

Ecological issues related to N deposition to natural ecosystems: research needs

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Abstract

There has and continues to be concern about the effects of elevated nitrogen (N) deposition on natural ecosystems. In this paper, research on natural ecosystems, including wetlands, heathlands, grasslands, steppe, naturally regenerated forests and deserts, is evaluated to determine what is known about nitrogen cycling in these ecosystems, the effects of elevated nitrogen on them and to identify research gaps. Aquatic ecosystems are not included in this review, except as they are part of the larger ecosystem. Research needs fall into several categories: (1) improved understanding and quantification of the N cycle, particularly relatively unstudied processes such as dry deposition, N fixation and decomposition/mineralization; (2) carbon cycling as affected by increased N deposition; (3) effects on arid ecosystems and other “neglected” ecosystems; (4) effects on complex ecosystems and interactions with other pollutants; (5) indicators and assessment tools for natural ecosystems.

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1. Introduction

Elevated nitrogen (N) deposition has been identified as a critical environmental concern of global proportions (Vitousek et al., 1997). I have been asked to cover the ecological issues related to N deposition to natural ecosystems. First, let me define “natural ecosystems”. There are very few truly “natural” or “pristine” ecosystems left on this planet, if we define natural as untouched by human impacts. However, if we define natural as unmanaged or relatively unmanaged, then I can identify biomes or large-scale ecosystems that we will consider as natural ecosystems. I am defining ecosystems at a rather large spatial scale, thus neglecting any discussion of microbial ecosystems, except as they might occur within the larger ecosystems. This does not mean these microbial systems are insensitive. For example, Wallenda and Kottke (1998), in their review of the relationship between ectomycorrhizae and N, concluded that effects are most obvious on the formation of fruiting bodies. However, they caution that this could reflect the relative lack of study of the below-ground effects as well as the apparent sensitivity of fruit bodies. The lack of understanding of effects of

N deposition on micro-ecosystems is an important research gap that is identified here but not discussed in any detail.

Examples of natural ecosystems that could be considered include water bodies (e.g., estuaries, lakes), deserts, wetlands (in all their diversity: e.g., bogs, wet heaths, fens, swamps), grasslands/prairies/steppes, heathlands, shrub lands, tundra and naturally regenerated forests. Aquatic ecosystems are not addressed in this analysis. Acidification of surface waters as a result of acidic deposition has been documented (Turner et al., 1990), and recovery, as sulfate deposition levels have decreased, has validated our understanding and modeling of this process (Stoddard et al., 1999). Eutrophication of estuaries as a result of high N loads, leading to hypoxic and anoxic zones, has been documented and is a serious concern (Paerl and Whitall, 1999). Note, however, that until recently, N deposition to large water bodies was relatively unquantified, so the extent of the impact from deposition is not well known. Recent data show that 15–35% of N in 40 estuarine systems in the USA derives from wet and dry deposition (Alexander et al., 2000).

Eutrophication occurs when N accumulates in an ecosystem. Many natural systems are N-limited, particularly those with high carbon accumulation, such as peatlands and tundra ecosystems, and therefore accumulate N. Fertilization with N increases available N, and can increase growth and productivity of some ecosystems. When the plants,

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animals and microbial biota are unable to utilize all of the available N, the system may be considered N-saturated, although there are several definitions of N saturation (Agren and Bosatta, 1988; Aber et al., 1989; Stoddard, 1994). Generally, N-saturated ecosystems can be thought of as those with a long-term amelioration of N limitations on biotic activity, along with a decrease in N retention capacity. Nitrogen-saturated terrestrial ecosystems that have been identified include a number of forest types (Stein and van Breemen, 1993; Peterjohn et al., 1996; Fenn et al., 1998), alpine tundra (Baron et al., 1994; Williams et al., 1996), chaparral (Riggan et al., 1994) and riparian wetlands (Hanson et al., 1994).

Symptoms of N saturation include elevated concentrations of nitrate, aluminum and hydrogen in surface waters, increased incidence of frost damage or other disrupted physiological functions, increased emissions of trace gases and increased cation leaching from the soil (Aber et al., 1989). As N saturation increases, growth and production decline and mortality may increase (Aber et al., 1995; McNulty et al., 1996).

Some of these symptoms have been demonstrated as a result of elevated deposition of N in natural ecosystems (Fenn et al., 1998). Other processes, particularly at the community level, are less well understood or have been studied in more managed ecosystems. It is particularly important to understand the implications of research on elevated N deposition for natural ecosystems, to identify areas where we do not understand these implications and to

address research gaps. Specifically, I was asked to identify research needs. From a very informal survey of colleagues in forest soils, and from my own review, I have placed these research needs into five categories: (1) the nitrogen cycle, (2) carbon cycling, (3) effects on arid and other neglected ecosystems, (4) effects on complex ecosystems and complex effects and (5) indicators. I will discuss what we do know about these topics and where I perceive the research gaps to be.

