

Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition

FRANK S. GILLIAM

Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510, USA

Summary

1 This review brings into focus what is known about the response of the herbaceous layer of forest ecosystems to increasing nitrogen deposition. The emphasis on forests in general is important for two reasons. First, forests often occupy areas receiving high rates of atmospheric deposition of N. Second, compared with herb-dominated communities, about which much is known regarding response to excess N, forests generally display greater biological and structural complexity. The more specific focus on the herbaceous layer – here defined as all vascular (herbaceous and woody) plants ≤ 1 m in height – is warranted because most of the species diversity of forests occurs in the herb layer.

2 Most responses of forest ecosystems to N saturation, defined here as ecosystem supply of N exceeding ecosystem demand for N, can be characterized by two complementary hypotheses, each emphasizing different facets of ecosystem structure and function. One focuses on ecosystem processes, such as net primary productivity, whereas the other addresses seasonal patterns of concentrations of NO_3^- in stream water. Although neither hypothesis considers the effects of chronically elevated N deposition on forest herbs, both share a prediction – a dramatic increase in availability of NO_3^- – that is relevant to forest herb response. Such a shift towards NO_3^- dominance has important implications for changes in herbaceous layer dynamics. For example, increases in soil NO_3^- pools can increase invasibility by exotic species. Also, because preferential use of NH_4^+ vs. NO_3^- can be highly species-specific among forest herbs, predominance of NO_3^- availability can bring about further changes in herb layer species composition. Also important to forest herbs is the tendency for enhanced mobility of NO_3^- to increase mobility and decrease availability of essential cations, such as Ca^{2+} .

3 The response of plant species of the herbaceous layer of forest ecosystems to excess N availability can arise from N-mediated changes in several processes. Here I identify six – competition, herbivory, mycorrhizal infection, disease, species invasions and exotic earthworm activity – and discuss how they respond to excess N and how this response affects the herb layer of forests. With the exception of the activity of exotic earthworms (which is correlated with, but not necessarily caused by, high N deposition), there is compelling evidence that all processes respond sensitively to N deposition and that this response generally leads to drastic shifts in species composition and decreases in biodiversity of forest herb communities.

4 A hypothesis is suggested – the nitrogen homogeneity hypothesis – that predicts loss of biodiversity in forest ecosystems experiencing chronically elevated N deposition. This hypothesis is based on the decrease in spatial heterogeneity of N availability that is typically high in forest soils under N-limited conditions.

Key-words: biogeochemistry, forest herbaceous communities, nitrogen saturation, vegetation science

Journal of Ecology (2006) **94**, 1176–1191
doi: 10.1111/j.1365-2745.2006.01155.x

Introduction

The human-caused increase in biologically reactive nitrogen (N) in the biosphere is a biogeochemical phenomenon that has consequences for plant biodiversity and thus embraces two distinct facets of plant ecology: biogeochemistry and vegetation science. Biogeochemists who understand the mechanisms of how excess N alters nutrient cycling in terrestrial ecosystems may be less aware of the processes that determine the composition of plant communities. Conversely, vegetation scientists who understand plant community dynamics may be less aware of the biogeochemical consequences of adding excess N to the environment. A primary impetus of this review, thus, is an attempt to bridge the gap between these two prominent ecological subdisciplines.

The main purpose of this review is to bring into focus what is known about the response of the herbaceous layer of forest ecosystems to increasing N deposition. The emphasis on forests in general is important for two reasons. First, forests occupy a high proportion of areas receiving high rates of atmospheric deposition of N, e.g. eastern North America and western Europe (Holland & Lamarque 1997). Second, compared with herb-dominated communities, about which much is known regarding response to excess N (Pennings *et al.* 2005; Suding *et al.* 2005), forests generally display greater biological and structural complexity. The specific focus on the herbaceous layer is warranted because most of the species diversity of forests occurs in the herb layer (Gilliam & Roberts 2003a).

My review will be organized into four sections. The first section will introduce the phenomenon of N saturation. This is not intended to provide an exhaustive review of the phenomenon; indeed, I would encourage readers to consider previous publications that do an excellent job reviewing N saturation, e.g. Fenn *et al.* (1998) or Aber *et al.* (2003). Rather, I will focus primarily on biogeochemical processes with a particular focus on aspects germane to forest plant species, e.g. the relationship between soil NO_3^- pools and invasibility, and NO_3^- vs. NH_4^+ use by herb layer species.

The second section will be a synthesis of published work on the effects of N additions on the forest herbaceous layer. Because the nature of the problem of excess N differs notably between North America and Europe, the way in which the effects of N on herbaceous vegetation has been studied also varies between these two regions. Consequently, I will distinguish between European and North American literature.

The third section will be devoted to identifying specific mechanisms – such as increased disease or decreased competitive ability – to explain observed responses of forest herbaceous layers to excess N availability. These will be posed as potentially complementary, rather than mutually exclusive, hypotheses to help understand and predict the effects of increasing N supply on forest herb communities.

The final section will be used to develop a general hypothesis of the negative effects of excess N on forests, one which has particular relevance to the herbaceous layer. Biodiversity is more than just the number and balance of different species occurring in an area; it also has a functional process component (Roberts & Gilliam 1995). Spatial and temporal heterogeneity in these processes (e.g. nutrient cycling, energy flow and species dynamics) contribute to the overall biodiversity of an ecosystem. This hypothesis will make a connection between excess N-mediated decreases in heterogeneity and decreases in species diversity of impacted forests, while predicting further decreases in the future in areas where N deposition remains unmitigated.

Note that for the sake of consistency I will use the term ‘herbaceous/herb layer’ throughout this review to refer to the lowest stratum of forest vegetation. As reviewed by Gilliam & Roberts (2003b), this layer is often, though not always, defined as comprising all vascular plants – woody and herbaceous – that are ≤ 1 m in height. Many aspects vary, however, across this facet of the plant ecological literature, including the specific height used to delimit the stratum and exclusion/inclusion of non-vascular plants (e.g. bryophytes). Gilliam & Roberts (2003b) also surveyed synonymous terms found in the literature, including ‘herbaceous/herb stratum’, ‘herbaceous understorey’, ‘ground layer’, ‘ground vegetation’ and ‘ground flora’. Again, for the sake of simplicity and consistency I will use ‘herbaceous/herb layer’, despite alternative terms used within given studies.

Nitrogen saturation

The N_2 gas that makes up 78% of our atmosphere is inert to virtually all living organisms, other than a small group (< 60 genera – Postgate 1982) of prokaryotes (i.e. symbiotic and non-symbiotic N-fixers). Furthermore, other than the high energy associated with lightning strikes that combines N_2 and O_2 ultimately to form NO_2 , N_2 enters into few non-anthropogenic, abiotic chemical reactions. As a result, N_2 is often referred to as non-reactive N in contrast to other forms, such as NO_3^- , NH_4^+ and NO_2 , that are collectively referred to as reactive N (N_r). Although the most inclusive sense of N_r (see Galloway *et al.* 2004 for a recent comprehensive review) comprises all forms of N that readily enter into reactions, including biochemical reactions (biologically active), photochemical reactions (photochemically active) and electromagnetic absorption (radiatively active), I confine my discussion here to biologically active N_r , particularly the predominantly plant-labile forms of NH_4^+ and NO_3^- .

Increases in anthropogenic N-fixation, including fossil-fuel combustion and the Haber–Bosch process for production of N fertilizers, have added increasing amounts of N_r to the biosphere. Galloway *et al.* (2004) estimated that total atmospheric deposition of NH_4^+ and NO_3^- to terrestrial ecosystems has increased from

17 Tg N year⁻¹ in 1860 to 64 Tg N year⁻¹ in the early 1990s, and projected further increases to 125 Tg N year⁻¹ by 2050. [Note: for simplicity I am presenting these as NH₄⁺ and NO₃⁻ rather than the more inclusive formulas NO_y and NH_x used by Galloway *et al.* (2004).] Thus, there will have been a nearly 10-fold increase in atmospheric deposition of N_r within the period of the last 200 years.

Although atmospheric deposition of N clearly has increased over this period, it is still quite spatially heterogeneous, with higher levels of N deposition generally being closely associated with high densities of human populations. For example, annual N deposition can vary 3–4-fold across the north-eastern USA, increasing from eastern Maine to western New York (Ollinger *et al.* 1993). Terrestrial ecosystems that receive high levels of N deposition are often predisposed to a phenomenon known as N saturation, which develops when the availability of N exceeds the total biological demand for N (Aber *et al.* 2003). Other factors, however, such as topography, vegetation and geology (i.e. parent materials), can also predispose ecosystems to N saturation to varying but important degrees (Williard *et al.* 2005). In parts of North America (particularly the eastern USA) and Europe there is a high degree of spatial coincidence of forests and chronically elevated atmospheric N deposition (Holland & Lamarque 1997). Consequently, most N-saturated ecosystems are forests.

Responses of forest ecosystems to N saturation can be generally characterized by two complementary hypotheses, each of which emphasizes different facets of ecosystem structure and function. The first, originally articulated by Aber *et al.* (1989), focuses on ecosystem processes, such as net primary productivity (which is predicted to decline at later stages of N saturation), whereas the other, described by Stoddard (1994), addresses seasonal patterns of concentrations of NO₃⁻ in stream water. Notably, neither hypothesis considers the effects of chronically elevated N deposition on forest biodiversity, particularly that of herb layer communities. They do, however, share a prediction that is relevant to forest herb response: a dramatic increase in availability of NO₃⁻ accompanied by change in N dynamics toward rapid movement of NO₃⁻ in N-saturated forest soils. Such a shift towards NO₃⁻ dominance has important implications for changes in herbaceous layer dynamics. For example, increases in soil NO₃⁻ pools can increase invasibility by exotic species (Fargione & Tilman 2005). Also, because preferential use of NH₄⁺ vs. NO₃⁻ can be highly species-specific among forest herbs (Marschner 1995; Muller 2003), predominance of NO₃⁻ availability can bring about further changes in herb layer species composition. Also important to forest herbs is the tendency for enhanced mobility of NO₃⁻ to increase mobility and decrease availability of essential cations, such as Ca²⁺ (Gilliam *et al.* 2005).

