Nitrogen critical loads for terrestrial ecosystems in low deposition areas

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The background document

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Foreword

In this background document I intend to briefly compile mainly empirical research focusing on effects of low doses of nitrogen on plant diversity in boreal and arctic ecosystems. When discussing plant diversity the processes governing growth of different plant species are important. I have in particular considered aspects of ecosystem biogeochemistry directly related to plant growth and interactions between plants and organisms (pathogens and herbivores) damaging them. It is important to keep in mind that ecosystem effects from adding nitrogen are extremely complex. Nitrogen can exist in various chemical forms in the biosphere and one single nitrogen molecule may cascade through various ecosystem compartments having impact on numerous processes. Although questions concerning effects from nitrogen deposition on natural ecosystems currently receive great attention from the international scientific community, not so many studies target biodiversity effects of <u>low</u> doses of nitrogen. This may partly be due to the way research normally is funded. Funding for a field experiment is often very short-time (3 – 5 years) and to be sure that results can be delivered within the funding period, high nitrogen doses are applied. These doses (50 – 100 kg N ha^{-1} yr^{-1}) are often irrelevant when compared to rates of nitrogen deposition currently received over boreal and arctic ecosystems in Europe and north-America (mainly in the range of 2 – 20 kg N ha^{-1} yr^{-1}). Obviously it is difficult, or even impossible, to extrapolate results from an experiment adding 50 kg N ha^{-1} at one single occasion to effects expected from adding 2 kg N ha^{-1} for 25 consecutive years.

 Empirical scientific approaches continuously deliver new knowledge on nitrogen effects on ecosystems. The development within the field needs to be acknowledged both by funding agencies (need to fund long-term nitrogen addition experiments) and by policy makers (need to make sure their decisions are based on sound and relevant science). I hope this workshop will contribute to both.

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Background

In April 2006 a CCE (Coordination Centre for Effects) Nitrogen Workshop was held under the Long Range Transboundary Air Pollution (LRTAP) Convention. The focus was effects of atmospheric nitrogen deposition on biological diversity of natural ecosystems and the connection between nitrogen enrichment and the ongoing climate change. It was clear that within Europe there are different opinions concerning the relevance of current recommended critical loads for nitrogen deposition (se Table 1). For parts of continental Europe with current nitrogen deposition loads sometimes as high as 80 – 100 kg nitrogen ha^{-1} yr^{-1} the current recommendations (in the range 5 to 25 kg N ha^{-1} yr^{-1}) would require a very substantial decrease of nitrogen emissions to the atmosphere. For parts of continental Europe, the U.K. and south Scandinavia currently receiving 10 – 20 kg N ha^{-1} yr^{-1} the recommendations would mean that not much need to be done about current emissions. For north Scandinavian boreal and arctic ecosystems the current recommendations for nitrogen critical loads greatly exceeds the current deposition of 1 – 3 kg N ha^{-1} yr^{-1}. The recommendations thus imply that these ecosystems are well suited to sustain current nitrogen loads, and that there would be no risks associated with even a quite substantial emission increase.

The critical load concept was launched in 1988 in order to evaluate negative effects of nitrogen and sulphur. It states that the critical load of a compound is the deposition load an ecosystem can endure without significant harmful effects according to present knowledge (Nilsson and Grennfelt 1988). For nitrogen it is important to acknowledge that due to the fact that it accumulates in ecosystems, the nitrogen critical load can be viewed as a "moving target". The nitrogen critical load of an ecosystem will depend on (1) *the sensitivity of ecosystem process to excess nitrogen*, and (2) *on the length of time nitrogen deposition will last*. For northern ecosystems, cold climate slows the biogeochemical nitrogen cycle and further strengthens the nitrogen limitation to primary production characterizing most terrestrial ecosystems. Apparently remote boreal and arctic ecosystems currently receiving low levels of nitrogen deposition may in the future confront fundamental changes due to eutrophication. However, so far nitrogen deposition impacts on these ecosystems have received relatively little attention in European air policy negotiation processes.