2. The nitrogen cycle

To better understand the effects of N deposition on ecosystems, we need to know how N moves through ecosystems and the processes involved in N cycling, and we must be able to quantify these reliably. Although a great deal of time and energy has been spent researching and quantifying the nitrogen cycle, in many different ecosystems (Clark and Roswall, 1981; Binkley et al., 2000), gaps still exist in our understanding of the components and rates of N cycling (Fig. 1). For example, one gap that is common to most natural ecosystems is the inability to accurately measure inputs of N. Nitrogen inputs can come in deposition (wet and dry), N_2 fixation (both symbiotic and associative), and, rarely, from geologic sources (Dahlgren, 1994). Inputs of N via dry deposition are seldom measured. Lovett (1992) measured wet, dry and fog deposition in several forested ecosystems and estimated dry deposition to be approxi-

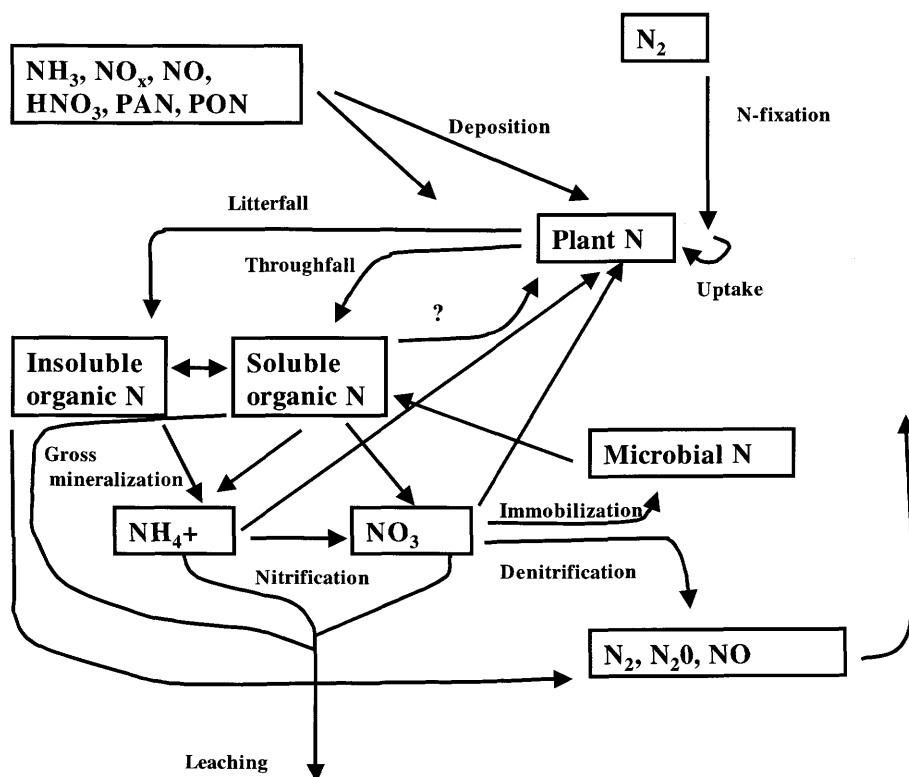


Fig. 1. Detailed N cycle. Adapted from Fisher and Binkley (2000).

mately 50% of the total N load at those sites. In other ecosystems, such as those in Mediterranean climates, the contribution of N from dry deposition may be almost 20 times greater than that from wet deposition (Fenn and Bytnerowicz, 1993; Bytnerowicz et al., 1996). In polar deserts of the high Arctic, it is believed that appreciable amounts of N are imported in feces of sea birds (Richter and Arndt, 2000), but little quantification has been done. Locally, deposition or capture of N from fog may be important, but its relevance on a larger scale is not well quantified.

Nitrogen fixation can contribute significantly to the available N pools in some natural ecosystems. Red alder (*Alnus rubra*) was found to contribute 50–150 kg N ha⁻¹ year⁻¹ (Binkley et al., 1994), a sufficient amount to create conditions of N saturation (van Miegroet and Cole, 1984; Fenn et al., 1998). Black locust (*Robinia pseudoacacia*) contributed from 35 to 300 kg N ha⁻¹ year⁻¹ (Boring and Swank, 1984). Most forest understory plants fix much lower amounts of N (<5 kg ha⁻¹ year⁻¹). In alpine tundra, in the Colorado Front Range, contributions from N-fixing plants were found to be a significant proportion of the N inputs to the community (Bowman et al., 1994, 1996) despite wide spatial heterogeneity in cover. Relatively few data exist for nonsymbiotic soil N fixation, but it is generally believed to be low (Binkley et al., 2000). However, in desert ecosystems cyanobacteria, bacteria and lichens comprising cryptobiotic crusts may be the primary source of N, through N fixation (Evans and Ehleringer, 1993).

