G.J. Heij and J.W. Erisman (Editors). Acid Rain Research: Do we have enough answers?

Ecological effects of atmospheric deposition on non-forest ecosystems in Western Europe

Roland Bobbink and Jan G.M. Roelofs

Department of Ecology, Research group Environmental Biology, University of Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

Abstract Mans activities pose a number of threats to natural vegetation. One of the major threats is the increase in atmospheric deposition. In this paper information on the ecological effects of increased atmospheric deposition upon non-forest ecosystems of high nature conservation importance (shallow soft-water lakes, heathlands, matgrass swards, and calcareous grasslands) have been presented. Empirical nitrogen critical loads are discussed and finally summarized.

1. INTRODUCTION

Most of earths biodiversity is found in (semi-)natural ecosystems, both in aquatic and terrestrial habitats. Mans activities pose a number of threats to the structure and the functioning of these ecosystems, and thus to the natural variety of plant and animal species. One of the major antropogenic threats is the increase in sulphur (SO_y) and nitrogen (NH_x and NO_y) air pollution. S and N pollutants have been shown to acidify ecosystems. Furthermore, N deposition may cause eutrophication, because nitrogen is limiting for plant growth in many of these (semi-)natural ecosystems. The impacts of increased nitrogen deposition upon biological systems are diverse, but the most important effects are: (i) direct toxicity of nitrogen gases and aerosols to individual species; (ii) soil-mediated effects upon vegetation; (iii) increased susceptibility to stress factors and, (iiii) changes in (competitive) relationships between species, resulting in loss of biodiversity.

The aim of this paper is to review information of ecological effects of an increase in atmospheric deposition upon West-European non-forest ecosystems of high nature conservation importance (shallow soft-water lakes, heathlands, matgrass swards, and calcareous grasslands).

2. SHALLOW SOFTWATER LAKES

In the lowlands of Western Europe many soft waters are found on sandy soils which are poor in calcium carbonate or almost devoid of it. The waters are poorly buffered and the concentrations of calcium in the water layer are very low; they are shallow and fully mixed water bodies, with periodically fluctuating water levels, and are mainly fed by rain water, and thus oligotrophic. These softwater ecosystems are characterized by plant communities from the phytosociological alliance LITTORELLION (Arts 1990; Schaminée *et al.* 1992). The stands of these communities are characterized by the presence of rare and endangered (Red-list) isoetids, such as *Littorella uniflora*, *Lobelia dortmanna*, *Isoetes lacustris*, *I. echinospora*, *Echinodorus* species, *Luronium natans* and many other softwater macrophytes. These soft waters are nowadays almost all within nature reserves and have become very rare in western Europe.

The effects of air pollutants on these soft waters have been intensively studied in the Netherlands both in field surveys and experimental studies. Field observations in ca. 70 soft waters (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 μeq l^{-1}), circumneutral (pH=5-6) and very poor in nitrogen (Roelofs 1983; Arts *et al.* 1990). The softwater sites where these plant species had disappeared, could be divided into two groups. In 12 of the 53 softwater sites eutrophication, resulting from enriched water, seemed to be the cause of the decline.

In the second group of lakes and pools (41 out of 53) another development had taken place: the isoetid species were 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 has been shown that the nitrogen levels of the water layer were higher in ecosystems where the natural vegetation had disappeared, compared with ecosystems where the LITTORELLION stands were still present (Roelofs 1983). This strongly suggests the detrimental effects of atmospheric nitrogen deposition in these softwater lakes.

A number of ecophysiological studies has revealed the importance of (i) inorganic carbon status of the water as a result of intermediate levels of alkalinity, and, (ii) low nitrogen concentrations, for the growth of the endangered isoetid macrophytes. Furthermore, almost all of the typical softwater plants had a relatively low potential growth rate. Increased acidity and higher concentrations of ammonium in the water layer clearly stimulated the development of *Juncus bulbosus* and submerged mosses such as *Sphagnum* and *Drepanocladus* species (Roelofs *et al.* 1984; Den Hartog 1986). It has also been shown in cultivation experiments that the nitrogen species involved (ammonium or nitrate) differentially influenced the growth of the studied species of water plants. Almost all of the characteristic softwater isoetids developed better with nitrate instead of ammonium addition, whereas *Juncus bulbosus* and aquatic mosses (*Sphagnum* & *Drepanocladus*), were clearly stimulated by ammonium nutrition (Schuurkes *et al.* 1986).

The effects of atmospheric deposition have been studied in small-scale softwater systems during a 2-year treatment with different artificial rainwaters. Acidification, without air-borne nitrogen input (sulphuric acid), has not resulted in a mass growth of *Juncus bulbosus* and a diverse isoetid vegetation remains present. However, after increasing the nitrogen concentration in the precipitation (as ammonium sulphate), similar changes in floristic composition as under field conditions have been observed: a dramatic increase in dominance of *Juncus* *bulbosus*, of submerged aquatic mosses and of *Agrostis canina* (Schuurkes *et al.* 1987). In these small-scale ecosystems, the recovery of the small-scale systems have been followed during ca. 8 years. Reduction of the acid load leads to a quick recovery of the acidified systems, whereas the situation in the eutrophied did not improved (personal observ. J.G.M. Roelofs).

