

20 Effects of Excess Nitrogen Deposition on the Herbaceous Layer of Eastern North American Forests

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The response of plant species of the herbaceous layer of forest ecosystems to excess nitrogen (N) availability can arise from N-mediated changes in several processes, including competition, herbivory, mycorrhizal infection, disease, and species invasions. This chapter discusses how these processes respond to excess N and how such responses affect the herb layer of forests, reviewing recent pertinent literature from both North America and Europe. There is compelling evidence that all processes potentially 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. A recently suggested hypothesis—the *N homogeneity hypothesis*—predicts a loss of biodiversity in forest ecosystems experiencing chronically elevated N deposition. The hypothesized mechanism for this response is a decrease in spatial heterogeneity of N availability that is typically high in forest soils under N-limited conditions. A great majority of studies on effects of N on plant diversity have been carried out in herb-dominated communities, with few in forest herb layer communities. Accordingly, more studies are needed, using both field gradient and manipulative approaches, in forest ecosystems, particularly in eastern North America where far fewer studies have been done.

NATURE OF EXCESS N IN THE ENVIRONMENT

Given the high rates of N deposition currently experienced in many parts of the biosphere, and its projected further increases in the future (Bobbink et al. 2010), it is not

surprising that there has been a notable recent rise in the number of studies investigating the effects of N on terrestrial ecosystems in general (De Schrijver et al. 2011; Goodale et al. 2011). On the other hand, there has been a rich history of experimental studies investigating the effects of N on species diversity in plant communities. The first and likely best-known of these is the Park Grass Experiment in Rothamsted, England (see Richardson 1938 and Silvertown et al. 2006 as early and recent references, respectively), initially established in 1856 to assist English farmers in enhancing forage production for cattle. Ongoing investigations at the Cedar Creek Natural Area in Minnesota (e.g., Clark and Tilman 2008) confirm results of this earlier work—excess N can profoundly alter species composition and decrease species diversity of plant communities. To date, N effects research has still been predominantly directed toward herb-dominated communities, with far fewer studies in forested ecosystems (Bobbink et al. 1998; Gilliam 2006; Clark et al. 2007; Stevens et al. 2010; De Schrijver et al. 2011). This is an unfortunate discrepancy, however, considering that forests often occupy areas receiving high rates of atmospheric deposition of N (e.g., eastern U.S. and central Europe) and generally display considerable structural complexity relative to herb-dominated systems. Indeed, despite the prominence of the overstory, most plant species diversity of forests is associated with the vegetation of greatest sensitivity to the effects of excess N—the herbaceous layer (Gilliam 2007).

The N_2 gas that comprises 78 percent of our atmosphere is inert to virtually all living organisms and enters into few non-anthropogenic, abiotic chemical reactions. Consequently, it is often referred to as non-reactive N (N_{nr}), in sharp contrast to other forms of N, such as NH_3 , NH_4^+ , NO_3^- , NO, and NO_2 , collectively referred to as reactive N (N_r), that do enter into biological or photochemical transformations. Increases in both high-energy combustion associated with fossil fuel consumption and use of the Haber-Bosch process for production of inorganic N fertilizers have enhanced otherwise naturally low rates of conversion of N_{nr} to N_r , chronically increasing amounts of N_r in the biosphere. Based on estimates from Galloway et al. (2004), total atmospheric deposition of NH_4^+ and NO_3^- in terrestrial ecosystems has increased from 17 Tg N yr^{-1} in 1860 to 64 Tg N yr^{-1} in the early 1990s, with projected further increases to 125 Tg N yr^{-1} by 2050. Thus, the projection over this 190-year period is that atmospheric deposition of N_r will increase nearly 10-fold. It is notable that, whereas N_r from vehicles and power plants in the eastern United States has decreased ~ 30 percent in the past decade in response to Clean Air Act regulations, N_r from fertilizer production and use has increased during this period (Pinder et al. 2011).

N LIMITATION VERSUS N SATURATION: INTERFACE OF BIOGEOCHEMISTRY AND VEGETATION SCIENCE

Although net primary productivity of most terrestrial ecosystems of the biosphere is still predominantly limited by availability of N (*N limitation*), anthropogenically enhanced atmospheric deposition of N in some regions of the biosphere has increased available N to levels that exceed the biotic demand for N (*N saturation*). Global patterns of increased atmospheric deposition of N_r are far from homogeneous, and highest rates understandably co-occur with areas of high human population density. In North America, these are also spatially coincidental with the distribution of forests, especially in the eastern United States (Gilliam et al. 2011). As a result, most N-saturated ecosystems are forests.

The phenomenon of N saturation represents an intriguing interface between biogeochemistry and vegetation science, as many of the biogeochemical consequences of N saturation are directly relevant to the structure and function of plant communities (Gilliam 2006). Primarily, these consequences are related to a notable change in the N cycle toward increasing dominance of nitrate (NO_3^-). Ammonium (NH_4^+) typically dominates in N-limited systems because NH_4^+ generated by ammonifying microbes is rapidly taken up by plant roots and immobilized by other microbial populations, leaving little for oxidation by nitrifying bacteria (autotrophic nitrification). However, during the sequence of stages leading to N saturation, NH_4^+ becomes increasingly available to nitrifier populations, as ammonification exceeds uptake and immobilization by plants and microbes, respectively. Increasing predominance of NO_3^- as the available form of N in forest soils may cause potentially rapid change in herb layer composition because (1) preferential use of NH_4^+ versus NO_3^- can be highly species-specific among plants, particularly among forest herbs (chapter 2, this volume; Boudsocq et al. 2012), and (2) increases in soil NO_3^- pools can increase invasibility by exotic species (chapter 13, this volume; Fargione and Tilman 2005). Increases in levels of NO_3^- in forest soils have also been shown to increase mobility and decrease availability of base cations, such as Ca^{2+} and Mg^{2+} (Gilliam et al. 2001).