Uptake by plants is an important retention mechanism, but is poorly quantified for most natural systems, and interactions at the leaf surface are poorly understood. Atmospheric N not only increases soil N but also results in exposure of vegetation surfaces to elevated levels of gaseous and particulate N, with subsequent deposition or interaction with leaf surfaces. Bytnerowicz et al. (1998) estimated capture of N by branches in conifer forests of Southern California, and found leaf capture of N in fog droplets could be locally important (Lovett, 1992). Storage of nitrogen is also poorly quantified. For example, in some forests, storage in understory vegetation can be significant relative to the understory (Fenn et al., 1998), but this has been investigated in only a few forests. This inability to measure uptake and storage precisely has led some forest soil scientists to speculate on “occult N”-accretion rates of N considerably greater than measured. These are often attributed to free-living N fixation organisms or other unmeasured variables, but they also may be attributed to uncertainty in our measurements (Binkley et al., 2000).

Organic forms of N are poorly quantified, and the cycling of organic N is not well understood for most ecosystems. For example, deposition of organic N is seldom measured, but can make up about 1/3 of the total N in bulk deposition (Morris, 1991). As another example, it is not known whether uptake of organic N is significant in forest ecosystems (Fisher and Binkley, 2000). However, many wetland plants can utilize organic N as well as low-molecular-mass amino

acids (Jonasson and Shaver, 1999), and ericaceous dwarf shrubs can utilize N from organic sources through their fungal symbionts (Read, 1993). The importance of dissolved organic nitrogen (DON) in streamwater exports for many natural ecosystems is not known, nor have the controls (particularly processes like non-biological incorporation into humus) been clearly elucidated. Dissolved organic N has been shown to be a major vector for N loss in old-growth forests (Sollins et al., 1980; Hedin et al., 1995). However, data from other forest sites suggest that DON export, expressed as a percent of total N export, decreases as total N leaching increases (Fisher and Binkley, 2000). Similarly, Currie et al. (1996) reported that the percent of DON in leachate from red pine (*Pinus resinosa*) and mixed hardwood stands decreased in response to fertilization. The vast majority of N in wetlands is in organic form, contained either in vegetation (live plants), plant detritus, macrofauna, micro-organisms, soil (soil organic matter or peat) or water (dissolved organic compounds or suspended sediments). Due to the rapid biological uptake of nutrients and extensive production of organic matter, wetlands generally export more organic N than inorganic N, even though nutrient inputs are often largely in inorganic form.

Outputs of nitrogen in soil solution and streamwater have been reasonably well quantified for a number of ecosystems, with the exception of DON, as described above, with considerable research conducted in forest ecosystems. However, the ecosystem attributes that control the accumulation and export of N in ecosystems are not sufficiently understood to produce reliable predictive models. Other forms of N loss, and their responsiveness to elevated deposition, are not as well quantified. For example, what are the effects of elevated N deposition on emissions of gaseous N? It has been suggested that N saturation of terrestrial ecosystems may drastically alter fluxes to the atmosphere of a number of radiatively active gases (CO₂, NO, NO₂, CH₄) (Fenn et al., 1998). The process of denitrification is a particular concern because the outcome is the production of nitrous oxide, which can react with ozone, potentially reducing the quantity of stratospheric ozone (Schimel, 1995). Denitrification requires low-oxygen conditions, such as those found in wetlands. Thus, it is surprising that losses of N via denitrification can be rapid in desert ecosystems, following precipitation events, approaching those of more mesic ecosystems (Peterjohn and Schlesinger, 1991; Evans and Belnap, 1999). In the forests of eastern North America, nitrous oxide seems to be the dominant trace gas produced in soil (through denitrification), while in southern California, NO emissions and nitrification are much more important (Fenn et al., 1998). Fertilization with N often leads to large increases in nitrous oxide production (Field et al., 1992). Although the effects of elevated N deposition on denitrification rates have not been well quantified in most natural ecosystems, a stimulation of nitrous oxide production might be expected (Goulding et al., 1998). Fertilization with N can also result in volatilization of ammonia, urea and other

forms of N. Gaseous losses have not been quantified for many natural systems, nor have natural (background) rates of loss been established for most ecosystems.

