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The response of understory herbaceous plants to nitrogen fertilization in forests of different land-use history

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ABSTRACT

Forests growing on former agricultural land often have reduced frequencies of many native forest herbs compared with forests that were never cleared for agriculture. A leading explanation for this pattern is that many forest herbs are dispersal limited, but environmental conditions may also hinder colonization. We examined the response of six forest herb taxa (*Arisaema triphyllum*, *Cimicifuga racemosa*, *Disporum lanuginosum*, *Osmorhiza* spp., *Polygonatum* spp., and *Prenanthes altissima*) to nitrogen (N) fertilization in forests with and without an agricultural history to investigate how N availability affects plant performance. The study was conducted in the southern Appalachian Mountains in western North Carolina, USA. There was a significant interaction between land-use history and N treatment for several species. In *A. triphyllum* and *Osmorhiza* spp., N fertilization increased aboveground biomass or leaf area more in the post-agriculture site than in the reference site. However, in the reference site, N fertilization depressed aboveground biomass or leaf area in the same taxa, as well as in *C. racemosa*. The foliar N concentration of these three taxa was elevated in fertilized plots regardless of land-use history, and there was no indication that the light environment differed among plots. These results suggest that some plants growing in post-agricultural stands may be N limited, whereas undisturbed stands in this region appear to be approaching N saturation. Thus, environmental conditions, and particularly N availability, may be an obstacle to the restoration of forest herb communities.

1. Introduction

Understanding the reasons for the persistent legacy of historical land use on herbaceous understory plants remains an important challenge for forest ecologists and mangers. Although previous human activity can affect entire plant communities, herbaceous understory plants are among the most sensitive taxa to historic disturbance due to their limited mobility, low recruitment, and short seed dormancy (Whigham, 2004). They also represent the majority of vascular plant diversity in temperate deciduous forests, making them a key group for conserving biodiversity (Gilliam and Roberts, 2003; Gilliam, 2007).

Differences between the understory communities of post-agricultural and undisturbed forests have been widely documented in both Europe and the US (see Flinn and Vellend, 2005 and Hermy and Verheyen, 2007 for a review of studies). Such studies overwhelmingly conclude that land-use history has a strong influence on contemporary patterns of plant diversity and distributions. Forests that have regrown following agricultural abandonment tend to have fewer forest-adapted plant species (Peterken and Game, 1984; Dzwonko and Loster, 1989; Bossuyt et al., 1999; Singleton et al., 2001) than continuously forested stands. Seed sowing and transplant experiments indicate that most species can germinate in post-agricultural forests (Graae et al., 2004; Verheyen and Hermy, 2004). However, adult plant performance can be either enhanced or depressed in post-agricultural forests (Donohue et al., 2000; Endels et al., 2004; Vellend, 2005; Fraterrigo et al., 2006c; Flinn, 2007; Jacquemyn and Brys, 2008). Additionally, sites enriched in nutrients as a result of past land use generally have higher species richness than undisturbed sites (Koerner et al., 1997; Graae, 2000; Dupouey et al., 2002). These patterns suggest that environmental conditions may influence the ability of species to recolonize post-agricultural forests.

Former agriculture can either increase or decrease the availability of soil nutrients, with the direction of the effect related to the use of organic amendments and livestock densities (McLauchlan, 2006). For instance, post-agricultural forests that

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were cultivated and amended with manure have elevated levels of nitrogen (N), whereas stands that were uncultivated but used as pastures are depleted in N relative to woodlots with no agricultural history (Compton and Boone, 2000). Nitrogen cycling rates are also higher in stands that have been cultivated and amended compared with those less intensively farmed (Compton and Boone, 2000). In eastern deciduous forests of North America, historic farming ranged in intensity, and contemporary forests exhibit both nutrient enrichment and impoverishment (Compton and Boone, 2000; Richter et al., 2000; Hooker and Compton, 2003; Fraterrigo et al., 2005).

Differences in adult plant performance may be related to the soil nutrient legacies of agriculture. Fraterrigo et al. (2006c) observed that the growth rate of several forest herbs was higher in post-agricultural forests relative to undisturbed forests. Growth rates were correlated with N and P in undisturbed forests but not in post-agricultural stands (Fraterrigo et al., 2006c). Endels et al. (2004) showed that soil nutrients, specifically N and P, were positively associated with adult plant performance in post-agricultural forests. In contrast, Vellend (2005) and Flinn (2007) found differences in adult plant performance that could not be explained by soil nutrient conditions (Vellend, 2005; Flinn, 2007). The effects nutrient legacies may be complex and depend on a variety of interacting factors such as types of uses, community-level responses, and edaphic conditions.