The second hypothesis of N saturation (Stoddard 1994) predicts that there should be elevated concentrations

of stream NO₃⁻ as N saturation progresses, accompanied by decreases in the magnitude of seasonal fluctuations of stream NO₃⁻ found in N-limited forests, in which there are measurable levels of NO₃⁻ during the dormant season that decline to nearly undetectable levels during the growing season. Peterjohn *et al.* (1996) clearly demonstrated this response for a mixed hardwood forest watershed at the Fernow Experimental Forest (FEF), West Virginia, experiencing chronically elevated ambient inputs of N. Analysing data from 1971 to 1994, they found that annual variability in stream NO₃⁻ concentrations decreased from a maximum coefficient of variation (which reflects the degree of seasonal fluctuation) of > 100% in 1975 to a minimum consistently < 20% from 1984 to the end of the sampling period. Thus, because NO₃⁻ leaching is pronounced during the growing season at N-saturated sites, ecosystem loss of cations can be substantial at a time when plant demand for cations is at a maximum. Furthermore, dormant-season losses of NO₃⁻ can facilitate loss of essential cations at a time when metabolic activities of plants are negligible and thus virtually incapable of mitigating such losses.

In addition to these effects of excess N on temporal dynamics of N processing, Gilliam *et al.* (2001) showed at this same site (FEF) that experimental additions of N to an entire watershed significantly decreased spatial heterogeneity of N processing, including net N mineralization and nitrification and uptake of N by prominent herb species, compared with a high degree of natural spatial heterogeneity on untreated reference watersheds. Decreases in spatial heterogeneity of soil N processing have important implications for the response of forest herbs – including composition, cover and biodiversity – to excess N deposition.

Response of the herbaceous layer to excess N

Field experiments investigating the effects of N availability on species composition and diversity of plant communities date back to the mid-19th century, with the first being the Park Grass Experiment in Rothamsted, England, established in 1856 (Richardson 1938). Although that experiment originally was designed to determine the effect of a variety of inorganic nutrient fertilizers on plant yield (and to compare it with the effect of manure), the early researchers also observed rapid and notable effects on species composition, particularly in response to additions of inorganic N. One of the more significant findings was that excess N greatly shifted species composition and decreased species diversity of herb communities. This response has been supported by even more extensive recent studies at the Cedar Creek Natural Area, Minnesota, that have focused specifically on the effects of a wide range of levels of N addition (Fig. 1). Regrettably, in contrast to numerous studies on effects of N on herb-dominated ecosystems (see Suding *et al.* 2005 for a meta-analysis of nine such sites in the USA), fewer have been done on forested ecosystems (Bobbink *et al.* 1998). This is a

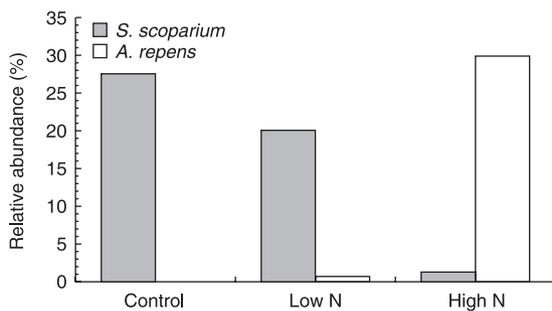


Fig. 1 Change in relative abundance (%) in response of important grass species (*Schizachyrium scoparium* and *Agropyron repens*) to experimental nitrogen (N) additions for 3 years, which were the following: Low N = 1 kg N ha⁻¹ year⁻¹, High N = 27.2 kg N ha⁻¹ year⁻¹. Figure based on data taken from Tilman (1987).

significant discrepancy because forest ecosystems generally display far greater structural and biological complexity than their herb-dominated counterparts, thus precluding extrapolation of findings from herb-dominated systems to forests, at least without empirical data to support such extrapolation.

SYNTHESIS OF RECENT RESEARCH ON STAND-LEVEL RESPONSES OF FOREST HERB LAYERS TO N

Problems associated with chronically elevated N deposition leading to N saturation were addressed earlier in Europe than in North America (e.g. Ågren & Bosatta 1988), in part because these problems arose earlier and were relatively more widespread in Europe. Excess wet deposition of N in Europe has largely been in the form of NH₄⁺ arising from NH₃ volatilization associated with agricultural practices (Asman *et al.* 1998; van Tol *et al.* 1998; Erisman & de Vries 2000; Krupa 2003). By contrast, anthropogenically elevated wet N deposition in North America has occurred more in the form of NO₃⁻, resulting from emissions of NO_x associated with high-energy combustion, including internal combustion engines of motor vehicles (USEPA 2002). Not surprisingly, then, more research on the biogeochemical effects of N deposition has been carried out in Europe than in North America, particularly in the form of co-ordinated networks such as NITREX (Wright & vanBreemen 1995), and more work on the effects of N on forest vegetation has also been done in Europe than in North America. For example, when Taylor *et al.* (1994) reviewed the effects of air pollutants on forests of North America they summarized numerous studies of biogeochemical and tree physiological responses of forest ecosystems to N deposition, but provided no data on the response of the herb layer. However, when Boxman *et al.* (1998) summarized vegetation and soil biota responses for the NITREX network, they presented no data on the effects of N manipulations on the herb community of European forests. A summary of results reviewed here is given in Table 1.

Table 1 A summary of studies examining the effects of excess N on the herbaceous layer of contrasting forest ecosystems

Ecosystem type	N treatment/deposition	Time	Response	Reference
Boreal forest, Sweden	50 kg N ha ⁻¹ year ⁻¹ /NH ₄ NO ₃	1 year	no change in biomass	Nordin <i>et al.</i> (1998)
Oak forests, Sweden	6–20 kg N ha ⁻¹ year ⁻¹ /gradient	NA	increases in nitrophilous, acid-tolerant species	Brunet <i>et al.</i> (1998)
Spruce/fir forest, Switzerland	30 kg N ha ⁻¹ year ⁻¹ /NH ₄ NO ₃	3 years	no significant response	Schleppi <i>et al.</i> (1999)
Scots pine plantation, Sweden	108 kg N ha ⁻¹ year ⁻¹ /NH ₄ NO ₃	9 years*	long-lived effects, significant decline in diversity	Strengbom <i>et al.</i> (2001)
Boreal forest, Sweden	< 3 to > 12 kg N ha ⁻¹ year ⁻¹ /gradient	NA	decline in occurrence/cover of ericaceous shrubs	Strengbom <i>et al.</i> (2003)
Hardwood forest, USA	35 kg N ha ⁻¹ year ⁻¹ /(NH ₄) ₂ SO ₄	2 years	no significant response	Gilliam <i>et al.</i> (1994)
Hardwood forest, USA	14 and 28 kg N ha ⁻¹ year ⁻¹ /(NH ₄) ₂ SO ₄	3 years	significant decline in cover	Hurd <i>et al.</i> (1998)
Red pine, USA	50 and 150 kg N ha ⁻¹ year ⁻¹ /(NH ₄)NO ₃	7 years	80% decline in density/90% decline in biomass	Rainey <i>et al.</i> (1999)
Hardwood forest, USA	35 kg N ha ⁻¹ year ⁻¹ /(NH ₄) ₂ SO ₄	6 years	no significant response	Gilliam <i>et al.</i> (2006)

*Time since termination of treatment, which was carried out as a tree growth fertilization experiment from 1971 to 1990.

Although some research on effects of N on the herb layer of European forests has employed experimental additions of N (Nordin *et al.* 2005), most published work has been based on sampling forest herb communities along gradients of atmospheric deposition of N or by utilizing forest fertilization, which was originally part of management practices to enhance tree growth, as surrogates for experimental treatments (e.g. Brunet *et al.* 1998; Strengbom *et al.* 2001, 2003). Furthermore, because excess N deposition in Europe is particularly pronounced as NH_4^+ and because nitrification of added NH_4^+ acidifies soil (Barber 1995), European studies often have emphasized the general effects of soil acidification on vegetation, in addition to the more specific effects of N (Falkengren-Grerup 1986, 1989; Økland *et al.* 2004).

Nordin *et al.* (1998) added N as ^{15}N double-labelled NH_4NO_3 to the herb layer of a boreal forest in northern Sweden at doses up to $50 \text{ kg N ha}^{-1} \text{ year}^{-1}$ and found no short-term response of biomass of species including *Vaccinium myrtillus*, *Deschampsia flexuosa* and bryophytes. They did find increases in concentrations of free amino acid N in plant tissue, suggesting a treatment-mediated increase in storage of N. The increase in storage of N has implications for effects of N on other facets of plant health and survival, such as susceptibility to herbivory and pathogenic fungal infection, that will be discussed later.

Brunet *et al.* (1998) employed multivariate methods to assess potential effects of N deposition on herb layer species of oak forests by sampling along a gradient of N deposition in southern Sweden. Species demonstrating increases in importance (cover) with increased N deposition were generally both nitrophilous and acid-tolerant. They concluded that N deposition influenced vegetation directly by increasing N availability and indirectly by increasing soil acidity.

Schleppi *et al.* (1999) treated experimental plots in Alptal, Switzerland, with NH_4NO_3 added at a rate of $30 \text{ kg N ha}^{-1} \text{ year}^{-1}$. Although the primary focus of that study was the response of the dominant tree species Norway spruce [*Picea abies* (L.) Karst] and silver fir (*Abies alba* Miller) to N additions, they also examined the herb layer and found no significant change in cover or composition following 3 years of treatment. They ascribed the lack of response to the complete dominance of the herb layer by perennial species, allowing N to be stored efficiently over indefinite periods in roots, stolons, bulbs and shoots (Schleppi *et al.* 1999).

Strengbom *et al.* (2001) used a creative approach to assess the response of herb layer species to increased N inputs by taking advantage of two separate forest fertilization experiments in northern Sweden. In one experiment, initiated in 1971, N had been added as NH_4NO_3 granules at varying rates up to $108 \text{ kg N ha}^{-1} \text{ year}^{-1}$, with that particular treatment having been terminated in 1990, 9 years prior to their study. The

authors carried out point-intercept measurements of herb layer plants in all treatment areas, thus allowing assessment of legacy effects of N deposition. Species composition, as measured via principal components analysis, was significantly different between control and treatment areas, and Simpson's diversity was significantly lower on treatment areas 9 years after cessation of N treatments in the first experiment. These responses arose to a great extent from sharp declines in ericaceous species, such as *V. myrtillus* and *V. vitis-idaea*, and increases in the nitrophilous grass, *D. flexuosa* (Fig. 2). The authors concluded that effects of increased N deposition on the herb layer of managed Swedish forests can be long-lived (Strengbom *et al.* 2001).