It may seem to the reader that nothing much is known about the N cycle. The N cycle, while fairly complex, is probably understood conceptually. Nitrogen budgets have been constructed for most natural ecosystems. However, the rates of the various processes are not quantified with much certainty. This is partly due to the dynamic nature of these processes, both temporally and spatially. Nitrogen cycling varies with temperature, moisture, disturbance (fire simultaneously affects inputs, storage and outputs, for example), and can even be expected to vary with successional stage (Reiners, 1981). In addition, the importance of the various processes varies among ecosystems. Continued refinement of the N cycle is needed and will require diligence to characterize the N cycle sufficiently so that reliable predictive models can be developed, much as they have been for the relatively simpler sulfur cycle.

3. Carbon cycling and utilization

In highly regulated production agriculture and one can include plantation forestry in this category, application of nitrogen fertilizers can increase growth or crop production. Since productivity of many natural ecosystems is limited by available N (Vitousek and Howarth, 1991), we can ask whether ambient rates of N deposition are sufficient to similarly alter productivity in natural ecosystems and significantly affect carbon cycling. There is great interest in this question now, particularly in relation to forests and the ability of terrestrial ecosystems to sequester and store carbon (C). There are areas of Europe where N deposition is significantly greater than in pristine areas, and where plant growth is believed to have increased as a result of elevated N deposition (Kauppi et al., 1992; Eriksson and Johansson, 1993). Increases in productivity may be achieved through changes in photosynthetic rates, altered carbon allocation or increases in leaf area (Tschlapinski and Norby, 1991; Medlyn and Dewar, 1996). Increased productivity in response to nutrient additions has been documented for northern freshwater wetlands (Chapin, 1980; Craft and Richardson, 1997). Li and Vitt (1997) reported that N additions increased production of two mosses (*Sphagnum fuscum* in a bog and *Tomethypnum nitens* in a rich fen) but not of two shrubs [common Labrador tea (*Ledum groenlandicum*) nor dwarf birch (*Betula pumila*) in the fen], suggesting multiple controls on productivity in these systems and the potential for differential responses. Numerous studies have evaluated the relationship between productivity and nutrients, particularly N, in grasslands. Generally, N fertilization will lead to increased productivity (Tilman, 1987; Bobbink, 1991; Tilman et al., 1994; Mamalos et al., 1995). However, additions of N did not increase biomass production in two native desert grasslands (White et al., 1990).

On a global scale, the extra storage of C due to atmospheric N deposition is estimated at 1 pg C year^{-1} (Norby, 1998). Most of that is attributed to storage in forest biomass, but there is uncertainty around that value, and the positive effect of N deposition on C sequestration declines as an ecosystem approaches N saturation and N retention decreases.

Elevated deposition of N may also affect soil C cycling—litter and soils were the major sinks of N identified in a review of forest fertilization studies (Johnson, 1992). Decomposition of organic matter may be affected by N deposition. Many studies have reported increased litter decomposition rates as a result of N fertilization of forests (Aber et al., 1989; Fenn, 1991), while other studies have reported slower decomposition (Adams and Angradi, 1996; Magill and Aber, 1998). Finally, there is some evidence that elevated N deposition may also inhibit methane production (Neff et al., 1994; West et al., 1998). For policy makers, this area probably needs more research to refine numbers and extend our understanding to other natural ecosystems.

4. Effects on arid ecosystems and other neglected ecosystems

Arid and semiarid lands cover about a third of the earth's land surface, yet there is relatively little research on N deposition effects on arid ecosystems. Searches of several extensive online databases revealed only a handful of publications on N cycling in deserts, mostly from deserts in the Southwestern US, and even fewer publications evaluated air pollution or fertilization effects on arid ecosystems. Because water is limited, the N cycle is different than in humid regions and not dominated by surface flows or wet deposition. Research conducted in the forests of southern California, a Mediterranean climate, suggests that dry deposition of N is 20 times as great as that from wet deposition, and is sufficient to lead to N saturation (Fenn et al., 1996). Effects of elevated N on coastal sage scrub and chaparral ecosystems have also been documented (Allen et al., 1998; Riggan et al., 1994). However, the impacts on most components of desert ecosystems are poorly understood. As mentioned earlier, many arid systems in the Western US and in the Arctic have traditionally been dominated by N-fixing components of cryptobiotic crusts that can represent 70% of the living cover in these deserts. Nitrogen fixation and N losses are very high in the vicinity of these crusts during and after precipitation events. Because arid ecosystems are often N-limited, the potential for significant impacts on N cycling and productivity is high. However, research on the effects of added N from atmospheric deposition on these desert ecosystems is limited to the temperate deserts of the Southwestern US. Other "hot" deserts and cold polar deserts have received scant research attention. Community composition research is particularly lacking in deserts.