Changes in soil nutrients may affect plant performance indirectly by enhancing competition among species. For example, both historic cultivation and pasturing can result in soil P enrichment, which can increase the potential that competitively dominant species will become established (de Keersmaeker et al., 2004). Once established, such species might negatively impact the performance of other species by depleting soil resources or decreasing light availability (Verheyen and Hermy, 2004). Other environmental factors, such as light availability, may limit adult plant performance as well (Jacquemyn and Brys, 2008).

Experiments that manipulate soil nutrient availability provide a means to assess the importance of nutrient limitation on forest herb recovery in sites where previous agriculture has led to nutrient impoverishment. A positive response to nutrient enrichment, such as increased biomass, might indicate that historically disturbed forests are resource limited, while a neutral response might indicate that other factors are inhibiting recovery. Because species vary in their ability to acquire and utilize nutrients, however, inter-specific differences can be expected.

Here, we compare the response of six understory herbaceous taxa to N enrichment in forests in the southern Appalachians with and without an agricultural history to examine the hypothesis that plants in post-agricultural stands are N limited. The taxa we selected (Table 1) are native, slow-growing perennials that are common occupants of eastern deciduous forests understories. We chose to manipulate N because an earlier study indicated that post-agricultural forests in this region have lower rates of N mineralization and thus decreased N availability (Fraterrigo et al., 2005). We measured plant morphological characteristics for three consecutive years and used them to estimate changes in biomass and leaf area as an index of species response to enrichment.

2. Methods

2.1. Study area

Our study was conducted in closed-canopy cove hardwood forests located in the Dillingham Creek watershed of the French Broad River Basin in Buncombe County, western North Carolina, USA. Soils were formed in residuum and possess mixed mineralogy, but all are well drained, upland mountain soils derived predominately from granite, gneiss and mica-schist. The two series present (Porters-Unaka complex) are classified as Typic Dystrudepts, acidic Inceptisols with humid moisture regimes (USDA NRCS). The vegetation is characteristic of the mixed mesophytic communities of the Southern Blue Ridge Province described by Braun (1950), with canopies dominated by tulip tree (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), oak (*Quercus* spp.), basswood (*Tilia americana*), hickory (*Carya* spp.) and sweet birch (*Betula lenta*). Similar species occur regardless of land-use history, but tulip tree is more abundant in post-agricultural forests than in undisturbed forests (Fraterrigo, unpublished data).

Historical land use consisted of subsistence agriculture and was determined from landowner interviews, rigorous examination of historical records, physical evidence (e.g., stand-age distribution, fences, stumps, road beds) and a chronosequence of aerial photographs (Fraterrigo et al., 2005). Fields were cleared in the late 1800s and early 1900s by girdling trees and were immediately planted with crops. The soil was not amended. As productivity declined, typically within fives or less, fields were converted to livestock pastures (Otto, 1987). Land abandonment in the 1930s allowed most land to revert to forest. In contrast, reference stands showed no evidence of human occupation or selective logging, and contained plant species typical of old-growth forests (e.g., *Dryopteris goldiana*).

We selected two sites, one with a history of agriculture (hereafter *post-agriculture*) and one reference stand. The sites are located in the same watershed and are similar with respect to geology, soil series, and terrain shape, but the reference site is higher in elevation (1150 m) than the post-agriculture site (850 m). These sites were chosen because their environmental conditions are similar and representative of those encountered in this region for each type of history (Fraterrigo et al., 2005).

Previous work indicated that potential N mineralization rates are an average of 89% lower in post-agriculture forests compared with reference forests in this region (Fraterrigo et al., 2005). Additionally, mean potential N mineralization in soils collected in 2001 from the sites in which this study was conducted were 9.5 ($NH_4 + NO_3$–N) kg ha^{-1} 28 d^{-1} in the post-agriculture site ($N = 68$ samples) and 14.5 (kg $NH_4 + NO_3$–N) kg ha^{-1} 28 d^{-1} in

Table 1

Taxa investigated in this study and mean (±1 SE) plant size, as measured in 2002 prior to fertilization. Differences in plant biomass between the post-agriculture site and the undisturbed site were tested with ANOVA. Values with non-matching superscripts are significantly different ($P < 0.05$).