Strengbom *et al.* (2003) conducted a synoptic survey of presence or absence of these same species (*V. myrtillus*, *V. vitis-idaea* and *D. flexuosa*) within 557 boreal forest stands throughout Sweden. Using results of an N-deposition model (MATCH – Langner *et al.* 1995), they divided Sweden into five classes of N deposition from < 3 to $> 12 \text{ kg N ha}^{-1} \text{ year}^{-1}$. The ericaceous species *V. myrtillus* and *V. vitis-idaea*, both regarded as keystone species of the herb layer of forests throughout Sweden (Niemelä *et al.* 1982), declined along the gradient, even at the lower rates of N deposition. In contrast to increases from experimentally applied N reported in Strengbom *et al.* (2001), *D. flexuosa* exhibited no significant pattern in response to the deposition gradient. They concluded that, given the importance of the two species negatively affected by increases in N, N deposition has contributed to a restructuring of the herb layer of much of the boreal forest of Sweden (Strengbom *et al.* 2003). In a review of many of these studies throughout Sweden, Nordin *et al.* (2005) echoed these conclusions, adding that small but chronic increases can cause profound changes in composition and structure of herb layer communities.

Despite the statistical limitations inherent in gradient studies (e.g. lack of true controls), these studies have

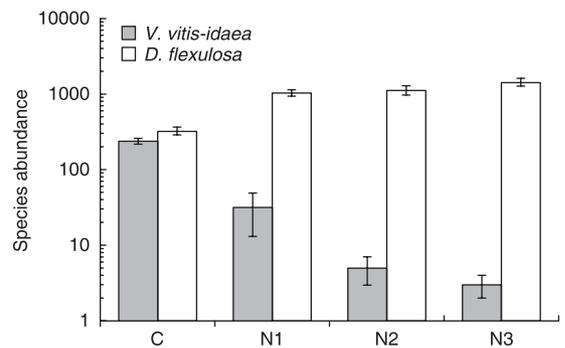


Fig. 2 Change in species abundance (measured as number of hits on a line transect) of dominant herbaceous layer species of Swedish boreal forests (*Vaccinium vitis-idaea* and *Deschampsia flexuosa*) in response to experimental nitrogen (N) additions 9 years following cessation of treatment, which were the following: N1 = $34 \text{ kg N ha}^{-1} \text{ year}^{-1}$, N2 = $62 \text{ kg N ha}^{-1} \text{ year}^{-1}$, N3 = $108 \text{ kg N ha}^{-1} \text{ year}^{-1}$. Figure drawn from data taken from Strengbom *et al.* (2001).

the advantage of reflecting the actual conditions of N deposition to which European forests are exposed. Although there is some understandable variation among forest types, vegetation scientists in Europe have clearly demonstrated that herb layer communities are sensitive to the range of anthropogenically elevated levels of N deposition. Furthermore, the gradient of N deposition is clearly related to spatial patterns of human populations across the European landscape.

North American research

Studies examining the response of the herbaceous layer to increases in N availability in North America generally have not employed the gradient analysis so common in Europe. Studies in North America more often use experimental additions of various forms of available N [e.g. NH_4NO_3 , $(\text{NH}_4)_2\text{SO}_4$, HNO_3]. In addition to determining effects of N on species composition and diversity of the herb layer, these studies also include effects on nutrient uptake (e.g. N and cations).

Beginning in 1989, N has been added to an entire watershed at FEF, West Virginia. Treatments are administered via three aerial applications (via helicopter) of $(\text{NH}_4)_2\text{SO}_4$ per year. March and November applications are made at approximately 7 kg N ha^{-1} , and July applications are approximately 21 kg N ha^{-1} , for a total of $35 \text{ kg N ha}^{-1} \text{ year}^{-1}$. Gilliam *et al.* (1994) reported results for the first year of this study, concluding that there was no response of the herbaceous layer following 3 years of treatment, including total herb cover and biomass, species richness and species diversity. In addition, there were no significant changes in tissue concentrations of plant nutrients for the herb layer as a whole (i.e. pooled across all species). However, working on a subset of sample plots used by Gilliam *et al.* (1994) and focusing on a single species – *Viola rotundifolia* – that occurred on all plots of the subset, Gilliam *et al.* (1996) found significantly higher foliar N in *V. rotundifolia* from the treatment watershed than in untreated control watersheds, accompanied by lower foliar Ca^{2+} and Mg^{2+} , in response to 4 years of treatment. They suggested that the N additions to the treatment watershed had simultaneously increased N availability and decreased nutrient cation availability to herb layer species (Gilliam *et al.* 1996).

Hurd *et al.* (1998) added N in two forms at varying rates at three sites in the Adirondack Mountains (Adirondack Park, New York). N was added biweekly as dissolved HNO_3 spray at the rate of $14 \text{ kg N ha}^{-1} \text{ year}^{-1}$ ($2\times$ ambient), whereas N was added as single applications in May of crystalline $(\text{NH}_4)_2\text{SO}_4$ at 14 and $28 \text{ kg N ha}^{-1} \text{ year}^{-1}$ ($2\times$ and $4\times$ ambient). They found that cover of prominent herbaceous species, *Oxalis acetosella*, *Maianthemum canadense* and *Huperzia lucidula*, in hardwood forests declined significantly after only 3 years of treatment, particularly in response to additions of $(\text{NH}_4)_2\text{SO}_4$. This decline appeared to have resulted from increased shading by the ferns, such as *Dryopteris intermedia* and *Dennstaedtia punctilobula*, which can

reduce light levels to the forest floor at peak growing season by as much as 70% (George & Bazzaz 2003). The observed response to N additions was more pronounced at sites experiencing lower inputs of atmospheric N.

Rainey *et al.* (1999) added N as NH_4NO_3 at rates of 50 and $150 \text{ kg N ha}^{-1} \text{ year}^{-1}$ to the forest floor of red pine stands of the Harvard Forest of western Massachusetts. Treatments began in 1988 with fertilizations applied as NH_4NO_3 solutions in six equal monthly applications. In 1991 and 1992 ^{15}N -labelled NH_4NO_3 was used in a tracer study on the low N ($50 \text{ kg N ha}^{-1} \text{ year}^{-1}$) treatment (Nadelhoffer *et al.* 1999). Recoveries of labelled N were low in more prominent herb layer species, namely *M. canadense* and *Trillium borealis*. However, N concentrations in these species were significantly higher in treatment vs. control plots, whereas cation concentrations were generally lower in treatment plots. This supported the earlier findings of Gilliam *et al.* (1996) at FEF that increased nitrification in forest soils under N-saturated conditions can decrease availability of nutrient cations, especially Mg^{2+} and Ca^{2+} . Following 7 years of N additions at Harvard Forest, density and biomass of herb layer species had declined by 80% and $\sim 90\%$, respectively. This was especially pronounced for the dominant species, *M. canadense*, which decreased in density from 216 in control plots to 44 and 14 stems m^{-2} in low N and high N treatments, respectively. Similarly, biomass of *M. canadense* decreased from 9 g m^{-2} in control plots to $1.5\text{--}0.5 \text{ g m}^{-2}$, respectively (Rainey *et al.* 1999).

Thus, both Hurd *et al.* (1998) and Rainey *et al.* (1999) found rapid responses (i.e. as short as 3 years following N treatments) of species of the herbaceous layer to experimental additions of N in hardwood forests of the eastern USA. In sharp contrast, Gilliam *et al.* (2006) concluded that 6 years of aerial applications of N to a central Appalachian hardwood-dominated watershed at FEF had no significant effects on the herb layer. This latter study essentially extended by an additional 3 years the sample period initially reported in Gilliam *et al.* (1994). They examined herb cover, composition and several diversity indicators, including the Shannon–Wiener index, species richness and species evenness, none of which was significantly different between treatment and control watersheds for any of the years sampled, 1991, 1992 and 1994. Consistent with the conclusion of Hurd *et al.* (1998) that sensitivity of the herb layer to N additions was largely a function of ambient N deposition, Gilliam *et al.* (2006) interpreted the lack of observed response as arising from the extremely high levels of N deposition at FEF – as much as $20 \text{ kg N ha}^{-1} \text{ year}^{-1}$ for total (wet plus dry) deposition (Gilliam & Adams 1996) – and that watershed soils were N-saturated prior to initiation of N treatments. Interestingly, meta-analysis of decomposition studies similarly revealed differing effects of N deposition on litter decomposition in relationship to ambient N. That is, experimental additions of N were found to stimulate

decomposition at field sites with low ambient N deposition (< 5 kg N ha⁻¹ year⁻¹), but inhibit decomposition at sites with high ambient N deposition (Knorr *et al.* 2005).

Specific effects of N on herb layer species – mechanisms of response

As suggested by these studies, the general patterns of response of the forest herbaceous layer to increasing N often, though not always, include the following: (i) initial increases in cover of the herb layer as a whole; (ii) decreases in species richness from loss of relatively numerous N-efficient species; (iii) decreases in species evenness from increasing dominance of relatively few high N-requiring species and (iv) declines in forest biodiversity as a result of decreases in both richness and evenness. In addition, these studies suggest that the response time of herb layer species to increases in N availability is inversely related to ambient N deposition. Thus, a rapid response should occur in areas receiving low levels of atmospheric deposition of N, such as that found for Hurd *et al.* (1998), whereas a more delayed response would be expected in areas receiving high N deposition, such as that found by Gilliam *et al.* (2006). Finally, explicit (and implicit) in many, if not most, of these studies is that increasing N supply enhances NO₃⁻ production and mobility, decreasing availability of essential soil cations.

Although some plants display predictable responses to N additions (Pennings *et al.* 2005), the response of plant species of the herbaceous layer of forest ecosystems to excess N availability can arise from several mechanisms. Suding *et al.* (2005) used a meta-analysis of the responses of over 900 plant species in 34 N-fertilization experiments carried out in herb-dominated ecosystems throughout the USA to examine mechanisms to explain losses in species diversity from N fertilization. They distinguished between functional-based and abundance-based mechanisms, where functional-based mechanisms operate at the level of plant functional groups (e.g. life history, photosynthetic pathway) and abundance-based mechanisms operate on an individual species' abundance (i.e. from rare to common), independent of functional type, wherein locally rare species may be more susceptible to local extinction from N treatment.

Here I take a different approach, and have identified six processes that have been shown both to respond to varying levels of N availability and to influence composition and diversity of forest herb communities. These are interspecific competition, herbivory, mycorrhizal infection, pathogenic fungal infection, species invasions and exotic earthworm activity. It is important to note that these are not mutually exclusive and that some may indeed interact synergistically to explain herb layer response to increasing N availability. For example, increasing N may increase foliar N concentrations, enhancing herbivory, which in turn may increase the likelihood of infection by pathogenic fungi. Furthermore, others may, in some specific instances, be

inseparable in their response to increasing N, i.e. changes in one of these processes may result from the response of another one. For example, increasing N may alter the outcome of interspecific competition indirectly because of its more direct effect on mycorrhizal infection. Nonetheless, I address these individually to assess their potential importance in determining the response of the forest herb layer to increasing N availability. The last mechanism – earthworm activity – is not a phenomenon that directly responds to N deposition. I include it here, however, because (i) there is often a close spatial correlation of N deposition and earthworm activity linked by high human population densities (e.g. north-eastern USA) and (ii) recent studies have demonstrated a profound influence of exotic earthworms on the herb layer of forests via alteration of soil properties. The general responses of these processes to excess N, as well as the relevance of those responses to the herb layer, are summarized in Fig. 3.