It became obvious that the observed changes occurred because of the effects of ammonium sulphate deposition, leading to both eutrophication and acidification. The increased levels of ammonium in the system stimulated directly the growth of plants such as *Juncus bulbosus*, whereas the surplus of the extra ammonium will be nitrified in these waters ($pH \geq 4.0$). During this nitrification process H^+-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 already occurred after 2-year treatment with ≥ 19 kg N ha^{-1} yr^{-1}. A reliable critical load for nitrogen deposition in these shallow softwater lakes is thus most likely below 19 kg N ha^{-1} yr^{-1} and probably between 5 and 10 kg N ha^{-1} yr^{-1}. 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 ca. 10-13 kg N ha^{-1} yr^{-1} (Arts 1990).

3. HEATHLANDS

Heathlands have for a long time been part in the West European landscape. Heaths are plant communities where the dominant life-form is that of the small-leaved dwarf-shrubs forming a canopy of 1 m or less above soil surface. Dwarf-shrub heathlands are wide spread in the atlantic and sub-atlantic parts of Europe. In these parts of the European continent natural heathland is limited to a narrow coastal zone. Inland lowland heathlands are certainly man-made (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 (Gimingham *et al.* 1979).

Until the beginning of this century, the balance of nutrient input and output was in equilibrium in the lowland heathlands of Western Europe. The original land use implied a regular, periodic removal of nutrients out of the ecosystem via grazing and sod removal (Heil & Aerts 1993). The original land use of the lowland heathland ceased in the early 1900s and the area occupied by this community decreased markedly all over its distribution area (e.g. Ellenberg 1988). Because of their conservational importance, many lowland heathlands have become nature reserves in recent years.

In W Europe many lowland dry-heathlands have become dominated by grass species. An evaluation, using aerial photographs, has shown that more than 35% of Dutch heathland has been altered into grassland (Van Kootwijk & Van der Voet 1989). It has been suggested that nitrogen eutrophication might be a significant factor in this transition to grasslands. Field and laboratory experiments affirm the importance of nutrients, especially in the early phase of heathland development (Heil & Diemont 1983; Roelofs 1986; Heil & Bruggink

1987; Aerts *et al.* 1990). However, *Calluna* can compete successfully with the grasses even at high nitrogen loading, if its canopy remains closed (Aerts *et al.* 1990). Apart from the changes in competitive interactions between *Calluna* and the grasses, heather beetle plagues, and nitrogen accumulation in the soil are important factors in the changing lowland heaths. Furthermore, evidence is growing that frost and drought sensitivity of the dominant dwarf-shrubs may also be affected by increasing nitrogen inputs.

In *Calluna* heathland outbreaks of the chrysomelid heather beetle (*Lochmaea suturalis)* occur frequently. The beetles feed exclusively on the green parts of *Calluna* and the closed *Calluna* canopy is opened over large areas and the interception of light by *Calluna* decreases strongly (Berdowski 1987; 1993). Thus the growth of the understorey grasses (*Deschampsia* or *Molinia*) will be enhanced significantly. In general (insect) grazing is affected by the nutritive value of the plant material. The nitrogen content is especially important in this respect. Experimental applications of nitrogen to heathland vegetation have demonstrated that the concentrations of this element in the (green) parts of *Calluna* increased (Heil & Bruggink 1987; Bobbink & Heil 1993). It is, therefore, very likely, that the frequency and intensity of the heather beetle outbreaks are stimulated by the increased atmospheric nitrogen input in Dutch heathland.

This hypothesis is supported by the observations of Blankwaardt (1977); he reported that from 1915 onwards heather beetle outbreaks have been observed in the Netherlands with an interval of ca. 20 years, whereas in the last 15 years the outbreaks occur within periods of less than 8 years. Furthermore, it has also been observed that during a heather beetle outbreak *Calluna* plants were more severely damaged in nitrogen-fertilized vegetation (Heil & Diemont 1983). Brunsting and Heil (1985) have done a rearing experiment with larvae of the heather beetle and demonstrated that the growth of the larvae of the heather beetle increased by higher leave nitrogen concentrations of *Calluna*. Van der Eerden *et al.* (1990) found no significant effect of ammonium sulphate treatments on total number and on biomass of the 1st stage larvae after an beetle outbreak. However, the development of subsequent larval stages has been accelerated by the application of ammonium sulphate in the artificial rain. Furthermore, heather beetle larvae had been put on *Calluna* shoots taken from plants which has been fumigated with ammonia in open top chambers (12 months; 4 to 105 µg m^{-3}) (Van der Eerden *et al.* 1991). Both the mass and the development rate of the larvae clearly increased with increasing concentrations of ammonia prior applied to *Calluna*. It can be concluded that nitrogen inputs influence the outbreaks of heather beetle, although the exact relationship between both processes needs further research.

Nowadays most Dutch heathlands are managed by mechanical 'sod removal'. It is likely that changes in the rate of nitrogen accumulation during secondary heathland succession will occur due to the increased nitrogen deposition. Berendse (1990) found a large increase in total nitrogen storage in the first 20/30 years after sod removal. Furthermore, he demonstrated that nitrogen mineralization was low in the first 10 years (ca. 10 kg N ha^{-1} yr^{-1}) after sod removal, but strongly increased in the next 20 years to 50-110 kg N ha^{-1} yr^{-1}.