Tundra ecosystems have received more research attention (Williams et al., 1996; Bowman et al., 1995; Baron et al., 1994), but much of the research on these ecosystems is in its early stages and comes from very few sites. There is a notable paucity of research evaluating N deposition effects on North American wetlands, although much fine research has been done on European wetlands. It is noteworthy that, whereas many European wetlands are thought of as limited by a single factor (generally N, but sometimes P), the few studies of North American wetlands show these are limited by multiple factors (Bedford et al., 1999).

5. Complex effects on complex ecosystems

The ecological literature is rife with studies of N effects on productivity and diversity of grasslands (van Hecke et al., 1981; Tilman, 1987; Bobbink, 1991; Mamalos et al., 1995). Fertilization of forest plantations has been studied extensively, if not always in great depth. However, the effects in more complex ecosystems (e.g., mixed-species forests, shrub lands or the more diverse wetlands) have not been extensively studied, particularly in North America. Unlike Europe, few studies of herbaceous or forested wetlands from North America have included direct measures of both nutrient availability and species diversity of bryophytes and vascular species. The effects of elevated N on complex ecosystems are likely to be manifest through differential direct effects, changes in reproductive success, altered herbivory, and/or altered competitive relationships. All of these could significantly change the nature and functioning of mixed species vegetative ecosystems.

Little evidence exists for direct toxic effects of elevated N deposition to trees and larger vegetation, except at very high inputs: ammonium deposition approaching $150 \text{ kg N ha}^{-1} \text{ year}^{-1}$ was found to cause mortality of Scots pine (*Pinus sylvestris*) in Europe (Fangmeier et al., 1994). A notable exception to the lack of toxic effects at ambient soil levels was reported for California sage (*Artemisia californica*), where nearly 100% mortality in a greenhouse was observed at soil N levels approximating those of field soils in polluted areas (Allen et al., 1998). However, excess N has been found to have direct toxic effects on a variety of ground vegetation. Some *Sphagnum* species are particularly sensitive (Morris, 1991). Moss cover at four wooded sites in the Scotland was found to decrease with increasing N deposition (Pitcairn et al., 1998). Declines in bryophytes and lichens (Bobbink et al., 1998; Lee and Caporn, 1998; Turkington et al., 1998) have been attributed to fertilization with N. Because lichens and bryophytes have little or no protective cuticle, they may be particularly susceptible to direct toxic effects. Thus, in a complex community, sensitivity to elevated N may vary among life forms, and the eventual results at the community level are difficult to predict.

Changes in seed production/reproduction have been documented in response to elevated N levels and could alter

complex communities. For example, nitrogen fertilization of heather (*Calluna vulgaris*) resulted in an increase in the number of flowers per shoot, greater density of flowering shoots and increased mass of individual seeds (Lee and Caporn, 1998). However, this was a short-term response, in an apparently N-deficient site. Significant changes in reproductive output of crowberry (*Empetrum nigrum*), in a sub-Arctic pine-birch forest, were reported as a result of nitric acid applications (Shevtsova and Neuvonen, 1997). The mass of individual berries was reduced, as were the number and yield of berries per unit of plant. Turkington et al. (1998) documented no change in cone or seed production of white spruce (*Picea glauca*) in Canada as a result of fertilization with NPK fertilizer. However, in seed orchards of loblolly pine (*Pinus taeda*), summer applications of ammonium nitrate are used to promote flowering (Schultz, 1997). Although relatively less information is available about hardwood tree species, Long et al. (1999) reported an increase in sugar maple (*Acer saccharum*) flower and seed production in response to applications of dolomitic lime, suggesting that low available Ca and Mg resulting from N saturation could adversely affect reproduction.

Herbivory by ungulates and rodents has been found to increase as a result of fertilization with N (Barrett, 1979; Severson and Medina, 1983; Hobbs et al., 1988). The higher nutrient content makes the vegetation much more attractive to herbivores. Selective browsing of particularly nutrient-rich species may also occur after fertilization (Gibbens and Pieper, 1962; DiTomasso and Aarssen, 1989). Insect herbivores, including many introduced exotic species such as gypsy moth (*Lymantria dispar*), also pose problems due to preferential grazing of higher N content vegetation. Additions of ammonium sulfate fertilizer to a hardwood-forested watershed in West Virginia, US, increased canopy arthropod abundance, particularly those classified as chewers (macro-lepidoptera, Curculinidea and Chrysomelidae; Butler, 1999). This increased abundance was believed to be related to higher levels of N-rich compounds, particularly amino acids, in the foliage. *C. vulgaris* plants receiving N fertilization were more severely damaged by the heather beetle (*Lochmae suturalis*) than plants in nonfertilized plots (Heil and Diemont, 1983). Significant outbreaks of heather beetle can open large areas of canopy and increase light penetration, which leads to enhanced growth of understory grasses such as wavy hair-grass (*Deschampsia flexuosa*) or purple moor-grass (*Molinia caerulea*) (Berdowski and Zeilinga, 1987; Pitcairn and Fowler, 1995; Bobbink et al., 1998).