Species or genus	Dispersal mechanism[†]	Root morphology[†]	Spread potential	Flowering phenology[†]	Maximum height (m)[†]	Biomass (g) post-agriculture site	Biomass (g) undisturbed site
Arisaema triphyllum	Ingested	Fibrous rhizome	Low	March–April	0.2–0.8	0.08 (0.01)	0.14 (0.06)
Cimicifuga racemosa	Passive	Fibrous rhizome	Low	May–July	2.5	6.86 (0.56)	7.52 (0.97)
Disporum lanuginosum	Ants, vertebrates	Elongate rhizome	High	April–May	0.4–1	0.80 (0.17)	0.77 (0.17)
Osmorhiza spp.	Adhesive	Fibrous rhizome	Low	April–May	0.1–1	0.29 (0.06)	0.25 (0.03)
Polygonatum spp.	Ingested	Elongate rhizome	High	April–June	0.2–2	0.74 (0.12)	0.56 (0.07)
Prenanthes altissima	Wind	Fibrous rhizome	Low	August–October	0.3–2	0.29 (0.02)[a]	0.13 (0.02)[b]

[†] Data from Radford et al. (1964) and Beattie and Culver (1981).

the reference site (N = 94 samples). Thus, we had evidence that the post-agriculture site had less available inorganic N. Total soil N was also lower in the post-agriculture site than in the reference site ($1.79\ \mathrm{g\ kg^{-1}}$ and $4.71\ \mathrm{g\ kg^{-1}}$, respectively), whereas as extractable soil P (post-agriculture: $49.7\ \mathrm{mg\ kg^{-1}}$; reference: $46.7\ \mathrm{mg\ kg^{-1}}$) and soil pH (post-agriculture: 5.7; reference: 5.2) were comparable. Soil bulk density was higher in the post-agriculture site ($0.87\ \mathrm{g\ cm^{-3}}$) than in the reference site ($0.32\ \mathrm{g\ cm^{-3}}$).

2.2. Fertilization and data collection

Within each site, we located eight blocks. Three 1 m × 1 m plots were established in each block and assigned one of three treatments in a completely randomized design. The treatments were: (i) *control* = no N addition; (ii) N1 = an amount of N approximately equal to the rate of net N mineralization in vegetatively similar forests without a history of human disturbance; and (iii) N3 = an amount of N approximately three times the rate of net N mineralization in vegetatively similar forests without a history of human disturbance. We computed the amount of N fertilizer needed to augment net N mineralization so that it was comparable to undisturbed forests as follows. We assumed that fertilizer additions would affect the area within the 1 m × 1 m plot to a depth of 12 cm, which represents approximately 92.4 kg of soil given the bulk density of soils in this area (Fraterrigo et al., 2006c). Multiplying the soil weight by an annual estimate of net N mineralization from a nearby, undisturbed forest dominated by tulip tree, birch, red oak, and hickory ($209\ \mathrm{mg\ N\ kg\ soil^{-1}}$; Knoepp and Swank, 1998), we determined that N mineralization would equal approximately $19.3\ \mathrm{g\ N\ year^{-1}}$ for the upper 12 cm of soil within a 1 m × 1 m plot. We thus added $20\ \mathrm{g\ N\ year^{-1}}$ to the N1 plots by hand casting 2.5 g of N in the form of 34–0–0 N–P–K commercial fertilizer monthly throughout the growing season (March–October) for two years (2003–2004). N3 plots received $60\ \mathrm{g\ N\ year^{-1}}$ by applying 7.5 g N over the same period. The total amount of inorganic N applied to each plot over the course of the study was thus 40 g and 120 g for the N1 and N3 treatments, respectively.

To determine canopy closure above each plot, we digitized the amount of open sky visible in hemispheric photographs of the forest canopy. One photograph was taken from a height of 1.5 m at each corner of each plot with a fish-eye lens mounted on a 35-mm camera. Photographic negatives were scanned and processed to classify photographs into open sky versus shaded pixels.

Prior to collecting data, we identified six understory herbaceous species or genera that differed in life-history characteristics but had a high frequency of occurrence in the study area (Table 1). For each of these taxa, we derived regression equations for aboveground biomass and leaf area by destructively sampling 10–15 individuals of every taxon (mean adjusted $r^2 = 0.95$) collected from locations outside the study area (see Fraterrigo et al., 2006c for regression equations). Individual stems and leaves were measured in the field and reweighed after oven-drying at 65 °C to a constant mass (c. 24 h). Digital image analysis was used to determine the leaf area of fresh leaves within 2 h of collection (O'Neal et al., 2002).

