SWEDISH ENVIRONMENTAL PROTECTION AGENCY

Effects of Nitrogen Deposition on Forest Ecosystems

Editors
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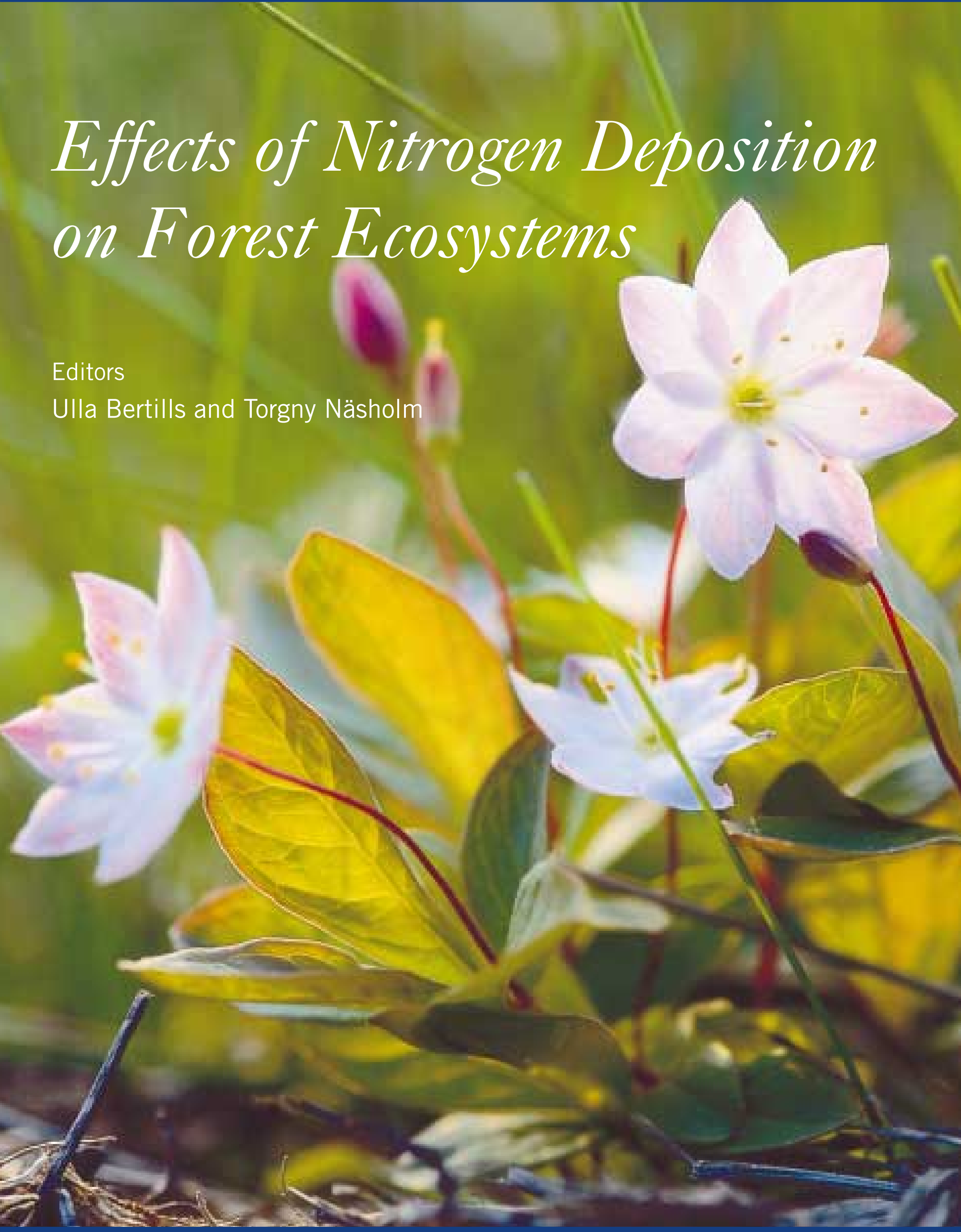

REPORT 5067

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PREFACE

The purpose of this report is to describe our present understanding of the effects of atmospheric nitrogen deposition on forests and forest soils. It is based on research carried out in the Swedish Environmental Protection Agency's project area ACIDIFYING SUBSTANCES AND TROPOSPHERIC OZONE. By setting the results of this research in an international context, we wish to present the knowledge that now exists regarding nitrogen deposition and its effects, and to describe the contribution which our project area has made to this knowledge. Most of the work within the project area was undertaken with funding from the Environmental Protection Agency's research allocation. When this allocation was discontinued, financial responsibility was taken over by the Swedish Foundation for Strategic Environmental Research (MISTRA), which thus provided support for the concluding phase of the work and the final reports.