Introduction

Traditionally impacts of nitrogen deposition on ecosystem processes have focused mainly on soil chemical processes and in particular on nitrogen leaching from ecosystems. Leaching occurs from an ecosystem when the external nitrogen supply exceeds the demand by plants and soil micro-organisms, and when the soil chemical capacity to bind nitrogen has been reached, which means that a situation of nitrogen saturation has been entered (Aber et al. 1989, Aber 1992). However, most boreal and temperate forest ecosystems have a high capacity to retain nitrogen, and over time nitrogen accumulates in the ecosystems. Nitrogen losses by leaching only occur when the capacity of the ecosystem to accumulate nitrogen has been saturated (which may take considerable time if the rate of nitrogen input is low). Nitrogen leaching from Swedish spruce forest has been detected at nitrogen deposition levels of 10 kg N ha^{-1} yr^{-1} (Näsholm et al. 1997) and

according to Dise and Wright (1995) there is a general trend in European forests that leaching is elevated as nitrogen deposition exceeds 9 kg N ha^{-1} yr^{-1}. Even so, nitrogen leaching draws no attention to initial effects of nitrogen deposition, such as effects on biodiversity. Although a very serious indication of ecosystem change, nitrogen leaching therefore appears to be an inadequate estimate to distinguish what is a harmful effect according to the definition of the critical load.

Another way to estimate effects of nitrogen deposition is to monitor biodiversity (i.e. changes in species composition of the vegetation). Nitrogen critical loads considering vegetation change were first set under the LRTAP Convention in 1992 and were revised in 1996 and 2002. Specific critical loads were recommended for different European habitats based on empirical data from field observations and experiments (Table 1).

Table 1. The table lists the current recommended critical loads of atmospheric nitrogen deposition to different European habitats set in respect to that no vegetation change should occur. These values were set by an expert workshop within the LRTAP convention in 2002 (Achermann and Bobbink 2002).

Recommended empirical critical loads for nitrogen (kg/ha/yr) to habitats	
Temperate and boreal forest	10 – 20
Tundra and heath	5 – 20
Grassland and tall forbs	10 – 25
Mire, bog and fen	5 – 20

There are two problems with the recommended critical loads. One is that at least some of the data they are based upon originate from field observations and nitrogen addition experiments performed in areas already exposed to large atmospheric nitrogen inputs for long time periods. It is likely that profound vegetation changes due to increased nitrogen supply took place in these areas prior to the experiments. If nitrogen addition experiments are conducted in areas already subjected to even moderate historical nitrogen deposition, important initial vegetation responses are neglected, and the effect of a certain nitrogen dose is underestimated. Another problem is that very few experiments have been performed applying low doses of nitrogen (< 10 kg N ha- yr^{-1}). So even though there is very little data demonstrating effects on biodiversity from nitrogen doses less than 10 kg N ha^{-1} yr^{-1}, there is even less data showing the opposite.

Aimes of the 2007 Stockholm Nitrogen Workshop

The focus of the workshop will be the influence of nitrogen deposition on ecosystem processes governing the biodiversity of northern latitude ecosystems currently receiving low rates of nitrogen deposition. Main expected results are:

- Guidelines for revised empirical critical loads for nitrogen in terrestrial ecosystems in low-deposition regions,
- Assessment of current scientific status of nitrogen-induced effects on vegetation in terrestrial ecosystems in low-deposition regions,
- Assessment of currently available modeling tools and recommendations for further research.

The conclusions and recommendations from the workshop will be delivered to the LRTAP Convention, in particular, to the International Cooperative Programme (ICP) on Modelling and Mapping (April 2007) and to the Working Group on Effect (September 2007).

Nitrogen deposition impacts on ecosystem processes

The increase of biologically reactive nitrogen in the biosphere is a biogeochemical phenomenon that has consequences for plant species diversity (Gilliam 2006). The linking between biogeochemistry and plant ecology is crucial to understand the consequences of nitrogen deposition on an ecosystem. There are several processes linking biogeochemistry to plant ecology, and vegetation responses to increased nitrogen supply arise from nitrogen inferring with several of these. The following section will briefly summarize the current state of knowledge on how nitrogen addition impacts (1) ecosystem biogeochemistry, (2) plant – soil interactions via mycorrhizal associations, (3) interactions between plants and organisms damaging them (pathogens and herbivores), and (4) plant interspecific competition.