Thus, the total organic matter and nitrogen amounts increased, as usual, during secondary succession after sod removal. However, this process is accelerated by the enhanced dry matter production and litter production of the dwarf-shrubs caused by the extra nitrogen inputs. Hardly any nitrogen disappeared from the system because nitrate leaching to deeper layers is only of minor importance in Dutch heathlands (De Boer 1989; Van Der Maas 1990). Nitrogen availability from atmospheric inputs, in addition to mineralization, is within a relatively short period of 10 years high enough to stimulate the transition of heathland to grassland, especially after the opening of the heather canopy by secondary causes.

It has been demonstrated that frost sensitivity in some tree species increased with increasing concentrations of air pollutants. This increase in frost sensitivity is sometimes correlated with the enhanced nitrogen concentrations in the foliage of the trees. Long-term effects of air pollutants on the frost sensitivity of *Calluna* and *Erica* may be expected, because of (i) the evergreen growth form of these species and, (ii) the increasing contents of nitrogen in the leaves of *Calluna*, associated with increased nitrogen deposition in the Netherlands. It is suggested that damage of the *Calluna* shoots in the successive severe winters of the mid-1980s is at least partly caused by the increased frost sensitivity.

After fumigation with sulphur dioxide (90 $\mu g\ m^{-3}$; 3 months) increased frost injury in *Calluna* was only found at temperatures which hardly occur in the Netherlands (< -20 °C) (Van der Eerden *et al.* 1990). Fumigation with ammonia of *Calluna* plants in Open Top Chambers during 4-7 month periods (100 $\mu g\ m^{-3}$) revealed that frost sensitivity was not affected in autumn (September or November), whereas in February, just before growth started, frost injury increased significantly at -12 °C (Van der Eerden *et al.* 1991). They also studied the frost sensitivity in *Calluna* vegetation which was artificially sprayed with 6 different levels of ammonium sulphate (3-91 kg N $ha^{-1}\ yr^{-1}$). The frost sensitivity of *Calluna* increased slightly, although significantly, after 5 months in vegetation treated with the highest level of ammonium sulphate (400 $\mu mol\ l^{-1}$; 91 kg N $ha^{-1}\ yr^{-1}$). However, frost sensitivity of *Calluna* decreased again two months later and no significant effects have been measured at that time. Thus, high levels of ammonia or ammonium sulphate seem to increase the frost sensitivity of *Calluna* plants, although the significance of this phenomenom is still uncertain at ambient nitrogen inputs.

It is shown that atmospheric nitrogen is the trigger for the changes of lowland dry-heathlands into grass swards in the Netherlands. A dynamic ecosystem simulation model has been used which integrated processes, such as atmospheric nitrogen input, heather beetle outbreaks, soil nitrogen accumulation, sod removal and competition between species, to establish nitrogen critical load in lowland dry-heathlands (Heil & Bobbink 1993). The model has been calibrated with data from field and laboratory experiments in the Netherlands. As an indicator of the effects of atmospheric nitrogen the proportion and increase of grasses in the heathland system are used. Atmospheric nitrogen deposition has been varied between 5 and 75 kg N $ha^{-1}\ yr^{-1}$ in steps of 5-10 kg N during different simulations. From these simulations it became obvious that the nitrogen critical load for the changes from dwarf-shrubs to grasses is 15-20 kg N ha^{-1} yr^{-1} (Fig. 1).

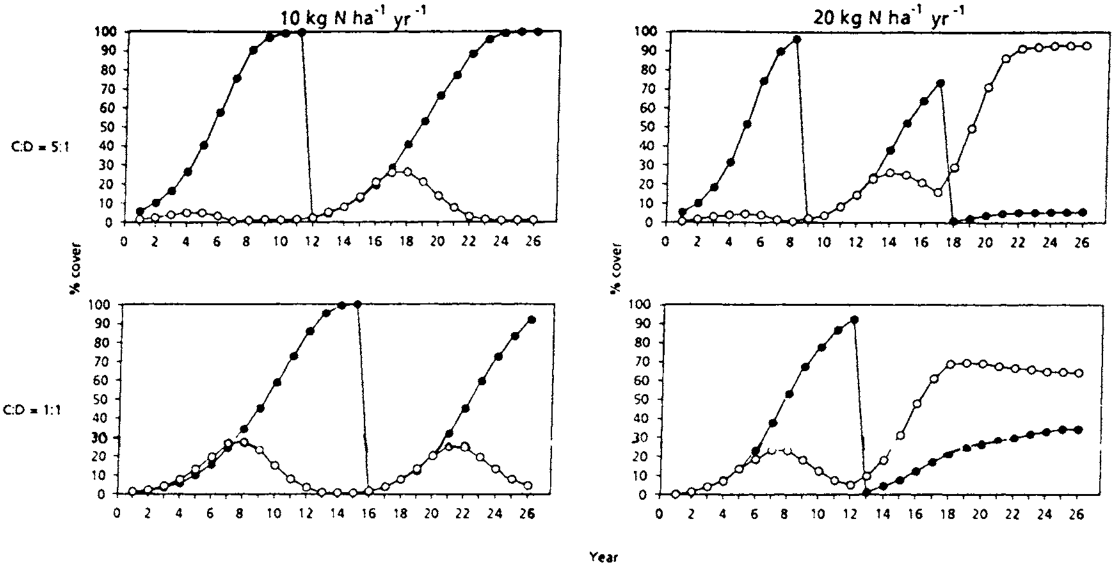

Fig. 1. Model results of interaction between *Calluna vulgaris* and *Deschampsia flexuosa* at two levels of atmospheric nitrogen deposition and two initial ratios of both species (C:D). The sudden reduction of *Calluna* cover is due to heather beetle attacks (adapted with permission from Heil & Bobbink 1993a). Closed circles: *Calluna*; open circles: *Deschampsia*.