INTERSPECIFIC COMPETITION

There is little consensus as to mechanisms explaining outcomes of interspecific competition (Aerts 1999). However, regardless of the actual mechanisms involved, most of the results of N additions to herb-dominated plant communities, such as those begun in Rothamsted in 1856 and that depicted in Fig. 1, have been suggested to arise from N-mediated changes in success of dominant species. For example, Wedin & Tilman (1993) found that *Schizachyrium scoparium* (an N-efficient species) out-competed *Poa pratensis* and *Agropyron scabra* (high N-requiring species) under conditions without added N, and did so in large part by taking up inorganic N in a way that decreased its availability to the high-N species. This supported what they called R*, the resource reduction model for competition (Wedin & Tilman 1993).

The dynamics of the herbaceous layer of forest ecosystems sharply contrast with those of herb-dominated systems in ways that are relevant to understanding the nature of interspecific competition and its response to increasing N availability. Although nutrients are certainly important for herb layer species, light is generally the primary limiting factor for understorey species of closed-canopied forests (Coomes & Grubb 2000; Neufeld & Young 2003). Furthermore, light directly reaching the forest understorey does so in discrete patches called 'sunflecks'. Such a light environment was described by Gilliam & Roberts (2003c) as a 'dynamic mosaic', to emphasize the variation in size and distribution of sunflecks at temporal scales from diurnal to seasonal and even successional (Brown & Parker 1994). Availability of nutrients such as N can display a great deal of patchiness in which plant roots not only compete interspecifically but also with soil microbes (Hodge *et al.* 2000). Although the degree of temporal variability of nutrients is generally much less than that of light, the typically high spatial heterogeneity of soil resources

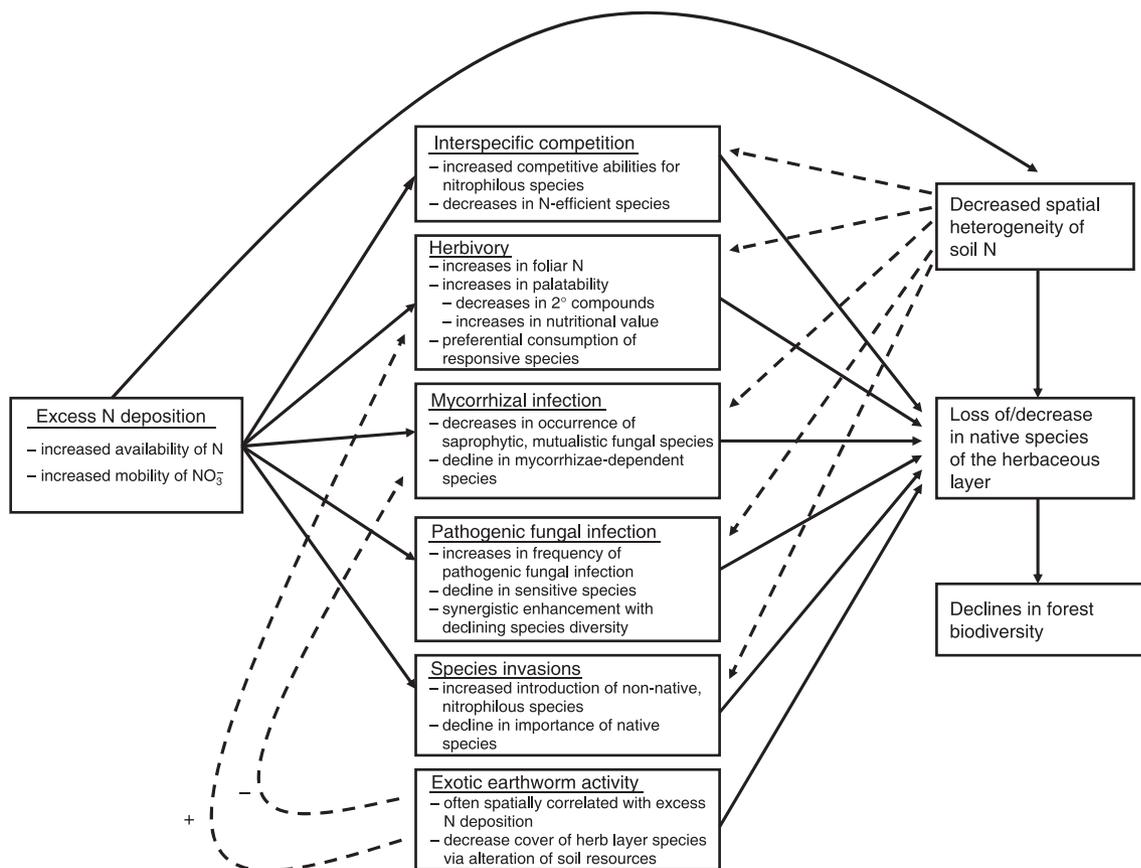


Fig. 3 Conceptual model of the direct effects of excess N on the herbaceous layer and soil N in forest ecosystems.

contributes measurably to species diversity of the herb layer (Beatty 2003).

It is important to note that the herbaceous layer in the broadest sense includes both herbaceous and woody species, which Gilliam & Roberts (2003b) referred to as 'resident' species (e.g. annual, biennial and perennial herbs that generally remain ≤ 1 m in height) and 'transient' species (e.g. seedlings and saplings of trees that have the ability to exceed this height), respectively, to highlight differences among species in time spent in this lowest vegetation stratum of forest communities. Tree seedlings, in particular, exhibit a wide range of tolerance among species to the spatially and temporally dynamic light environment of the forest floor (Kobe *et al.* 1995). Thus, the success of transient species to emerge from the herb stratum depends to a large extent on competitive interactions with resident species.

Both light and N have been shown to limit herb layer species synergistically. Based on an extensive review, Coomes & Grubb (2000) concluded that light alone limits plant growth under high moisture/nutrient conditions. In support of this observation, Anderson (2003) showed that N uptake by a variety of herb species increased with N supply, but did so to a greater degree in unshaded vs. shaded conditions. The initial response of the herbaceous layer to increases in deposition of N, then, would be to lessen limitation by N and increase limitation by light. Eventually, however, further excess N would have a direct effect on competitive

abilities of herb layer species. The resource reduction model for competition (Wedin & Tilman 1993) predicts that plants gain competitive superiority by utilizing essential resources in such a way that decreases availability of those resources to other plants. Thus, chronic inputs of high N to a forest would give a competitive disadvantage to N-efficient plants (e.g. *Schizachyrium scoparium* – Fig. 1) because they are unable to draw down available soil N that is constantly re-supplied via atmospheric deposition.

Admittedly, the high light and low N conditions at such herb-dominated communities (e.g. Cedar Creek Natural History Area) are in sharp contrast to conditions typical of a forest understory (Gilliam & Roberts 2003c). However, Price & Morgan (2006) demonstrated similar results for a herb-rich forest in Australia. They concluded that increased soil N (along with phosphorus and potassium as N–P–K fertilizer) increased competitive exclusion of species adapted to low N availability, resulting in declines in species initially dominant prior to treatment.

HERBIVORY

Consumption of plant material, whether by vertebrate or invertebrate herbivores, is one of several disturbances that can have a profound impact on the herbaceous layer of forests (Roberts & Gilliam 2003; Roberts 2004). Furthermore, herbivory has been shown to interact with

nutrient availability to regulate species composition of the herb layer in some forest ecosystems (John & Turkington 1995). The degree to which herbivores consume plant material for their energy and nutritional demands is a function of several factors, the more important of which involve the nutritional value and palatability of plant tissue. Bison, for example, selectively graze in burned tallgrass prairie, even though unburned areas are of equal access, largely because leaves of dominant prairie grasses are higher in N and lower in unpalatable compounds in burned compared with unburned prairie (Knapp *et al.* 1999).

Turkington *et al.* (2002) summarized results of a 10-year study on effects of N fertilization on herbivory in herb communities of boreal forests Canada. Their primary impetus was to test hypotheses of 'bottom-up control' of vegetation composition, wherein resource (e.g. N) availability is the primary determinant, vs. 'top-down control', wherein herbivores themselves are predominant. They concluded that soil resources, especially N availability, were more important in determining herb community composition, and that herbivore activity was more of a response variable, rather than an additional driver, in these forests.

Herb layer species in forests receiving chronically elevated N deposition will undergo luxury uptake of N (Muller 2003), increasing foliar N concentrations and creating the potential to alter herbivore activity. Hartley & Mitchell (2005) found that additions of N increased grazing consumption of species adapted to low-N soils and did so in a way that shifted herb community composition. Anderson (2003) found that most herb layer plants receiving experimental N additions were more susceptible to vertebrate herbivory than those in control plots, but that this was not consistent for all species, suggesting a species-specific response.

Throop & Lerdau (2004) provided perhaps the most extensive review of work on the effects of N deposition on insect herbivory. They concluded that, despite finding an expected degree of variability among studies, the most probable mechanisms to explain such effects were related to deposition-mediated changes in quality and availability of forage plant tissue, especially those related to tissue chemistry, including increases in amino acid (e.g. glutamine and arginine) content and simultaneous decreases in carbon (C)-based defensive secondary compounds (e.g. condensed tannins and phenolics). Using the CENTURY model (Parton *et al.* 1988), Throop *et al.* (2004) demonstrated that the response of herbivory to increased N can have major impacts on ecosystem-level processes, such as C cycling. Nordin *et al.* (1998) demonstrated similar results for low-growing ericaceous shrubs in Sweden, wherein Lepidoptera larvae were found to increase their consumption of foliar material with greater application rates of N.

May & Killingbeck (1992) demonstrated that simulated defoliation measurably decreases plant fitness and concluded that this occurs primarily because

herbivory decreases the host plant's ability to reclaim essential nutrients (i.e. nutrient resorption), thus interfering with nutrient dynamics within the plant. Wise & Abrahamson (2005) further showed that herbivory-mediated reductions in plant fitness were more sensitive under conditions of high N availability. This suggests that herb layer species in forests receiving high levels of N deposition may suffer simultaneous reductions in biomass and fitness as a result of N-induced increases in herbivory. Ultimately, N-mediated increases in herbivory should lead to pronounced shifts in species dominance of the herb layer via preferential consumption by herbivores of those plants that demonstrate greatest sensitivity to increased N availability.