Biogeochemistry

Under normal circumstances input of external biologically reactive nitrogen to boreal and arctic ecosystems is highly restricted. Even so, very few plant species within these ecosystems are capable to form symbiotic relations with N_2-fixing microorganisms. Mainly common boreal forest bryophytes and *Sphagnum* spp. have been found to harbor N_2 fixing cyanobacteria on leaf-surfaces, and it has been estimated that approximately 1.5 kg N ha^{-1} yr^{-1} can be fixed to the ecosystem via continuous moss-carpets (DeLuca et al. 2002). Nitrogen fixed via this pathway does however not become available to higher plants until bryophytes decompose.

The below ground compartment of boreal and arctic ecosystems contain large stores of nitrogen in the organic material. Most of this nitrogen is bound to dead organic matter, mainly humus, which is turned over very slowly (between 20 and 500 years depending on soil horizon) (Tamm and Östlund 1960). Only a minor portion of nitrogen cycles within the ecosystem and is directly available for plant uptake. Soil nitrogen transformation rates, notably net nitrification have been shown to increase with nitrogen inputs

(Falkengren-Grerup et al. 1998, Gundersen et al. 1998, Vestgarden & Kjønaas 2003). However, very few experiments using relevant nitrogen loads have been performed in areas with low background deposition, such as ecosystems at high latitudes (i.e. Robinson et al. 2004, Brenner et al. 2005). It can be hypothesized that due to the lower nitrogen demand for plant growth in boreal and arctic ecosystems (due to the temperature limitation to growth and the low turnover rate of nitrogen) these ecosystems are more vulnerable to the effects of nitrogen deposition than temperate ecosystems. For example, addition of as little as 5 kg N ha^{-1} yr^{-1} to a high arctic ecosystem in Svalbard appeared to exceed the ecosystem nitrogen retention capacity (Robinson et al. 2004).

Plant species have different abilities to take up different nitrogen forms. In ecosystems characterized by nitrogen limitation and low temperatures, the dissolved nitrogen pool is dominated by NH_4^+ and/or organic nitrogen forms like free amino acids (Nordin et al. 2001, Jones and Kielland 2002, Nordin et al. 2004). Studies have demonstrated that various boreal tree species as well as many boreal and arctic dwarf-shrubs and herbs have only limited capacity to utilize NO_3^- (Chapin et al. 1993, Kronzucker et al. 1997, Nordin et al. 2001, Nordin et al. 2004). In contrast, plant species adapted to nitrogen rich habitats (some of them with capacity to invade ecosystems as nitrogen supply increases), often exhibit high capacities to take up NO_3^- but only limited capacity to take up organic nitrogen (Bowman and Steltzer 1998, Nordin et al. 2001, Nordin et al. 2006). In many areas of Europe and north-America nitrogen deposition is comprised of equal parts of NH_4^+ and NO_3^-. When assessing effects of nitrogen deposition, it is important to consider that plant species exhibit differences in their capacities to utilize NO_3^-. Although the effect of nitrogen deposition to an ecosystem is mainly related to the quantity of nitrogen deposited, also the qualitative aspect needs to be recognized.

Mycorrhizal infection

Mycorrhizal symbioses are fundamentally important for the aboveground – belowground linkage in ecosystems (Read 1991). The mycorrhizal association forms the link by which plants can access organic nitrogen forms not available for direct uptake by plant roots. In nitrogen poor ecosystems the mycorrhizal association is fundamental to provide plants access to nitrogen, and non-mycorrhizal plants are suppressed (Read & Perez-Moreno 2003). Mycorrhizal associations are sensitive to the soil nitrogen supply and both abundance and species diversity of ecto-mycorrhizal fungi in the soil have been demonstrated to change in response to increased ecosystem nitrogen input (Peter et al. 2001, Lilleskov et al. 2002, Dighton et al. 2004, Nilsson et al. 2005). The strongest response of ecto-mycorrhiza to nitrogen enrichment is however seen above ground as sporocarp production can cease at high nitrogen input (Peter et al. 2001, Strengbom et al. 2001). The response of ericoid mycorrhiza (an endo-mycorrhizae) associated with ericaceous plants to increased soil nitrogen supply is less well studied than the corresponding responses of ecto-mycorrhiza. However, mycorrhizal infection of *Calluna vulgaris* roots declined significantly along a nitrogen deposition gradient from 85 % at 2 kg N ha^{-1} yr^{-1} to 14 % at 10 kg N ha^{-1} yr^{-1} (Yesmin et al. 1996).

