

Chapter 14: **Effects of airborne nitrogen pollutants on vegetation: critical loads**

Introduction

Most of the earth's biodiversity is found in (semi-)natural ecosystems, both in aquatic and terrestrial habitats. Human activities pose a number of threats to the structure and functioning of these ecosystems, and thus to the natural variety of plant and animal species. One of the major threats is the increase in airborne nitrogen pollution (NO_x and NH_y) in recent decades. Nitrogen is the limiting nutrient for plant growth in many of the (semi-)natural ecosystems. Most of the plant species from these (semi-)natural habitats are adapted to nutrient-poor conditions, and can only compete successfully on soils with low nitrogen levels (1,2). Nitrogen is the only nutrient whose cycling through the ecosystem is almost exclusively regulated by biological processes. To establish reliable critical loads for nitrogen, it is essential to understand the effects of nitrogen on these ecosystem processes. The critical loads for nitrogen depend on (a) the type of ecosystem; (b) the land use and management in the past and present; and (c) the abiotic conditions, especially those that influence the nitrification potential and immobilization rate in the soil. Where possible, these points are taken into account in this section.

The impacts of increased nitrogen deposition on biological systems are diverse, but the most important effects are: (a) direct toxicity of nitrogen gases and aerosols to individual species; (b) soil-mediated effects on vegetation; (c) increased susceptibility to secondary stress factors; and (d) changes in (competitive) relationships between species, resulting in loss of biodiversity.

The main aim of this chapter is to update the previous WHO guideline for airborne nitrogen deposition on vegetation, which was established at 30 kg/ha per year (3). The effects of increased nitrogen supply will be reviewed with respect to changes in vegetation and fauna in terrestrial and aquatic (semi-)natural ecosystems. Observed and validated changes will be used as an indication for the effects of nitrogen deposition. Based on these, data guidelines (critical loads) for nitrogen deposition (4) are presented for freshwater ecosystems (shallow soft-water bodies, lakes and streams) and terrestrial ecosystems (wetlands and bogs, species-rich grasslands, heathlands and forests). Finally, an overview of the guidelines is given and gaps in knowledge are discussed.

Effects of nitrogen deposition on freshwater ecosystems

The acidifying effects of airborne nitrogen compounds are only briefly summarized in this section, as critical loads for acidity, including nitrogen, are relatively well established (5–7).

Shallow soft-water lakes

In the lowlands of western Europe, many soft-water lakes are found on sandy soils that are poor in calcium carbonate or almost devoid of it. The waters are poorly buffered and have very low calcium concentrations. These lakes are shallow, fully mixed water bodies, with periodically fluctuating water levels. They are fed mainly by rain water, and are therefore oligotrophic. Their ecosystems are characterized by plant communities from the phytosociological alliance Littorellion (8–12) and include rare and endangered isoetids such as *Littorella uniflora*, *Lobelia*

dortmanna, *Isoetes lacustris*, *I. echinospora*, *Echinodorus* species, *Luronium natans* and many other soft-water macrophytes. (For more details on these communities see Schoof-van Pelt (8) and Schaminée et al. (13).) Such soft-water bodies are nowadays almost all within nature reserves and have become very rare in western Europe. *L. uniflora* was present at more than 230 sites in the Netherlands in the early 1950s, of which only some 40 still exist, and there has been a marked decline in amphibians (14).

The effects of nitrogen pollutants have been intensively studied in the Netherlands, in both field surveys and experimental studies. Field observations in some 70 soft-water bodies with well developed isoetid vegetation in the 1950s showed that the waters in which these macrophytes were still abundant in the early 1980s were poorly buffered (alkalinity 50–500 meq/litre), neutral (pH 5–6) and very poor in nitrogen (15,16). The sites from which these plant species had disappeared could be divided into two groups. In 12 of 53 sites, eutrophication resulting from inlet of enriched water seemed to be the cause of the decline. In this group of non-acidified waters, plant species such as *Myriophyllum alterniflorum*, *Lemna minor* or *Riccia fluitans* had become dominant, and high concentrations of phosphate and ammonium were measured in the sediment. In some of the larger of the water bodies, no macrophytes were found at all as a result of dense plankton bloom.

In the second group of 41 sites, the isoetid species had been replaced by dense stands of *Juncus bulbosus* or aquatic mosses such as *Sphagnum cuspidatum* or *Drepanocladus fluitans*. This clearly indicates acidification of these soft waters in recent decades, probably caused by enhanced atmospheric deposition. In the same field study, it was shown that the nitrogen levels in the water layer were higher in ecosystems where the natural vegetation had disappeared than in those where the Littorellion stands were still present (15). This strongly suggests the detrimental effects of atmospheric nitrogen deposition in these soft-water lakes.

Ecophysiological studies have revealed the importance of the inorganic carbon status of the water, as a result of intermediate levels of alkalinity, and of the low nitrogen concentrations for the growth of the endangered isoetid macrophytes. Furthermore, almost all of the typical soft-water plants were shown to have a relatively low potential growth rate. Increased acidity and higher concentrations of ammonium in the water layer clearly stimulated the development of *J. bulbosus* and submerged mosses such as *Sphagnum* and *Drepanocladus* spp. (17,18). In addition, cultivation experiments have shown differences in the influence of nitrogen species (ammonium or nitrate) on the various species of water plants studied. Most of the characteristic soft-water isoetids developed better following addition of nitrate than with ammonium, whereas *J. bulbosus* and aquatic mosses were clearly stimulated by ammonium nutrition (19,20).

The effects of atmospheric deposition were studied in small-scale soft-water systems during a two-year treatment with different artificial rain waters. Acidification, without airborne nitrogen input (sulfuric acid), did not result in a mass growth of *J. bulbosus* and a diverse isoetid vegetation remained present. After increasing the nitrogen concentration in the precipitation (as ammonium sulfate), however, similar changes in floristic composition as under field conditions were observed: a dramatic increase in the dominance of *J. bulbosus*, submerged aquatic mosses and *Agrostis canina* (21). It became obvious that these changes had occurred because of the effects of ammonium sulfate deposition, leading to both eutrophication and acidification. The increased levels of ammonium in the system directly stimulated the growth of plants such as *J. bulbosus*, whereas the surplus of the extra ammonium is nitrified in these waters (pH 4.0). During this nitrification process hydrogen ions are produced, which increase the acidity of the

system. The results of this study clearly demonstrated that the changes in composition of the vegetation had already occurred after two-year treatment with nitrogen at a rate of 19 kg/ha per year. A reliable critical load for nitrogen deposition in these shallow soft-water lakes is thus most likely to be below 19 kg/ha per year and probably 5–10 kg/ha per year. This value is supported by the observation that the strongest decline in the species composition of the Dutch Littorellion communities has coincided with nitrogen loads of around 10–13 kg/ha per year (12).

Lakes and streams

There is ample evidence that an increase of acidic and acidifying compounds in atmospheric deposition has resulted in the recent acidification of lakes and streams in geologically sensitive regions of Scandinavia, western Europe, Canada and the United States (6,22). This acidification is characterized by a decrease in pH and acid neutralizing capacity, and by increases in concentrations of sulfate, aluminium and, sometimes, nitrate and ammonium. It has already been shown, with different approaches (field surveys, laboratory studies, whole-lake experiments), that these changes have had dramatic consequences for plant and animal species (macrofauna, fish) and for the functioning of these aquatic ecosystems.

The critical loads of acidity for aquatic ecosystems were established in 1988 and 1992 based on steady state-water chemistry models. These models incorporate both sulfur and nitrogen acidity and the calculations take into account base cation deposition, internal alkalinity production or base cation concentrations, and nitrate leaching from the water system. The critical loads are thus site-specific (sensitive or non-sensitive areas) and also depend on the local hydrology and precipitation. The critical loads for nitrogen acidity (kg/ha per year) for the most sensitive lakes and streams are:

1. Scandinavian waters: 1.4–4.2 (5–7)
2. alpine lakes: 3.5–6.1 (23)
3. humic moorland pools: 3.5–4.5 (21,24)

In many areas with high water alkalinity and/or high base-cation deposition, the values of the critical load for nitrogen acidity are much higher than those for sensitive fresh waters. So far, the (possible) effects of nitrogen eutrophication by ammonia/ammonium or nitrate deposition are hardly incorporated in the establishment of critical loads of nitrogen, except for shallow softwater lakes. This is because primary production in almost all aquatic ecosystems is limited by phosphorus, and thus nitrogen enrichment has been considered unimportant in this respect (25). This certainly holds for those aquatic ecosystems considered above, where the critical load with regard to acidifying effects are certainly more relevant than the effects of nitrogen eutrophication. It is, however, to be expected that alpine lakes, waters with low background of nitrogen and humic lakes are sensitive to nitrogen enrichment (7). The effects of nitrogen eutrophication (including ammonia/ammonium) in these waters need further research and should be incorporated into critical loads for nitrogen in future. It is not currently possible to present reliable critical loads of nitrogen eutrophication in these kinds of aquatic ecosystem. For an overview of the critical loads see Table 2 (page 26).

Effects of nitrogen deposition on ombrotrophic bogs and wetlands

A common feature of these systems is the anaerobic nature of their waterlogged soils, characterized by a low redox potential, high concentrations of toxic reduced substances and high rates of denitrification (26,27).

Ombrotrophic (raised) bogs

Ombrotrophic bogs, which receive all their nutrients from the atmosphere, are particularly sensitive to airborne nitrogen loads. These bogs are acidic, wet areas and are very common in the boreal and temperate parts of Europe. Because of the abiotic conditions, decomposition rates are slow, favouring the development of peat. In western Europe and high northern latitudes, typical plant species include bog mosses (*Sphagnum* spp.), sedges (*Carex* and *Eriophorum* spp.) and heathers (*Andromeda*, *Calluna* and *Erica* spp.). Insectivorous plants such as *Drosera* spp. are especially characteristic for these bogs; they compensate for low nutrient concentrations (nitrogen) by trapping and digesting insects (28).

Clear effects of nitrogen eutrophication have been observed in Dutch ombrotrophic bogs. The composition of the moss layer in the small remnants of the formerly large bog areas has changed markedly in recent decades as nitrogen loads (especially as ammonium/ammonia) have increased to 20–40 kg/ha per year; the most characteristic *Sphagnum* species are replaced by more nitrophilous (moss) species (29). A national survey of Danish ombrotrophic bogs has shown a decline of the original bog vegetation together with an increase of more nitrogen-dependent species in areas with ammonia depositions greater than 25 kg/ha per year (30,31).