Although less investigated than what has been presented here, two other facets of herbivory merit mention in the context of excess N-mediated responses: below-ground herbivory and higher trophic levels. Stevens & Jones (2006) demonstrated that, although fine roots (< 1.0 mm diameter) responded sensitively to fertilizer treatments, root herbivore activity also responded to such treatments, suggesting that excess N not only stimulates above-ground, but also below-ground, herbivory. Focusing on C:N stoichiometry in plant and animal tissues (i.e. $C:N_{\text{plants}} \gg C:N_{\text{herbivores}} > C:N_{\text{predators}}$), Denno & Fagan (2003) provided evidence that N limitation may promote omnivory among carnivorous arthropods. This suggests that excess N could have impacts on higher trophic levels of forest ecosystems.

MYCORRHIZAE

Mycorrhizal associations compose a well-known mutualistic relationship between vascular plant root and fungal symbionts, and are quite common among species of the herbaceous layer of forests (Whigham 2004). Among the considerable benefits conferred to the plant by the fungus, including increased access to nutrients, protection against pathogens and enhanced water-use efficiency (Smith & Read 1997), mycorrhizal plants are particularly superior competitors compared with non-mycorrhizal plants in nutrient-limited soils, largely because of their fungal-enhanced abilities to take up nutrients, such as N (Read & Perez-Moreno 2003).

One particular type of endomycorrhizae – ericoid mycorrhizae – is associated with ericaceous plants, which are especially well adapted to characteristics of many older forest soils – highly acidic, weathered and infertile (Read 1996; Perotto *et al.* 2002). Ericoid mycorrhizae also allow host plants to take up amino acids and complex nitrogenous organic compounds (Grelet *et al.* 2005). These fungal symbionts, however, exhibit notable sensitivity to increases in N deposition. Yesmin *et al.* (1996) found that ericoid mycorrhizal infection declined significantly along an N deposition gradient, from $84.5 \pm 3.1\%$ at $2 \text{ kg N ha}^{-1} \text{ year}^{-1}$ to $14.5 \pm 2.6\%$ at $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$.

Wallenda & Kottke (1998) reviewed the literature on field experiments investigating the effects of added N

on ectomycorrhizae and found that there was little effect of N on below-ground populations. They did, however, find measurable shifts in above-ground (i.e. sporocarp) communities, as did Lilleskov *et al.* (2002), generally concluding that increased N decreases ectomycorrhizal diversity. Similarly, using a combination of N deposition gradient and glasshouse studies, Dighton *et al.* (2004) found that ectomycorrhizae declined significantly with increased N in soils from New Jersey pine barren forests. Other studies have found less notable effects of increasing N on ectomycorrhizae (Lilleskov & Bruns 2001).

Synthesizing the extensive results of the NITREX network in Europe, Brandrud & Timmermann (1998) envisaged the response of mycorrhizae to N enrichment as occurring in three phases. In Phase 1 there is a rapid decrease in above-ground diversity and sporocarp production by mycorrhizal fungi; below-ground mycorrhizae and fine-roots of host species are usually not affected. By Phase 2, generally sensitive fungi disappear, with below-ground structures variably affected. Finally, Phase 3 occurs with an essentially complete disappearance of sporocarp production, along with sharp declines in density of below-ground mycorrhizae and fine-roots of host species.

Although it lies largely beyond the scope of this review, Read & Perez-Moreno (2003) developed an ecosystem gradient model relating changes in mycorrhizal communities to changes in N form and availability in terrestrial ecosystems that is relevant to this discussion. They envisaged a gradient from (1) soils with little N mineralization and no nitrification dominated by organic N cycling and plants commonly supporting ericoid and ectomycorrhizal fungi with well-developed saprotrophic capabilities, to (2) soils with limited N mineralization dominated by a more diverse assemblage of plants supporting ericoid, ecto- and arbuscular mycorrhizae, to (3) soils with high nitrification potential and dominated by NO_3^- availability and plants supporting arbuscular mycorrhizae with limited or no saprotrophic capabilities (Read & Perez-Moreno 2003). This gradient is consistent with findings of Eaton & Ayres (2002), who demonstrated that early-successional mycorrhizae were characterized by having low N mineralization efficiency, whereas late-successional fungal species exhibited high mineralization efficiency. Forests experiencing N saturation from excess N deposition can quickly change from (2) to (3), with one of the immediate impacts being a pronounced shift in species composition of the herbaceous layer. Superimposed on this scenario for forests of eastern North America is the paucity of old-growth forests (McCarthy 2003). Thus, forest of extremely late-successional stages, as envisaged by Eaton & Ayres (2002), are relatively rare in this region.

DISEASE

Most work carried out on the effects of excess N on the frequency and occurrence of plant diseases, primarily

pathogenic fungal infections, has been carried out in Swedish forests (Nordin *et al.* 1998, 2006; Strengbom *et al.* 2001, 2002, 2003, 2006). The herbaceous layer of these forests is generally dominated by low-growing ericaceous species of the genus *Vaccinium*. As previously discussed, these species are known to decline with increasing N loading as the result of the elimination of their fungal symbionts – ericoid mycorrhizae (Read & Perez-Moreno 2003). However, they also are impacted by excess N through significant and substantial increases in the rate of fungal infections. Strengbom *et al.* (2003) found this response by sampling Swedish forests along a gradient of N deposition. Similar patterns were found using experimental additions of N (Nordin *et al.* 1998; Strengbom *et al.* 2006). Indeed, Strengbom *et al.* (2002) found that increases in N-enhanced pathogenic fungal infections can be rapid and can further result in major shifts in herb layer species dominance within 3 years of treatment.

N-mediated changes in pathogenic fungal infections have also been shown to covary with other factors, both abiotic and biotic. Strengbom *et al.* (2006) found that individuals of host plant *Vaccinium myrtillus* were proportionally more susceptible to the parasitic fungus *Valdensia heterodoxa* when exposed to 12.5 and 50 kg N ha⁻¹ year⁻¹ added as granular NH_4NO_3 compared with untreated control plots. They also found that the incidence of disease was significantly and positively correlated with precipitation, with the higher summer precipitation enhancing the effects of added N. Nordin *et al.* (2006) demonstrated the contrast between vascular plant response vs. pathogenic response to added N in boreal forests. Plant species discriminated between the form of added N: N-efficient species exhibited no response, high-N-requiring species responded mostly to NO_3^- and bryophytes responded to NH_4^+ . By contrast, occurrence of pathogenic fungi increased in response to all additions of N, regardless of the form in which it was added.

Mitchell *et al.* (2003) considered the additional interactions of elevated CO_2 and decreased plant species diversity with the effects of excess N on pathogenic fungal infection of several herbaceous species. They developed a metric called ‘pathogen load’, which they defined as the relative (%) leaf area infected by fungi, to quantify these responses. They found that all three variables (elevated CO_2 , decreased diversity and increased N) increased pathogen load on several herb species, in some cases interactively. The response to N was particularly pronounced for N-efficient species, such as C4 grasses. The most profound response of pathogen load was not to N, but to diversity. Plots with one or four species had greater than twice the pathogen load as plots with nine or 16 species. This finding has important relevance to long-term, though indirect, effects of N on herb layer communities. That is, N-mediated declines in herb diversity may make forest herb communities more susceptible to pathogenic fungi.

Invasion of non-native species in undisturbed forests with closed, intact canopies is generally rare (Luken 2003). Recent work, however, has shown that species invasions can be facilitated by increasing N supply. Although most work has been done in non-forest ecosystems such as grasslands, shrublands and deserts (Padgett & Allen 1999; Brooks 2003; Fenn *et al.* 2003), recent studies suggest that N limits the invasibility of the herbaceous layer of both conifer and hardwood forests (Cassidy *et al.* 2004). Thus, N-saturated forests would be particularly susceptible to introduction of exotic species.

Much of the observed, excess N-mediated increase in invasibility of forest herb layer communities appears to be related to one of the hallmark symptoms of N saturation: increases in net nitrification, resulting in increased availability and mobility of NO_3^- in impacted soils. Fargione & Tilman (2005) found that increases in biomass of invasive species were significantly related to increasing soil NO_3^- . They further concluded that soil NO_3^- was the best predictor of success for species that invaded experimental monocultures.

Windham (2002) presented a compelling mechanism to explain this response. Because much of the N deposited from the atmosphere occurs as NO_3^- , she undertook a comparative study to examine variation in the ability of native vs. exotic species to utilize NO_3^- , measured as levels of nitrate reductase activity (NRA) in leaves and roots (Muller & Janiesch 1993), across a gradient in NO_3^- deposition across North America and in southern Chile. Results demonstrated notably higher use of NO_3^- by exotic species, as evidenced in ranges of potential NRA: 0–186 $\text{nmol NO}_2^- \text{g}^{-1} \text{h}^{-1}$ for native species and 145–1291 $\text{nmol NO}_2^- \text{g}^{-1} \text{h}^{-1}$ for exotic species. These results were consistent with earlier work by Kourtev *et al.* (1999), who found that NRA was generally higher in the invasive species *Berberis thunbergii* and *Microstegium vimineum* than in native species at adjacent sites in hardwood forests of northern New Jersey. Windham (2002) suggested that NO_3^- deposition creates a 'low light/high nitrate' niche in forests that favours exotic herb layer species which are better adapted to produce NRA more quickly than native species. Accordingly, invasive exotic species are generally better able to take advantage of higher soil NO_3^- , and do so at the expense of native species.

Furthermore, it is quite likely that positive feedbacks can develop to further exacerbate increases in invasions of forest herbaceous layers by exotic species that are caused by excess soil NO_3^- . Ehrenfeld *et al.* (2001) examined invasion of the herb layer of hardwood stands of northern New Jersey by the two exotic species studied by Kourtev *et al.* (1999): *B. thunbergii* and *M. vimineum*. They found that soil in which these species grew had higher pH and net N mineralization and nitrification than soil occupied by native species, results which were found both in the field and under the

more controlled conditions of the glasshouse. Higher pH in impacted soil was probably the result of preferential uptake of NO_3^- by the exotic species (Marschner 1995; Ehrenfeld *et al.* 2001). In a review of studies of this phenomenon that included 56 invasive species, Ehrenfeld (2003) concluded that most invasives had the ability to alter the N cycle of forest soils drastically, particularly by increasing N availability, altering rates of N fixation, and producing litter of lower C : N ratios that decomposes more rapidly than that of co-occurring native species. Thus, a dangerous feedback can develop when (i) excess N deposition increases N availability in forest soils that (ii) enhances the success of exotic species invading the herbaceous layer that (iii) further alter N dynamics of forest soil by maintaining high levels of available NO_3^- that (iv) simultaneously gives a competitive advantage to invasive species themselves and (v) a disadvantage to native species. The result is a further drastic shift in species composition and decrease in biodiversity of the herb layer.