Plant disease

Plant diseases and herbivores can serve as important drivers mediating effects from various environmental changes on plant community species composition (e.g. Mitchell and Reich 2003). In boreal spruce forest, damage on the dominant understorey dwarf-shrub *Vaccinium myrtillus* from pathogens increased in response to adding 12.5 or 50 kg N ha^{-1} yr^{-1} (Nordin et al. 1998, Strengbom et al. 2002, Nordin et al. 2006). A similar pattern existed under a gradient of nitrogen deposition as pathogen damage to the shrub became more frequent in areas were N deposition exceeded 6 kg N ha^{-1} yr^{-1} (Strengbom et al. 2003). Pathogen damage to *V. myrtillus* often occurs in well-defined patches of the shrub canopy. In such patches the shrubs become leaf-less early in the season and more fast-growing competing plants (mainly the graminoid *Deschampsia flexuosa*) proliferate from increased nitrogen supply due to the increased light availability (Strengbom et al. 2002, Strengbom et al. 2004). However, also fungal infections on *D. flexuosa* have been found to increase at increased nitrogen supply (Nordin et al. 2006).

The boreal mire is another ecosystem type which has been well characterized concerning nitrogen mediated changes in pathogenic fungal infections of ericaceous shrub species. Wiedermann et al. (2007) demonstrated that damage from several species of fungi infecting *V. oxycoccus* and *Andromeda polifolia* increased from nitrogen additions.

Both in boreal forest and on mires it has been found that nitrogen mediated changes in pathogenic fungal infections covary with other factors. Effects from the pathogen *Valdensia heterodoxa* infecting *V. myrtillus* is positively correlated with summer precipitation, with higher precipitation enhancing the effect of added nitrogen (Strengbom et al. 2006). On *D. flexuosa* the two pathogens *Uromyces airae-flexuosae* and *Telimenella gangraena* showed opposite responses to drought stress; *U. airae-flexuosae* decreased, while *T. gangraena* increased in response to drought treatment (Nordin et al. 2006). For the boreal mire it was found that warming had a negative influence on infection of most pathogens on *V. oxycoccus* and *A. polifolia* (Wiedermann et al. 2007). This was in contrast to the commonly held view that global warming will result in increased disease problems for plants (e.g. Roy et al. 2004). Such contradictive results stresses that more knowledge is needed to produce relevant scenarios predicting effects from increased nitrogen supply in combination will global warming on plant – pathogen interactions.

Herbivory

The concentrations of nitrogen based proteins and amino acids in plant foliage determine its quality as feed for herbivores. Consequently, foliage nitrogen concentration is the best single predictor of host plant quality (e.g. Mattson 1980). Although numerous studies have linked grazing by large and small mammals to changes in plant community structure and function (see for example Pastor & Cohen 1997, Niemelä et al. 2001), it is less well understood to what extent insect herbivory affect plant community dynamics (e.g. Throop et al. 2004). Often a strong positive relationship between foliar nitrogen concentrations and insect survivorship, growth and reproduction has been demonstrated (Mattson 1980, Scriber and Slansky 1981, White 1993). Insect consumption response to nitrogen are however both positive and negative, since some species increase consumption in response

to nitrogen rich food while other decrease consumption to keep nitrogen intake constant (Woods 1999, Meyer 2000). Positive effects of nitrogen at the level of the individual insect can scale up to enhanced populations sizes (but this response is not universal) (Strauss 1987, Kytö et al. 1996). In boreal forest *Operophtera brumata* (Lepidoptera: Geometridae) and the closely related *O. fagata* are polyphagous moths using *V. myrtillus* as their main host plant. During their larval stage in late spring and early summer, *Operophera* spp. are normally found grazing annual shoots of *V. myrtillus* although in outbreak situations the complete *V. myrtillus* aboveground structure can be consumed. It was demonstrated that nitrogen fertilization (12.5 kg N ha^{-1}) of *V. myrtillus* increased damage to the annual shoots from *Operopthera* spp. larvae (Nordin et al. 1998). However, presence of larval predators (birds) counteracted the positive effects on larvae from nitrogen, and was a factor strongly influencing the extent of damage to *V. myrtillus* from grazing (Strengbom et al. 2005).