We recorded the morphological characteristics (stem height and diameter and leaf length and width) of all individuals of each taxon in each 1 m × 1 m plot. Measurements were collected during mid-June 2002–2004, when taxa were at peak biomass. We used the regression equations to estimate annual aboveground biomass and leaf area for each individual based on their morphology and summed across taxa in each plot. To determine relative change, we subtracted the total biomass or leaf area in 2002 (initial) from the total biomass or leaf area in 2004 (final) and divided the result by the total initial value for each taxon in each plot. We also recorded percentage cover of all herbaceous species in each plot during 2002, prior to fertilization.

We collected leaf samples during mid-June 2004 for chemical analysis. Five mature and unsenesced leaves were removed from three or more plants of each taxon in each plot and transported to the laboratory where they were oven dried (65 °C), weighed, and ground in a Wiley mill for nutrient analysis. We determined total N content in plant tissue samples using Kjeldahl digestion followed by colorimetric assay on an Alpkem autoanalyzer (OI Analytical, Wilsonville, OR, USA).

2.3. Statistical analyses

We compared changes in the aboveground biomass and leaf area of each taxon across treatment levels and sites using mixed effects analysis of variance (SAS v.9.1, SAS Institute Inc.). Changes in aboveground biomass were expressed as a relative proportion by dividing the change in biomass or leaf area by the initial value of these variables, which was observed prior to fertilization. Models included site, treatment and the treatment × site interaction as fixed effects, and block nested in site as a random effect. A similar model was used to analyze differences in foliar chemistry. Where mixed effects ANOVA indicated a significant interaction between treatment and site, the response to fertilization was evaluated again, but for each site individually. We tested for differences among all treatments within a site using Tukey's test. We also tested for differences in initial plant size (total biomass in 2002 prior to fertilization) between the sites using mixed effects analysis of variance with site as a fixed effect and block nested in site as a random effect.

3. Results

Among sites with different land-use histories, initial plant size and growth rates were similar. In five of the six taxa we investigated, plant size prior to fertilization did not vary between sites, which had different histories (Table 1). However, *Prenanthes altissima* had significantly greater biomass in the post-agriculture site compared to the reference site ($F_{1,446} = 9.34$, $P = 0.02$).

Similarly, plant growth between 2002 and 2004 differed between sites in only two taxa. *Arisaema triphyllum* showed a greater relative increase in total aboveground biomass in the reference site (0.71 ± 0.23 g) than in the post-agriculture site (0.32 ± 0.07 g; $F_{1,28} = 11.31$, $P < 0.01$). In contrast, *P. altissima* showed a greater relative increase in the reference site (2.29 ± 0.38 g) than in the post-agriculture site (1.06 ± 0.31 g; $F_{1,29} = 13.98$, $P < 0.01$).

In response to fertilization, aboveground plant biomass varied with site and among taxa. In *A. triphyllum*, fertilization significantly reduced growth in total aboveground biomass compared to the control in the reference site, but had no effect on growth in the post-agriculture site (treatment × site: $F_{2,28} = 11.03$, $P < 0.01$; Fig. 1). In contrast, the N3 treatment increased total aboveground biomass in *Osmorhiza* spp. in the post-agriculture site but had no effect in the reference site (treatment × site: $F_{2,21} = 3.98$, $P = 0.05$; Fig. 1). Fertilization significantly increased aboveground biomass in *P. altissima*, but there was no difference in the response among the sites (treatment: $F_{2,29} = 4.76$, $P = 0.03$; Fig. 1). The other taxa showed no response to fertilization.

Change in leaf area was significantly different between sites in one taxa. *Polygonatum* spp. showed a greater relative increase in leaf area in the post-agriculture site ($584 \pm 104\ \mathrm{cm^2}$) than in the reference site ($226 \pm 54\ \mathrm{cm^2}$; $F_{1,20} = 11.37$, $P < 0.02$). Leaf area response to fertilization, however, varied with site and among taxa. *A. triphyllum* showed a significant increase in leaf area in the post-agriculture site under the N1 treatment, but no change under the N3 treatment or in the reference site (treatment × site: $F_{2,28} = 4.97$, $P = 0.03$; Fig. 2). By comparison, fertilization resulted in a smaller increase in leaf area in the reference site but had no significant effect