Because herbivory may differentially affect species in a stand and affect tree health and regeneration capacity, changes in species richness or evenness can occur. Effects can be subtle (decreased vigor) to catastrophic (widespread mortality and loss of one or more species).

Competitive relationships may be affected through altered nutrient regimes, preferential herbivory, changes in microclimate, altered growth patterns, or altered stand structure. Effects may be manifested through changes in species rich-

ness, evenness or both (DiTomasso and Aarssen, 1989). For example, Bobbink et al. (1998) reported that long-term N enrichment from acidic deposition led to competitive exclusion of naturally occurring species by more nitrophilic plants, particularly under nutrient-poor conditions. An increase in nitrophilic species, which are often tall and densely growing, can result in decreased competitive ability of small and slow-growing species (Falkengren-Grerup, 1986) and eventual declines in diversity. A similar response was observed when tundra was fertilized (Bowman et al. 1995). They reported a shift from forb-dominated to grass-dominated communities, due to the greater capacity of alpine graminoids to sequester N. A reduction in species number and the increasing dominance of a few grass species, in response to N fertilization, have been well documented in the Rothamsted Park Grass experiment (UK) (Tilman et al., 1994) and at the Cedar Creek Long-Term Ecological Research Site in Minnesota (US) (Inouye and Tilman, 1995). On extremely nutrient-poor soils, on the other hand, species richness may increase as a result of N enrichment because of invasion by exotic species (Bobbink et al., 1998). The exotic species often become extremely good competitors with slight increases in fertility.

Legumes may be particularly susceptible to N-induced competition effects. Fertilization with NPK was found to eradicate a leguminous species [birdsfoot trefoil (*Lotus corniculatus*)] from a meadow community, while common bent grass (*Agrostis capillaris*) populations increased (Zarzycki, 1983). In the same study, additions of P, K, Na and Mg without N encouraged the growth of leguminous species such as meadow vetchling (*Lathyrus pratensis*) and red clover (*Trifolium pratense*).

Significant changes in soil fertility could alter competitive relationships among wetland plants and threaten species adapted to those infertile habitats (Bobbink et al., 1998). Both N and P were implicated in decreasing the cover of *Sphagnum* in peatlands in Sweden (Backeus, 1980). In Dutch heathlands, van Breemen and van Dijk (1988) documented an increase in grass species at the expense of ericaceous species as a result of high N deposition, a trend also documented by Berendse and Elberse (1990). In the first half of the 20th century, the evergreen dwarf shrub cross-leaved heath (*Erica tetralix*) dominated most wet heathlands in the Netherlands. During the last 20–30 years, the perennial grass *M. caerulea* has increased in abundance in these heathlands to the point that most *Erica*-dominated communities have been replaced by monocultures of *Molinia*.

Although forest communities have received less research attention than grassland or wetland communities, no studies have been identified that have documented changes in tree species composition in response to elevated N. However, several studies have identified changes in ground/field layer vegetation of forests as a result of altered nutrient status. In conifer forests in Europe, an increase in grasses such as *D. flexuosa* and herbs such as chickweed wintergreen (*Trientalis europaea*) has been documented in response to

fertilization with N or N plus lime (Nams et al., 1993; Kellner and Redbo-Torstensson, 1995; Hallbäck and Zhang, 1998). Nitrogen additions to boreal spruce stands resulted in increases in nitrophilous species, such as *D. flexuosa*, and decreases in dwarf shrubs, such as *Vaccinium* spp., and other ericaceous plants (Mitka, 1987; Kellner and Redbo-Torstensson, 1995; Pitcairn et al., 1998) through altered competitive relationships. Turkington et al. (1998) noted changing understory species composition in Canadian spruce stands due to increased cover of graminoids such as *Festuca* and herbs such as *Epilobium*, with N additions. Also noted were decreases in N-fixing vegetation (*Lupinus*, *Peltigera*) (Turkington et al., 1998). Rainey et al. (1999) noted a decrease in biomass and abundance of Canada mayflower (*Maianthemum canadense*) and hay-scented fern (*Dennstaedtia punctilobula*) after 7 years of fertilization of a red pine (*P. resinosa*) plantation in Massachusetts (US). These decreases resulted in changes in relative abundance of all understory species.