4. MATGRASS SWARDS & SPECIES-RICH WET HEATHLANDS

In recent decades, besides the transition from dwarf-shrub dominated to grass dominated heathlands, a reduced species diversity in these ecosystems has been observed. Species of the acidic NARDETALIA grasslands and the related dry- and wet-heathlands (CALLUNO-GENISTION and ERICION TETRALICES) seem to be especially sensitive. Many of these herbaceous species (e.g. *Arnica montana*, *Antennaria dioica*, *Dactylorhiza maculata*, *Gentiana pneumonanthe*, *Genista pilosa*, *Genista 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 of these species that they can not survive (Van Dam *et al.* 1986). Dwarf-shrubs as well as grass species are nowadays dominant in former habitats of these endangered species.

Enhanced nitrogen fluxes onto the nutrient-poor heathland soils lead to an increased nitrogen availability in the soil. However, most of the deposited nitrogen in W Europe originates from ammonia/ammonium deposition and may also cause acidification as a result of nitrification. Whether eutrophication or acidification or a combination of both processes is important, depends on pH, buffer capacity and nitrification rates of the soil. Roelofs *et al.* (1985) found that in dwarf-shrub dominated heathland soils nitrification has been 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 from the habitats of the endangered species, due to its somewhat higher pH and higher buffer capacity. In soils within the pH range of 4.1-5.9, the produced acidity is buffered by cation exchange processes (Ulrich 1983). The pH will drop when calcium is depleted and this may cause the decline of 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 have been done 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)* (Van Dobben 1991). The dominant species indeed have a lower pH optimum (3.5 and 4.0, respectively) than the endangered species (4.2-6.0). However, the endangered species could survive very low pH without visible injuries during this short experimental period.

The pH decrease may indirectly result in an increased leaching of base cations, increased aluminium mobilization and thus enhanced Al/Ca ratios of the soil (Van Breemen *et al.* 1982). Furthermore, the reduction of the soil pH may inhibit nitrification and result in ammonium accumulation and consequently increased NH_4/NO_3 ratios. In a recent field study the characteristics of the soil of several of these threatened heathland species have been compared with the soil characteristics of the dominant species. Generally the endangered species grow on soils with higher pH, lower nitrogen content, and lower Al/Ca ratios than the dominant species. The NH_4/NO_3 ratios were higher in the dwarf-shrub dominated soils compared with the ratios in the soil of the endangered species. Fennema (1990; 1992) has demonstrated that soils from locations where *Arnica* is still present, had higher pH and lower Al/Ca ratios than soils of former *Arnica* stands. However, he found no differences in total soil nitrogen and NH_4/NO_3 ratios. Both these studies indicate that high Al/Ca ratios or even increased NH_4/NO_3 ratios are associated with the decline of these species. However, no significant effects of Al and Al/Ca on growth rates have been observed in hydroculture experiments at high nutrient levels in which the effects of Al and Al/Ca ratios on root growth and survival rate were studied (Pegtel 1987; Kroeze *et al.* 1990; Van Dobben 1991). However, results of a hydroculture experiment with *Arnica* showed that this species is very sensitive to enhanced Al/Ca ratios at intermediate or low nutrient levels, whereas another Red-list species (*Cirsium dissectum)* is also very sensitive for high ammonium concentrations and high NH_4/NO_3 ratios (Fig. 2) (De Graaf *et al.* 1994).

Pot experiments with acidic heathland soil have indicated that increased NH_4/NO_3 ratios, because of ammonium accumulation, have caused a decreased vitality of *Thymus*. Only in artificially buffered soils, nitrification rates were high enough to balance ammonium and nitrate. Thymus plants on these soils were vital despite high nitrogen applications (Houdijk *et al.* 1993). Hydroculture experiments with this plant species confirmed that increased NH_4/NO_3 ratios affected the cation uptake (Houdijk 1993). At present, however, 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 species mostly disappear before dwarf-shrubs are replaced by grasses, leads to the assumption that their critical load is lower than the critical load for the transition to grasses (thus < 15-20 kg N ha^{-1} yr^{-1}).