Competition

The majority of nitrogen addition experiments results in increased success for a limited number of plant species that consequently will dominate the plant community. This has been attributed to that species vary in their nitrogen use efficiency (i.e. productivity per unit nitrogen taken up) as well as their nitrogen loss rate. Under low nitrogen conditions slow-growing species with high nitrogen use efficiency and low nitrogen loss rates becomes dominant (Aerts and Van der Peijl 1993, Aerts 1995, Aerts and Chapin 2000). This nitrogen conserving strategy is however sub-optimal under nitrogen rich conditions as fast-growing, less nitrogen conservative species with higher nitrogen loss rates will become dominate (Aerts and Van der Peijl 1993, Aerts and Chapin 2000). For understorey vegetation in forest ecosystems another important factor (besides nitrogen supply) that governs growth and interspecific competition is light (Coomes and Grubb 2000, Strengbom et al. 2004). The initial response of forest understorey plants to increased nitrogen supply is a decreased limitation to growth by nitrogen, while the limitation by light increases.

In boreal forest ecosystems where the ground-vegetation is dominated by *V. myrtillus* a nitrogen load of 6 kg N ha^{-1} yr^{-1} has been found to cause increased abundance of *D. flexuosa* (Kellner & Redbo-Torstensson 1995, Nordin et al. 2005). Kellner & Redbo-Torstensson (1995) also found an increased density of the herb *Trientalis europaea* at this nitrogen load. Decreased abundance of the normally dominant *V. myrtillus* occurs in fertilization experiments adding 12.5 kg N ha^{-1} yr-1 (Strengbom et al. 2002) and *V. myrtillus* abundance decreases in south-Sweden where nitrogen deposition loads exceeds 6 kg N ha^{-1} yr^{-1} (Strengbom et al. 2003). Forest ground-vegetation dominated by *V. vitis-idaea* appears to respond slightly differently to nitrogen deposition as the response is more slow compared to the *V. myrtillus* vegetation type. While *V. myrtillus* dominated vegetation respond significantly within four years when adding 6 kg N ha^{-1} yr^{-1}, *V. vitis-idaea* dominated vegetation does not (Lena Widermann personal communication). However, if a high nitrogen load persist for long time period, the abundance of *V. vitis-idaea* do decline and the abundance of grasses increase (Strengbom et al. 2001).

From arctic ecosystems there are few published studies that have examined effects on vegetation from low doses of nitrogen. However, an experiment manipulating soil

temperature in a sub-arctic birch forest in Abisko, Sweden, demonstrated that warming enhanced soil nitrogen mineralization rates (Hartley et al. 1999). Warming caused the supply of plant available nitrogen to increase with *c*. 5 kg N ha^{-1} yr^{-1} (i.e. Hartley et al. 1999). The greater nitrogen availability likely contributed to the increased growth of *V. myrtillus*, *V. vitis-idaea* and *Empetrum hermaphroditum* together dominating the forest ground vegetation (Hartley et al. 1999). In the fifth year of warming no positive effect on plant growth was observed indicating that the long-term response might be quite different from the short-term one (Hartley et al. 1999), and unfortunately the experiment was terminated after five years. For Alaskan tussock tundra experimental warming has been found to increase growth of the overstorey shrub, *Betula nana*, while growth of the understorey shrub *V. vitis-idaea* is suppressed (Hobbie and Chapin 1998). Other experiments have also demonstrated increased abundance of graminoids (Hollister et al. 2005), which also have been reported from experiments manipulating nitrogen supply (adding as much as 100 kg N ha^{-1} yr^{-1}) (see for example Parsons et al. 1994, 1995, Chapin and Shaver 1996).