Changes in floristic composition of ground vegetation have also been noted in hardwood forests and attributed to altered competitive relationships. Falkengren-Grerup (1986) surveyed 34 deciduous forests in southern Sweden, originally surveyed in 1949–1970, and reported significant increases in the number of species present and in the cover of nitrophilic species. The increase is mainly due to new species appearing in later surveys, in particular, species with high nitrogen demands, such as narrow-leaved fireweed (*Chamaenerium angustifolium*), raspberry (*Rubus idaeus*), wood stitchwort (*Stellaria nemorum*) and ground elder (*Aegopodium podagraria*). Thimonier et al. (1992) reported an increase in nitrophilous species in response to N in a mixed hardwood forest in France. Lovett and Rueth (1999) reported that beech (*Fagus grandifolia*) and sugar maple (*A. saccharum*) respond differently to N accumulation from atmospheric deposition. These differences could affect overall stand/ecosystem response.

Many of the research studies reported here were single-factor studies. Although enlightening, these studies do not tell us much about ecosystem function in a complex environment ('the real world'). The interaction of atmospheric N with other factors needs more research. For example, N fertilization can increase tree growth (Auchmoody and Smith, 1977; Lamson, 1988; Nams et al., 1993; Turkington et al., 1998), leading to a denser canopy that could lead to light limitations of field layer species (Kellner and Redbo-Torstensson, 1995; Högbom and Högborg, 1991). Carroll et al. (1999) documented such reductions in abundance of bryophytes and lichens on and under *C. vulgaris* as a result of changes in the structure of the canopy that decreased light penetration. In addition, in mixed species stands, some tree species respond to fertilizer while others do not (Lamson, 1988) resulting in differential growth and changes in stand characteristics. Other elemental deficiencies or toxicities may be exacerbated by atmospheric N deposition or may moderate the response. For example, high N deposition in

the Netherlands apparently induced a phosphorus deficiency in Douglas-fir (*Pseudotsuga menziesii*) stands (Mohren et al., 1986), and Bowman et al. (1995) found N and P colimited production in Colorado wet meadows.

The sensitivity of various organisms to the mix of pollutants to which they are exposed (the interaction of N with other air pollutants) has not been well studied. The interaction between N deposition or N gases and ozone on vegetation or other organisms has been investigated; however, most of these studies involved individual plant species in controlled settings. For example, growth of current-year foliage of loblolly pine (*P. taeda*) was more sensitive to elevated ozone concentrations when seedlings were grown in soils with higher levels of N (Tjoelker and Luxmoore, 1991). However, the influence of ozone on foliar carbohydrates of red spruce (*Picea rubens*) saplings was not modified by foliar N level (Amundson et al., 1995). Bäck et al. (1996) reported a negative interaction of nitrous oxide and ozone on birch (*Betula pubescens*). Photosynthesis was inhibited at lower exposure of the combined pollutants than for each gas alone.

Finally, the interactions of N with changing atmospheric carbon dioxide concentrations, and a changing climate, need to be understood. Research on tundra ecosystems in Alaska suggests that climate change is already affecting species composition in this particularly sensitive ecosystem, and the interaction with N may be difficult to separate.

6. Indicators/assessment tools

How can we tell if we have a problem, and how can we assess its magnitude? What useful information can we provide to policy makers? What are the indicators of ecosystem change? A number of variables have been used to assess N saturation and N status of ecosystems. Export of nitrate in streamwater is one that is commonly used (Aber et al., 1989; Stoddard, 1994; Fenn et al., 1998). However, natural streamwater concentrations and export of nitrate are not well quantified for all natural ecosystems, nor is it an applicable indicator for all ecosystems. For example, loss by leaching to groundwater or in streamwater is very low in arid ecosystems (Peterjohn and Schlesinger, 1990). Likewise, surface runoff is usually considered nil in deserts, although N losses during infrequent hydrologic events is not well quantified. Our ability to predict streamwater nitrate concentrations or exports is limited and the focus of much ongoing research. Williard et al. (1997) reported that total N in the upper 10 cm of the mineral soil was the best single predictor of nitrate exports within the Appalachian/mid-Atlantic region. In the Integrated Forest Study, however, N mineralization was the factor most highly correlated with nitrate leaching (van Miegroet et al., 1992). There is probably no single best indicator of N status of an ecosystem, but rather a suite of variables that can be used together to indicate status. Fenn and Poth (1998) proposed such a

suite of nutrient-cycling parameters that would serve as indicators of forest N status for western US forests. The list included nitrate concentrations in foliage and soil, foliar N:P, soil C:N, stream nitrate concentrations and fluxes and plant growth response to additional N.