We would like to express our sincere thanks to all the researchers who have contributed to this report, and in particular to Peringe Grennfelt for providing the questions in the 'Questions and answers' sections.

Thanks are also due to Margot Wallin and Johan Wihlke at the Environmental Protection Agency for their painstaking work on the layout of the report and the diagrams, and to Martin Naylor for his excellent translation.

ULLA BERTILLS & TORGNY NÄSHOLM

Stockholm and Umeå, 2000

Earlier reports from the project area
ACIDIFYING SUBSTANCES AND TROPOSPHERIC OZONE:

GROUND-LEVEL OZONE – A THREAT TO VEGETATION
Swedish Environmental Protection Agency Report 4970
EDITOR: HÅKAN PLEIJEL
(Swedish version: Report 4969)

RECOVERY FROM ACIDIFICATION IN THE NATURAL ENVIRONMENT.
PRESENT KNOWLEDGE AND FUTURE SCENARIOS
Swedish Environmental Protection Agency Report 5034
EDITORS: PER WARFVINGE AND ULLA BERTILLS
(Swedish version: Report 5028)

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EXECUTIVE SUMMARY

Many forest ecosystems in Sweden receive appreciable inputs of nitrogen in the form of atmospheric deposition resulting from human activities. Nitrogen deposition is an international problem, since emissions in one country often give rise to effects in another. Of the current deposition of nitrogen oxides in Sweden, some 85% originates from emissions in other countries, and for ammonia the corresponding figure is 65%.

International agreements have been entered into to curb emissions of both nitrogen oxides and ammonia. Deposition of nitrogen currently exceeds what are known as 'critical loads' with respect to eutrophication throughout southern Sweden. Furthermore, there is much to suggest that emissions of nitrogen – and particularly of ammonia – will remain high over the coming decade. Environmental research to improve our understanding of how these emissions affect forests is therefore crucial.

Nitrogen is a very important plant nutrient, and in most cases its availability is a major limiting factor for growth in forest ecosystems. Most of the nitrogen supplied to a forest by deposition ends up in the soil, where it is rapidly taken up and turned over by plants and micro-organisms. In moderate amounts, deposition of nitrogen can above all increase biological activity, and often growth. However, plants and micro-organisms do not have an unlimited capacity to absorb this element. Large inputs, in fertilizers or deposition, will result in the biological capacity for nitrogen retention being exceeded. In an ecosystem in which such a surplus of nitrogen exists, the excess can easily be leached from the soil, polluting ground and surface waters.

Nitrogen deposition causes eutrophication (nutrient enrichment) of the forest ecosystem, with the result that organisms adapted to a severe nitrogen limitation are replaced by others which are more competitive at higher levels of nitrogen.

To enhance our understanding of the effects nitrogen deposition is having and has had on forests, several experiments have been carried out in which nitrogen has been applied to forest ecosystems. From these studies, mainly involving coniferous forests, the following results have emerged:

- The quantities of nitrogen in *soil* are increasing, and there is a long-term risk of nitrogen saturation and hence increased leaching of nitrogen into lakes and watercourses. Forest soils in southern Sweden have a large capacity to retain nitrogen and, what is more, retention increases with the scale of deposition. The carbon/nitrogen ratio of the soil is an important factor affecting nitrogen retention. European experiments have revealed a clearly increased risk of nitrogen leaching at C/N ratios of less than 25. High deposition of nitrogen may also result in an increased release of carbon from bogs.

- *Trees* are not damaged even by relatively high levels of nitrogen. However, additions of nitrogen do cause a number of changes to their biochemistry and structure, which can in turn make them more sensitive to frost, drought, insect attack or fungal infection, for example. There is no evidence in the literature, though, of clear changes in trees' resistance to such stress factors.

- The *flora* of deciduous forests subjected to nitrogen inputs shows a marked shift towards more nitrophilous species. In severely nitrogen-limited coniferous forests, even small doses of nitrogen rapidly produce a distinct effect, in that growth of grasses is promoted at the expense of bilberry. In such forests, the species composition of mycorrhizal fungi also changes dramatically. Nitrogen deposition results in there being fewer mushrooms and berries to pick in these forests.

- When *nitrogen deposition decreases*, the nutrient status of trees rapidly shifts in the direction of nitrogen limitation. The soil pool of inorganic nitrogen decreases rapidly, as does leaching of nitrate. Thus, several of the serious adverse effects of nitrogen deposition are reversed relatively quickly when deposition abates. However, ground- and field-layer vegetation respond more slowly, and a similar inertia probably applies to other components of the forest ecosystem. It could conceivably take a long time for species which have declined significantly as a result of nitrogen deposition to recolonize a site.