The effects of atmospheric nitrogen deposition on ombrotrophic bogs have also been studied intensively in the United Kingdom (32,33). Many characteristic *Sphagnum* species are now largely absent from affected ombrotrophic bog areas, such as the southern Pennines of England. Atmospheric nitrogen deposition has more than doubled in these areas to around 30 kg/ha per year, compared with areas with healthy *Sphagnum* growth. Most of the nitrogen deposition in the United Kingdom comes from the deposition of nitrogen oxides, in contrast with the situation elsewhere in western Europe, although the importance of ammonia/ammonium is also increasing (34). Several studies in British bogs have shown that increased supplies of nitrogen have been rapidly absorbed and utilized by bog mosses (*Sphagnum* spp.), reflecting the importance of nitrogen as a nutrient and its scarcity in unpolluted regions (35,36). The high nitrogen loadings are, however, supraoptimal for the growth of many characteristic *Sphagnum* species, as demonstrated by restricted development in growth experiments and transplantation studies between clean and polluted locations. In areas with high nitrogen loads, such as the Pennines, the growth of *Sphagnum* is generally lower than in unpolluted areas (33). After transplantation of *Sphagnum* from an “unpolluted” site to a bog in the southern Pennines, a rapid increase in nitrogen content from about 12 to 20 mg/g dry weight was observed (37). Further, a large increase in nitrogen-containing amino acids (arginine) in the moss shoots was found, indicating a nutritional imbalance. In field experiments in northern and southern Sweden, a nitrogen limitation of the growth of (*Sphagnum*) was observed. Other nutrients, especially phosphorus, may however become secondarily limiting to plant growth when nitrogen inputs reach a certain threshold (38).

Increased nitrogen content of the bog mosses may also lead to an increased decay rate of the peat, as nitrogen content strongly influences decomposition rates (39). A short-term experiment in Swedish ombrotrophic bogs indicated that the decomposition rate of *Sphagnum* peat was more influenced by the phosphorus content of the material than by the nitrogen content, although some relation with nitrogen supply was observed (40). Further evidence is needed to evaluate long-term effects.

All these studies clearly indicate the detrimental effects of atmospheric nitrogen on the development of the bog-forming *Sphagnum* species. Moreover, enhanced nitrogen deposition

can influence the competitive relationships in nutrient-deficient vegetation such as bogs. The effects of additional nitrogen on populations of *Drosera rotundifolia* has been studied in a 4-year fertilization experiment in Swedish ombrotrophic bogs (41). Experimental nitrogen applications above 10 kg/ha per year (as ammonium nitrate) clearly affected the population of this insectivorous species, significantly reducing the establishment of new individuals and plant survival. This decrease in the total population density of the characteristic bog species was not caused by toxic effects of nitrogen, but by enhanced competition for light with tall plants, such as *Eriophorum* and *Andromeda* spp., which responded positively to the increased nitrogen.

The British and Scandinavian studies show that increased nitrogen loads strongly affect ombrotrophic bog ecosystems, in particular because of the high nitrogen retention capacity and closed nitrogen cycling. The negative effect on the growth of bog mosses and changes in the competitive relationship between the prostate dominants and the subordinate plant species lead to a reduction in biodiversity. A quite reliable critical load for nitrogen in these ombrotrophic bogs is 5–10 kg/ha per year, although additional long-term studies with enhanced nitrogen (both nitrogen oxides and ammonia/ammonium) are needed to validate this figure.

Mesotrophic fens

Fens are wetland ecosystems that are typical of alkaline to slightly acidic habitats in many European countries. The alkalinity is due to groundwater draining from surrounding rocks or sediments that are relatively high in calcium carbonate. Most of these fen ecosystems are characterized by rare and endangered plant species; they also contain many *Carex* species and are rich in forbs (e.g. *Pedicularis palustris*, orchids). The effects of nitrogen enrichment on mesotrophic fens have been intensively studied in the Netherlands (42,43), where many are managed as hay meadows with removal of the plant material; true fens and are now restricted to nature reserves.

A considerable increase of tall graminoids (grasses or *Carex* spp.) with a somewhat higher potential growth rate has been observed after experimental nitrogen addition in three Dutch fen ecosystems (42,44). This caused a significant decrease in the diversity of the subordinate plant species. In one site, with a long history of hay-making, it has been shown that phosphorus deficiency was also a major factor in the productivity of the system, since much of this element was removed with the hay (42,43). Using the results of fertilization trials and nutrient budget studies in these fen ecosystems (43,45), with their relatively closed nitrogen cycle, it seems reasonable to establish a critical nitrogen load of 20–35 kg/ha per year, based on the nitrogen output for usual management. In some fen ecosystems the critical nitrogen load based on the change in diversity may be substantially higher, because of the limitation of productivity by phosphorus (42,46). In this situation, however, the risks of nitrogen losses to surface water or groundwater will increase, and these effects should also be incorporated in the evaluation. High rates of denitrification could also influence the establishment of critical loads for these fen ecosystems, and requires further investigation.

Intertidal freshwater and salt-water marshes

In the wetland ecosystems discussed above, the nitrogen cycle is more closed than that of intertidal marshes. The data on atmospheric nitrogen inputs to the nitrogen cycling in intertidal fresh- and salt-water marshes (with large prostrate graminoids as *Spartina*, *Typha* or *Carex* spp.) are reviewed by Morris (47). It has become evident that nitrogen inputs in these marsh ecosystems via surface water (>100 kg/ha per year) are much higher than that due to atmospheric loading. Many studies have shown that in non-tidal freshwater marshes

denitrification is very high and there is a very large output of nitrogen from the ecosystem (see Morris (47) for a full list of references). Because of the combined effect of these processes, atmospheric nitrogen deposition is of only minor importance for intertidal marshes, so that it is not useful to establish a critical load for airborne nitrogen in these systems. In his review, Morris (47) formulates a critical load for atmospheric nitrogen in wetland ecosystems of about 20 kg/ha per year.

It is concluded that it is more appropriate to make a distinction for different types of wetland, as shown earlier. For an overview of the critical loads see Table 2 (page 26).

Effects of nitrogen deposition on species-rich grasslands

Almost all of the research on the effects of atmospheric deposition on terrestrial vegetation has focused on ecosystems (e.g. forest, heathland and bogs) on poorly buffered, acidic soils. Semi-natural grasslands with a traditional agricultural use have also been an important part of the landscape in western and central Europe. They are now becoming rarer and a number have been set aside as nature reserves in several European countries (28,48). These ecosystems are generally poor in nutrients, because of long agricultural use with low levels of manure and removal of plant parts by grazing or hay-making. They are characterized by many species of low stature and of nutrient-poor soils (49). Although these grasslands are nowadays rare, the proportion of endangered (Red List) plant and animal species is very high (50). Many experiments have shown that application of artificial NPK fertilizer alters these grasslands, producing tall, species-poor stands dominated by a few highly productive crop grasses (51–53). To maintain high species diversity, fertilization should therefore be avoided. It is thus to be expected that these species-rich grasslands will be affected by increased atmospheric nitrogen input (49,54,55).

Many semi-natural grassland types are present in western and central Europe. Most belong to the so-called neutral grasslands (Molinio-Arrhenatheretea; moist to moderately dry), to the dry calcareous grasslands (Festuco-Brometea) or to the acid grasslands on very poor soils (Nardetalia). For a detailed description see Ellenberg (28) and Van Dijk (50). To obtain critical loads for nitrogen for all these grasslands, it would be essential to study the effects of nitrogen eutrophication in a representative range within these communities. Detailed data are, however, scarce. Therefore, the results of an integrated research programme on nitrogen eutrophication in Dutch calcareous grasslands are used here as a target study to obtain information on observed changes in this type of grassland caused by enhanced nitrogen input and a reliable estimate of the critical nitrogen load in these well buffered, non-acidic systems.

Calcareous grasslands

Calcareous grasslands are communities on limestone, which is widespread in the hilly and mountainous regions of western and central Europe. Subsoils consist of different kinds of limestone with high contents of calcium carbonate (> 90%) covered by shallow, well buffered rendzinas (A/C-profiles; topsoil pH 7–8; calcium carbonate content around 10%). Soil depth is 10–50 cm and the availability of nitrogen and phosphorus is low. These systems are found mainly on slopes with limestone in the subsoil and a deep groundwater table. European calcareous grasslands are chiefly Mesobromion communities; a temperate grassland type found in areas with precipitation quantities of 500–900 mm per year (56). Plant productivity is low and peak standing crop is 150–400 g/m². The vegetation canopy is open and low (10–20 cm).

Calcareous grasslands are among the most species-rich plant communities in Europe and contain a large number of rare and endangered species. Their area declined sharply during the second half of the twentieth century (57,58) and some remnants have become nature reserves. Specific management is needed to maintain the characteristic calcareous vegetation and prevent natural succession towards woodland (59,60). The calcareous grasslands in the Netherlands are located in the extreme south near Maastricht, and most of them are cut in autumn and the hay removed (61).

Nitrogen enrichment and vegetation composition

The effects of nitrogen enrichment on vegetation composition have been investigated in two field experiments in the Netherlands (62,63). Potassium (100 kg/ha per year), phosphorus (30 kg/ha per year) or nitrogen (100 kg/ha per year) or a complete NPK fertilizer were applied over three years. The nitrogen (ammonium nitrate) was applied in two nature reserves with opposite aspects (north and south). Total above-ground biomass increased considerably, as expected, after three years of the complete fertilizer, and there was a moderate increase in above-ground dry weight with nitrogen (some 330 g/m² compared with about 210 g/m² in the untreated plots). Dry weight distribution of species was dramatically affected by nutrient treatments. Following nitrogen treatment, the dry weight of the grass species *Brachypodium pinnatum* was some three times higher than in the control plots. Nitrogen application also resulted in a drastic reduction in the biomass of forb species (including several Dutch Red List species) and of the total number of species. This decrease in species diversity is caused not by nitrogen toxicity but by a change in the vertical structure of the grassland vegetation. The growth of *Brachypodium* was strongly stimulated, reducing light quantity and quality for other species where growth declined rapidly (62,63). Similar effects were also been observed in a five-year permanent plot study using a factorial design (64).

Besides this decrease in phanerogamic plant species, many characteristic lichens and mosses have disappeared in recent years (65). This is partly caused by the indirect effects of extra nitrogen (66). Data on the effects of nitrogen eutrophication on the species-rich fauna of calcareous grassland are not currently available. Nevertheless, it is very likely that the faunistic diversity, especially of insects, will also be reduced when tall grasses come to dominate the vegetation, thus decreasing the abundance of many herbaceous flowering species as host or forage plants.