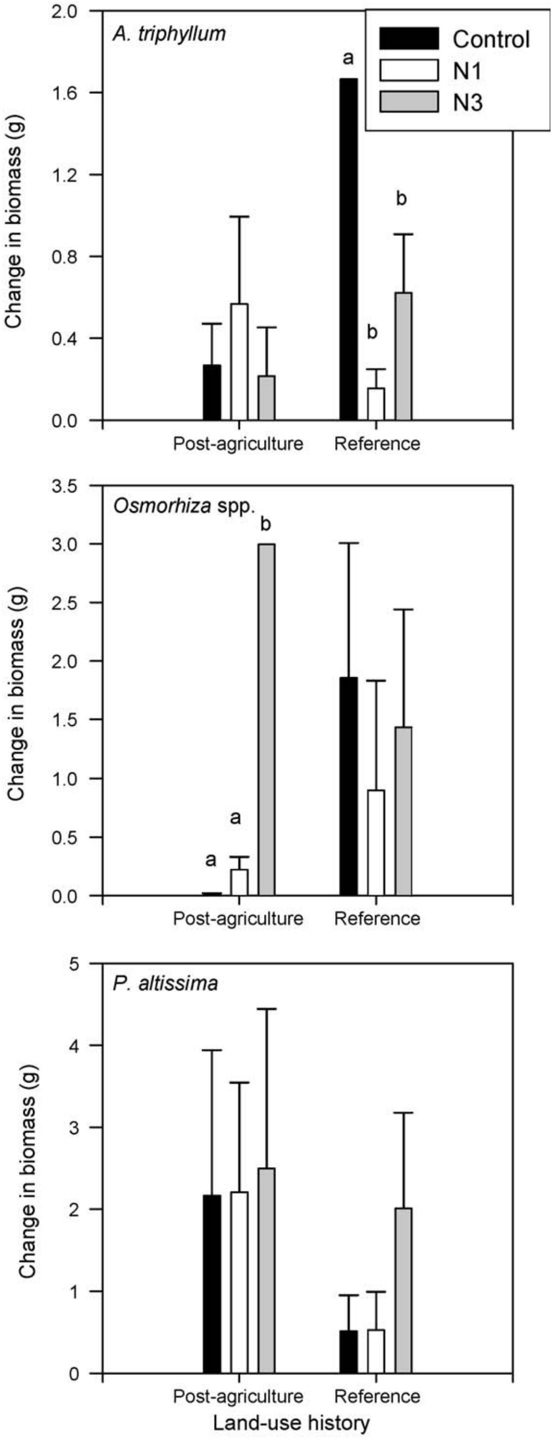

Fig. 1. Mean relative change (±1 SE) in aboveground biomass of the three taxa investigated in this study that responded to N fertilization. Different lowercase letters above bars indicate significant differences between treatment groups within each site based on Tukey's test.

in the post-agriculture site in *Cimicifuga racemosa* (treatment × site: $F_{2,17} = 12.39$, $P = 0.005$; Fig. 2) and *Osmorhiza* spp. (treatment × site: $F_{2,21} = 5.38$, $P = 0.03$; Fig. 2). *Disporum lanuginosum* showed an increase in leaf area with fertilization regardless of site (treatment: $F_{2,23} = 5.90$, $P = 0.02$). Finally, there was no effect of fertilization on leaf area in either *P. altimssima* or *Polygonatum* spp.

Analysis of foliar tissue indicated that plants in fertilized plots were N enriched, although this effect varied by taxon (Fig. 3). The taxa that showed a treatment response included *A. triphyllum* ($F_{2,24} = 15.84$, $P = 0.001$), *Osmorhiza* spp. ($F_{2,27} = 28.63$, $P < 0.001$) and *P. altissima* ($F_{2,30} = 22.48$, $P < 0.01$). *C. racemosa* showed a marginal though non-significant increase in foliar N concentration ($F_{2,19} = 2.36$, $P = 0.16$). In addition, *P. altissima* had significantly higher foliar N concentration in the post-agriculture site (3.4 ± 0.13%) than in the reference site (2.8 ± 0.14%) regardless of N treatment ($F_{1,30} = 25.90$, $P < 0.001$).

Total herbaceous cover was higher in the reference site than in the post-agriculture site prior to fertilization. Mean cover was 87% in the reference forest and 72% in the post-agriculture forest ($F_{1,48} = 10.2$, $P < 0.01$). Canopy closure ranged from 90% to 95% and did not differ between sites ($F = 0.43$, $P = 0.51$), suggesting that plants experienced similar light environments regardless of land-use history.