To understand and predict the effects of nitrogen deposition on forest ecosystems, we have to have recourse to experimental studies of various kinds. At the same time, it has to be admitted that experiments provide only fragmentary knowledge. Many nitrogen fertilization experiments have been relatively small-scale. What is more, most of the experiments conducted were not set up specifically to study the consequences of atmospheric inputs of nitrogen, but primarily to investigate forest productivity. These studies have consequently covered a relatively narrow range of forest types and, furthermore, they have involved patterns of nitrogen application which do not tally very closely with atmospheric deposition. Given all these factors, we are not in a very good position to predict the effects of nitrogen deposition.

Many European countries have considerably higher deposition levels than Sweden, and there leaching of nitrogen from forest soils is a very major environmental problem. In Sweden, deposition of nitrogen has not caused the same problems, and many Swedish forest ecosystems have evolved with a severe nitrogen limitation. The organisms inhabiting them are thus adapted to meagre supplies of nitrogen and some will therefore probably decline or disappear altogether as a result of deposition. The only way of preventing this is to reduce emissions of nitrogen as rapidly as possible.

THE NITROGEN PROBLEM IN HISTORICAL PERSPECTIVE

TRYGGVE PERSSON

Views of nitrogen (chemical symbol N), which is an essential constituent of the proteins and nucleic acids of cells, have changed dramatically in recent decades. For most of human history, plant-available forms of this element have been in short supply. This is the case in forested areas, too: at our latitudes, nitrogen is usually the limiting factor for the growth of forest trees. After the Second World War, the use of artificial fertilizers rose sharply, and emissions of nitrogen oxides from motor vehicles and industrial processes also increased. As a result, far more nitrogen than before was brought into circulation. Nitrogen was therefore no longer simply a factor of production; in certain respects, it also became an environmental problem.

From the middle of the 1980s, nitrogen began to be seen as one of the most problematic of pollutants, in the light of mounting evidence that excess amounts of it could have adverse effects. These effects included:

- infants becoming ill as a result of high nitrate levels in drinking water,
- lakes, rivers and streams suffering eutrophication and becoming choked with plant growth,
- blooms of toxic algae,
- increased formation of ozone due to nitrogen oxides, harming plants and human health,
- intensification of the greenhouse effect and damage to the ozone layer at high altitudes, caused by emissions of nitrous oxide,
- effects on biodiversity, and
- incipient nitrogen saturation and declining productivity of forest land (Cowling *et al.* 1998).

In many cases, atmospheric deposition of nitrogen took the place of sulphur deposition as the chief focus of environmental concern. However, nitrogen and nitrogen deposition differ in several respects from sulphur and sulphur deposition. An input of nitrogen not only tends to boost tree productivity; it affects virtually every organism in the forest ecosystem. It therefore changes far more processes in this ecosystem than an input of sulphur. This report describes some of the effects of nitrogen deposition that have been studied more closely. A number of these effects are clearly detrimental, such as increased leaching of nitrate or reduced forest growth at very high levels of nitrogen. Others need to be described in detail before it can be established whether or not they represent a threat. In a few cases, deposition of nitrogen has consequences that can be regarded as either desirable or undesirable, depending on one's point of view. In areas where nitrogen is the growth-limiting factor, deposition of this element stimulates forest growth, and such an effect is of course welcome to the owners of forests. It can also be regarded as beneficial in terms of binding more carbon dioxide in plant biomass and hence reducing net emissions of this greenhouse gas to the atmosphere. At the same time, there is cause for concern if nitrogen deposition affects the vascular plant and macrofungal floras of the forest floor in such a way as to reduce their species richness.

Our understanding of how nitrogen is cycled and how it affects the natural environment is based on research that began in the days of Carl Linnaeus. Table 1.1 presents some of the milestones in the history of nitrogen research.

One of the first breakthroughs in thinking in this area came when Liebig showed that, in addition to sunlight and water, plants needed mineral salts to grow, and not what Linnaeus referred to as 'humus'. Other breakthroughs followed when microbiologists began to understand how nitrogen could be converted from one form to another. A further advance in thinking occurred when scientists began to discover that certain plants, chiefly those with mycorrhizas, were able to take up nitrogen even though it was not present in a mineral form. Liebig's conclusions thus had to be partly revised. In recent years, Näsholm and co-workers (1998), among others, have shown that several forest plants are able to take up simple forms of organic nitrogen (amino acids) in the field. The suspicion that roots with mycorrhizas can take up organic nitrogen has, however, existed since the 19th century.