Nitrogen enrichment and nutrient storage

The seasonal distribution of nutrients after nitrogen fertilization in spring (120 kg/ha as ammonium nitrate) has been studied with the repeated harvest approach (67). Results show a significantly increased peak standing crop of *Brachypodium* spp. This grass has a very efficient system of nitrogen acquisition and redistribution from senescent shoots into its well developed rhizome system. *Brachypodium* can benefit from the extra nitrogen redistributed to the below-ground rhizomes by enhanced growth the following spring. The distribution of nitrogen has also been quantified in two three-year fertilization experiments, showing that *Brachypodium* strongly monopolized (>75%) nitrogen storage, both above and below ground, with increasing nitrogen availability (62,63).

Nitrogen cycling and accumulation in calcareous grassland can be significantly influenced by two major outputs from the system: leaching from the soil and removal by management regimes. Nitrogen losses by denitrification in dry calcareous grasslands are low (<1 kg/ha per year), because of good drainage (68).

Critical load

The most important output of nitrogen from calcareous grassland is by exploitation or management. From the 1950s onwards, almost all of the calcareous grasslands in the Netherlands were cut in autumn and the hay removed. The annual nitrogen removal in the hay varies slightly between years and sites, but in general some 17–22 kg/ha is removed with the usual management (63,69). The ambient nitrogen deposition in Dutch calcareous grasslands is high (35–40 kg/ha per year) (70) and is nowadays the major nitrogen input to the system. Legume species also occur in calcareous vegetation, and provide additional nitrogen of the order of 5 kg/ha per year.

The nitrogen mass balance of Dutch calcareous grasslands is summarized in Table 1, from which it is clear that they nowadays significantly accumulate nitrogen (16–26 kg/ha per year). A critical nitrogen load can be determined with a steady-state mass balance model (71). Assuming a critical long-term nitrogen immobilization rate of 0–6 kg/ha per year, the critical nitrogen load can be derived by adding the nitrogen fluxes due to net uptake, denitrification and leaching, corrected for input by fixation. Thus 14–25 kg/ha per year is considered as the critical nitrogen load for this system. Nitrogen cycling within the system (between plants and soil) is not used in this calculation.

Table 1. Nitrogen mass balance (kg/ha per year) for dry calcareous grassland in the Netherlands

Input		Output	
Atmospheric deposition	35–40	Harvest	17–22
Nitrogen fixation	5	Denitrification	1
		Soil leaching	1
Total	40–45	Total	19–24

Addition of nitrogen to calcareous grassland in England generally encouraged the dominance of grasses (72,73). In these studies, nitrogen application at 50–100 kg/ha per year resulted in strong dominance by *Festuca rubra*, *F. ovina* or *Agrostis stolonifera*. However, *Brachypodium* spp. and *Bromus erectus*, the most frequent species in continental calcareous grassland, were absent from these British sites, so the data are not comparable in this respect. Following a survey of data from a number of conservation sites in southern England, Pitcairn et al. (74) concluded that *Brachypodium* had expanded in the United Kingdom during the twentieth century. They considered that much of the early spread could be attributed to a decline in grazing pressure, but that more recent increases had, in some cases, taken place despite grazing or mowing, and might be related to nitrogen inputs. A study of chalk grassland, however showed no substantial change in species composition over the 20 years between 1970 and 1990, a period when nitrogen deposition is thought to have increased to 15–20 kg/ha per year (75). *Brachypodium* was present in the sward but had not expanded as in the Dutch grasslands. In a linked experimental study, applications of nitrogen to eight forbs and one grass (*Brachypodium*) at levels of 20, 40 and 80 kg/ha per year for two years did not result in *Brachypodium* becoming dominant. This indicates that the effects of nitrogen are sometimes counteracted by adequate management or prohibited by phosphorus limitation.

Apart from the Netherlands, the effects of enhanced nitrogen inputs have been little investigated in continental European calcareous grasslands. Data on a fertilization experiment with the alvar grassland (a thin-soiled vegetation over flat limestone) on the Swedish island of Öland suggest that the vegetation hardly responds at all to applications of nitrogen or phosphorus (76). Only irrigation combined with nutrients caused an increase in grasses, a phenomenon probably caused by the low annual precipitation in the area.

Increased nitrogen availability is probably of major importance in many European calcareous grasslands. An increased availability of nitrogen is indicated by an enhanced growth of some “tall” grasses, especially of stress-tolerant species that have a slightly higher potential growth rate and efficient nitrogen utilization. Which of the grass species will increase at enhanced nitrogen inputs depends on the original species composition. Furthermore, the difference between the Dutch and British results may reflect differences in management; the effects of grazing in the British grasslands could have offset any competitive advantage the grasses may have obtained from additional nitrogen. The figures of critical nitrogen load to these calcareous grasslands could be influenced by management, and long-term studies are needed to quantify the effects of management and phosphorus limitation on excess nitrogen inputs.

Other semi-natural grasslands

Productivity in grasslands is strongly influenced by nutrients, as shown in many agricultural studies (1). It is also well known that large amounts of fertilizer alter almost all grassland types into tall, species-poor swards dominated by a few highly productive crop grasses (51–53,77). Most of these species-rich grasslands are deficient in nitrogen and/or phosphorus, and are thus characterized by plant species of nutrient-poor habitats. It is thus likely that these grasslands are sensitive to nitrogen eutrophication from the atmosphere (49,54). It is therefore important to establish critical nitrogen levels for the species-rich grasslands as well, although data from experiments with nitrogen application in these semi-natural grasslands are scarce.

A classical experiment on the effects of nutrients on neutral grasslands is the Park Grass experiment at Rothamsted in England, which has been in existence since 1856 (78). After the application of nitrogen (48 kg/ha per year) as ammonium sulfate or sodium nitrate, the vegetation became very poor in species and dominated by grasses such as *Holcus lanatus* and *Agrostis* spp. The effects of nutrients on dry and wet dune grasslands (calcium carbonate 1%) on sandy soils have been studied at Braunton Burrows in the west of England (80). Nutrients were applied for two years (nitrogen at 40 kg/ha per year) using a factorial design for nitrogen and phosphorus. Nitrogen proved to be the most important nutrient in stimulating the growth of *Festuca rubra* and *Poa pratensis*, leading to a significant reduction in the abundance of many small plants such as prostrate phanerogamic species, mosses and lichens (79). In this coastal area with low nitrogen deposition (currently about 10 kg/ha per year) the vegetation of dune grasslands is at present still species-rich, whereas in many Dutch dune grasslands with higher nitrogen loading (20–30 kg/ha per year) many grasses have increased in abundance and it has become a problem to maintain diversity. Recent studies of the response of mesotrophic grasslands in the United Kingdom have shown that additions as small as 25 kg/ha per year can lead to changes in species diversity after several years of fertilizer additions, and that changes take place more rapidly at higher rates of addition (80). This indicates that many of these semi-natural grasslands are also sensitive for nitrogen eutrophication, and that the critical loads are likely of the same magnitude or slightly higher (20–30 kg/ha per year) than in calcareous grasslands.

Many semi-natural grassland types occur in Europe, especially in the montane-subalpine regions, and contain a large proportion of the biodiversity of that area. It is important to emphasize the effects of nitrogen eutrophication in these grasslands, too, because nitrogen deposition is beginning to increase in these remote regions. Data are too scarce to establish a reliable critical load for these grasslands, but it may nevertheless be expected that most of these grasslands are sensitive to nitrogen and that the critical nitrogen load is probably lower than for lowland calcareous grasslands. For an overview of the critical loads see Table 2 (page 26).

Effects of nitrogen deposition on heathlands

Heathlands have long been part of the western European landscape. Various types of plant community have been described as heath, but the term is applied here to plant communities where the dominant species are small-leaved dwarf shrubs forming a canopy 1 metre or less above the soil surface. Grasses and forbs may form discontinuous strata, and there is frequently a ground layer of mosses or lichens (81,82). Dwarf shrub heathlands occur in various parts of the world, especially in montane habitats, but are widespread in the atlantic and subatlantic parts of Europe. In these parts of the European continent, natural heathland is limited to a narrow coastal zone. Inland lowland heathlands are certainly semi-natural, although they have existed for several centuries. Lowland heaths are widely dominated by some Ericaceae, especially *Calluna vulgaris* in the dry and *Erica tetralix* in the wet heathlands (81). In these heaths, development towards woodland has been prevented by mowing, burning, sheep grazing and sod removal.

Until the beginning of the twentieth century, nutrient input and output was in equilibrium in the lowland heathlands of western Europe (82,83). The original land use implied a regular, periodic removal of nutrients from the ecosystem through grazing and sod removal (84). Sod removal was practised less systematically in many Scandinavian and Scottish heathlands (84), where *Calluna* was renewed by burning at regular intervals varying from 4–6 years in southern Sweden to 15–20 years in western Norway (85,86). The original use of the lowland heathland ceased in the early 1900s, and the area occupied by this community decreased markedly all over its distribution area (28,82,87). Because of their conservational importance, many lowland heathlands have become nature reserves in recent years. Dwarf shrub heathlands may be divided into four categories according to broad differences in habitat: dry heathlands, wet heathlands, montane heathlands and arctic-alpine heathlands.

Inland dry heathlands

During the last few decades, the equilibrium between nutrient input and output has been disturbed. In western Europe, many lowland heathlands have become dominated by grass species. An evaluation, using aerial photographs, has shown that more than 35% of Dutch heathland has been transformed into grassland (88). Similar changes have been observed in recent years in south-west Norway, the area having the largest local emission of ammonia as well as the heaviest nitrogen input through long-range deposition in Norway (89). It has been suggested that nitrogen eutrophication might be a significant factor in this transition to grassland, and field and laboratory experiments affirm the importance of nutrients, especially in the early phase of heathland development (10,90–92). Nevertheless, *Calluna* spp. can compete successfully with grasses even at high nitrogen loading if its canopy remains closed (92). Heather beetle plagues and nutrient accumulation in the soil are also important factors in the

changing lowland heaths. Furthermore, evidence is growing that the frost sensitivity of the dominant dwarf shrubs may also be affected by increasing nitrogen inputs.