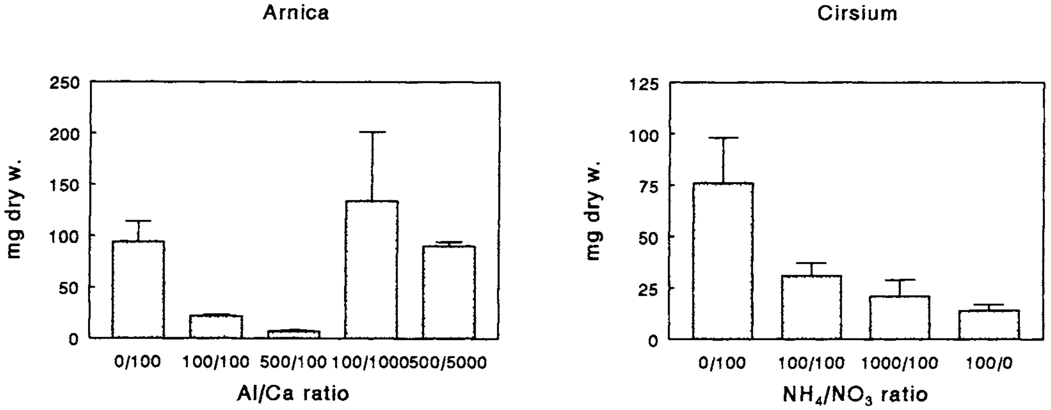

Fig. 2. Plant dry weight of *Arnica montana* (A) after cultivation on water cultures with different Al/Ca ratios and of *Cirsium dissectum* (B) on cultures with different ammonium/nitrate ratios. The ratios are given in µmol l^{-1} (adapted with permission from De Graaf *et al.* 1994).

5. CALCAREOUS GRASSLANDS

Calcareous grasslands are communities on limestone, which is wide spread 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 rendzina soils (A/C-profiles; pH of the top soil: 7-8 with calcium carbonate content of ca. 10%). The depth of the soil varies between 10-50 cm and the availability of nitrogen and phosphorus is low. A large part of the European calcareous grasslands are MESOBROMION communities; a grassland type found in areas with precipitation quantities between 500-900 mm per year (Willems 1982). Plant productivity is low and peak standing crop is in general between 150-400 g m^{-2}. Calcareous grasslands are among the most species-rich plant communities in Europe and contain a large number of rare and endangered species. These semi-natural grasslands decreased strongly in area during the second half of this century (e.g. Wolkinger & Plank 1981). Some remnants became nature reserve in several European countries. To maintain the characteristic calcareous vegetation a specific management is needed to prevent their natural succession towards woodland (e.g. Ellenberg 1988).

The effects of nitrogen enrichment in Dutch calcareous grasslands on vegetation composition have been investigated in field experiments (Bobbink *et al.* 1988, Bobbink 1991). Either potassium (100 kg K ha^{-1} yr^{-1}), phosphorus (30 kg P ha^{-1} yr^{-1}) or nitrogen (100 kg N ha^{-1} yr^{-1}) as well as a complete fertilization (N+P+K) have been applied during 3 years to study 'long-term' effects on vegetation composition. Total above-ground biomass increased considerably, as expected, after three years of N+P+K fertilization. In the separate application of nutrients, a moderate increase in above-ground dry weight was only seen with nitrogen addition: ca. 330 g m^{-2} compared with ca. 210 g m^{-2} in the untreated plots. Dry weight distribution of the species was dramactically affected by nutrient treatments. In the N-treated vegetation the dry weight of the grass species *Brachypodium pinnatum* was ca. 3 times higher than in the control plots (Fig. 3).

Nitrogen application resulted furthermore in a drastic reduction of the biomass of forb species (including several Dutch Red List species) and of the total number of species (Fig. 3). The observed decrease in species diversity in the nitrogen treated vegetation is certainly not caused by nitrogen toxicity, but by the change in vertical structure of the grassland vegetation. The growth of *Brachypodium* is strongly stimulated and its overtopping leaves reduce the light quantity and quality in the vegetation. It overshadowed the other characteristic species and growth of these species declined rapidly (Bobbink *et al.* 1988; Bobbink 1991). The effects of excess nitrogen supply on the massive expansion of *Brachypodium* and a drastic reduction in species diversity have also been observed in a long-term permanent plot study using a factorial design (Willems *et al.* 1993.)

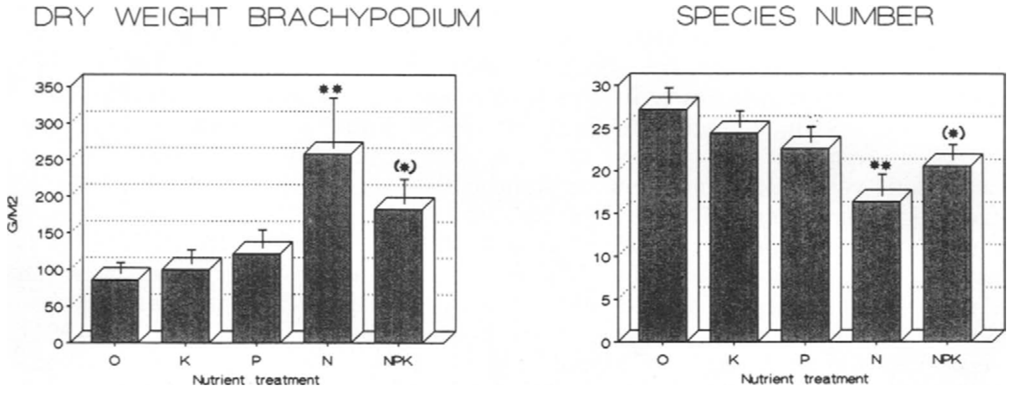

Fig. 3. Above-ground biomass of *Brachypodium* (g m^{-2}) and phanerogamic species number (per 50x50 cm) after 3 years of nutrient additions (adapted with permission from Bobbink 1991). (*): $p<0.10$; **: $p<0.01$.