N-SENSITIVE PROCESSES POTENTIALLY AFFECTING THE HERB LAYER

As suggested, several processes are sensitive to change mediated by enhanced atmospheric deposition of N that potentially influence herb layer dynamics. It is coincidental that the primary geographic scope of this book—eastern North America—experiences some of the higher rates of N deposition in the world (Gruber and Galloway 2008; Bobbink et al. 2010). Thus, understanding herb layer dynamics in this highly N-impacted region has broad application over other impacted areas. Moreover, such understanding is also important in application of knowledge toward effective conservation policies (see Critical Loads for N Deposition below).

The principal N-mediated change in soil N processing is the simultaneous increase in N availability and increasing predominance of NO_3^- as the available form of N uptake. Because nitrification in excess of NO_3^- uptake results in net H^+ production, in some cases, chronic excess N can increase soil acidity (Kelly et al. 2011). Thus, one of the immediate changes in herb layer composition is an increase in the predominance of species that are nitrophilic, preferential NO_3^- -uptake species, acidophilic, or some combination of these.

I suggest the following as a general pattern of response of the herbaceous layer of temperate deciduous forests of eastern North America, with the degree to which this occurs being largely influenced by antecedent N conditions in the soil (Hurd et al. 1998). Initially, there should be an overall increase in biomass of the herb layer as the forest shifts from N limitation toward N saturation (i.e., a fertilizer effect). This will be followed by a loss of N-efficient species and a general decrease in species richness, which can represent a rapid decline in plant biodiversity because of the relative high numbers of such species (fig. 20.1). The next stage will be an increasing predominance of nitrophilic species. As there are far fewer of these species in N-limited forests (fig. 20.1), this will further negatively impact forest biodiversity by decreasing species

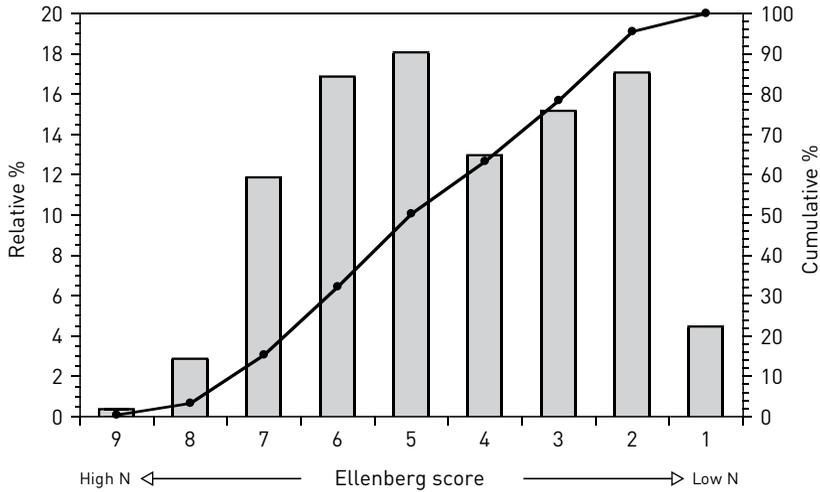


FIGURE 20.1 Relative and cumulative percentages of number of species within Ellenberg N groups, with N demand being highest for 9 and lowest for 1, for ~1,900 vascular plant species of Great Britain.

equitability (evenness). It has been further suggested that decreases in evenness can be further exacerbated by the clonal nature of many of these nitrophilic species (Eilts et al. 2011).

MECHANISMS FOR N-MEDIATED RESPONSE OF HERB LAYER

In a previous synthesis and review (Gilliam 2006), I developed a conceptual model (fig. 20.2) to articulate several processes sensitive to N deposition that have the potential to alter herb layer composition and dynamics, ultimately resulting in N-mediated declines in forest biodiversity. Because of their relevance to the discussion of this chapter, I summarize these here.

Interspecific Competition

Most work on the effects of additions of N on the outcomes of interspecific competition has been carried out on herb-dominated plant communities and has demonstrated notable N-mediated changes in success of dominant species. Early work at Cedar Creek demonstrated that N-efficient species (e.g., *Schizachyrium scoparium*) outcompeted high N-requiring species (e.g., *Poa pratensis* and *Agropyron scabra*) under N-limited conditions by taking up inorganic N to the extent that it was below the requirement of the high-N species (i.e., R^* , the resource reduction model for competition—Wedin and Tilman 1993).