Heathland canopies have a strong filtering effect on air pollutants, in which a varying canopy structure is an important factor. It has been shown that for sulfur and nitrogen, bulk deposition accounts for only some 35–40% of total atmospheric input (91,93). Total atmospheric deposition of nitrogen was found to be 30–45 kg/ha per year in the heathland sites in the eastern part of the Netherlands. More than 70% of the total nitrogen input was deposited as ammonium or ammonia (93,94). Although data for nitrogen inputs in other European lowland heathlands are lacking, it is very likely that the nitrogen deposition has also increased in many European agricultural regions in recent years (95,96).

Heather beetle outbreaks

In *Calluna* heathland, outbreaks of the chrysomelid heather beetle (*Lochmaea suturalis*) occur frequently. The beetles feed exclusively on the green parts of *Calluna*, with the result that the canopy is opened over large areas (97,98) and the growth of understorey grasses (*Deschampsia*, *Molinia*) is significantly enhanced. In general, insect grazing is affected by the nutritive value of the plant material, the nitrogen content being especially important in this respect (99). Nitrogen concentrations in the green parts of *Calluna* increased when nitrogen was experimentally applied to heathland vegetation (91,94). It is therefore very likely that the frequency and intensity of heather beetle outbreaks are stimulated by the increased atmospheric nitrogen input in Dutch heathland. This hypothesis is supported by the fact that, although from 1915 onwards outbreaks occurred in the Netherlands roughly every 20 years, in the last 15 years outbreaks have occurred every 8 years or less (100). Furthermore, it has also been observed that during a heather beetle outbreak nitrogen-fertilized *Calluna* plants were more severely damaged (90).

Brunsting & Heil (101) demonstrated that the growth of heather beetle larvae was increased by higher nitrogen concentrations in the leaves of *Calluna*. A study on the effects of spraying covered *Calluna* plants with ammonium sulfate on the growth of heather beetle showed no significant effect of the treatment on the total number and biomass of the first-stage larvae. However, the development of subsequent larval stages was accelerated by the application of ammonium sulfate, the third-stage larvae increasing by 20% compared with control larvae (102). In another experiment (103), larvae were placed on *Calluna* shoots taken from plants fumigated with ammonia in open-top chambers for 12 months at 4–105 mg/m³. After 7 days the larvae were counted and weighed. Both the mass and the development rate of the larvae clearly increased with increasing concentrations of ammonia.

The heather beetle has recently been found in south-west Norway, and is probably an important cause of death of *Calluna* populations in this region (104). It can be concluded that nitrogen inputs influence outbreaks of heather beetle, although the exact relationship between both processes needs further research.

Nutrient accumulation in the soil

In the past, Dutch inland heathlands were grazed by sheep and sod was generally removed at intervals of 25–50 years (82). Nowadays these heathlands are mostly managed by mechanical sod removal. Sod removal can restore the heathland vegetation if a seed bank of the original heathland species is still present (106). Increases in organic matter and in the amounts of nitrogen in the system during secondary succession are well known (106). It was shown in the 1970s that during secondary heathland succession the above- and below-ground biomass and the

amount of litter increased (81,107). It is likely that changes in nitrogen accumulation will occur due to the increase in atmospheric deposition in the last few decades.

Berendse (108) found a large increase in plant biomass, soil organic matter and total nitrogen storage in the first 20–30 years after sod removal. Moreover, nitrogen mineralization was low in the first 10 years (about 10 kg/ha per year) but strongly increased in the next 20 years to 50–110 kg/ha per year. Regression analysis of total nitrogen storage against years after sod removal revealed an annual increase in nitrogen of some 33 kg/ha per year (probably somewhat lower in the first years and higher in the later years) (108). These values are in good agreement with nitrogen deposition measured in Dutch heathlands in the late 1980s (93).

Thus, as is usual, the organic matter in the soil increased rapidly during secondary succession after sod removal, which removed almost all of the soil organic matter. However, this process is accelerated by enhanced dry matter production and litter production by the dwarf shrubs caused by the extra nitrogen input. Nitrogen accumulation in the system also increased, and hardly any nitrogen disappeared from the system because nitrate leaching to deeper layers is only of minor importance in Dutch heathlands, as shown by De Boer (109) and Van Der Maas (110). Within the relatively short period of 10 years, nitrogen availability from atmospheric inputs, in addition to mineralization, is high enough to stimulate the transition of heathland to grassland, especially after the opening of the heather canopy by secondary causes.

Frost sensitivity

It has been shown that frost sensitivity in some tree species increases with increasing concentrations of air pollutants (111,112). This increase in frost sensitivity is sometimes correlated with higher nitrogen concentrations in the foliage of the trees. Air pollution can be expected to have long-term effects on the frost sensitivity of *Calluna* and *Erica* spp., owing to the fact that they are evergreens and that the increased nitrogen deposition in the Netherlands and Norway is shown to increase the nitrogen content of *Calluna* leaves (91,103). It is suggested that the damage to *Calluna* shoots in the successive severe winters of the mid-1980s was at least partly due to increased frost sensitivity.

The effects of sulfur dioxide, ammonium sulfate and ammonia on frost sensitivity in *Calluna* have been studied by Van Der Eerden et al. (102). After fumigation with sulfur dioxide (90 mg/m³ for 3 months) increased frost injury in *Calluna* was found only at temperatures that occur only infrequently in the Netherlands (lower than –20 °C). Frost sensitivity was not affected in autumn (September or November) when *Calluna* plants were fumigated with ammonia in open-top chambers for 4–7 months at 100 mg/m³, whereas in February, just before growth started, frost injury increased significantly at –12 °C (103). Similar fumigation during the winter in England also caused increased frost sensitivity, but the applied concentrations of ammonia were high (140–280 mg/m³) (113).

Van Der Eerden et al. (103) studied frost sensitivity in *Calluna* sprayed with six different levels of nitrogen as ammonium sulfate (3–91 kg/ha per year). Frost sensitivity increased slightly, though significantly, after five months at the highest level of ammonium sulfate (400 mmol/litre, equivalent to nitrogen at 91 kg/ha per year) compared with the control. Nevertheless, the frost sensitivity of *Calluna* decreased again two months later, and no significant effects of ammonium sulfate application on frost hardiness were found at that time. The effects of ammonium nitrate on frost sensitivity in *Calluna* on peaty soils were studied in North Wales (114). In contrast to the above-mentioned studies, the frost sensitivity of *Calluna*, quantified by

two methods, significantly decreased in the nitrogen-treated plants after 32 months of application at 0–120 kg/ha per year. This decrease in frost sensitivity was most obvious in October.

Thus, high levels of ammonia or ammonium sulfate seem to increase the frost sensitivity of *Calluna* plants, although the significance of this phenomenon is still uncertain at ambient nitrogen inputs; ammonium nitrate even reduces the frost sensitivity of *Calluna*. Currently, the relationship between frost sensitivity and nitrogen inputs is insufficiently quantified to use it for a precise assessment of critical loads in this respect.

It has been shown that atmospheric nitrogen is the trigger for the change of lowland dry heathland into grassland in the Netherlands. In the United Kingdom, studies on three heaths revealed a decline in *Calluna* and an increase in grasses; the authors concluded that an increase in nitrogen deposition was at least partly responsible for the changes, but also noted that the management had also changed (74). A wider assessment of heathlands in south-eastern England showed that in some cases *Calluna* had declined and subsequently been invaded by grasses, while other areas were still dominated by dwarf shrubs (115). This clearly stresses the importance of management for the maintenance of dwarf shrubs in heathland.

A simulation model was used to integrate the various processes (such as atmospheric nitrogen input, heather beetle outbreaks, soil nitrogen accumulation, sod removal and competition between species) to establish the critical loads of nitrogen deposition in lowland dry heathlands (116,117). The model was calibrated with data from field and laboratory experiments in the Netherlands, and the proportion and increase of grasses in the heathland system were used as an indicator of the effects of atmospheric nitrogen. Atmospheric nitrogen deposition varied between 5 and 75 kg/ha per year in steps of 5–10 kg, from which it was clear that the critical nitrogen load for change from dwarf shrubs to grasses is 15–20 kg/ha per year.

Inland wet heathlands

The western European lowland wet heathlands are dominated by the dwarf shrub *Erica tetralix* (28). These communities are generally richer in plant species than the dry heathlands. In recent decades a drastic change has been seen in the species composition of Dutch wet heathlands, many originally dominated by *Erica* having become monospecific stands of *Molinia*. Together with *Erica*, almost all of the rare plant species have disappeared from the system, and it has been suggested that the change was brought about by atmospheric nitrogen eutrophication.

Competition experiments using micro-ecosystems have clearly shown that *Molinia* is a better competitor than *Erica* at high nitrogen availability: after two years of applying nitrogen (150 kg/ha per year) the relative competition strength of *Molinia* compared with *Erica* had doubled (118). A three-year field experiment with nitrogen application at about 160 kg/ha per year also indicated that *Molinia* is able to out-compete *Erica* at high nitrogen availabilities (119). In contrast to the competitive relationship between *Calluna* and the grasses, *Molinia* can out-compete *Erica* without opening the canopy. This is because the *Erica* canopy is lower than that of *Calluna*, so that *Molinia* can outgrow *Erica* if enough nitrogen is available. In this respect it is also important that outbreaks of heather beetle do not occur; up to now no frost damage has been observed in this community.

In many Dutch wet heathlands, the accumulation of litter and humus has led to increased nitrogen mineralization (100–130 kg/ha per year) (120). In the first 10 years after sod removal,

the annual nitrogen mineralization is very low, but afterwards it increases strongly. This nitrogen accumulation can be greatly influenced by increased deposition, because the leaching of soil nitrogen from wet heathlands is extremely low (108). The observed nitrogen availabilities are high enough to turn *Erica*-dominated wet heathlands into monospecific stands of *Molinia*.

Berendse (121) developed a wet heathland model to simulate carbon and nitrogen dynamics during secondary succession. He incorporated in this model the competitive relationships between *Erica* and *Molinia*, the litter production from both species, soil nitrogen accumulation and mineralization, leaching, atmospheric nitrogen deposition and sheep grazing. He simulated the development of lowland wet heathland after sod removal, because almost all of the Dutch communities are already strongly dominated by *Molinia* and it is impossible to expect changes in this situation without drastic management. Using the biomass of *Molinia* with respect to *Erica* as an indicator, his results suggested 17–22 kg/ha per year as the critical load for the transition of lowland wet heathland into grassland (122). The decrease in rare forbs is partly caused by shading by *Molinia*, but some species had already disappeared before the increase in *Molinia* began.