With the repeated harvest approach it has been shown that *Brachypodium* had a very efficient nitrogen acquisition and a very efficient withdrawal from its senescent shoots into its well-developed rhizome system (Bobbink *et al.* 1989). It thus benefits from the extra nitrogen redistributed to the below-ground rhizomes by enhanced growth in the next spring. After 3-year of nitrogen addition *Brachypodium* had strongly monopolized (>75%) the nitrogen storage in both the above-ground and below-ground compartments of the vegetation with increasing nitrogen availability (Bobbink *et al.* 1988; Bobbink 1991).

Nitrogen cycling and accumulation in calcareous grassland can be significantly influenced by two major outputs from the system: (i) leaching from the soil, and (ii) removal with management regimes. Nitrogen losses by denitrification in dry calcareous grasslands are low (<1 kg N ha^{-1} yr^{-1}) (Mosier *et al.* 1981). Ammonium and nitrate leaching has been studied in Dutch calcareous grasslands by Van Dam *et al.* (1992). Both the water fluxes and the solute fluxes at different soil depths have been measured over two years in untreated vegetation and in calcareous grassland vegetation sprayed with ammonium sulphate (50 kg N ha^{-1} yr^{-1}). The observed nitrogen leaching from the untreated vegetation is very low (0.7 kg N ha^{-1} yr^{-1}), and only 2% of the total atmospheric deposition of N. After two-weekly spraying of ammonium sulphate, nitrogen leaching has significantly increased to 3.5 kg N ha^{-1} yr^{-1}, although this figure is also a very small proportion (4%) of the nitrogen input (Van Dam *et al.* 1992). It is thus evident that calcareous grassland ecosystems almost completely retain nitrogen in the system. This is caused by a combination of enhanced plant uptake (Bobbink *et al.* 1988; Bobbink 1991) and increased immobilization in the soil organic matter (Van Dam *et al.* 1992).

The most important output of nitrogen from the calcareous grassland is by exploitation or management. From the 1950s onwards almost all of the calcareous grasslands in the Netherlands were mown in autumn with removal of the hay. The annual nitrogen removal in the hay varies slightly between years and sites, but in general between 17-22 kg N ha^{-1} is removed from the system with the usual management (Bobbink 1991; Bobbink & Willems 1991). The ambient nitrogen deposition in Dutch calcareous grasslands, as determined by Van Dam (1990), is high (35-40 kg N ha^{-1} yr^{-1}) and is nowadays the major nitrogen input to the system. Legume species (*Leguminosae*) also occur in calcareous vegetation, and form an additional nitrogen input with the nitrogen-fixing microorganisms in their root nodules (ca. 5 kg N ha^{-1} yr^{-1}). The nitrogen mass balance of Dutch calcareous grasslands is summarized in Table 1. It is obvious that calcareous grasslands nowadays significantly accumulate nitrogen (16-26 kg N ha^{-1} yr^{-1}) in the Netherlands. A critical nitrogen load can be determined with a steady-state mass balance model (e.g. De Vries 1994). Assuming a critical long-term immobilization rate for N of 0-6 kg N ha^{-1} yr^{-1}, the critical nitrogen load can be derived by adding the N fluxes due to net uptake, denitrification and leaching, corrected for the N input by fixation. Thus, 14-25 kg N ha^{-1} yr^{-1} is considered as nitrogen critical load for this system.

Table 1. Nitrogen mass balance (kg N ha^{-1} yr^{-1}) for dry calcareous grassland in the Netherlands.

INPUT		OUTPUT	
Atmospheric deposition	35-40	Harvest	17-22
Nitrogen fixation	5	Denitrification	1
		Soil leaching	1

6. CONCLUSION: EMPIRICAL NITROGEN CRITICAL LOADS

In this paper the effects of nitrogen deposition on (semi-)natural non-forest ecosystems are evaluated with published evidence. Empirical critical loads for excess nitrogen deposition are summarized in Table 2.

Table 2. Summary of nitrogen critical loads (kg N ha^{-1} yr^{-1}) to non-forest ecosystems. ## reliable; # quite reliable and (#) best guess (after Bobbink *et al.* 1992; Bobbink & Roelofs 1995).

	Critical load	*Indication*
Shallow soft-water lakes	5-10 ##	Decline isoetid species
Mesotrophic fens	20-35 #	Increase tall graminoids, decl. diversity
Ombrotrophic bogs	5-10 #	Decrease Sphagnum and subordinate species, increase tall graminoids
Calcareous grassland	14-25 ##	Increase tall grass, decline diversity
Neutral-acid grassland	20-30 #	Increase tall grass, decline diversity
Lowland dry-heathland	15-20 ##	Transition heather to grass
Lowland wet-heathland	17-22 ##	Transition heather to grass

7. REFERENCES

Aerts, R. Berendse, F. De Caluwe, H. & Schmitz, M. 1990. Competiton in heathland along an experimental gradiet of nutrient availability. Oikos 57: 310-318.

Arts, G.H.P. 1990. Deterioration of atlantic soft-water systems and their flora, a historical account. PhD thesis, University of Nijmegen.

Arts, G.H.P., Van Der Velde, G., Roelofs, J.G.M. & Vanv Swaay, C.A.M. 1990. Successional changes in the soft-water macrophyte vegetation of (sub)atlantic, sandy, lowland regions during this century. Freshwater Biol. 24: 287-294.

Berdowski, J.J.M. 1987. The catastrophic death of *Calluna vulgaris* in Dutch heathlands. PhD thesis, University of Utrecht.