4. Discussion

Of the six taxa we investigated, only *A. triphyllum* and *Osmorhiza* spp. showed significantly greater increases in biomass or leaf area in the post-agriculture site compared with the reference site following N fertilization, and thus supported the hypothesis of N limitation. In contrast, fertilization reduced growth in aboveground biomass or leaf area in three species in the reference site. Species-specific responses to N availability and interspecific competition may explain these trends. In his review of studies investigating forest herb response to excess N deposition, Gilliam (2006) observed that herb layers tend to initially increase in cover with increasing N and then decrease in species richness. He argued that the latter response is a signal of the onset of N saturation as numerous N-efficient species are lost, possibly due to increased interspecific competition with nitrophilous species (Gilliam, 2006). In the present study, the reference site initially had higher percent cover of herbaceous species and therefore presented a more competitive environment for the individual plants living therein. As we added N, interspecific competition may have increased further in the reference site, resulting in reduced growth in aboveground biomass. Our findings thus suggest that the reference site is approaching N saturation, whereas the post-agriculture site shows no sign of excess N availability.

The discrepancy in the N-saturation stage of our sites may be a direct result of land-use history. Previous land use can precondition forest response to N deposition by increasing N limitation via the extraction of N from a site by agricultural conversion (Aber et al., 1998). Consequently, forests with a history of agriculture and logging are accumulating N, even as undisturbed forests lose N through nitrification and leaching (Goodale and Aber, 2001; Compton et al., 2007; McLauchlan et al., 2007). However, landscape position may also be important, as the reference site was located at a higher elevation than the post-agriculture site, and high elevation areas tend to receive more N deposition (Weathers et al., 2000).

Still, fertilization stimulated productivity in only two taxa in the post-agriculture site. We expected more taxa to increase in biomass or leaf area with fertilization if the site was truly N limited. One reason that taxa may have responded differently to N fertilization in our study is that their abilities to acquire nutrients can vary. Light is one of the most limiting resources in moist, rich forest understories (Coomes and Grubb, 2000) and can substantially alter the capacity of a plant to absorb available nutrients (Aerts and Chapin, 2000). While the light environment, measured here as canopy closure, did not differ among plots, some taxa may have experienced light limitation due to differences in phenology and stature (Givnish, 1982). For example, species that leaf out and flower early have more access to light resources and thus should have a greater demand for nutrients (Muller, 1978; Blank et al., 1980; Peterson and Rolfe, 1982; Neufeld and Young, 2003).