For bottom-layer bryophytes it has been reported that most dominant boreal forest species decline as nitrogen input increases (Huttunen et al. 1980, Hallingbäck 1992, Mäkipää 1995, Forsum et al. 2006, Nordin et al. 2006). Bryophyte responses to nitrogen exposure are however species specific, and as common boreal feather-moss species like *Hylocomium splendens*, decline in abundance in response to nitrogen exposure, species like *Brachythecium* spp. and *Plagiothecium* spp. increase (Strengbom et al. 2001, Mäkipää and Heikkinen 2003). Not many experiments have explicitly targeted at what nitrogen load species composition bryophyte dominated plant community changes. Bryophytes are highly efficient in taking up and retaining supplied nitrogen in their tissues (Gordon et al. 2001, Turetsky 2003). Nitrogen taken up by bryophytes in excess of what is needed for growth and maintenance is accumulated in the moss tissues, largely in the form of free amino acids (Nordin et al. 1998, Limpens and Berendse 2003, Forsum et al. 2006). For *Sphagnum fuscum*, *S. magellanicum* and *S. rubellum* nitrogen addition (between 10 and 100 kg N ha^{-1} at one single occasion) resulted in decreased growth which correlated to elevated tissue concentrations of amino acids (Gunnarsson & Rydin 2000, Nordin and Gunnarsson 2000). Continuous nitrogen addition (10 kg N ha^{-1} yr^{-1}) to a boreal mixed mire dominated by *S. balticum* caused decreased bryophyte biomass production and abundance, while abundance of vascular bog species (*Eriophorum vaginatum*, *Andromeda polifolia* and *Vaccinium ocyccocus*) increased (Gunnarsson et al. 2004, Wiedermann et al. 2007). For the highly nitrogen sensitive boreal forest bryophyte *H. splendens* it has been demonstrated that although subjected to high nitrogen input (50 kg N ha^{-1} yr^{-1} for eight consecutive years) resulting in elevated tissue nitrogen concentrations and decreased abundance, nitrogen uptake rates does not decline (Forsum et al. 2006). Thus accumulation of nitrogen in bryophyte tissues may in the long-term turn out to be detrimental (Jones et al. 2001). However, when assessing effects from nitrogen input on bryophytes it is important to note that bryophyte abundance in an ecosystem is governed also by several other environmental factors (besides nitrogen input). In particular high moisture and moderately cool temperatures are favorable for moss growth (Økland 1995). Under such conditions negative effects from nitrogen

exposure can be counteracted, as nitrogen accumulated in bryophyte tissues can be converted into new biomass.

The link between nitrogen deposition and biodiversity

There is an ongoing debate concerning how biodiversity influences ecosystem functioning and provision of ecosystem services (like productivity, carbon sequestration and nitrogen retention) (see for example Loreau et al. 2001, Hooper et al. 2005, Wright et al. 2006). In general a positive relationship between biodiversity and the provision of ecosystem services has been proposed, due to the assumption of more effective utilization of available ecosystem niches at high than at low biodiversity (Tilman 1997, Grime 2002, Cardinale et al. 2006, Kahmen et al. 2006). In addition it has been suggested that overall ecosystem stability increases with biodiversity (Tilman 1996, Naeem and Li 1997, Yachi and Loreau 1999, Chapin et al. 2000, Hooper et al. 2005). However, recent work has proposed that biodiversity effects on ecosystem stability are dependent on the nature of disturbance the ecosystem confronts. While biodiversity effects on buffering of nutrient perturbations and invading species are positive, the effects on buffering influences of warming and drought seems to be neutral or slightly negative (Balvanera et al. 2006).

When discussing biodiversity it should be kept in mind that the concept includes both number and composition of genotypes, species, functional groups of species and landscape units in a given system. However, biodiversity has often been equated to species richness and other components have frequently been underestimated. There is an emerging agreement that that the effects of biodiversity on ecosystem processes should be attributed to the functional traits of individual species and their interactions, rather than to species number *per se* (Tilman 1999, Diaz and Cabido 2001, Naeem and Wright 2003, Reich et al. 2004, Cardinale et al. 2006). An important question currently debated is whether there is a classification scheme that can group species together to effectively describe the functional diversity of an ecosystem? Grouping species assumes that the traits of importance are discrete rather than continuously distributed among species and that the variance in traits is smaller within than between species (Chapin et al. 1996). Consequently, if multiple traits are responsible for controlling an ecosystem function, these traits should be correlated within species. Conventional functional classification schemes (mostly grouping species according to life-form) have been found to have low predictive precision of ecosystem functioning (Wright et al. 2006). Alternative schemes based on ecophysiological and/or morphological traits of species may capture more of the variation that leads to effects on ecosystem functioning (Reich et al. 2003, Mouillot et al. 2005, Kahmen et al. 2006). Due to the complications related to classifying species into relevant functional groups, it has sometimes been assumed that plant species richness can serve as a surrogate for functional richness (see for example Tilman 1999). Although the two types of richness often are correlated, it has been argued that this relationship is not sufficiently universal to justify using species richness as a reliable proxy for functional richness (e.g. Diaz & Cabido 2001).