In contrast to herb-dominated communities wherein nutrients, especially N, can be particularly limiting to herbaceous species, closed-canopied forests are generally light-limited. Direct light only reaches the forest understory in discrete patches called *sunflecks* (chapter 3, this volume), creating a *dynamic mosaic*, in which the size and distribution of sunflecks vary widely across temporal and spatial scales (Gilliam and

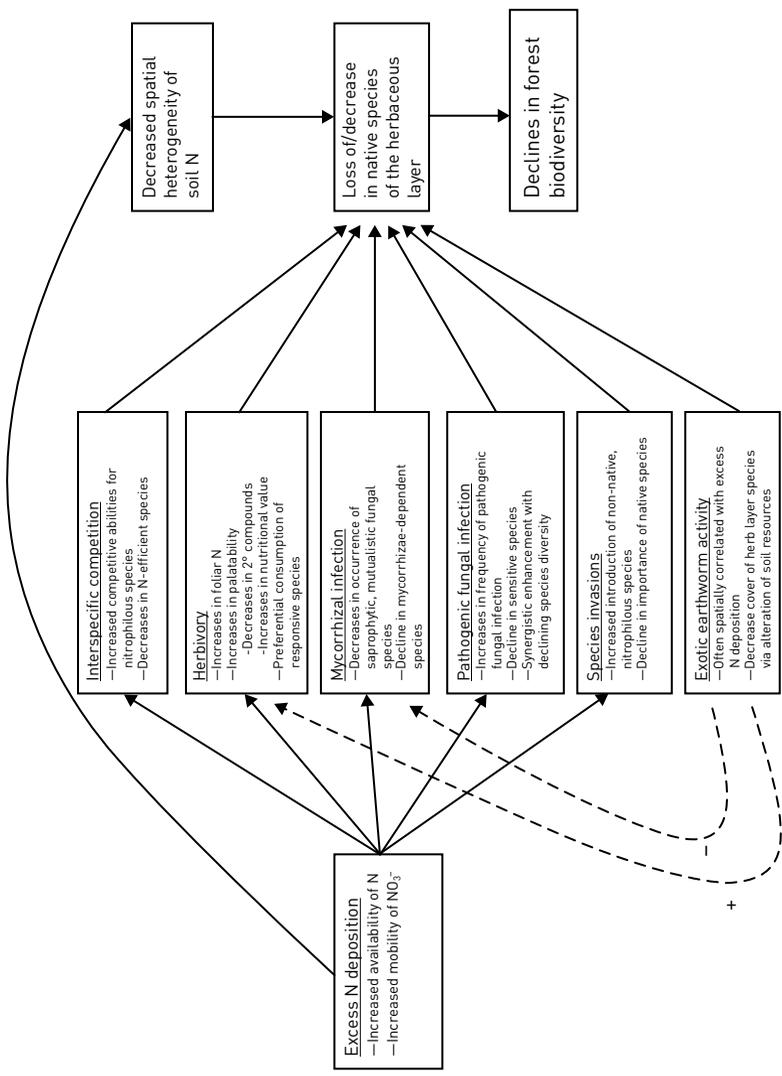


FIGURE 20.2 Conceptual model of the direct effects of excess N on the herbaceous layer and soil N in forest ecosystems (Gilliam 2006, used by permission). Note that although “exotic earthworm activity” is part of the original model of Gilliam (2006), it is not discussed in this chapter.

Roberts 2003). Nitrogen availability can exhibit considerable spatial heterogeneity (patchiness) in which plant roots compete interspecifically and with soil microbes (Hodge et al. 2000). Although temporal variation in nutrient availability is usually much less than availability of light, high spatial heterogeneity of soil resources is important in maintaining species diversity of the herb layer (chapter 8, this volume).

Given that the resource reduction model for competition (Wedin and Tilman 1993) predicts that plants gain competitive superiority by usurping essential soil resources and decreasing availability to other plants, high inputs of N to a forest should give a competitive disadvantage to N-efficient plants because these plants will be decreasingly able to deplete available soil N constantly resupplied via atmospheric deposition. Price and Morgan (2007) demonstrated this process experimentally for an herb-rich forest in Australia. They concluded that increased soil N promoted competitive exclusion of species adapted to low N availability, resulting in declines in species initially dominant prior to treatment.

Herbivory

Herbivory by vertebrate and invertebrate animals can exert a profound influence on the herbaceous layer of forests (chapters 13, 16, and 17, this volume; Roberts 2004). Intensity of herbivory is influenced by numerous factors, particularly nutritional value and palatability of plant—especially foliar—tissue. Chronically elevated N deposition can stimulate herb layer species to undergo luxury uptake of N (chapter 2, this volume), which increases foliar N concentrations and creates the potential to alter herbivore activity. Hartley and 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.

In their synthesis and review of research on effects of N deposition on insect herbivory, Throop and Lerda (2004) found a great degree of variability among studies, but concluded that the most likely mechanisms explaining N-enhanced herbivory were via deposition-mediated changes in quality and availability of forage plant tissue, especially those related to tissue chemistry. This included increases in content of amino acids, such as glutamine and arginine, and simultaneous decreases in carbon-based defensive secondary compounds, including condensed tannins and phenolics. Ultimately, increases in herbivory from excess N deposition potentially result in profound shifts in species composition/dominance of the herb layer through preferential consumption of those plants most sensitive to increased N availability.

Mycorrhizae

The well-known mutualistic relationships between vascular plant roots and fungal symbionts known as mycorrhizae are very common among herbaceous layer species (Whigham 2004). Plants get considerable benefits from the fungus, including increased access to nutrients, protection from pathogens, and increased water-use efficiency (Smith and Read 1997). Also, relative to non-mycorrhizal plants, mycorrhizal plants are superior competitors in nutrient-limited soils, primarily because of their fungal-enhanced abilities to take up nutrients, such as N (Read and Perez-Moreno 2003). Conversely, excess N can alter this competitive dynamic.