Arctic and alpine heathlands

Semi-natural *Calluna* heathlands are found in the lowlands along the Norwegian coast to a latitude of 68° N, showing distinct floristic gradients in the south–north direction, inland from the coast and from lowland to upland areas (122). In central parts of western Norway, the floristic composition changes at about 400 m above sea level as alpine species occur regularly in the heaths. At this altitude, oceanic upland *Calluna* and *Erica* heaths merge into alpine heaths of naturally occurring, non-anthropogenic communities. Some oligotrophic alpine heaths also contain *Calluna*, but most heaths in Fennoscandia and in European parts of Russia are dominated by other ericoid species (*Vaccinium* spp., *Empetrum nigrum*, *Arctostaphylos* spp., *Loiseleuria procumbens* and *Phyllodoce caerulea*) as well as *Betula nana*, *Juniperus communis* and *Salix* spp. Many heath types have a more or less continuous layer of mosses and lichens. Related heaths are found in alpine regions in the British Isles, in Iceland, in southernmost Greenland, in northern Russia and on siliceous rocks in the Alps (28,123,124).

Alpine and arctic habitats have many ecological characteristics in common, although the climatic conditions are more severe in the arctic regions than in most alpine regions. The growing season is short (3–3.5 months in the low arctic zone), air and soil temperatures are low, winds are frequent and strong, and the distribution of plant communities depends on the distribution of snow during winter and spring. Most alpine and all arctic zones are influenced by frost activity or solifluction, except for soils in the low alpine and semiarctic zones, where podzolic soils are found. Decomposition of organic matter and nutrient cycling are slow, and a large amount of the nitrogen input is stored in the soil, in forms that cannot be used by plants (1). The low nutrient availability limits primary production. Most species are adapted to a strict nitrogen economy, and their nitrogen indicator values are generally low (125).

A study on the nitrogen balance of an arctic area in Alaska found that the most important sources of nitrogen were fixation (75%) and ammonia in precipitation (22%) (126). Most of the nitrogen input is retained in living biomass, and only very little is leached from the soil. Denitrification is also low, partly due to nutrient deficiency. Nevertheless, nitrogen metabolism as such does not seem to be inhibited by low soil temperatures (127). Nitrogen fixation in arctic habitats has been studied in bacteria, soil algae, lichens and legumes (128,129). Blue-green algae are especially important in this respect, either free-living species, those associated with

mosses, or phycobionts in lichens (e.g. *Peltigera*, *Nephroma* and *Stereocaulon*). The rate of fixation depends on temperature and moisture, and thus varies throughout the year (130).

It is to be expected that arctic and alpine communities are sensitive to increased atmospheric nitrogen input because nitrogen retention is very efficient, although primary production is also strongly regulated by factors other than nitrogen (temperature, moisture) (2). The effects of increased nitrogen availability on alpine/tundra vegetation have been studied in several fertilization experiments. In most of these experiments complete NPK fertilizer was used, although sometimes nitrogen was applied separately. The results showed that:

1. in alpine and arctic vegetation, nitrogen is quickly absorbed by phanerogamic species and incorporated into their tissues, while the increase in nitrogen contents differs for graminoids, deciduous and evergreen species (131–134);
2. phanerogamic plant species respond to nitrogen application in different ways: increased growth and biomass, enhanced number of tillers, more flowers, and changes in phenology (135);
3. some phanerogamic species are damaged or even killed at high doses of nitrogen fertilization (135); and
4. changes in species cover and composition are likely when nitrogen is applied for a longer period (5–10 years).

All these studies concentrated on effects on phanerogamic species, providing little information on the effects of nitrogen on cryptogams. Many authors, however, stress that nitrogen fixation will probably decrease when atmospheric deposition increases in arctic and alpine ecosystems. In forest studies, it has already been shown that *Cladonia* spp. and some mosses are very sensitive to addition of nitrogen. It is often stated that these ecosystems are sensitive to air pollutants, but critical loads for nitrogen are rarely investigated. We suggest, however, that the critical nitrogen load for arctic and alpine heaths is lower than that for lowland heathland, at 5–15 kg/ha per year.

Matgrass swards

In recent decades, besides the transition from dwarf-shrub-dominated to grass-dominated heathlands, a reduced species diversity has been observed. Species of the acidic Nardetalia grasslands and the related dry and wet heathlands (Calluno-Genistion and Ericion tetralicis) seem to be especially sensitive. Many of these herbaceous species (e.g. *Arnica montana*, *Antennaria dioica*, *Dactylorhiza maculata*, *Gentiana pneumonanthe*, *Genista pilosa*, *G. tinctoria*, *Lycopodium inundatum*, *Narthecium ossifragum*, *Pedicularis sylvatica*, *Polygala serpyllifolia* and *Thymus serpyllum*) are declining or have even become locally extinct in the Netherlands. The distribution of these species is related to small-scale, spatial variability of the heathland soils. It is suggested that atmospheric deposition has caused such drastic abiotic changes that these species cannot survive (136). Dwarf shrubs as well as grass species now dominate the former habitats of these endangered species.

Enhanced nitrogen fluxes on to the nutrient-poor heathland soils lead to an increased nitrogen availability in the soil. Nevertheless, most of the deposited nitrogen in western Europe originates from ammonia/ammonium deposition and may also cause acidification as a result of nitrification. Whether eutrophication or acidification, or a combination of the two, is decisive depends on the pH, buffer capacity and nitrification rate of the soil. Roelofs et al. (137) found that in dwarf-shrub-dominated heathland soils, nitrification was inhibited at pH 4.0–4.2, and

that ammonium accumulated while nitrate decreased to almost zero at these or lower pH values. Furthermore, nitrification has been observed in the soils of the habitats of endangered species, owing to their somewhat higher pH and higher buffer capacity. In soils within the pH range 4.1–5.9, the produced acidity is buffered by cation exchange processes (138). The pH will drop when calcium is depleted and this may cause a decline in those species that are generally found on soils with somewhat higher pH. To study the pH effects on root growth and survival rate, hydroculture experiments were conducted over 4-week periods with several of the endangered species (*Arnica*, *Antennaria*, *Viola*, *Hieracium pilosella* and *Gentiana*) and with the dominant species (*Molinia* and *Deschampsia*) (139). The dominant species had a lower pH optimum (3.5 and 4.0, respectively) than the endangered species (4.2–6.0), but the endangered species could nevertheless survive very low pH without visible injury during this short experimental period.

Reduced pH may indirectly result in an increased leaching of base cations, increased aluminium mobilization and thus enhanced aluminium:calcium ratios in the soil (140). Furthermore, reduction of the soil pH may inhibit nitrification and result in ammonium accumulation and consequently increased ammonium:nitrate ratios. In a field study, the characteristics of the soil of several of these threatened heathland species were compared with the soil characteristics of the dominant species (*Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea*) (141). In general, the endangered species grew on soils with higher pH, lower nitrogen content and lower aluminium:calcium ratios than the dominant species. The ammonium:nitrate ratios were higher in the dwarf-shrub-dominated soils compared with the soil of the endangered species. Fennema (143,143) demonstrated that soils from locations where *Arnica* is still present had higher pH and lower aluminium:calcium ratios than soils of former *Arnica* stands, although he found no differences in total soil nitrogen and ammonium:nitrate ratios. Both these studies indicate that high aluminium:calcium ratios or even increased ammonium:nitrate ratios are associated with the decline of these species. Nevertheless, no significant effects of aluminium or aluminium:calcium ratio on growth rates have been observed in hydroculture experiments in which the effects of these factors on root growth and survival rate were studied (139). Comparable experiments with *Arnica* and *Deschampsia* (144) and with *Antennaria*, *Viola*, *Filago minima* and *Deschampsia* (145) showed similar results. However, results of a hydroculture experiment with *Arnica* showed that this species is very sensitive to enhanced aluminium:calcium ratios at intermediate or low nutrient levels (146). Pot experiments have indicated that increased ammonium:nitrate ratios lead to decreased vitality in *Thymus* spp., and hydroculture experiments with the same species confirmed that increased ammonium:nitrate ratios affect the cation uptake (147). In a pot experiment, *Thymus* spp. planted on acid heathland soil and on artificially buffered heathland soil was sprayed with ammonium nitrogen at 0, 15 and 150 kg/ha per year for six months (141). In this relatively short period a deposition of 15 kg/ha per year on the acid soil did not lead to ammonium accumulation. As a result of nitrification, soil pH decreased faster compared with no deposition. At the highest deposition (150 kg/ha per year), nitrification rates in the acid heathland soils were too low to prevent ammonium accumulation, and increased ammonium:nitrate ratios probably caused the decline of the species. Only in the artificially buffered soils with higher pH were nitrification rates high enough to balance ammonium and nitrate. *Thymus* plants thrived on these soils despite very high total nitrogen contents.

At present, there is too little information available on these rare heathland and acidic grassland species to formulate a critical load for nitrogen. The observation that these heathland species mostly disappear before dwarf shrubs are replaced by grasses, however,

leads to the assumption that their critical load is lower than the that for the transition to grasses (15–20 kg/ha per year). For an overview of the critical loads see Table 2 (page 26).

Effects of nitrogen deposition on forests

Forests tree species

Until recently, the growth of the vast majority of the forest tree species in the northern hemisphere was limited by nitrogen. In forestry, nitrogen fertilization was used to increase wood production (2). An increase in the supply of an essential nutrient such as nitrogen will stimulate tree growth, and the initial impact of enhanced nitrogen deposition will therefore be a fertilizer effect. Nevertheless, continued high inputs of nitrogen produce negative effects on tree growth (1). Until the mid-1980s, almost all of the research on forest decline had focused on acidification, but it has now become evident that enhanced nitrogen deposition may also be important in recent forest decline.

The effects of high atmospheric nitrogen are very complex (54,148–150). Chronic nitrogen deposition may result in “nitrogen saturation”, whereby enhanced nitrogen inputs no longer stimulate tree growth but start to disrupt ecosystem structure and function, and increased amounts of nitrogen are lost from the ecosystem in the leachate (2,151,152). The nitrogen input at which such saturation occurs depends on a number of factors, including the amount of deposition, the vegetation and soil types and management history. The following indirect processes, besides the direct effects of gaseous pollutants on the shoots, are important.

1. Soil acidification, due to nitrification of ammonium, leads to accelerating leaching of base cations, and in poorly buffered soils to increased dissolution of aluminium, which can damage the development of fine roots and mycorrhizas and thus reduce nutrient uptake (138,153).
2. Whether ammonium will accumulate in a soil depends strongly on the nitrification rate and the deposition levels (154). Ammonium accumulation will lead, apart from an initial growth stimulation and changes to the root:shoot ratio, to an imbalance in the nutritional state of the soil and concomitantly of the trees (137,155–157). Accumulation of nitrates in the ecosystem may also lead to eutrophication.