In general it has been demonstrated that eutrophication decreases ecosystem biodiversity (i.e. species richness) (Bobbink et al. 1998, Gough et al. 2000, Strengbom et al. 2001, Stevens et al. 2004, Bonanomi et al. 2006, Stevens et al. 2006). So far, not many studies

have addressed whether nitrogen induced species loss also have affected ecosystem functioning (but see Knops et al. 2002, Dijkstra et al. 2004, Bragazza et al. 2006). The relationship between species richness and ecosystem productivity is often described by a hump-shaped curve in which species richness is considered a function of productivity, i.e. species richness is low in the least productive ecosystems, highest at moderate levels of productivity and then low again at very high levels of productivity (e.g. Grime 1973, Loreau et al. 2001, Mittelbach et al. 2001). In this context productivity has mainly been equated to the ecosystem's nutrient supply, but sometimes also climatic variables and light has been more explicitly considered. Most studies examining effects of increased nitrogen supply on species richness have been performed in moderately productive ecosystems and have (in agreement with the suggested hump-shaped curve) resulted in species loss and increased dominance of a few species. According to the described hump-shaped model, nitrogen addition to the least productive ecosystems would instead increase species richness, although so far not many studies have reported results from nitrogen addition studies conducted in such ecosystems (but see Jonasson 1992). As increased biodiversity in boreal and arctic environments often require establishment of new plant species, the scares support for the hypothesis may just be due to lack of long-term experimental data.

The ecological consequences of biodiversity loss due to human activities have aroused considerable interest and also controversy during recent time. Expert opinions consider that nitrogen deposition will be the third greatest driver of biodiversity loss at the global scale (after land use and climate) over the coming century (Sala et al. 2000). To asses nitrogen deposition effects on ecosystem biodiversity it is important to consider not only effects on species richness per se, but also effects on functional richness. In addition, although nitrogen deposition normally results in species loss from recipient ecosystems, it should be considered that for the least productive north-latitude ecosystems nitrogen deposition may result in increased biodiversity.

Tools for monitoring nitrogen deposition effects on biodiversity

The ground vegetation of an ecosystem is the component first and most markedly affected by nitrogen deposition. However, it is often very difficult to establish what effects nitrogen deposition has had on the vegetation in a specific area, since vegetation is also affected by a number of other factors. In environmental monitoring simple and cost-effective methods are needed to survey the landscape over whole regions. Mainly two different approaches have been used to monitor effects of nitrogen deposition on vegetation; (1) the assignment of nitrogen indices to species, and (2) analyses of plant biochemistry.

1. Nitrogen indices for plant species have been suggested as one method to assess effects of nitrogen deposition on vegetation. The idea is that by defining species according to their nitrogen requirements, one can assess the nitrogen status of a habitat by an inventory of its flora. The most frequently used index is Ellenberg's (1992) indicator values that have been assigned to a great number of European vascular, bryophyte and lichen species. The Ellenberg index characterizes a

species according to a range of variables of which soil nitrogen availability at the site where the species is normally found is one of the more important. Another simpler index is FNIS that characterize a species according to its occurrence in relation to soil ammonification and nitrification (Diekmann and Falkengren-Grerup 1998). A limitation with both these indices is that they are developed explicitly for temperate ecosystems. Also it is only possible to assess changes that have already occurred, and the monitoring results cannot predict future changes.

