content, and decreased biomass and stem density of species occurring under N deposition. Though this system has not reached N saturation according to some definitions (N leaving the ecosystem is not greater than N inputs sensu Agren and Bossatta 1988), the understory plant community has been affected by N additions, and effects differed significantly by species. The understory fern (*D. punctilobula*), abundant in the Ambient plot, decreased dramatically in N addition treatments. Biomass and stem density of *M. canadense* declined as a result of chronic N additions. Cation imbalances, possibly due to increased NO_3 leaching, may be an important mechanism leading to the observed declines. On the other hand, *T. borealis* showed no negative effects of N additions. This species had lower tissue N concentrations in the Ambient treatment and greater increases in tissue N with fertilizer treatments, showing that it was able tolerate a wide range of soil N conditions. Cation concentrations in *T. borealis* were not significantly changed with treatment. The differences in how these three species were affected by chronic N inputs has resulted in changes in the composition of the understory plant community.

For both common species, the large and significant increase in $\delta^{15}N$ in tissues suggests that significant quantities of NO_3 are being lost. It appears that N is available in this system above biotic demand, and may also be responsible for decreases in biomass and nutrient cation concentrations in some species. We propose that the chemistry of the understory plants in our study reflects the change in N cycling in these systems, and could be used as an indicator of N saturation.

Acknowledgments

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