As a consequence of all these processes, the health of the trees declines and their sensitivity to drought, frost, insect pests and pathogens can increase markedly (54). These phenomena may also play a secondary, but certainly not unimportant, role in the dieback of forest trees.

Although many tree species occur in natural forest ecosystems, almost all studies on air pollution have concentrated on a few forestry tree species from acidic, nutrient-poor soils. Most of these species are conifers (*Picea*, *Pinus* and *Pseudotsuga* spp.) and the following section will focus mainly on the long-term soil-mediated effects on these trees. Available data on broad-leaved species (*Fagus*, *Quercus*) are also considered. Soil acidification *per se* is only shortly reviewed, because the critical load for acidity and tree growth is well established (158,159).

Soil-mediated changes in nutritional status

It has been shown that in areas with high ammonia/ammonium deposition, ammonium accumulates in acid forest soils that have little or no nitrification. Van Dijk & Roelofs (155) found ammonium accumulation in damaged *Pinus* and *Pseudotsuga* stands receiving nitrogen at 60–100 kg/ha per year, even though the soil pH was no different from that in healthy stands.

This build-up of ammonium leads to increased ammonium:base-cation ratios (137,154), a reduction of base cation uptake, and eventually nutritional problems. Critical ratios of excess ammonium to base cations were determined using different ammonium sulfate spraying treatments (154). Values above 5, 10 and 1 for, respectively, ammonium:potassium, ammonium:magnesium and aluminium:calcium ratios in soil extracts gave nutritional problems in the coniferous species studied. In soils with no or a low nitrification rate, around 11 kg/ha per year is a reliable critical load to prevent critical ammonium:cation ratios, whereas in soils rich in base cations, with moderate to high nitrification rates, the critical loads are higher (> 50 kg/ha per year) (154).

Nutritional status following enhanced nitrogen inputs is affected by both ammonium accumulation and soil acidification. Base cation concentrations in the soil are reduced by leaching, whereas base cation uptake by plants is reduced by excess ammonium or aluminium. Moreover, root growth is decreased (see below). Laboratory, greenhouse and field measurements in Germany, the Netherlands and southern Sweden (155,157,160–166) have shown that this complex of factors produces severe deficiencies of magnesium and potassium in coniferous trees. Most of these studies were conducted in areas of high nitrification or involved experiments with large nitrogen inputs of 40–100 kg/ha per year.

It has been observed that the magnesium and phosphorus concentrations in leaves of *Fagus sylvatica*, a common deciduous tree in Europe, decreased significantly from 1984 to 1992 in permanent plots in north-west Switzerland. Further, the magnesium concentrations in the leaves of young *F. sylvatica* had previously decreased significantly over a 4-year period at fertilization rates of 25 kg/ha per year (167). In Sweden, suboptimal concentrations of magnesium and potassium in *Fagus* leaves were found in areas with the highest nitrogen deposition (168) and addition of nitrogen enhanced nutritional imbalance in a 120-year-old *Fagus* stand (169). It is thus obvious that this species is also sensitive to nutritional imbalances induced by enhanced nitrogen supply.

Base cations are also lost from the canopy by increased leaching, linked to high amounts of atmospheric deposition (93,137,170). High nitrogen inputs increase the organic nitrogen concentration in conifer needles to supra-optimal levels (155,171). Nitrogen-rich free amino acids, especially arginine, significantly increased in *Picea abies* needles with a high nitrogen concentration (> 1.5%) (155,162,172,173) and in *Fagus* leaves (171).

Although there is clear evidence that high ammonia/ammonium loads produced adverse changes in the nutritional status and growth of the coniferous and broad-leaved trees studied, it is difficult to deduce a critical load for nitrogen because of the complexity of the ecosystem. A quite reliable critical load for nitrogen deposition on beech tree vitality is about 15–20 kg/ha per year, as demonstrated in the experiments in Switzerland (167).

The results of the European Commission's nitrogen saturation study (NITREX), which incorporates long-term experiments in both clean and nitrogen-polluted areas with whole-ecosystem manipulation of nitrogen inputs, are providing important evidence on the effects of nitrogen deposition on tree vitality and ecosystem health. Atmospheric deposition of nitrogen was reduced from 40 to 2 kg/ha per year from 1989 onwards in a nitrogen-saturated *Pinus sylvestris* stand in the Netherlands (165,174,175), by replacing the throughfall water with clean water. Nitrogen concentrations in the upper soil and the fluxes of this element through the soil profile decreased. As a result, base cation leaching and the ratios of ammonium to various

cations also decreased, while potassium and magnesium concentrations in the needles increased significantly. The needle nitrogen concentrations were reduced only slightly, but were significantly lower than in the needles of the control plots. The concentration of arginine, a free amino acid, decreased significantly in the needles of the trees given clean water. Furthermore, tree growth was higher after four years of clean throughfall than in the control plots with high nitrogen deposition. Up to now, no changes in the mycorrhizal status or in the undergrowth have been observed (165,176). This experiment clearly demonstrates the detrimental effects of enhanced atmospheric nitrogen deposition on the nutritional balance of conifers.

Susceptibility to frost

It has been suggested that the sensitivity of trees to secondary stress factors is increased by high nitrogen loading (54,148). In field fertilization experiments, it is often observed that tree growth starts earlier in the season, which may increase damage by late frost. Furthermore, it has been shown, after nutrient applications, that frost damage to *Pinus sylvestris* increased considerably at needle nitrogen concentrations above 1.8% (111), although other experiments indicated that improved nitrogen status reduced frost damage (177–179). Only a few data are available with respect to frost damage in direct relation to airborne nitrogen deposition. After exposure to ammonia and sulfur dioxide, *P. sylvestris* saplings became more frost sensitive ($< -10\text{ }^{\circ}\text{C}$) compared with control plants (112), yet field site investigations in areas with low ammonia/ammonium pollution (about 4 mg/m^3) and in highly polluted areas (40 mg/m^3) showed that the frost sensitivity of *P. sylvestris* was not higher (and was sometimes even lower) in the polluted area than in the other investigated sites. After the experimental treatment with ammonia (53 mg/m^3) the growth of the trees had increased, indicating that the observed change in frost sensitivity might occur through physiological changes and nutrient imbalances.

The effects of simulated acid mist containing sulfate, ammonium, nitrate and hydrogen ions on the frost sensitivity of *Picea rubens* has been studied in several experiments (180,181). The results revealed that sulfur compounds strongly affect the frost sensitivity of coniferous trees, but that the impact may be mediated by the nutritional status (nitrogen:base cation ratio) of the trees (181). Overall, the effects of increased nitrogen inputs on frost sensitivity remain speculative, and there are insufficient data for assessment of critical load.

Susceptibility to drought

The water uptake of conifers may also be affected by increasing nitrogen deposition, caused by an increased shoot:root ratio and a reduction in the length of fine roots. Indeed, the vitality of many tree species in regions with high nitrogen deposition in the Netherlands was particularly low in the dry years in the mid 1980s, but revived in the following normal years (149). A high nitrogen supply is generally considered a negative effect on the development of fine roots and mycorrhizas, although positive effects are also mentioned (182). In a pot experiment, nitrogen at 0, 48 or 480 kg/ha per year as ammonium sulfate was applied to young plants of *Pinus sylvestris*, *P. nigra* and *Pseudotsuga menziesii* (161). After seven months, the coarse root biomass had not changed but the fine root biomass had decreased by 36% and mycorrhizal infection had decreased by 63% at the highest rate of application. In the Dutch NITREX study the fine root biomass and the number of root tips of *P. sylvestris* increased after nitrogen deposition was reduced to pre-industrial levels, indicating a restricted root growth and nutrient uptake capacity at the ambient nitrogen load of some 40 kg/ha per year (165,176).

In a hydroculture experiment with *P. nigra* at pH 4.0, an increase in coarse/fine root ratio was found after increasing the ammonium concentration to 5000 mmol/litre. Furthermore, a clear

relationship was found between the nitrogen content of the fine roots and mycorrhizal infection (measured as the number of dichotomously branched roots). In another hydroculture experiment, 2700 mmol/litre nitrate had hardly any effect on the mycorrhizal development of *Picea abies* seedlings inoculated with *Lactarius rufus* (183). Similarly, 2700 mmol/litre ammonium had only a slight negative effect on mycorrhizal development, although a reduction in root growth was seen. A pot experiment with *P. abies* demonstrated an optimal mycorrhizal frequency when the mineral nitrogen content of the soil was 40 mg/kg dry soil, while at 350 mg/kg a 95% reduction in mycorrhizal frequency was found (184). In this study no correlation was found with soil pH. Application of nitrogen as ammonium sulfate at 300 kg/ha per year to a 35-year-old *Picea sitchensis* stand produced a 15% reduction in mycorrhizal frequency in the following year (185). In a pot experiment, nitrogen was applied at 0–400 kg/ha per year as ammonium or nitrate to young *P. sylvestris* inoculated with *Paxillus involutus* (186). A reduction in the amount of mycorrhizal root tips and the number of sclerotia was found at application rates above 10 kg/ha per year.

Besides the above-mentioned data for coniferous trees, it had been shown that the shoot:root ratios of young *Fagus sylvatica* trees, grown in containers with acid forest soil, significantly increased from about 1 to 2–3 after a 4-year experimental application of nitrogen (25 kg/ha per year or more) (167).

It is thus likely that enhanced nitrogen inputs affect drought sensitivity through changes to shoot:root ratios, the number of fine roots and the ectomycorrhizal infection of the roots. Nevertheless, the data on this aspect of reduced tree vitality are too scarce to enable any calculation of a critical load for nitrogen.

Susceptibility to pathogens

There may also be significant effects of fungal pathogens or insect pests associated with increasing nitrogen deposition. The foliar concentrations of nitrogen increased markedly in tree needles or leaves in experiments with nitrogen additions, and also in forest sites with high atmospheric nitrogen loading (137,155,169). Grazing by mammals and insects generally increases with increasing palatability of the leaves or shoots, and nitrogen is of major importance for the palatability of plant material (99). Secondary plant chemicals such as phenolics are important for the resistance of plants to insect attacks, which increases with the concentration of phenolics. In this respect, it may be important that the total amount of phenolics of *Fagus* leaves in a 120-year-old stand decreased by more than 30% compared with the control after nitrogen fertilization at about 45 kg/ha per year (169). An ecologically important relationship between nitrogen enrichment and insect pests has been quantified for lowland heathland (98,101), but corresponding data for forest ecosystems are still scarce.