In Sweden, the long-term forest experiments established by Carl Olof Tamm and his successors have played a major part in developing our understanding of how nitrogen inputs affect forests and soils (Helmisaari & Helmisaari 1992), but also of how nitrogen cycling itself is affected by different treatments, such as nitrogen fertilization, experimental acidification, liming, applications of ash, whole-tree harvesting and clear felling. Some of the experiments that have generated most knowledge are listed in table 1.2 overleaf. Many of the results which form the core of this report stem from these experiments.

TABLE 1.1. Milestones in nitrogen research. Sources: Stålfelt 1960 and others.

YEAR	DISCOVERY OR IDEA
1747	LINNAEUS launches the idea that plants live on the humus formed by the decomposition of plants and animals (the theory of humus).
1840	JUSTUS VON LIEBIG shows that growth of agricultural crops is dependent on the salts present in the soil.
1862	Microbiologist LOUIS PASTEUR suggests that nitrification (formation of nitrate) is a biological process.
1876	Forest researcher E. EBERMAYER shows that forest trees need mineral salts.
1885	A. B. FRANK proposes that plants with mycorrhizas should be able to take up organic nitrogen from forest soils (see also below).
1920–40	Forest researchers H. HESSELMANN, L.-G. ROMELL and C. MALMSTRÖM show by fertilization experiments that nitrogen is the limiting factor for forest growth.
1946	A. G. NORMAN writes that it should be possible to use the stable isotopes ^{13}C and ^{15}N to quantify various transformations of nitrogen.
1950–60	The forest researchers C. O. TAMM in Sweden and P. J. VIRO in Finland set up fertilization experiments involving varying doses of nitrogen, phosphorus, potassium and other nutrients. Some of these experiments are still in progress.
1958	Using ^{15}N techniques, S.-L. JANSSON shows that soil micro-organisms utilize ammonium in preference to nitrate.
1985–86	D. READ's research group (BAJWA, ABUZINADAH *et al.*) in Sheffield show that members of the heath family with ericoid mycorrhizas and trees with ectomycorrhizas can take up organic nitrogen.
1993	F. S. CHAPIN *et al.* show that organic nitrogen can also be taken up by non-mycorrhizal sedges in Arctic environments.

International emission abatement agreements have achieved cuts in emissions of nitrogen compounds, both reduced (ammonia/ammonium) and oxidized (nitrogen oxides/nitrate), and will bring about further reductions in the years ahead. However, as yet we do not know how far-reaching the environmental effects of these decreases will be. One possibility is that they will result in a less marked nutrient imbalance in forest trees and recovery in terms of biodiversity in affected areas of Sweden. Another possibility is that their effects will be more limited, since soils have already been 'charged' with nitrogen.

The chapters that follow will shed light on the effects of nitrogen deposition on forest ecosystems. An account will be given of how nitrogen deposition has changed over time, what happens to deposited nitrogen once it has entered the soil, how it affects trees and other vegetation, and what happens when nitrogen inputs are reduced. It is our hope that this report will provide a fair picture of the current state of knowledge and hence provide a basis for effective action to tackle the nitrogen problem.

TABLE 1.2. Long-term experiments at Swedish forest sites which shed light on the effects of nitrogen on tree growth, nutrient status, soil chemistry, soil biology, leaching, and cycling of carbon and nitrogen. Examples of other questions which they answer are given in the table. N1, N2 and N3 refer to increasing doses of nitrogen fertilizer, with N1 averaging between 30 and 40 kg of nitrogen per hectare per year. Source: Nohrstedt *et al.* 1999.

EXPERIMENT	BEGAN	TREATMENTS	QUESTIONS ANSWERED
Stråsan (Norway spruce)	1967	N1, N2, N3 combined with P, K, PK and CaPK	Effects of nutrient combinations. Critical loads. Recovery processes.
Norrliden (Scots pine)	1971	N1, N2, N3 combined with P, K, PK; $CaCO_3$, acidification	Significance of nutrient combinations. Critical loads. Recovery. Effects of liming.
Flakaliden (Norway spruce)	1987	Solid fertilizer, irrigation, irrigation with fertilization, warming, CO_2	Effects of increased temperature and CO_2 concentrations. Maximum tree productivity with no nitrate leaching.
Asa (Norway spruce)	1987	Solid fertilizer, irrigation, irrigation with fertilization	Maximum tree productivity with no nitrate leaching.
Skogaby (Norway spruce)	1988	Solid fertilizer, irrigation, irrigation with fertilization, drought, ash	Effects of supraoptimal N/S fertilization on trees and soils. Effects of irrigation, drought, ash, N-free fertilizers.
Gårdsjön (Norway spruce)	1989	Roof experiment (low deposition)	Effects of decreased/increased deposition.
	1991	Application of ^{15}N fertilizer	
Farabol (Norway spruce)	1976	N fertilization, $CaCO_3$, S powder followed by clear felling	Post-felling effects of additions of lime, acid and N fertilizer.
Hasslöv (Norway spruce)	1984	Different doses of dolomite	Effects of liming N-rich soils in southern Sweden.