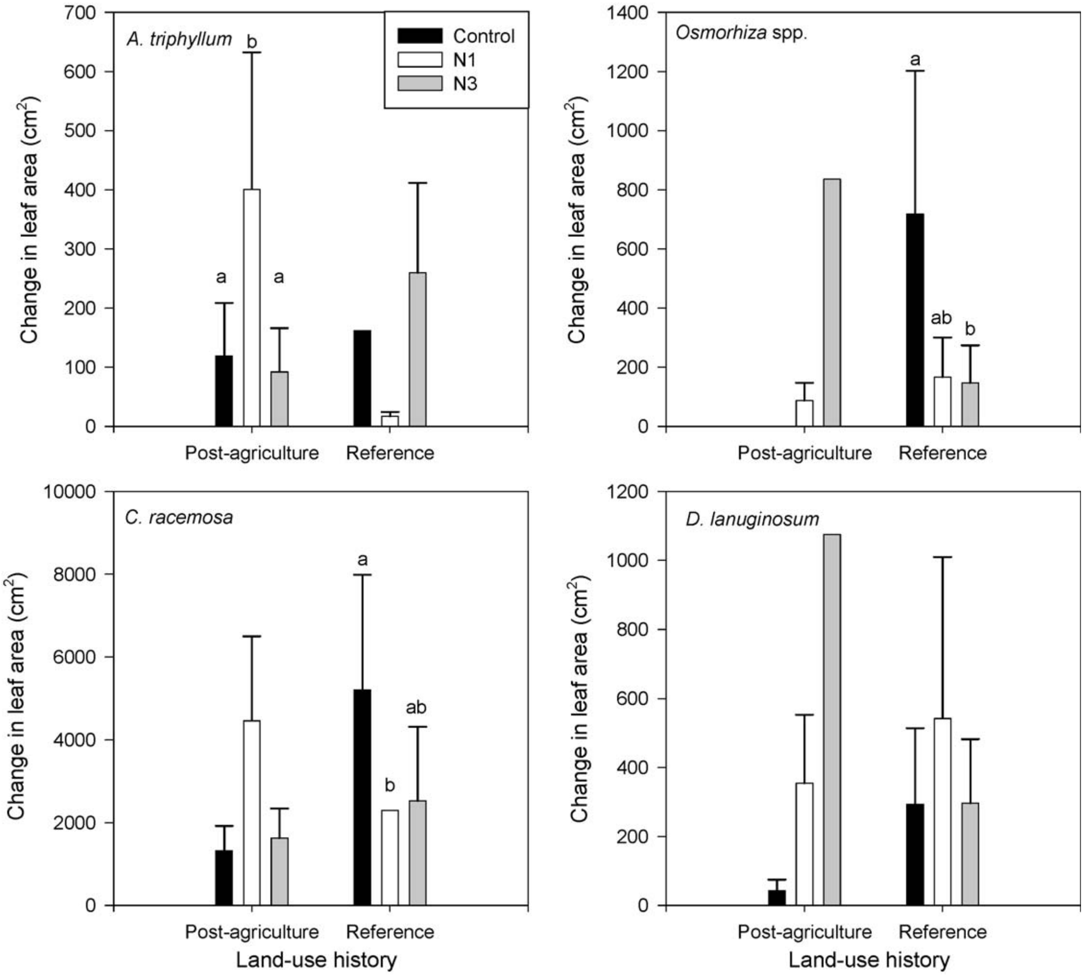

Fig. 2. Mean relative change (±1 SE) in leaf area of the four taxa investigated in this study that responded to N fertilization. Different lowercase letters above bars indicate significant differences between treatment groups within each site based on Tukey's test.

Accordingly, both *A. triphyllum* and *Osmorhiza* spp., which have early flowering periods (Table 1), showed elevated levels of foliar N with fertilization. Foliar N concentrations were elevated in both the post-agriculture and reference site, however; thus, N uptake alone does not explain the larger increase in biomass or leaf area that these that taxa exhibited in the post-agriculture site compared with the reference site. Species that are tall in stature should likewise have a higher demand for N due to enhanced light access, but our results did not generally support this hypothesis.

The effects of past land use on plant performance in historically altered forests remain equivocal. The soil nutrient legacies of agriculture clearly account for some of the variation in the patterns observed in this and other studies. Where agriculture has led to nutrient enrichment, plant performance tends to be enhanced (Endels et al., 2004; Fraterrigo et al., 2006c), whereas in the present study we found evidence that nutrient impoverishment limits the growth of some taxa. Yet even these patterns vary among species (Verheyen and Hermy, 2004; Fraterrigo et al., 2006c; Flinn, 2007). For example, as in a previous study (Fraterrigo et al., 2006c), we found that *A. triphyllum* performed better in the reference site than in the post-agriculture site, while the opposite was true for *P. altissima*. Frequently, previous agriculture has no discernable effect on soil nutrients, which causes the rejection of hypotheses implicating nutrient availability (Vellend, 2005; Jacquemyn and Brys, 2008). Soil nutrient availability can be highly variable among post-agricultural forests, however, which may obscure potential relationships between soil nutrients and plant performance (Fraterrigo et al., 2005). Indeed, accounting for variation in soil nutrients and light availability can equalize apparent differences in plant size and abundance in forests with different histories (Fraterrigo et al., 2006b; Flinn, 2007).

The role of competition may also be important and can vary among systems. In Europe, researchers have documented differences in competition between recent and ancient stands, mainly as a result of the higher abundance of *Urtica dioica* in post-agricultural forests (de Keersmaeker et al., 2004; Endels et al., 2004). Due to its high stature, *U. dioica* can overshadow many common woodland herbs, with negative consequences for seeding and juvenile survival (Endels et al., 2004; Verheyen and Hermy, 2004). However, in the present study, total herbaceous cover was actually slightly lower in the post-agriculture stand than in the reference stand. Thus, it is unlikely that competition for light and nutrients was higher in the post-agriculture site.

Belowground dynamics can also contribute to competitive differences, but have not been widely examined. There is some evidence for differences in the microbial community between post-agricultural and reference stands. Specifically, post-agricultural forests have a lower abundance of arbuscular mycorrhizal fungi than reference stands (Fraterrigo et al., 2006a). Because mycorrhizal fungi can contribute to N nutrition (Smith and Read, 1997), we might expect plants that do not form this mutualism to respond more vigorously to the addition of nitrogen compared with those that have mycorrhizal associations.