EARTHWORM ACTIVITY

There is no apparent causal relationship between excess N deposition and introduction and activity of exotic earthworm species. Even so, Kourtev *et al.* (1999) found that introduced (European) earthworm populations were significantly and substantially higher in soil that supported invasive species. Thus, enhanced activity of exotic earthworms can add to the positive feedback mechanism just described. In addition, exotic earthworms have been shown to decrease colonization rates of mycorrhizae in forests of north-east USA (Lawrence *et al.* 2003). Activity of exotic earthworms also is often spatially correlated with excess N because both often arise from human activity (Gundale *et al.* 2005), especially in areas of high densities of human populations.

Considering the effect that earthworm activity can have on herbaceous communities (Bohlen *et al.* 2004), such a spatial coincidence can confound the direct effects of excess N with those of earthworms. Bohlen *et al.* (2004) provided stunning photographic evidence of the effects of exotic earthworms in forests of northern Minnesota. Among the apparent effects were: general lack of herb layer cover, areas of exposed mineral soil from a greatly reduced litter layer, and exposed roots of canopy trees from disappearance of forest floor. Gundale (2002) surveyed 28 populations of the rare fern *Botrychium mormo* and found that local extirpation of this species was directly associated with the introduced earthworm *Lumbricus rubellus*.

Much of the change in the herbaceous layer caused by exotic earthworms results from worm-mediated alterations in soil nutrient dynamics. Gundale (2002) found thinner O horizons in soils occupied by *L. rubellus* and suggested that the associated decline in *B. mormo* was related to the dependence of *B. mormo* on nutrients in the O horizon. Hale *et al.* (2005) examined soil characteristics of northern hardwood forests of

Minnesota that had been invaded by European earthworms. Because glaciated soils such as those they studied lack native earthworm populations, they were able to assess effects directly by comparing invaded vs. non-invaded sites. They found that earthworm activity rapidly decreased the O horizon, but increased thickness, bulk density and total organic matter content of the A horizon; percentage organic matter and fine-root density of the A horizon decreased (Hale *et al.* 2005).

In addition to these indirect effects of exotic earthworms on herb communities via alteration in soil conditions, other effects can be more direct. For example, herbaceous layer species can experience direct mortality when earthworms consume forest floor from beneath them (James & Cunningham 1989). Herb layer species may also suffer reduced reproduction and survival from earthworm activity via consumption and deep burial of seeds, alteration of germination microclimate, and increased susceptibility to vertebrate herbivory (Bohlen *et al.* 2004).

Clearly, excess N deposition does not directly increase the introduction and activity of non-native earthworm species in forest ecosystems, and vice versa. However, these two anthropogenic disturbances display a high enough degree of spatial coincidence, and indeed their effects are often quite similar enough, that their impacts on the herbaceous layer must be considered in many instances to occur in tandem.

The nitrogen homogeneity hypothesis: a general hypothesis of herb response to excess N in forest ecosystems

This final section will be used to develop a general hypothesis of the negative effects of excess N on forests, one which has particular relevance to the herbaceous layer. Biodiversity can be seen as more than just the number of different species occurring in an area. It also has a functional process component (Roberts & Gilliam 1995). Thus, spatial heterogeneity in processes such as nutrient cycling contributes to the overall biodiversity of an ecosystem. This hypothesis will make a connection between excess N-mediated decreases in spatial heterogeneity of soil N processing and decreases in species diversity of impacted forests.

Spatial heterogeneity in essential resources contributes to maintenance of plant species diversity, although the degree to which this operates is still open to considerable debate (see Stevens & Carson 2002 for a recent discussion). Hutchings *et al.* (2003) argued that the spatial extent of patches (e.g. of high vs. low N) relative to the spatial extent of root systems of plants in the patches determines how sensitive this relationship is. They concluded that spatial heterogeneity of soil resources, such as N, plays an important role in influencing structure and composition of plant communities.

Intuitively, however, it is clear that increasing heterogeneity (i.e. patchiness) in availability of an essential

nutrient, such as N, in forest soils would give rise to coexistence of greater numbers of species through minimizing or even obviating competitive exclusion. This is especially valid for herb layer communities, wherein the spatial distribution of species is influenced greatly by spatial heterogeneity of soil nutrient availability (Beatty 2003; Small & McCarthy 2003; Whigham 2004).

Spatial heterogeneity of N processing (e.g. N mineralization, nitrification) is typically high in forest soils (Laverman *et al.* 2002), the result of several factors, including effects of spatial variability in chemistry of tree litter (Aubert *et al.* 2005). However, watershed-scale research at the FEF has shown that one of the effects of excess N inputs on terrestrial ecosystems is to decrease the high ambient degree of spatial heterogeneity in soil N dynamics, including both soil and plant processing of N (Gilliam *et al.* 2001, 2005). Although not statistically significant, net nitrification was higher on a watershed (WS3) treated with 35 kg N ha⁻¹ year⁻¹ than two untreated control watersheds (Fig. 4). More important, however, spatial variability in net nitrification (measured as coefficient of variation of means based on seven sample plots within each watershed) was approximately four times higher in the control watersheds than in the treated watershed. Similarly, the available pool of NO₃⁻ in soils was generally higher in WS3 than in the control watersheds, whereas spatial variability was 3–4 times higher in control watersheds than in WS3 (Fig. 4). Gilliam *et al.* (2001) reported similar contrasts for spatial variability in foliar N concentrations of herb layer species, litter N and soil N, all of which

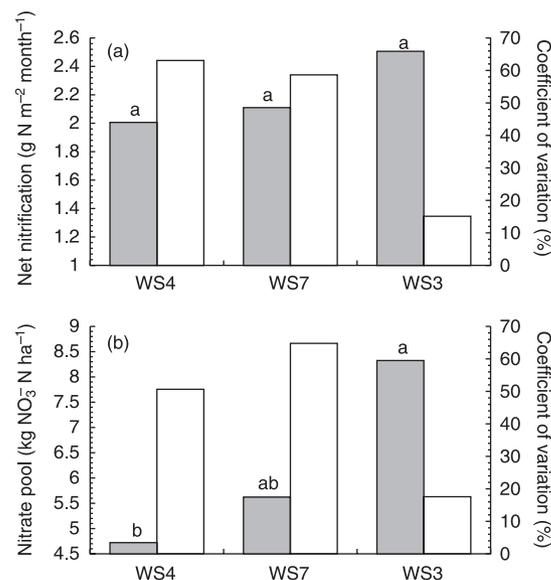


Fig. 4 Spatial variation in N-treated (WS3) vs. untreated (WS4 and WS7) watersheds at the Fernow Experimental Forest, West Virginia. (a) Shaded bars represent mean net nitrification; means with the same letter are not significantly different at $P < 0.05$. Open bars are coefficients of variation associated with each mean. (b) Shaded bars represent mean soil NO₃⁻ pools; means with the same letter are not significantly different at $P < 0.05$. Open bars are coefficients of variation associated with each mean.

exhibited greater spatial heterogeneity on the untreated control watersheds.

From both a biogeochemical and a plant standpoint, one of the more serious results of N saturation in forest ecosystems is the profound shift in the nature of N cycling from one predominated by processing of organic N to one dominated by the mobility of NO_3^- . Biogeochemically this is important because of the highly mobile, anionic nature of this inorganic form of N. Thus, when NO_3^- is produced in excess of plant and microbial demand, it moves easily through the mineral soil, leaching essential cations, such as Ca^{2+} , with it, decreasing their availability to forest plants. With respect to plant response, this increase in soil NO_3^- availability is important for several reasons. Many of the specific responses of the herbaceous layer to excess N previously discussed – and summarized in Fig. 3 – arise directly from increased NO_3^- availability and uptake by plants, including: (i) increasing competitive abilities for a small number of nitrophilous species, (ii) increases in herbivory, (iii) decreases in mutualistic fungi, (iv) increases in pathogenic fungi and (v) enhanced invasibility by exotic species that are highly competitive under conditions of high soil NO_3^- . All of these, alone and in combination, have the potential to cause net reductions in species richness of the herb layer and, ultimately, in the biodiversity of impacted forests.

I suggest that, in addition to these well-documented responses, an additional response be added: that of reducing the naturally high degree of spatial heterogeneity in soil N availability. In other words, not only does N saturation shift the N cycle toward NO_3^- mobility, but it also results in more homogeneous availability of N in the soil. When increased spatial homogeneity in soil N availability is coupled with responses summarized herein (Fig. 3), excess N can be seen to be especially effective in decreasing the species diversity of the herb layer.

Such a response will certainly vary among ecosystem types, with some being more, and other less, sensitive to change. However, given the ubiquitous importance of N in controlling the structure and function of forest ecosystems (Vitousek & Howarth 1991) and the increasingly ubiquitous nature of anthropogenically enhanced N deposition (Galloway *et al.* 2004), all forests are potentially susceptible to the negative impacts of excess N. The nitrogen homogeneity hypothesis predicts that N saturation ultimately will decrease forest biodiversity (Fig. 3).

It should be clear from this review that whereas much is known about the biogeochemical responses of forests to excess N deposition (Fenn *et al.* 1998; Aber *et al.* 2003) and about the ecology of the herbaceous layer (Gilliam & Roberts 2003a; Whigham 2004), far less is known about the dynamics of herb layer communities in N-saturated forests. Certainly, this represents an area in need of further research. For example, among the processes affected by excess N discussed herein, mechanisms for N-mediated invasion

of non-native species appear among the least understood, yet species invasions represent one of the more serious threats to forest biodiversity. Thus, future research on the ecology of the herbaceous layer in impacted forests will be at once interesting and essential.

Acknowledgements

I would like to thank the following individuals for their invaluable contributions in improving the quality of this paper: Mary Arthur, Jeffrey May, Nicole Turrill Welch, Dennis Whigham and Lisa Windham. I also thank David Gibson, Editor, *Journal of Ecology*, for his initial invitation to write this review and Robert Jones, Associate Editor (and two anonymous referees) for making excellent suggestions that greatly improved the quality of this paper.