The critical loads concept was developed to quantify the environmental effects of air pollutants and to facilitate regulation of emissions of air pollutants, and has been used most widely in Europe. A critical load for nitrogen has been defined as “the highest load that will not cause chemical changes leading to long-term harmful effects on the most sensitive ecological systems” (Nilsson, 1986). Establishment of these critical levels has raised numerous questions and identified research needs, while stimulating much discussion among scientists. Pardo and Driscoll (1993) reviewed four mass balance methods used for calculating critical loads for nitrogen deposition for forest ecosystems and identified several deficiencies and limitations. Many data gaps were found to exist, requiring extrapolation from the relatively few site-specific data. The proposed critical load figures in Europe have tended to be set successively lower as research methods improved and data became available (Swedish NGO Secretariat on Acid Rain, 1998). A related issue is the identification of natural or background levels of the indicators used, for example, leaching of nitrate to groundwater or streams. As mentioned earlier, rates of N input are not well quantified for all ecosystems, and setting critical loads without knowing current levels accurately, or without understanding “natural” levels, may be counterproductive.

A major conclusion of Pardo and Driscoll's (1993) analysis was that, because of the complexity of the N cycle, it is not possible to obtain a single critical load for the whole ecosystem. One needs to synthesize several critical loads, reflecting different components of the ecosystem, different ecological effects of elevated N deposition or different management histories. For example, as *Sphagnum* is probably more sensitive to elevated N deposition than the trees under which it grows, critical loads based on the sensitivity of trees may not be appropriate if *Sphagnum* is a critical part of the ecosystem. This raises the question, what is the most sensitive receptor? Within a broad geographical area, or political boundary, what is the most sensitive ecosystem, and how do we quantify that? In addition, critical loads are established for single pollutants. If synergistic effects occur between pollutants, the critical levels should reflect this.

7. Conclusions

Clearly, there are gaps in our knowledge of atmospheric N effects on natural ecosystems. A more rigorous accounting of the N cycle in all natural ecosystems would address many of these deficiencies. Additional work on interactions within complex terrestrial ecosystems, and with complex atmospheric environments, is clearly needed. There are

some very specific research questions to be addressed, and some natural ecosystems that require more specific research.

A glaring omission in this discussion of effects on terrestrial ecosystems is the lack of discussion of effects on fauna. This discussion has focused almost exclusively on the vegetative component of terrestrial ecosystems. Research does exist on acid rain effects on some fauna (Graveland, 1990; Longcore et al., 1993; Eeva et al., 1997). One example of a significant effect of elevated N deposition on fauna is illuminating. Elevated ammonium deposition in the Netherlands is credited with leading to a decreased nesting success in the great tit (*Parus major*), due to egg shell thinning. Accelerated leaching of calcium from the soil has decreased calcium availability to snails (the calcium is utilized in building shells). Decreased calcium availability in the prey (snails) has led to lower calcium levels in the predator (the great tit), resulting in thinner, more porous egg shells (Graveland et al., 1994). Long-term effects of declining great tit populations are hypothesized. Fauna that use a particular plant species for food or cover could be negatively affected if increasing N deposition alters vegetative species composition. This is a relatively unexplored field, and therefore a research need. However, I would add that rather than a whole series of dose–response studies on the many and diverse fauna of these ecosystems, a “big-picture” approach is needed. Indeed, a larger perspective is needed to integrate some of the complexities described earlier.

Part of this big picture must include “bigger” temporal scales. Even in studies in annual grasslands, early observation results were not always sustained over longer time periods. In one of the longer term studies on grasslands, more than a decade was needed before equilibrium was reached and conclusions could be drawn (Inouye and Tilman, 1995). Chapin et al. (1993) evaluated responses of arctic tundra to changes in climate and nutrients and found that short-term (3 years) responses were poor predictors of longer term (9 years) changes in community composition. With long-lived tree species with limited rates of dispersal or establishment, or harsh or highly variable climates such as deserts, the outcome of manipulations that alter competitive relationships are not easy to predict based on only a few years of data. One modeling study suggested that elevated N inputs could change the direction of succession from an open oligotrophic bog toward a mesotrophic bog dominated by trees (Logofet and Alexandrov, 1984). Therefore, there is a pressing need for long-term research and monitoring. Such research programs exist (e.g., the Long-Term Ecological Research Program [LTER] and the Intensive Site Ecosystem Monitoring Program [ISEM] of the US Forest Service) and can meet some of the research needs identified here. Indeed, much of the data presented has come from LTER or ISEM sites. Continued support for such research programs is essential.

Integration of individual research sites is necessary, particularly integration across biomes and the artificial

boundaries that we have created (out of necessity) to simplify our research. The interactions across and between aquatic and terrestrial ecosystems are particularly poorly charted. A framework for assessing effects over long time-frames and larger spatial areas and rigorous experimental designs are needed to provide important information for scientists, land managers and policy makers.

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