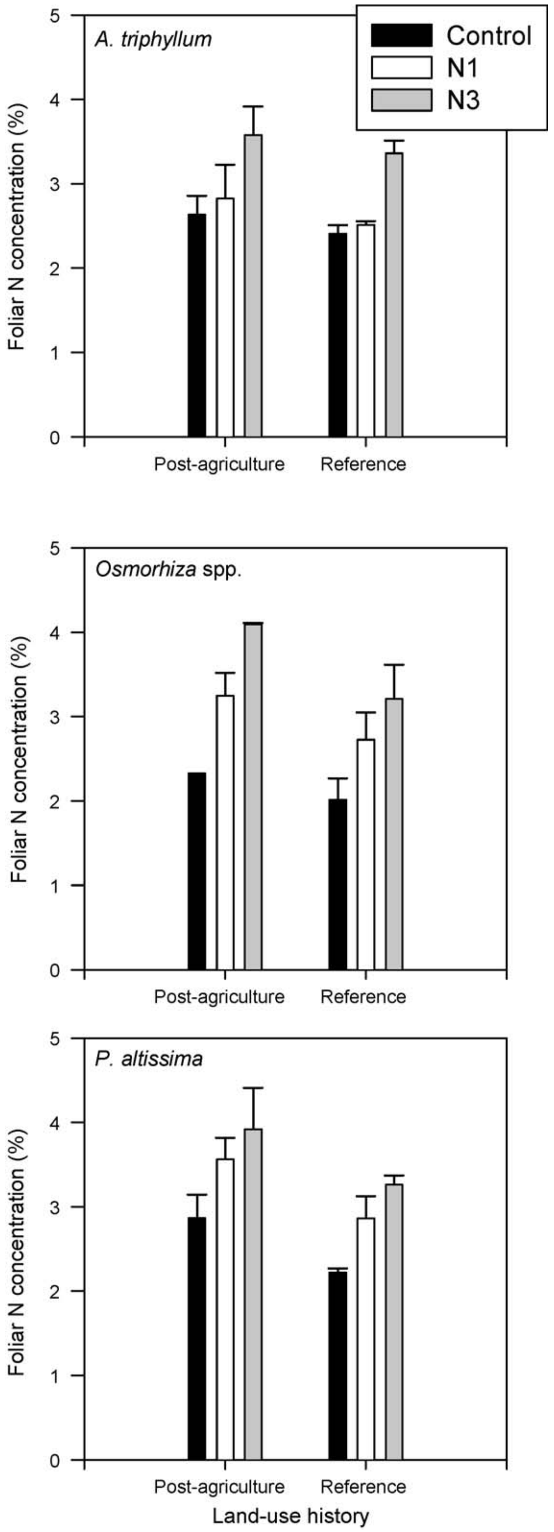

Fig. 3. Mean foliar nitrogen concentration (±1 SE) of the three taxa investigated in this study that showed elevated levels of foliar N in response to N fertilization.

One caveat of our study is that we did not examine how belowground biomass changed with fertilization. It is possible that plants in reference stands could have stored added N in their roots rather than translocating it to aboveground parts. Yet even this strategy would suggest that plants in the reference stand were less N limited because luxury consumption occurs when nutrients are in excess of immediate growth requirements (Chapin, 1980). Additional studies of belowground dynamics are needed to fully resolve this question.

To our knowledge, there have been no other studies that have examined the response of forest understory species to N fertilization in sites that differ in land-use history. Studies that have manipulated N in the herbaceous layer of forest understories have generally done so in order to examine the effects of atmospheric N deposition on the herb layer. Our results are generally consistent with the findings of such studies, which show that adding N to the herbaceous layer initially increases cover when forests are not N saturated (Hurd et al., 1998; Gilliam, 2006; Gilliam et al., 2006).

5. Conclusion

Dispersal limitation is considered the primary obstacle to the recovery of forest herbs in historically altered forests. This perspective implies that forest–herb communities can be restored by introducing seeds into post-agricultural forests. In contrast, our study suggests that the performance of some taxa may be inhibited by nutrient limitation as well. Low nutrient availability may not hamper initial establishment, but may eventually compromise the colonization of reforesting areas by reducing plant vigor. Species are likely to respond in diverse ways to nutrient limitation, however, with soil conditions acting as a differential filter to alter community composition and the relative importance of species. Understanding the effects and nutrient limitation on the population structure of a variety of forest herbaceous species is therefore an important goal for future research.

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