Berdowski, J.J.M. 1993. The effect of external stress and disturbance factors on *Calluna*-dominated heathland vegetation. In: Aerts, R. & Heil, G.W. (Eds.), Heathland: Patterns and Processes in a changing environment. Geobotany 20, Kluwer, Dordrecht, pp. 85-124. Berendse, F. 1990. Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. J. Ecol. 78: 413-427.

Blankwaardt, H.F.H. 1977. Het optreden van de heidekever (*Lochmaea suturalis* Thomson) in Nederland sedert 1915. Entomologische Berichten. 37: 34-40. (In Dutch).

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. J. Appl. Ecol. 28: 28-41.

Bobbink, R., Bik, L. & Willems, J.H. 1988. Effects of nitrogen fertilization on vegetation structure and dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland. Acta Bot. Neerl. 37: 231-242.

Bobbink, R., Den Dubbelden, K.C. & Willems, J.H. 1989. Seasonal dynamics of phytomass and nutrients in chalk grassland. Oikos 55: 216-224.

Bobbink, R. & Willems, J.H. 1991. Impact of different cutting regimes on the performance of *Brachypodium pinnatum* in Dutch chalk grassland. Biol. Conserv. 56: 1-21.

Bobbink, R., Boxman, D., Fremstad, E., Heil, G., Houdijk, A. & Roelofs, J. (1992). Critical loads for nitrogen eutrophication of terrestrial and wetland ecosystems based upon changes in vegetation and fauna. In: Grennfelt, P. & Thörnelöf, E. (Eds.), Critical loads for nitrogen. Nord (Miljörapport) 41, 111-159. Nordic Council of Ministers, Copenhagen.

Bobbink, R. & Heil, G.W. 1993. Atmospheric deposition of sulphur and nitrogen in heathland ecosystems. In: Aerts, R. & Heil, G.W., Heathland: Patterns and Processes in a changing environment. Geobotany 20, Kluwer, Dordrecht, pp.25-50.

Bobbink, R. & Roelofs, J.G.M. (1955). Empirical nitrogen critical loads: update since Lökeberg (1992). In: Sutton, M.A. (ed.). Critical loads for nitrogen. A workshop report of the UN/ECE meeting in Grange-over-Sands, xx-xx. UK Ministery of the Environment.

Brunsting, A.M.H. & Heil G.W. 1985. The role of nutrients in the interaction between a herbivorous beetle and some competing plant species in heathlands. Oikos 44: 23-26.

De Boer, W. 1989. Nitrification in Dutch heathland soils. PhD thesis, Agricultural University of Wageningen.

De Graaf, M.C.C., Verbeek P.J.M., Cals, M.J.R. & Roelofs, J.G.M. 1994. Effectgerichte Maatregelen in matig mineraalrijke heide en schraallanden. Eindrapport monitoringsrapport eerste fase. Vakgroep Oecologie, Katholieke Universiteit Nijmegen.

Den Hartog, C. 1986. The effects of acid and ammonium deposition on aquatic vegetations in the Netherlands. In: Proceedings 1st. Internat. Symposium on water milfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Vancouver, Canada, pp. 51-58.

De Vries, W. 1994. Soil response to acid deposition at different regional scales. PhD Thesis, Agricultural University of Wageningen.

Ellenberg, H. 1988. Vegetation ecology of Central Europe. Cambridge Univ. Press, Cambridge.

Fennema, F. 1990. Effects of exposure to atmospheric SO_2, NH_3 and $(NH_4)_2SO_4$ on survival and extinction of *Arnica montana* L. and *Viola canina* L.. RIN, Arnhem, The Netherlands. Report no. 90/14, 1-61.

Fennema, F. 1992. SO_2 and NH_3 deposition as possible causes for the extinction of *Arnica montana* L. Water Air Soil Poll. 62: 325-336.

Gimingham, C.H., Chapman, S.B. & Webb, N.R. 1979. European heathlands. In: Specht, R.L. (ed.) Ecosystems of the world, 9A. Elsevier, Amsterdam, pp.365-386.

Heil, G.W. & Diemont, W.H. 1983. Raised nutrient levels change heathland into grassland. Vegetatio 53: 113-120.

Heil, G.W. & Bruggink, M. 1987. Competition for nutrients between *Calluna vulgaris* (L.) Hull and *Molinia caerulea* (L.) Moench. Oecologia 73: 105-108.

Heil, G.W. & Aerts, R. 1993b. General introduction. In: Aerts, R. & Heil, G.W. , Heathland: Patterns and Processes in a changing environment. Geobotany 20, Kluwer, Dordrecht, pp. 1-24.

Heil, G.W. & Bobbink, R. 1993. Impact of atmospheric nitrogen deposition on dry heathlands: a stochastic model simulating competition between Calluna vulgaris and two grass species. In: Aerts, R. & Heil, G.W., Heathland: Patterns and Processes in a changing environment. Geobotany 20, Kluwer, Dordrecht, pp. 181-200.

Houdijk, A.L.F.M. 1993. Atmospheric ammonium deposition and the nutritional balance of terrestrial ecosystems. PhD Thesis, University of Nijmegen.

Houdijk, A.L.F.M., Verbeek, P.J.M., Van Dijk, H.F.G. & Roelofs, J.G.M. 1993. Distribution and decline of endangered herbaceous heathland species in relation to the chemical composition of the soil. Plant Soil 148: 137-143.