From 1982 to 1985, an epidemic outbreak of the pathogenic fungus *Sphaeropsis sapinea* was observed in coniferous forest (mainly *P. nigra*) in the Netherlands, which affected whole stands and was especially severe in the south-east with its high airborne nitrogen deposition (137). Van Dijk et al. (162) showed that trees in the infected stands had a significantly higher leaf nitrogen concentration, occurring together with higher soil ammonium levels, compared with the uninfected stands. Most of the additional nitrogen in the needles of the affected stands was stored as nitrogen-rich free amino acids, especially arginine. Proline concentrations were also higher in the infected trees, indicating a relation with water stress (162).

The effects of *Sphaeropsis* have also been studied by De Kam et al. (171). Two-year-old *P. nigra* plants were grown for three years in pots and given five treatments with ammonium sulfate from a very low nitrogen level to some 300 kg/ha per year, in combination with two levels of potassium sulfate. The 5-year-old plants were then inoculated with *Sphaeropsis*. Bark necrosis was much higher in the plants treated with ammonium sulfate, whereas in the plots with high levels of potassium sulfate necrosis was low. Effects of ammonium sulfate on fungal damage were observed at nitrogen levels as low as 75 kg/ha per year, but were very significant in the plants treated with 150 kg/ha per year. After potassium addition fungal necrosis was greatly reduced (171).

In beech forests in north-western Switzerland, a significant positive correlation was found between the nitrogen:potassium ratios in the leaves and necrosis caused by *Nectria ditissima* (167). Experimental inoculation of *F. sylvatica* with *N. ditissima* at different applications of nitrogen clearly increased the dieback of new leaves and shoots. Furthermore, infestation of *F. sylvatica* with beech aphids (*Phyllaphis fagi*) was also affected by nitrogen availability. The degree of infestation with the aphid increased significantly with enhanced leaf nitrogen:phosphorus ratios (167). Although evidence for nitrogen-mediated changes in susceptibility to fungal pests and insect attacks has until now been based on observations of only few species, it is obvious that trees became more susceptible to these attacks with increasing nitrogen enrichment and this may play a crucial role in the dieback of some forest stands.

A critical load for nitrogen had been established at 11 kg/ha per year (at no or low nitrification) to > 50 kg/ha per year in highly nitrifying soils, based on nutritional imbalance of coniferous species (154). Recent evidence on the health of *F. sylvatica* in acidic forests indicates a critical load of 15–20 kg/ha per year based on both field and experimental observations. Elevated nitrogen deposition can seriously affect tree vitality via a complex web of interactions, such as susceptibility to frost and drought. Pathogens may play an important role in tree decline, but it is not currently possible to combine the observed processes and effects to give an overall critical nitrogen load for tree health.

Tree epiphytes, ground vegetation and ground fauna

Ground-living and epiphytic lichens and algae

The effects of sulfate as an acidifier on epiphytic lichens have been extensively studied over a long period (187,188). Sulfate was the dominant airborne pollutant in the past, and it has been shown that most epiphytic lichens are more negatively affected by acidity than by nitrogen compounds (except nitrate). Most lichens have green algae as the “photobiont” and are affected by acidity but not by nitrogen; some even react positively to nitrogen (187). Nevertheless, 10% of all lichen species in the world have blue-green algae as the photobiont, and these are negatively affected not only by acidity but also by nitrogen. Most of the north-west European lichens with blue-green algae live on the soil surface or are tree epiphytes. They include the most pollution-sensitive lichens, and are threatened with extinction. This is probably caused by increased nitrogen deposition, which inhibits the functioning of the blue-green algae. In the Netherlands, for example, all of the blue-green algae lichens that were present at the end of the nineteenth century are missing today. In Denmark, 96% of the lichens with blue-green algae are extinct or are under threat. Furthermore, the blue-green algae lichens are strongly over-represented on the Red List of the European Union countries (189).

Very few data exist to establish a critical load for nitrogen for these lichens with blue-green algae. Nohrstedt et al. (190) investigated the effects of nitrogen application (as ammonium nitrate or calcium nitrate) on ground-living lichens (*Peltigera aptosa* and *Nephroma arcticum*) with blue-green algae as the photobiont. The plots were treated once, three times or four times with nitrogen at 120, 240 or 360 kg/ha. After a short time *Peltigera* and *Nephroma* had disappeared and even 19 years later no recolonization had occurred. Nevertheless, it is impossible to transform these very high doses to critical loads. The effects of air pollutants on lichens are usually related to concentrations in the air or in the precipitation. For tree epiphytes stem flow is most relevant, whereas for ground-living lichens throughfall will be more important. Although much research is still needed, it has been suggested that a load as low as 5–15 kg/ha per year is critical for the growth of these blue-green algal lichens (189). These lichens may be the most sensitive components of some forest ecosystems and will thus determine the critical load for these systems.

Free-living green algae, especially of the genus *Pleurococcus* (syn. *Protococcus*, *Desmococcus*) are strongly stimulated by enhanced nitrogen deposition. They cover practically all outdoor surfaces not subject to frequent desiccation in regions with high nitrogen deposition, such as in Denmark and the Netherlands. Results from Sweden show that these algae do not colonize spruce needles in regions with a total deposition (throughfall) lower than about 5 kg/ha per year (191). In areas with deposition above 20 kg/ha per year, the green algal cover of the needles is so thick and the algae colonize so quickly that this may impede the photosynthesis of the spruce trees.

Ground vegetation

In a site in central Netherlands the forest vegetation was investigated in 1958 (nitrogen input around 20 kg/ha per year) and in 1981 (around 40 kg/ha per year). All lichens disappeared during this period and a strong increase in *Deschampsia flexuosa* and *Corydalis claviculata* was found. A large representative sample test (N = 2000) covering some 90% of the Dutch forests, revealed in the mid-1980s that *Galeopsis tetrahit*, *Rubus* spp., *Deschampsia flexuosa*, *Dryopteris cathusiana*, *Molinia caerulea*, *Poa trivialis* and *Urtica dioica* are among the 40 most common forest plants (192,193). In Sweden, *Quercus robur* stands in two geographical areas with different nitrogen deposition were compared, with special emphasis on nitrogen indicator species (194). The stands were quite comparable except for the nitrogen inputs, 6–8 kg/ha per year and 12–15 kg/ha per year, respectively. In the stand with the highest deposition the soil solution was more acidic, probably due to acidic deposition as well (around 10 kg sulfur per ha per year), and it was estimated that acidification of the soil had accelerated during the last 30–50 years. *Urtica dioica*, *Epilobium augustifolium*, *Rubus idaeus*, *Stellaria media*, *Galium aparine*, *Aegopodium podagraria* and *Sambucus* spp. were more common in the most polluted site. Thus, in both the Netherlands and Sweden species indicating nitrogen enrichment became common (28).

Comparable observations were reported in studies examining the changes in soil and vegetation in *Quercus* and *Fagus* stands in southern Sweden (195,196). The studies showed a reduction in exchangeable base cations, a doubling of aluminium over the previous 35 years, and a decrease in soil pH with the disappearance of several species when the pH dropped below a certain threshold. In spite of soil acidification some species had increased their cover, and the most plausible explanation seems to be the increased nitrogen deposition, which is around 15–20 kg/ha per year in southern Sweden and has doubled since 1955. A marked increase in cover was found for *Lactuca muralis*, *Dryopteris filix-mas*, *Epilobium augustifolium*, *Rubus idaeus*,

Melica uniflora, *Aegopodium podagraria*, *Stellaria holostea* and *S. nemorum*, some of these species being nitrogen indicators. Despite soil acidification, acid-tolerant species (*Deschampsia flexuosa*, *Maianthemum bifolium* and *Luzula pilosa*) did not increase. A distinct decrease was observed for *Dentaria bulbifera*, *Pulmonaria officinalis* and *Polygonatum multiflorum*. Furthermore, Rosen et al. (197) found a significant positive correlation between the increase in *Deschampsia flexuosa* cover in the last 20 years in the Swedish forests and the pattern of nitrogen deposition.

In a large semi-natural *Fagus–Quercus* forest in north-east France, some 50 permanent vegetation plots were described in 1972 and 1991. Besides a number of moderately acidic habitats, the changes in species composition on calcareous soils were followed. During the study period, a significant increase in nitrophilous ground flora was observed in these high-pH (about 6.9) stands. This indicates that at this location (with ambient deposition of 15–20 kg/ha per year) a distinct effect of increasing nitrogen availability could be detected (198).

In addition to this evidence from site comparison over time, the effects of nitrogen enrichment on forest ground vegetation have been determined in some experimental studies. From 1968 to 1985, three sites in a 30-year-old *Pinus sylvestris* forest in Lisselbo (central Sweden) were given nitrogen at 0, 20, 40 and 60 kg/ha per year (as ammonium nitrate plus an ambient deposition of 10 kg/ha per year). The original ground vegetation consisted of *Calluna vulgaris*, *Vaccinium vitis-idea*, *V. myrtillus*, *Cladonia* spp., *Cladina* spp. and the mosses *Dicranum* spp., *Pleurozium* spp. and *Hylocomium* spp. The first changes were observed within 8–15 years, and after about 20 years the experimental plots were compared and statistically analysed. At levels above 20 kg/ha per year (plus ambient deposition) the original species disappeared and were replaced by *Epilobium augustifolium*, *Rubus idaeus*, *Deschampsia flexuosa*, *Dryopteris carthusiana* and the moss *Brachythecium oedipodium* (188,198). In another experiment at Lisselbo, the combined effects of acidification (addition of sulphuric acid, pH 2.0) and nitrogen fertilizer (0 and 40 kg/ha per year) were investigated. Increased nitrogen seemed to be the most important parameter: the same species mentioned above increased in cover. Acidification was the second significant parameter: all species disappeared, except for the moss *Pohlia nutans* at high additions of acidity (192,199).

In southern Sweden, the effects of the application of nitrogen (60–180 kg/ha per year) as ammonium nitrate over a 5-year period was studied in stands of *Fagus sylvatica* (200). There was a large reduction in biomass of the ground vegetation with the application of nitrogen and the frequency of most herb layer species declined significantly. Soil measurements revealed that, in addition to eutrophication, the acidification of the soil solution was also important for the decline of the original ground vegetation. In an experiment on the effects of nitrogen fertilization on bryophytes, it appeared that *Brachythecium oedipodium*, *B. reflexum* and *B. starkei* increased significantly at fertilization levels up to 60 kg/ha per year, although at higher doses these species tended to decline. *Hylocomium splendens* and *Pleurozium schreberi* declined strongly at nitrogen doses of 30–60 kg/ha per year (201).