Several studies (e.g., Lilleskov et al. 2002, 2008; van Diepen et al. 2011) have found notable change in fungal sporocarp (aboveground) communities in response to increased

N, suggesting the likelihood of similar N-mediated alteration in ectomycorrhizal diversity. Dighton et al. (2004) used both an ambient N deposition gradient and an experimental greenhouse approach in demonstrating that ectomycorrhizae declined significantly with increased N in soils from New Jersey pine barren forests. Thus, it is likely that for forests receiving elevated levels of N deposition, herb layer composition and diversity may be negatively impacted via declines/loss of numerous mycorrhizal plant species.

Disease

Excess N has been shown to increase occurrence and degree of pathogenic fungal infections in a variety of plant species (Mitchell et al. 2003). Strengbom et al. (2006) found that the host plant *Vaccinium myrtillus* was more susceptible to the parasitic fungus *Valdensia heterodoxa* when exposed to 12.5 and 50 kg N ha⁻¹ yr⁻¹ compared to untreated control plots, and that the incidence of disease was significantly and positively correlated with summer precipitation. Nordin et al. (2006) reported a species-specific plant response to added N in boreal forests, one that contrasted with effects on pathogenic fungi. Plant species discriminated between the forms of added N: High-N-requiring species responded primarily to NO₃⁻, and bryophytes responded to NH₄⁺, whereas N-efficient species exhibited no response. In contrast, frequency of pathogenic fungi increased in response to all additions of N, regardless of the form in which it was added.

Mitchell et al. (2003) examined interactions of elevated CO₂ and decreased plant species diversity with effects of excess N on pathogenic fungal infection of several herbaceous species. They developed a metric called “pathogen load”—relative (%) leaf area infected by fungi—to quantify responses. All variables (elevated CO₂, decreased diversity, and increased N) increased pathogen load on several herb species, often interactively. Response to N was particularly pronounced for N-efficient species, but the most pronounced response of pathogen load was not to N, but to diversity. Plots with one or four species had > 2 times the pathogen load as plots with nine or 16 species. This finding has important relevance for long-term 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.

Invasive Species

Although invasion of nonnative species in undisturbed forests with closed canopies are generally rare (chapter 15, this volume), considerable work has shown that species invasions can be facilitated by increasing N supply. These studies suggest that N limits the invasibility of the herbaceous layer of both conifer and hardwood forests (Gurevitch et al. 2008). Thus, N-saturated forests would be particularly susceptible to introduction of exotic species (Ehrenfeld 2010).

It is further likely that positive feedbacks can reinforce increases in invasions of forest herbaceous layers by exotic species via excess soil NO₃⁻. Ehrenfeld et al. (2001) examined invasion of the herb layer of New Jersey hardwood stands by two exotic species—*Berberis thunbergii* and *Microstegium vimineum*—and found that soil in which these species grew had higher pH and net N mineralization/nitrification than soil occupied by native species. Higher pH in impacted soil was largely the result of preferential uptake of NO₃⁻ by the exotic species (Marschner 1995; Ehrenfeld et al.

2001). Ehrenfeld (2003) provided a synthesis of studies of this phenomenon and concluded that most of the 56 invasive species reviewed had the ability to drastically alter the N cycle of forest soils, 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 precarious 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. As a result, there is substantial change in species composition and decrease in biodiversity of the herb layer following N-mediated increases in species' invasions.

SYNTHESIS OF N-RESPONSE STUDIES IN FORESTS

Research Approaches

As with most studies of effects of atmospheric deposition on terrestrial plant communities, research approaches toward determining the response of plant biodiversity to increasing N deposition can generally be divided into two broad categories: observational versus manipulative studies (Dunne et al. 2004). Each of these approaches has innate strengths and weaknesses that are largely mutually exclusive. Observational studies tend to be more common in Europe (Brunet et al. 1998; Strengbom et al. 2003; Stevens et al. 2010; Verheyen et al. 2012), whereas manipulative studies are generally more common in North America (Gilliam et al. 1994, 2006; Hurd et al. 1998; Rainey et al. 1999), South America (Siddique et al. 2010; Ochoa-Hueso et al. 2011), and Asia (Lu et al. 2010, 2011).

Observational, or gradient, studies to examine the potential effects of excess N on plant biodiversity typically lack experimental manipulations, instead characterizing variation in plant species composition over a given region experiencing widely varying amounts of N deposition. Among the scientific strengths associated with gradient studies, perhaps the most important is the ability to examine plant response to N under unaltered, ambient conditions, including cyclical processes related to seasonal change. In addition, N deposition occurs in these studies (1) without the "pulse" phenomenon associated with experimentally added N, and (2) in an ambient balance of forms of reactive N (including NH_4^+ , NO_3^- , and organic N) via both wet and dry processes. Weaknesses of the N deposition gradient approach are primarily related to the fact that it is essentially a variation of space-for-time substitution often used in studies of plant succession (chapter 11, this volume). As such, these studies carry with them the unavoidable confounding effects of other environmental factors/gradients, including soil properties and microclimatic variables. Despite any limitations, gradient studies offer excellent insight into effects of N on plant biodiversity.

Manipulative, or experimental, approaches to studying the effects of excess N on plant biodiversity involve controlled addition of N in various forms and amounts to plots and, much more rarely, entire watersheds. A strength of this approach, especially for studies employing experimental plots (often $10\text{ m} \times 10\text{ m}$, but also as small as $1\text{ m} \times 1\text{ m}$), includes greater statistical power in data analysis related to use of replicated treatments. In addition, because of the more controlled nature of these experiments, they lack the problems of confounding of other environmental factors inherent in gradient studies. However, the weaknesses of manipulative studies arise out of their limitations in simulating natural processes. Thus, their form (usually NH_4^+ , NO_3^- , or

both) of N addition and timing/amount of N addition often poorly resemble ambient atmospheric N deposition processes. For example, the amount of N added will almost invariably represent a “pulse” of N not normally experienced under ambient conditions. As with gradient-based approaches, these manipulative studies have greatly enhanced our understanding of plant diversity responses to excess N. In addition, synoptic-scale analyses and meta-analyses of plot-based experiments have yielded still further insights (Suding, et al. 2005; Pennings et al. 2005; De Schrijver et al. 2011).