References

- Aber, J.D., Goodale, C.L., Ollinger, S.V., Smith, M., Magill, A.H., Martin, M.E., Hallett, R.A. & Stoddard, J.L. (2003) Is nitrogen deposition altering the nitrogen status of northeastern forests? *Bioscience*, **53**, 375–389.
- Aber, J.D., Nadelhoffer, K.J., Steudler, P. & Melillo, J.M. (1989) Nitrogen saturation in northern forest ecosystems. *Bioscience*, **39**, 378–386.
- Aerts, R. (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant–soil feedbacks. *Journal of Experimental Botany*, **50**, 29–37.
- Ågren, G.I. & Bosatta, E. (1988) Nitrogen saturation of terrestrial ecosystems. *Environmental Pollution*, **54**, 185–197.
- Anderson, W.B. (2003) Interactions of nutrient effects with other biotic factors in the herbaceous layer. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 91–101. Oxford University Press, New York.
- Asman, W.A.H., Sutton, M.A. & Schrjöring, J.K. (1998) Ammonia: emission, atmospheric transport and deposition. *New Phytologist*, **139**, 27–48.
- Aubert, M., Bureau, F. & Vincelas-Akpa, M. (2005) Sources of spatial and temporal variability of inorganic nitrogen in pure and mixed deciduous temperate forests. *Soil Biology and Biochemistry*, **37**, 67–79.
- Barber, S.A. (1995) *Soil Nutrient Bioavailability: a Mechanistic Approach*, 2nd edn. John Wiley & Sons, New York.
- Beatty, S.W. (2003) Habitat heterogeneity and maintenance of species in understory communities. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 177–197. Oxford University Press, New York.
- Bobbink, R., Hornung, M. & Roelofs, J.G.M. (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology*, **86**, 717–738.
- Bohlen, P.J., Scheu, S., Hale, C.M., McLean, M.A., Migge, S., Groffman, P.M. & Parkinson, D. (2004) Non-native invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment*, **2**, 427–435.
- Boxman, A.W., Blanck, K., Brandrud, T.-K., Emmett, B.A., Gundersen, P., Hogervorst, R.F., Kjønaas, O.J., Persson, H. & Timmermann, V. (1998) Vegetation and soil biota response to experimentally-changed nitrogen inputs in coniferous forest ecosystems of the NITREX project. *Forest Ecology and Management*, **101**, 65–79.

- Brandrud, T.K. & Timmermann, V. (1998) Ectomycorrhizal fungi in the NITREX site at Grdsjn, Sweden; below and above-ground responses to experimentally-changed nitrogen inputs 1990–1995. *Forest Ecology and Management*, **101**, 207–214.
- Brooks, M.L. (2003) Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology*, **40**, 344–353.
- Brown, M.J. & Parker, G.G. (1994) Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Canadian Journal of Forest Research*, **24**, 1694–1703.
- Brunet, J., Diekmann, M. & Falkengren-Grerup, U. (1998) Effects of nitrogen deposition on field layer vegetation in south Swedish forests. *Environmental Pollution*, **102**, 35–40.
- Cassidy, T.M., Fownes, J.H. & Harrington, R.A. (2004) Nitrogen limits an invasive perennial shrub in forest understory. *Biological Invasions*, **6**, 113–121.
- Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs*, **70**, 171–207.
- Denno, R.F. & Fagan, W.F. (2003) Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology*, **84**, 2522–2531.
- Dighton, J., Tuininga, A.R., Gray, D.M., Huskins, R.E. & Belton, T. (2004) Impacts of atmospheric deposition on New Jersey pine barrens forest soils and communities of ectomycorrhizae. *Forest Ecology and Management*, **201**, 131–144.
- Eaton, G.K. & Ayres, M.P. (2002) Plasticity and constraint in growth and protein mineralization of ectomycorrhizal fungi under simulated nitrogen deposition. *Mycologia*, **94**, 921–932.
- Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503–523.
- Ehrenfeld, J.G., Kourtev, P. & Huang, W. (2001) Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications*, **11**, 1287–1300.
- Erisman, J.W. & de Vries, W. (2000) Nitrogen deposition and effects on European forests. *Environmental Review*, **8**, 65–93.
- Falkengren-Grerup, U. (1986) Soil acidification and vegetation changes in deciduous forest in southern Sweden. *Oecologia*, **70**, 339–347.
- Falkengren-Grerup, U. (1989) Soil acidification and its impact on ground vegetation. *Ambio*, **18**, 339–347.
- Fargione, J.E. & Tilman, D. (2005) Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, **8**, 604–611.
- Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T.S., Johnson, D.W. & Neitlich, P. (2003) Ecological effects of nitrogen deposition in the western United States. *BioScience*, **53**, 404–420.
- Fenn, M.E., Poth, M.A., Aber, J.D., Baron, J.S., Bormann, B.T., Johnson, D.W., Lemly, A.D., McNulty, S.G., Ryan, D.F. & Stottlemeyer, R. (1998) Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. *Ecological Applications*, **8**, 706–733.
- Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend, A.R. & Vörösmarty, C.J. (2004) Nitrogen cycles: past, present, and future. *Biogeochemistry*, **70**, 153–226.
- George, L.O. & Bazzaz, F.A. (2003) The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. *The Herbaceous Layer in Forests of Eastern North America* (eds F. S. Gilliam & M. R. Roberts), pp. 265–282. Oxford University Press, New York.
- Gilliam, F.S. & Adams, M.B. (1996) Wetfall deposition and precipitation chemistry for central Appalachian forest. *Journal of the Air and Waste Management Association*, **46**, 978–984.
- Gilliam, F.S., Adams, M.B. & Yurish, B.M. (1996) Ecosystem nutrient responses to chronic nitrogen inputs at Fernow Experimental Forest, West Virginia. *Canadian Journal of Forest Research*, **26**, 196–205.
- Gilliam, F.S., Hockenberry, A.W. & Adams, M.B. (2006) Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest. *Journal of the Torrey Botanical Society*, **133**, in press.
- Gilliam, F.S., Lyttle, N.L., Thomas, A. & Adams, M.B. (2005) Soil variability along a nitrogen mineralization/nitrification gradient in a nitrogen-saturated hardwood forest. *Soil Science Society of America Journal*, **69**, 247–256.
- Gilliam, F.S. & Roberts, M.R. (2003a) *The Herbaceous Layer in Forests of Eastern North America*. Oxford University Press, New York.
- Gilliam, F.S. & Roberts, M.R. (2003b) Introduction: conceptual framework for studies of the herbaceous layer. *The Herbaceous Layer in Forests of Eastern North America* (eds F. S. Gilliam & M. R. Roberts), pp. 3–11. Oxford University Press, New York.
- Gilliam, F.S. & Roberts, M.R. (2003c) The dynamic nature of the herbaceous layer: synthesis and future directions for research. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 323–337. Oxford University Press, New York.
- Gilliam, F.S., Turrill, N.L., Aulick, S.D., Evans, D.K. & Adams, M.B. (1994) Herbaceous layer and soil response to experimental acidification in a central Appalachian hardwood forest. *Journal of Environmental Quality*, **23**, 835–844.
- Gilliam, F.S., Yurish, B.M. & Adams, M.B. (2001) Temporal and spatial variation of nitrogen transformations in nitrogen-saturated soils of a Central Appalachian hardwood forest. *Canadian Journal of Forest Research*, **31**, 1768–1785.
- Grelet, G.-A., Meharg, A.A. & Alexander, I.J. (2005) Carbon availability affects nitrogen source utilisation by *Hymenoscyphus ericae*. *Mycological Research*, **109**, 469–477.
- Gundale, M.J. (2002) Influence of exotic earthworms on the soil organic matter horizon and the rare fern *Botrychium mormo*. *Conservation Biology*, **16**, 1555–1561.
- Gundale, M.J., Jolly, W.M. & Deluca, T.H. (2005) Susceptibility of a northern hardwood forest to exotic earthworm invasion. *Conservation Biology*, **19**, 1075–1083.
- Hale, C.M., Frelich, L.E., Reich, P.B. & Pastor, J. (2005) Effects of European earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, USA. *Ecosystems*, **8**, 911–927.
- Hartley, S.E. & Mitchell, R.J. (2005) Manipulation of nutrients and grazing levels on heather moorland: changes in *Calluna* dominance and consequences for community composition. *Journal of Ecology*, **93**, 990–1004.
- Hodge, A., Stewart, J., Robinson, D., Griffiths, B.S. & Fitter, A.H. (2000) Competition between roots and soil microorganisms for nutrients from nitrogen-rich patches of varying complexity. *Journal of Ecology*, **88**, 150–164.
- Holland, E.A. & Lamarque, J.-F. (1997) Modeling bio-atmospheric coupling of the nitrogen cycle through NO_x emissions and NO_y deposition. *Nutrient Cycling in Agroecosystems*, **48**, 7–24.
- Hurd, T.M., Brach, A.R. & Raynal, D.J. (1998) Response of understory vegetation of Adirondack forests to nitrogen additions. *Canadian Journal of Forest Research*, **28**, 799–807.
- Hutchings, M.J., John, E.A. & Wijesinghe, D.K. (2003) Toward understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology*, **84**, 2322–2334.