Kroeze, C., Pegtel, D.M. & Blom, C.J.C. 1989. An experimental comparison of aluminium and manganese susceptibility in *Antennaria dioica*, *Viola canina*, *Filago minima* and *Deschampsia flexuosa*. Acta Bot. Neerl. 38: 165-172.

Mosier, A.R. Stillwel, M. Paton, W.J. & Woodmansee, R.G. 1981. Nitrous oxide emissions from a native shortgrass prairie. Soil Sci. Soc. Am. J. 45: 617-619.

Moss, B. 1988. Ecology of fresh waters - Man and Medium. Blackwell, Oxford.

Pegtel, D.M. 1987. Effects of ionic Al in culture solutions on the growth of *Arnica montana* L. and *Deschampsia flexuosa* (L.) Trin. Plant Soil 102:85-92.

Roelofs, J.G.M. 1983. Impact of acidification and eutrophication on macrophyte coomunities in soft waters in the Netherlands. I. Field observations. Aquat. Bot. 17: 139-155.

Roelofs, J.G.M. 1986. The effect of airborne sulphur and nitrogen deposition on aquatic and terrestrial heathland vegetation. Experientia 42: 372-377.

Roelofs, J.G.M., Schuurkens, J.A.A.R. & Smits, A.J.M. 1984. Impact of acidification and eutrophication on macrophyte coomunities in soft waters in the Netherlands. II. Experimental studies Aquat. Bot. 18: 389-411.

Roelofs, J.G.M., Kempers, A.J., Houdijk, A.L.F.M. & Jansen, J. 1985. The effect of air-borne ammonium on *Pinus nigra* var. *maritima* in the Netherlands. Plant Soil 84: 45-56.

Schaminée, J.H.J., Westhoff, V. & Arts, G.H.P. 1992. Die Strandlinggesellschaften (Littorelletea Br.-Bl. et Tx. 43) der Niederlande, in europäische Rahmen gefasst. Phytocoenologia 20: 529-558.

Schuurkens, J.A.A.R., Kok, C.J. & Den Hartog, C. 1986. Ammonium and nitrate uptake by aquatic plants from poorly buffered and acidified waters. Aquat. Bot. 24: 131-146.

Schuurkes, J.A.A.R. Elbers, M.A., Gudden, J.J.F. & Roelofs, J.G.M. 1987. Effects of simulated ammonium sulphate and sulphuric acid rain on acidification, water quality and flora of small-scale soft water systems. Aquat. Bot. 28: 199-225.

Ulrich, B. 1983. Interaction of forest canopies with atmospheric constituents: SO_2, alkali and earth alkali cations and chloride. In: Ulrich, B. & Pankrath, J. (eds.) Effects of accumulation of air pollutants in forest ecosystems. D. Reidel Publ., Dordrecht, pp.33-45. Van Breemen, N., Burrough, P.A., Velthorst, E.J., Dobben, H.F. van, Wit, T. de, Ridder, T.B. & Reijnders H.F.R. 1982. Soil acidification from atmospheric ammonium sulphate in forest canopy throughfall. Nature 299: 548-550.

Van Dam, D. 1990. Atmospheric deposition and nutrient cycling in chalk grassland. PhD thesis, University of Utrecht.

Van Dam, D. Van Dobben, H.F. Ter Braak, C.F.J. & De Wit, T. 1986. Air pollution as a possible cause for the decline of some phanerogamic species in The Netherlands. Vegetatio. 65: 47-52.

Van Dam, D. Heil, G.W. Bobbink, R. & Heijne, B. 1992. Impact of atmospheric deposition on nutrient cycling in chalk grassland: throughfall, canopy exchange, nitrogen turnover and input/output budgets. Oecologia.

Van Der Eerden L.J. Dueck, Th.A. Elderson, J. Van Dobben, H.F. Berdowski, J.J.M. & Latuhihin M. 1990. Effects of NH_3 and $(NH_4)_2SO_4$ deposition on terrestrial semi-natural vegetation on nutrient-poor soils. Report IPO/RIN.

Van Der Eerden, L.J. Dueck, Th. A. Berdowski, J.J.M. & Greven, H. & Van Dobben, H.F. 1991. Influence of NH_3 and $(NH_4)_2SO_4$ on heathland vegetation. Acta Bot. Neerl. 40: 281-297.

Van Der Maas, M.P. 1990. Hydrochemistry of two douglas fir ecosystems and a heather ecosystem in the Veluwe, The Netherlands. Report Agricultural University of Wageningen.

Van Dobben, H.F. 1991. Integrated effects (Low vegeatation). In: Heij, G.J. & Schneider, T., Acidification research in the Netherlands Final report of the Dutch Priority Programme on Acidification. Elsevier, Amsterdam, pp 464-524.

Van Kootwijk, E.J. & Van der Voet, H. 1989. De kartering van heidevergrassing in Nederland met de Landsat Thematic Mapper sattelietbeelden. Report RIN 89/2, Arnhem (In Dutch).

Willems, J.H. 1982. Phytosociological and geographical survey of Mesobromion communities in Western Europe. Vegetatio 48: 227-240.

Willems, J.H., Peet, R.K. & Bik, L. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. J. Veg. Science 4: 203-212.

Wolkinger, F. & Plank, S. 1981. Dry grasslands of Europe. Council of Europe, Strasbourg.