Temperate Forests

Gilliam (2006) reviewed the literature on effects of N on herbaceous layer dynamics of temperate forests of both eastern North America and Europe, the principle regions wherein this work was being conducted, with the main focus having been on effects on species diversity. The purpose of this section is to examine work published since that time.

EASTERN NORTH AMERICA

Regrettably, few, if any, eastern North American studies of the effects of N on herb layer dynamics published since 2006 have focused explicitly on responses of herb layer species composition and diversity to added N. However, studies have examined other facets of N response, such as interactions with patterns of land use and light availability and effects on invasive species that are directly relevant to influencing herb layer species composition and maintaining biodiversity.

Fraterrigo et al. (2009) studied responses of six herb taxa to N fertilization in forests of contrasting land use history in western North Carolina, with an emphasis on whether forests developed on former agricultural land. By adding three levels of N to paired plots in native (reference) versus post-agricultural stands, they found a significant interaction between N and land use for three taxa (*Arisaema triphyllum*, *Osmorhiza* spp., and *Cimicifuga racemosa*). In general, responses to N were more pronounced in post-agricultural stands. They concluded that post-agricultural forests may have been more N-limited, whereas native stands were approaching N saturation.

Focusing on the potential for N to influence invasions of exotic species (chapter 12, this volume), Gurevitch et al. (2008) determined interactive effects of light (via experimental gap formation) and N on establishment of seedlings of native and exotic woody species (i.e., transient species, chapter 1, this volume) in forests of Long Island, New York. Consistent with predictions of Gilliam and Turrill (1993), they found that light was more profound in its effect than was added N; however, they also found that invasive species responded more sensitively than did native species to N. They concluded that the response of invasive forest species to excess N is complex and, therefore, often unpredictable.

Also addressing the potential for invasive species to exhibit different growth response to N than native species, Ross et al. (2011) examined effects of adding different forms of available N (i.e., NH_4^+ versus NO_3^-) on native and exotic herb layer species from forests of New Jersey. They found a highly species-specific response to added N, largely but not solely related to invasiveness status. Invasive species *Microstegium vimineum* responded significantly via increases in stem height/relative

growth rate and biomass to both forms of N. Surprisingly, native *Hamamelis virginiana* and invader *Berberis thunbergii* exhibited N-response patterns similar to each other, responding to both forms of added N, whereas native *Vaccinium pallidum* responded only to NH_4^+ . Their conclusions supported those of Gurevitch et al. (2008) that the complexity of plant-environment interactions of invasive species precludes broad generalizations regarding the response, and subsequent effects, of species invasions to excess N.

Gilliam (2014) summarized ecosystem responses to N as part of an ongoing, watershed-based experimental study in north-central West Virginia. Whole-watershed studies are far less common than plot-based studies, due largely to the greater logistical challenges associated with carrying out experimental treatments on such a broad scale. These studies lack the statistical advantage of plot experiments, and in fact are subject to the problem of pseudoreplication (Hurlbert 1984). However, they have the advantage of examining responses on a more realistic spatial scale. Most watershed-scale manipulations have focused on responses to disturbances, such as forest harvesting, whereas those that have employed experimental N additions generally have examined only biogeochemical responses.

One watershed (WS3) at the Fernow Experimental Forest (FEF), West Virginia, has received aerial applications (via helicopter/airplane) of N since 1989. Gilliam et al. (1994) reported no response of the herb layer following two years of application, and Gilliam et al. (2006) reported similar lack of response following six years of N treatment. However, repeated sampling in 2003 indicated a substantial decline of species diversity of the herbaceous layer in response to aerial N additions, a decrease that appears to be related to loss of species and increased total cover (Gilliam 2014). Most of this has arisen from increases in cover of shade-intolerant *Rubus* spp. from < 1 percent in 1991 to ~ 15 percent in 2003. In fact, *Rubus* spp. cover was 5 percent of total herb layer in cover on WS3 and increased to > 35 percent of total herb cover by 2003. These increases have come at the expense of one of the more diverse taxa in these forests—*Viola* spp.

EUROPE

Working in forests of central Sweden, Strengbom and Nordin (2008) took advantage of N fertilization treatments initially designed for enhancing tree growth to experimentally examine residual (long-lived) effects of excess N on herb layer cover and diversity measures, with their treatment plots having received 150 kg N ha⁻¹ over 20 years prior to their study. They found that the herb layer of the N-fertilized stand had significantly higher cover, lower evenness, and lower biodiversity, and concluded that excess N can exert long-term negative effects on the herb layer. Strengbom and Nordin (2012) followed their 2008 study with a field experiment to determine the interactive effects of forest harvesting and N additions in these same stands. Using a harvesting x fertilization factorial design, they found that species of the herb layer were more sensitive to N additions in harvested than in non-harvested stands.