- James, S.W. & Cunningham, M.R. (1989) Feeding ecology of some earthworms in Kansas tallgrass prairie. *American Midland Naturalist*, **121**, 78–83.
- John, E. & Turkington, R. (1995) Herbaceous vegetation in the understorey of the boreal forest: does nutrient supply or snowshoe hare herbivory regulate species composition and abundance? *Journal of Ecology*, **83**, 581–590.
- Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C. & Towne, E.G. (1999) The keystone role of bison in North American tallgrass prairie. *Bioscience*, **49**, 39–50.
- Knorr, M., Frey, S.D. & Curtis, P.S. (2005) Nitrogen additions and litter decomposition: a meta-analysis. *Ecology*, **86**, 3252–3257.
- Kobe, R.K., Pacala, S.W., Silander, J.A. Jr & Canham, C.D. (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, **5**, 517–532.
- Kourtev, P.S., Huang, W.Z. & Ehrenfeld, J.G. (1999) Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. *Biological Invasions*, **1**, 237–245.
- Krupa, S.V. (2003) Effects of atmospheric ammonia (NH₃) on terrestrial vegetation: a review. *Environmental Pollution*, **124**, 179–221.
- Langner, J., Persson, C. & Robertson, L. (1995) Concentration and deposition of acidifying air pollutants over Sweden: estimates for 1991 based on the MATCH model and observations. *Water, Air, and Soil Pollution*, **85**, 2021–2026.
- Laverman, A.M., Borgers, P. & Verhoef, H.A. (2002) Spatial variation in net nitrate production in a N-saturated coniferous forest soil. *Forest Ecology and Management*, **161**, 123–132.
- Lawrence, B., Fisk, M.C., Fahey, T.J. & Suárez, E.R. (2003) Influence of non-native earthworms on mycorrhizal colonization of sugar maple (*Acer saccharum*). *New Phytologist*, **157**, 145–153.
- Lilleskov, E.A. & Bruns, T.D. (2001) Nitrogen and ectomycorrhizal fungal communities: what we know, what we need to know. *New Phytologist*, **149**, 154–158.
- Lilleskov, E.A., Fahey, T.J., Horton, T.R. & Lovett, G.M. (2002) Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. *Ecology*, **83**, 104–115.
- Luken, J.O. (2003) Invasions of forests in the eastern United States. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 283–301. Oxford University Press, New York.
- Marschner, H. (1995) *Mineral Nutrition of Higher Plants*, 2nd edn. Academic Press, London.
- May, J.D. & Killingbeck, K.T. (1992) Effects of preventing nutrient resorption on plant fitness and foliar nutrient dynamics. *Ecology*, **73**, 1868–1878.
- McCarthy, B.C. (2003) The herbaceous layer of eastern old-growth deciduous forests. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 163–176. Oxford University Press, New York.
- Mitchell, C.E., Reich, P.B., Tilman, D. & Groth, J.V. (2003) Effects of elevated CO₂, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. *Global Change Biology*, **9**, 438–451.
- Muller, R.N. (2003) Nutrient relations of the herbaceous layer in deciduous forest ecosystems. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 15–37. Oxford University Press, New York.
- Muller, E.K.H. & Janiesch, P. (1993) *In vivo* nitrate reductase activity in *Carex pseudocyperus* L. the influence of nitrite-ammonium concentration ratios and correlation with growth. *Journal of Plant Nutrition*, **16**, 1357–1372.
- Nadelhoffer, K.J., Downs, M.R. & Fry, B. (1999) Sinks for 15N-enriched additions to an oak forest and a red pine plantation. *Ecological Applications*, **9**, 72–86.
- Neufeld, H.S. & Young, D.R. (2003) Ecophysiology of the herbaceous layer in temperate deciduous forests. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 38–90. Oxford University Press, New York.
- Niemelä, P., Tahvanainen, J., Sorjonen, J., Hokkanen, T. & Neuvonen, S. (1982) The influence of host plant growth form and phenology on the life strategies of Finnish macrolepidopterous larvae. *Oikos*, **39**, 164–170.
- Nordin, A., Näsholm, T. & Ericson, L. (1998) Effects of simulated N deposition on understory vegetation of a boreal coniferous forest. *Functional Ecology*, **12**, 691–699.
- Nordin, A., Strengbom, J. & Ericson, L. (2006) Responses to ammonium and nitrate additions by boreal plants and their natural enemies. *Environmental Pollution*, **141**, 167–174.
- Nordin, A., Strengbom, J., Witzell, J., Näsholm, T. & Ericson, L. (2005) Nitrogen deposition and the biodiversity of boreal forests: implications for the nitrogen critical load. *Ambio*, **34**, 20–24.
- Økland, T., Bakkestuen, V., Økland, R.H. & Eilersten, O. (2004) Changes in forest understorey vegetation in Norway related to long-term soil acidification and climatic change. *Journal of Vegetation Science*, **15**, 437–448.
- Ollinger, S.V., Aber, J.D., Lovett, G.M., Millham, S.E., Lathrop, R.G. & Ellis, J.M. (1993) A spatial model of atmospheric deposition for the northeastern U.S. *Ecological Applications*, **7**, 459–472.
- Padgett, P.E. & Allen, E.B. (1999) Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. *Plant Ecology*, **144**, 93–101.
- Parton, W.J., Stewart, J.W.B. & Cole, C.V. (1988) Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry*, **5**, 109–131.
- Pennings, S.C., Clark, C.M., Cleland, E.E., Collins, S.L., Gough, L., Gross, K.L., Milchunas, D.G. & Suding, K.N. (2005) Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *Oikos*, **110**, 547–555.
- Perotto, S., Giralanda, M. & Martino, E. (2002) Ericoid mycorrhizal fungi: some new perspectives on old acquaintances. *Plant and Soil*, **244**, 41–53.
- Peterjohn, W.T., Adams, M.B. & Gilliam, F.S. (1996) Symptoms of nitrogen saturation in two central Appalachian hardwood forests. *Biogeochemistry*, **35**, 507–522.
- Postgate, J.R. (1982) *The Fundamentals of Nitrogen Fixation*. Cambridge University Press, Cambridge.
- Price, J.N. & Morgan, J.W. (2006) Vegetation dynamics following resource manipulations in herb-rich woodland. *Plant Ecology*, in press.
- Rainey, S.M., Nadelhoffer, K.J., Silver, W.L. & Downs, M.R. (1999) Effects of chronic nitrogen additions on understory species in a red pine plantation. *Ecological Applications*, **9**, 949–957.
- Read, D.J. (1996) The structure and function of the ericoid mycorrhizal root. *Annals of Botany*, **77**, 365–374.
- Read, D.J. & Perez-Moreno, J. (2003) Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist*, **157**, 475–492.
- Richardson, H.L. (1938) The nitrogen cycle in grassland soils: with especial reference to the Rothamsted Park Grass Experiment. *Journal of Agricultural Science*, **28**, 73–121.
- Roberts, M.R. (2004) Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany*, **82**, 1273–1283.
- Roberts, M.R. & Gilliam, F.S. (1995) Patterns and mechanisms of diversity in forested ecosystems: implications for forest management. *Ecological Applications*, **5**, 969–977.
- Roberts, M.R. & Gilliam, F.S. (2003) Response of the herbaceous layer to disturbance in eastern forests. *The Herbaceous Layer*

- in *Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 302–320. Oxford University Press, New York.
- Schleppi, P., Muller, N., Edwards, P.J. & Bucher, J.B. (1999) Three years of increased nitrogen deposition do not affect the vegetation of a montane forest ecosystem. *Phyton*, **39**, 197–204.
- Small, C.J. & McCarthy, B.C. (2003) Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. *Plant Ecology*, **164**, 37–48.
- Smith, S.E. & Read, D.J. (1997) *Mycorrhizal Symbiosis*, 2nd edn. Academic Press, San Diego.
- Stevens, M.H.H. & Carson, W.P. (2002) Resource quantity, not resource heterogeneity, maintains plant diversity. *Ecology Letters*, **5**, 420–426.
- Stevens, G.N. & Jones, R.H. (2006) Patterns in soil fertility and root herbivory interact to influence fine-root dynamics. *Ecology*, **87**, 616–624.
- Stoddard, J.L. (1994) Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences. *Environmental Chemistry of Lakes and Reservoirs* (ed. L.A. Baker), pp. 223–282. ACS Advances in Chemistry Series no. 237, American Chemical Society, Washington, DC.
- Strengbom, J., Englund, G. & Ericson, L. (2006) Experimental scale and precipitation modify effects of nitrogen addition on a plant pathogen. *Journal of Ecology*, **94**, 227–233.
- Strengbom, J., Nordin, A., Näsholm, T. & Ericson, L. (2001) Slow recovery of boreal forest ecosystem following decreased nitrogen input. *Functional Ecology*, **15**, 451–457.
- Strengbom, J., Nordin, A., Näsholm, T. & Ericson, L. (2002) Parasitic fungus mediates change in nitrogen-exposed boreal forest vegetation. *Journal of Ecology*, **90**, 61–67.
- Strengbom, J., Walheim, M., Näsholm, T. & Ericson, L. (2003) Regional differences in occurrences of understorey forest species reflect differences in N deposition. *Ambio*, **32**, 91–97.
- Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D.G. & Pennings, S. (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences USA*, **102**, 4387–4392.
- Taylor, G.E. Jr, Johnson, D.W. & Andersen, C.P. (1994) Air pollution and forest ecosystems: a regional to global perspective. *Ecological Applications*, **4**, 662–689.
- Throop, H.L., Holland, E.A., Parton, W.J., Ojima, D.S. & Keough, C.A. (2004) Effects of nitrogen deposition and insect herbivory on patterns of ecosystem-level carbon and nitrogen dynamics: results from the CENTURY model. *Global Change Biology*, **10**, 1092–1105.
- Throop, H.L. & Lerdau, M.T. (2004) Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. *Ecosystems*, **7**, 109–133.
- Tilman, D. (1987) Secondary succession and the patterns of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, **57**, 189–214.
- van Tol, G., van Dobben, H.F., Schmidt, P. & Klap, J.M. (1998) Biodiversity of Dutch forest ecosystems as affected by receding groundwater levels and atmospheric deposition. *Biodiversity and Conservation*, **7**, 221–228.
- Turkington, R., John, E., Watson, S. & Secombe-Hett, P. (2002) The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-year study. *Journal of Ecology*, **90**, 325–337.
- United States Environmental Protection Agency (2002) *Nitrogen: multiple and regional impacts. Clean Air Markets Programs, EPA-430-R-01-006*. USEPA Clean Air Markets Division, Washington, DC.
- Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry*, **13**, 87–115.
- Wallenda, T. & Kottke, I. (1998) Nitrogen deposition and ectomycorrhizas. *New Phytologist*, **149**, 154–158.
- Wedin, D. & Tilman, D. (1993) Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs*, **63**, 199–229.
- Whigham, D.F. (2004) Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology and Systematics*, **35**, 583–621.
- Williard, K.W.J., DeWalle, D.R. & Edwards, P.J. (2005) Influence of bedrock geology and tree species composition on stream nitrate concentrations in mid-Appalachian forested watersheds. *Water, Air, and Soil Pollution*, **160**, 55–76.
- Windham, L. (2002) Does atmospheric nitrate deposition promote understorey plant invasions? Nitrate reductase assays say yes. *Bulletin of the Ecological Society of America*.
- Wise, M.J. & Abrahamson, W.G. (2005) Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos*, **109**, 417–428.
- Wright, R.F. & vanBremen, N. (1995) The NITREX project – an introduction. *Forest Ecology and Management*, **71**, 1–5.
- Yesmin, L., Gammack, S.M. & Cresser, M.S. (1996) Effects of atmospheric nitrogen deposition on ericoid mycorrhizal infection of *Calluna vulgaris* growing in peat soils. *Applied Soil Ecology*, **4**, 49–60.

Received 7 March 2006

Revision accepted 8 May 2006

Handling Editor: Robert Jones