2. Another method suggested as useful for assessing effects of nitrogen deposition on vegetation is measuring amino acid concentrations of plant tissues (Näsholm et al. 1994, Pitcairn et al. 2003). According to this idea elevated amino acid concentrations in tissues of a plant would denote that nitrogen uptake exceeded the plant's capacity to convert nitrogen to growth. This would indicate a risk for others species (with a better capacity to convert nitrogen to growth) to take over the habitat. An advantage with the method would be that instead of just assessing changes that already occurred, predictions of future changes would be possible to make. However, in perennial vascular species amino acids are also used for seasonal nitrogen storage (supporting rapid spring growth at the time of year when soil nitrogen supply is not sufficient to meet plant nitrogen demand) (Ohlson et al. 1995, Nordin and Näsholm 1997). Thus it appears difficult to interpret whether amino acid accumulation in a plant occurs in response to excessive nitrogen uptake, or just in response to the seasonal nitrogen storage cycle.

Apparently both the above described methods have certain limitations. So are there other simple methods to monitor effects of nitrogen on vegetation on the landscape level? Recent research has demonstrated that patterns of plant disease can be closely correlated to plant nitrogen status. Increases in disease incidence in response to increased nitrogen supply may occur long before actual changes in vegetation species composition does (Nordin et al. 1998, Strengbom et al. 2002). Monitoring of plant disease may thus be a very sensitive measure of nitrogen effects on vegetation. This approach was tested in a north-south gradient of increasing nitrogen deposition over Sweden. It was demonstrated that disease incidence of *Valdensia heterodoxa* on *Vaccinium myrtillus* was higher in the south as nitrogen deposition exceeded 6 kg N ha^{-1} yr^{-1} (Strengbom et a. 2003). The abundance of *V. myrtillus* as well as *V. vitis-idaea* decreased along the same gradient of increased nitrogen deposition (Strengbom et al. 2003).

The link between empirical data and ecological modeling

To overcome obstacles related to observing nitrogen effects on vegetation ecological modeling can be useful. Observations of how ecosystems respond to environmental changes collected from experiments or large scale environmental monitoring schemes often exist only for rather limited periods of time, and from only a few geographical regions. To make predictions of ecosystem responses to environmental changes over time spans like decades or even centuries, and over vast geographical regions, computer models of ecosystems are important tools complementing observations. Also in the planning of management activities, in for example forestry, and for long-term sustainable

land use, models provide an important predictive tool. Under the LRTAP convention models are used to assess the ecosystem effects of different emission scenarios. This requires an ongoing work developing models based on sound ecosystem science and continuously incorporating new knowledge in the models.

Within this context a LRTAP Convention workshop was held on nitrogen processes and dynamic modeling in October 2005 in Brighton (U.K.). The workshop assessed both biogeochemical N modeling and modeling N impacts on ecosystem biodiversity. So far modeling efforts have dealt mainly with biogeochemical N modeling while modeling of N impacts on biodiversity has been initiated rather recently. Obviously the two types of models need to be closely linked. When modeling N impacts on biodiversity, soil abiotic variables are used as drivers of vegetation change, and biogeochemical N modeling may be used to predict these abiotic variables.

The workshop concluded that vegetation models are currently developed in several different European countries and they are either based on large-scale vegetation surveys (for example MOVE, NTM, BERN, GBMOVE) or experimental data (for example VEG). There are some general similarities between models (particularly those based on survey data) but there are also important differences including that different models use different abiotic variables for N biogeochemistry (organic soil horizon C/N ratio, soil solution N, N availability).

The Brighton workshop listed some outstanding challenges for the currently used vegetation models:
- More extensive testing, particularly against long-term datasets
- Expansion of testing and application beyond the geographical region for which model dose-response relationships have been parameterised
- Prediction of rare species
- Representation of lag times (e.g. due to species persistence, dispersal)
- Incorporation of feedbacks with biogeochemical models (e.g. changes in litter quality due to species change)
- Consideration of the differential effects of oxidised and reduced nitrogen.

The workshop also concluded that priorities for future work on modeling nitrogen impacts on biodiversity include:
- The collection of new data to identify and verify the most suitable abiotic N variables for predicting vegetation responses
- Testing and comparison of different models at the same sites
- Adaptation, testing and upscaling of models for new countries/biogeographical regions (particularly areas not included in current model coverage, such as Mediterranean and Alpine regions, and Eastern Europe)
- Incorporation of biodiversity models within dynamic modeling work undertaken for the Convention, e.g. target loads for N as a nutrient.

Acknowledgments

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