Because herb layer dynamics can directly influence development of seedlings/juveniles of overstory species (chapter 14, this volume), it is important to determine how N-mediated changes in herb layer cover/composition might mitigate this influence. Diwold et al. (2010) investigated this by using soil C/N ratios as a surrogate for N processing and availability in forest soils of the Northern Limestone Alps of Austria

to examine relationships with herb cover, with focus on effects on tree seedlings. They found that N availability was not only positively correlated with herb cover, but that increases in herb cover had a negative effect on recruitment and growth rate of seedlings of one of the dominant hardwood species, *Acer pseudoplatanus* (L.).

Hedwall et al. (2011) studied the effects of frequency of N fertilization on herb layer species composition and diversity in forests of southern Sweden, including bryophyte species, which can be quite prominent in these forests, in their analysis. Although the plots receiving N treatments exhibited altered species composition and decreased diversity, relative to control plots for vascular, there was no significant response found for bryophyte species. All responses increased with increasing frequency of N additions. Hedwall et al. (2011) concluded that increased N will lead to long-term change in herb layer dynamics at the scale of individual stands and possibly that of the landscape.

N HOMOGENEITY HYPOTHESIS

There is increasing evidence that spatial variability (heterogeneity) in soil resources, such as essential nutrients, exerts a profound influence in creating and maintaining high species diversity in plant communities, including the herb layer of forest ecosystems (Hutchings et al. 2003; Lundholm 2009; Costanza et al. 2011; García-Palacios 2012; chapter 8, this volume). In a synthesis paper, Bartels and Chen (2010) reviewed 130 relevant studies from the peer-reviewed literature and found that both resource supply (quantity) and heterogeneity were important in maintaining herb layer diversity, but that heterogeneity was more important in disturbed forests, a condition that characterizes most forests of eastern North America. Costanza et al. (2011) analyzed data from 150 nested vegetation plots from North and South Carolina and found consistently positive relationships between heterogeneity and herb species richness, independent of spatial scale.

One of the early observations in the ongoing whole-watershed N experiment at Fernow Experimental Forest, West Virginia, wherein N is added aerially three times per year at a rate of 35 kg N ha⁻¹ yr⁻¹, was that the N treatment increased extractable soil NO₃⁻ and soil solution NO₃⁻. A more novel finding, however, was that the treatment also substantially decreased the spatial heterogeneity of these variables in the 35 ha treatment watershed (Gilliam et al. 2001). This observation led to the development of the *N homogeneity hypothesis* (Gilliam 2006).

Assumptions and Predictions

The primary assumptions of the N homogeneity hypothesis arise from the previously discussed relationship between spatial heterogeneity of soil resources and diversity of plant communities, focusing on spatial heterogeneity of available N in forest ecosystems. Relatively undisturbed forests typically display a high degree of spatial heterogeneity, with spatially discrete areas of high and low rates of N mineralization in soils. High heterogeneity of soil N should maintain high diversity, particularly at the landscape scale, by creating a patchwork of areas of high soil N—referred to as “islands of fertility” by Schlesinger et al. (1996) and as “hot spots” by McClain et al. (2003)—that support nitrophilous species, and areas of low soil N that support non-nitrophilous, low-N-requiring species. A final assumption of the hypothesis is that high rates of atmospheric N deposition will decrease spatial heterogeneity (increase homogeneity)

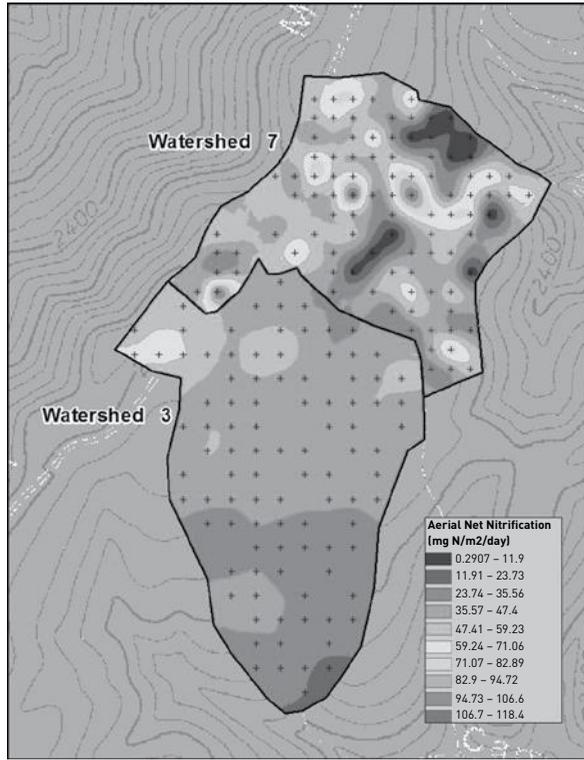


FIGURE 20.3 Spatial patterns of net nitrification in soils of reference (WS7) and N-treated (WS3) watersheds at Fernow Experimental Forest, West Virginia. See text for description of N treatments. Figure used with permission of William Peterjohn, West Virginia University, Morgantown, WV.

of N by increasing N availability of the low-N matrix. These assumptions are supported by work carried out at the Fernow Experimental Forest, West Virginia (fig. 20.3).

Accordingly, the N homogeneity hypothesis predicts that excess N deposition will lead to decreases in spatial heterogeneity of N availability and that such N-mediated decreases will lead to decreases in biodiversity of the herb layer of impacted forests. By homogenizing patterns of N availability (i.e., maintaining high levels of soil N throughout the landscape), increased excess N in atmospheric deposition will give a competitive advantage to the relatively few nitrophilous species (see fig. 20.1) that will outcompete non-nitrophilous plant species.