Macrofungi and mycorrhizas

During the last two decades, an increasing number of reports have mentioned a decrease in species diversity and in the abundance of macrofungi. These changes can probably be attributed to indirect effects of air pollution, in particular to increases in the amount of available nitrogen (possibly in combination with acidification) and/or to reduced tree vitality with concomitant reduction of assimilate transport to the roots and mycorrhizas (202).

When comparing sites over time, there were marked differences in the number of fruiting bodies of macrofungi. Most studies in western Europe, however, reveal that the number of ectomycorrhizal fungal species has declined (202). In the Netherlands, the average number of ectomycorrhizal species per foray declined significantly from 71 in the period 1912–1954 to 38 between 1973 and 1982. Similar changes have been observed in Germany: 94 ectomycorrhizal species found between 1950 and 1979 in the Völklinger area (Saarland) have not been recorded recently. From the 236 species found between 1918 and 1942 in the Darmstadt area of Germany, only 137 were recorded in the early 1970s – a loss of 99 species, including many mycorrhizal fungi (202). In contrast to the decline in mycorrhizal fungi, the number of saprotrophic species remained practically unchanged, while the number of lignicolous species increased. This may be related to soil acidification with an increase in aluminium, since the proportion of forest areas in western Europe with a soil pH under 4.2 increased from less than 1% in 1960 to 15% in 1988 (203).

Arnolds (202,204) concluded that acidification has very little effect on the diversity of ectomycorrhizal fungi, but rather triggers changes in species composition. He regarded the increased nitrogen flux to the forest floor as the most important factor in the decline of mycorrhizal fungi. Another study (205) found a negative correlation between the total nitrogen input in mature *Pinus sylvestris* stands and the abundance of fruiting bodies of ectomycorrhizal fungi. Similar results were obtained in a study comparing two sites with *Picea abies* in the Göttingen area of Germany (206). An obvious negative relation was found between nitrogen input (23 versus 42 kg/ha per year) and ectomycorrhizal species – 85 basidiomycetes including 21 ectomycorrhizas (25%) at the less polluted site compared with 55 basidiomycetes including 3 ectomycorrhizas (5%) at the most polluted site. Environmental factors other than nitrogen did not differ significantly. The negative impact of nitrogen seems to hold true only for mature forests (205). Jansen & de Vries (207) found maximum fruiting body production at about 25 kg/ha per year in over 20-year-old *Pseudotsuga menziesii* stands. Meyer (184) found a similar optimum when *Picea abies* was planted in soil mixed with different amounts of sawdust having a high carbon:nitrogen ratio.

Experiments with nitrogen fertilizers have indicated some of the same results as mentioned above. In a fertilization trial with simulated nitrogen deposition in a *Fagus* forest in southern Sweden (ambient nitrogen deposition 15–20 kg/ha per year), applying nitrogen (60 and 180 kg/ha per year) as ammonium nitrate caused almost all mycorrhizal species to cease fruiting body production within 3–4 years (208). In contrast, several decomposer species increased in fruiting body production. Wood decomposers showed no obvious reaction to the treatment. No fruiting bodies were recovered when nitrogen was applied at 300 kg/ha to *P. sylvestris* stands as liquid manure (209). The mycorrhizal frequency of the roots, however, was still 55% as compared to 87% in the control. Nitrogen as ammonium nitrate applied at 112 kg/ha to 11-year-old *P. taeda* stands reduced the number of fruiting bodies by 88% and the number of mycorrhizas per unit of soil volume by 14% (210). In the Lisselbo experiment, the number of fruiting bodies strongly decreased with each dose of nitrogen fertilizer (211). Another study with nitrogen applications (as ammonium sulfate or nitrate) of 0, 30 and 60 kg/ha per year to young *Pinus sylvestris* stands found that in general fruiting body production was more negatively influenced by the higher ammonium levels than by nitrate levels (212). The mycorrhizal frequency and the number of mycorrhizas per unit of soil volume were not influenced. It is concluded that fruiting body production is much more sensitive to nitrogen enrichment than mycorrhizal formation. Another investigation in a *Picea abies* stand at the Swedish NITREX

study found that fruiting body production by mycorrhizal species decreased after only 1.5 years when nitrogen (as ammonium nitrate) was applied at 35 kg/ha (213).

In contrast to the observations mentioned above, some studies have shown an increase in the number of fruiting bodies of insensitive mycorrhizal fungi after nitrogen fertilization, for example: *Paxillus involutes* (up to 240 kg/ha as mixed forms of nitrogen (214), ureum (215) or ammonium sulfate (216)); *Laccaria bicolor* (215); and *Lactarius rufus* (216).

Soil fauna

Almost all studies on changes in faunal species composition due to nitrogen enrichment have been conducted in arable fields or agricultural grasslands using complete fertilization, and thus cannot be used to substantiate critical loads for semi-natural forest ecosystems (217). The relationship between acidity and soil fauna has also been studied in northern coniferous forests, but only very few studies have incorporated the effects of nitrogenous compounds (218). The abundance of nematodes, oligochaets and microarthropods (especially *Collembola*) increased in some studies but decreased in others after application of high doses of nitrogen fertilizer (>150 kg/ha per year) (219–221). A reduction in the nitrogen deposition in a *Pinus sylvestris* stand (NITREX site at Ysselsteyn, the Netherlands) to pre-industrial levels increased the species diversity of microarthropods, owing to reduced dominance of some species (175). At present, however, it is unfortunately not possible to use these few data to formulate a critical load for changes in forest soil fauna due to increased nitrogen deposition. The effects of enhanced nitrogen input on soil fauna are a serious gap in knowledge and certainly deserve more attention in future research.

Based on the results presented in this overview, the critical nitrogen load for changes in the ground vegetation in both coniferous and deciduous acidic forest is 15–20 kg/ha per year. The critical load for changes in fruiting body production by ectomycorrhizal fungi is probably about 30 kg/ha per year, while the that for changes in mycorrhizal frequency in tree roots is certainly considerably higher. There are insufficient data on the effects of enhanced nitrogen deposition on faunal components of forest ecosystems to allow critical loads to be set. A probably sensitive component of forest ecosystems are epiphytic or ground-living lichens with blue-green algae as the photobiont; these have an estimated critical nitrogen load of 5–15 kg/ha per year. A summary of critical nitrogen loads is given in Table 2.

Table 2. Summary of guidelines for nitrogen deposition (kg/ha per year) to (semi-)natural freshwater and terrestrial ecosystems

Ecosystem	Critical load	Indication
Shallow soft-water lakes	5–10 ^a	Decline in isoetid species
Mesotrophic fens	20–35 ^b	Increase in tall graminoids; decline in diversity
Ombrotrophic (raised) bogs	5–10 ^b	Decrease in <i>Sphagnum</i> and subordinate species; increase in tall graminoids
Calcareous species-rich grasslands	14–25 ^a	Increase in tall grasses; decline in diversity
Neutral-acid species-rich grasslands	20–30 ^b	Increase in tall grasses; decline in diversity
Montane-subalpine grasslands	10–15 ^c	Increase in tall graminoids; decline in diversity
Lowland dry heathlands	15–20 ^a	Transition from heather to grass
Lowland wet heathlands	17–22 ^a	Transition from heather to grass
Species-rich heaths/acid grasslands	7–15/20 ^b	Decline in sensitive species
Arctic and alpine heaths	5–15 ^c	Decline in lichens, mosses and evergreen dwarf shrubs; increase in grasses and herbs
Coniferous forests (acidic, managed)	10–15 ^b	Tree health; nutrient imbalance (low nitrification rate)
Coniferous forests (acidic, managed)	20–50 ^b	Tree health; nutrient imbalance (moderate to high nitrification rate)
Coniferous forests (acidic, managed)	15–20 ^a	Changes in ground flora
Deciduous forests (acidic, managed)	15–20 ^b	Tree health; nutrient imbalance; shoot–root ratio
Deciduous forests (acidic, managed)	15–20 ^b	Changes in ground flora
Forests (acidic, unmanaged)	Unknown	Unknown
Forests (calcareous)	15–20 ^c	Changes in ground flora

^a Reliable (a number of published papers of various studies show comparable results).

^b Quite reliable (the results of some studies are comparable).

^c Best guess (no data are available for this type of ecosystem); critical load based on knowledge of ecosystems likely to be more or less comparable.

Guidelines

The first edition of this volume (3) set a guideline for total nitrogen deposition of 30 kg/ha per year to protect sensitive vegetation. In this edition, in the light of new evidence based on observed changes in vegetation and reductions in biodiversity, critical loads for nitrogen have been formulated (Table 2). As most research efforts have focused on acidification in forestry, serious gaps in knowledge exist on the effects of enhanced nitrogen deposition on (semi-)natural terrestrial and aquatic ecosystems. The following gaps in knowledge are most important.

1. Quantified effects of enhanced nitrogen deposition on fauna in all reviewed vegetations are extremely scarce.
2. More research is needed in Mediterranean, tropical and subtropical vegetation zones.
3. The critical load for nitrogen deposition to arctic and alpine heathlands is largely speculative.
4. More research is needed into the effects of nitrogen on forest ground vegetation and (ground) fauna, because most research has focused on the trees.

5. Little is known of the effects of nitrogen in neutral/calcareous forests, which are not sensitive to acidification.
6. More long-term research is needed in montane/subalpine meadows, species-rich grasslands and ombrotrophic bogs.
7. The long-term effects of enhanced atmospheric nitrogen in grassland and heathland of high nature conservation importance under different management regimes are insufficiently known and may affect the critical load.
8. The possible differential effects of the deposited nitrogen species (NO_x or NH_y) are insufficiently known to differentiate between them in establishing critical loads.
9. Long-term effects of nitrogen eutrophication in (sensitive) aquatic ecosystems (freshwater and marine) need further research.

Nitrogen is the only nutrient whose cycling through ecosystems is almost exclusively regulated by biological processes. To establish reliable guidelines, it is crucial to understand the long-term effects of increased nitrogen deposition on these processes in a representative range of ecosystems. It is thus very important to quantify the effects of nitrogen loads on (semi-)natural terrestrial and freshwater ecosystems by manipulating nitrogen inputs in long-term ecosystem studies in unaffected and affected areas. These data are essential to validate the presented critical loads, and to develop robust dynamic ecosystem models reliable enough to calculate critical loads for nitrogen deposition in (semi-)natural ecosystems.

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