Tests of Hypotheses in Literature

Since its original appearance in 2006, the N homogeneity hypothesis has been reviewed in synthesis papers (e.g., Lu et al. 2008; Fujimaki et al. 2009; García-Palacios 2012) and addressed, either explicitly or implicitly, in several studies. All but one study (Bernhardt-Römermann et al. 2010) provided evidence either in direct support of or consistent with predictions of the N homogeneity hypothesis (e.g., Eilts et al. 2011). Hülber et al. (2008) sampled > 120 plots throughout the ~ 90 ha Northern Limestone Alps in Austria and found results indicating that homogenization of site

conditions from long-term high levels of N deposition leads to a homogenization of forest floor vegetation. They concluded that these limestone areas with such diverse soil conditions at the broader landscape scale are negatively affected by airborne N deposition, supporting predictions of the hypothesis. Combining a plant function type (PFT) and non-manipulative N gradient (soil N 0.6–1.1 percent) approach, Bernhardt-Römermann et al. (2010) sampled 20 relevés in a ~ 24 ha deciduous forest of southern Germany to test the N homogeneity hypothesis. Of the seven PFTs they identified (based on leaf persistence, height of plant, seed mass, and flowering phenology), they found that the greatest numbers were associated with high-N plots, inconsistent with predictions of the hypothesis. Hedwall et al. (2011) examined fertilized and unfertilized plots in forest stands of middle and southern Sweden to assess effects of N on herb layer composition and species richness. Fewer vascular plant species were observed on fertilized plots than on control plots, although numbers of bryophyte species remained unchanged. These authors reported support for the N homogeneity hypothesis, finding that fertilized plots also showed a lower variance in species composition and a lower Shannon's diversity index than unfertilized plots. Indeed, fertilized plots were more similar to each other than unfertilized plots were to each other over the geographical range (Hedwall et al. 2011). García-Palacios et al. (2012) added another dimension to this response—belowground processes—in a synthesis study that strongly supported the N homogeneity hypothesis.

In contrast to the lack of herb layer response at Fernow Experimental Forest, West Virginia, following two and six years of N additions to WS3 (Gilliam et al. 1994, 2006;

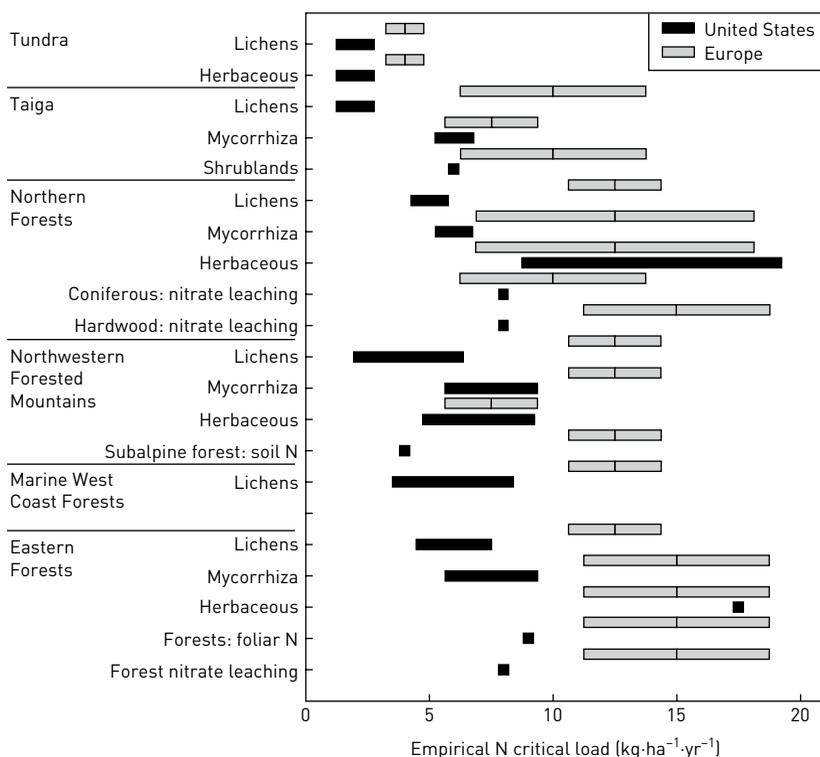


FIGURE 20.4 Empirical critical loads for nitrogen in Europe and the U.S. Taken from Pardo et al. (2011); used by permission.

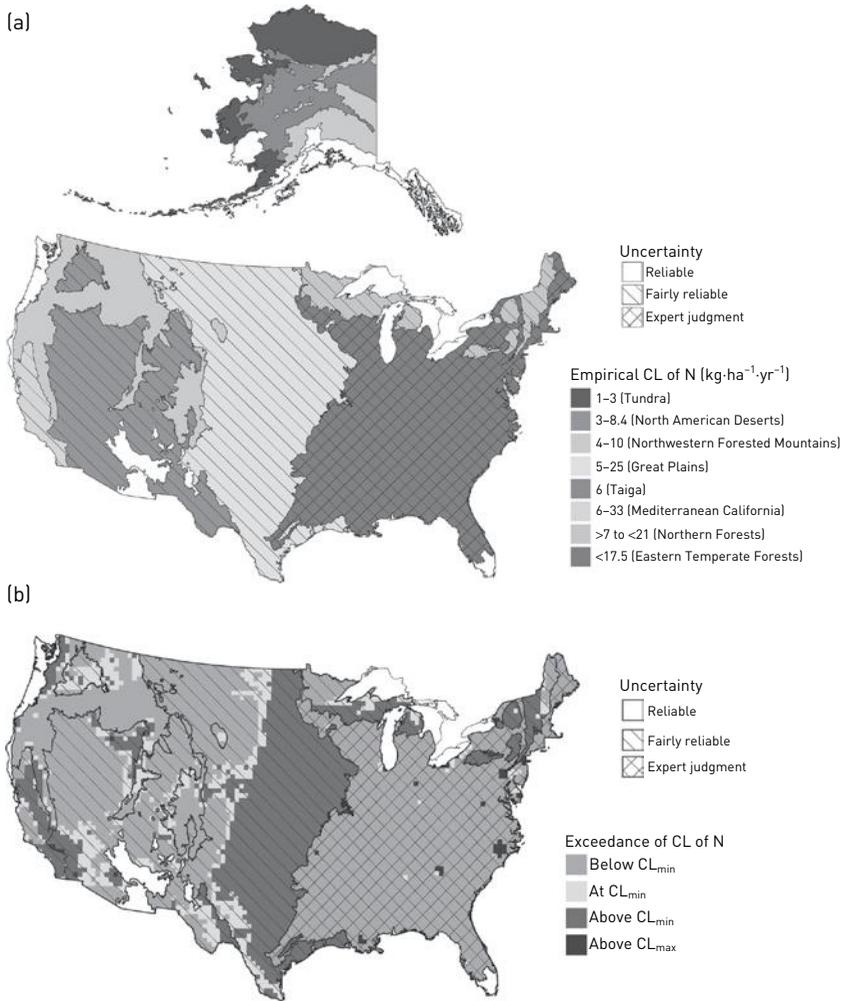


FIGURE 20.5 Maps of (a) critical loads of N for herbaceous plants and shrubs by ecoregion in the U.S., and (b) exceedances of N for herbaceous plants and shrubs by ecoregion in the U.S. Taken from Pardo et al. (2011); used by permission.

respectively), Gilliam (2014) reported reductions in species diversity—related both to decreased richness and evenness—following 14 years of treatment. This was primarily related to increases in cover of clonal *Rubus* spp., which was initially (1991) a minor component (~ 1 percent relative cover) of the herb layer, but was ~ 15 percent of the herb layer in 2003. Contemporaneously with these increases in cover, spatial variability of cover of *Rubus* spp. has decreased on WS3, consistent with declines in spatial variability of soil N (Gilliam and Adams 2011), supporting the N homogeneity hypothesis. Other studies (e.g., Strengbom and Nordin 2008; Hedwall et al. 2011) have found excess N-mediated increases in *Rubus* spp. Furthermore, the clonal nature of species, such as *Rubus* spp., has been shown to contribute measurably to increases in homogeneity of herb layer composition. For example, Eilts et al. (2011) found strongly consistent negative effects of clonal plants on species richness of herb-dominated communities, effects that were greatest at high fertility and when soil resources were applied at a scale at which rhizomatous clonal species could integrate across resource patches.

CRITICAL LOADS FOR N DEPOSITION

Recent integrative models to study the effects of N on plant diversity are being incorporated into determination of *critical loads* for N deposition. This is a concept developed originally in Europe, but it is now being used in North America (Pardo et al. 2011). By definition, the critical load for N is the level of N deposition below which there are no harmful ecological effects of excess N. Critical load is distinguished from *target load*, which is the level of N deposition established by policymakers to protect sensitive ecosystems, considering such criteria as economic costs for reduction of N emissions. Critical loads are generally determined via three approaches: empirical (based on observations, such as those reviewed above), simple mass balance (using inputs/outputs of N), and dynamic models (expanding the steady-state models by incorporating internal feedbacks, including ecosystem N accumulation). Until recently, critical load approaches have been largely based on N biogeochemistry (e.g., examining effects on base cations, soil fertility, and foliar chemistry). However, more recent studies have begun to include effects of N on plant biodiversity as a major response variable and critical load criterion (Nordin et al. 2005; Bobbink et al. 2010; Posch et al. 2011; Pardo et al. 2011). Based on results taken from Pardo et al. (2011), examples of critical load determinations are given in figs. 20.4 and 20.5. From these data, it appears that much of the eastern U.S. is below critical loads for N.

CONCLUSIONS

It is clear that excess N has the potential to substantially alter species composition and decrease biodiversity of the herbaceous layer of forests of eastern North America, and to do so in ways that are distinctive from other forms of forest disturbance. The literature is replete with studies confirming that increasing N in forests from N limitation to N saturation can not only alter soil N biogeochemistry and deplete nutrient cations, but it can also (1) alter competition to give advantages to fewer nitrophilous species, (2) increase intensity and degree of herbivory, (3) increase frequency of mycorrhizal infection, (4) increase occurrence and severity of fungal pathogens, and (5) enhance species invasions. Such responses of all these processes can contribute to N-mediated changes in forest herb layer community dynamics.

The N homogeneity hypothesis that predicts loss of biodiversity in forest ecosystems experiencing chronically elevated N deposition has largely been supported in the literature, as several studies have reported increased soil N heterogeneity—coupled with declines of herb layer diversity—with increasing N supply, particularly at the stand and landscape scales. As this is a hypothesis that is easily tested through manipulative field studies, I suggest that more studies be carried out to examine its application in a variety of forest types, particularly in eastern North America, where rates of N deposition can be notably high. Indeed, given the dearth of studies within this region on the effects of N on herb layer diversity, especially relative to more numerous studies carried out in Europe, I strongly urge that more emphasis be placed on such investigations in general, both by biogeochemists and vegetation scientists.