INTERNATIONAL NEGOTIATIONS AND NATIONAL ENVIRONMENTAL OBJECTIVES

ULLA BERTILLS AND PERINGE GRENNFELT

It has long been recognized that nitrogen oxides and ammonia are transported across national frontiers in a similar way to sulphur. The role of nitrogen compounds as a factor in acidification and behind changes in the structure and functioning of ecosystems was also elucidated at an early stage. Not until the mid-1980s, though, did the countries of Europe begin to show any real interest in acting on this knowledge.

At the international level, nitrogen compounds have primarily received attention in the framework of the Convention on Long-Range Transboundary Air Pollution (CLRTAP). In addition, atmospheric transport and deposition of nitrogen compounds have been addressed under the marine environment conventions relating to the Baltic (HELCOM) and the North Sea (OSPAR). The European Community/European Union has also highlighted the nitrogen problem, initially through its Large Combustion Plants Directive, adopted in 1988, and through various directives in the area of road transport. In recent years, nitrogen compounds have been addressed as part of the EU's strategies on acidification and tropospheric ozone.

Convention on Long-Range Transboundary Air Pollution

Following initiatives from Sweden and other countries, international negotiations were launched with the aim of reducing pollutant emissions to the atmosphere. They resulted in an agreement, the Convention on Long-Range Transboundary Air Pollution, being drawn up in 1979 under the auspices of the United Nations Economic Commission for Europe (UNECE). This Convention came into force in 1983.

The first protocol to reduce emissions of nitrogen oxides was signed in 1988. This protocol proved a fairly undemanding agreement, its objective being merely to ensure that 1994 emissions were no higher than 1987 levels. On the other hand, it did receive quite broad support, with a total of 26 signatories. Twelve of the countries concerned, including Sweden, signed a separate agreement declaring their intention of reducing emissions by 30% by 1998, from the level prevailing during a year of their choice between 1980 and 1986.

Despite the modest requirement laid down in the 1988 protocol, i.e. that emissions should not increase up to 1994, several countries (seven, according to the statistics) had difficulty meeting it. As for the countries that pledged a 30% reduction, the outcome has proved even more discouraging: probably not even half of them have attained their more ambitious target. Overall, however, European emissions of nitrogen oxides are falling and, according to available statistics (EMEP 1999), they have been reduced by almost 20% since 1987. Over the same period, Sweden's emissions have decreased by around 35%.

Ammonia – European emissions of which are of the same order of magnitude as those of nitrogen oxides (calculated in tonnes of nitrogen) – was not dealt with at all in the 1988 protocol. Several countries have nevertheless taken steps to curb agricultural losses of nitrogen to both air and soil. According to the statistics, these measures reduced emissions by about 20% between 1987 and 1996.

After a second sulphur protocol, based on critical loads, had been signed in 1994, negotiations began on a new protocol relating to nitrogen. From the outset, it became clear that the parties to the Convention had widely differing priorities when it came to reducing nitrogen oxide emissions. Most of the countries on the continent saw high ozone levels as the main reason for taking action, while the Nordic countries were primarily concerned about nitrogen's role in acidification and eutrophication. Some countries referred to high urban concentrations of nitrogen dioxide as the key argument for a protocol.

In addition, the countries involved considered it imperative that critical loads and cost-effective action should remain the guiding principles for the negotiations. Since it was not easy to distinguish the contributions of nitrogen oxides to different effects, it was felt that the only viable approach was to try to develop a protocol that would take into account both a range of effects (acidification, eutrophication, and the effects of ground-level ozone on vegetation and health) and a number of different substances (nitrogen oxides, ammonia, volatile organic compounds and sulphur dioxide). The agreement that has since been negotiated under the Convention reflects this approach and has accordingly been described as a 'multi-pollutant, multi-effect' protocol. The Protocol to Abate Acidification, Eutrophication and Ground-level Ozone, as it is officially known, was signed in Göteborg, Sweden, on 1 December 1999 and is expected to reduce European emissions of sulphur by 63%, nitrogen oxides by 41%, volatile organic compounds by 40% and ammonia by 17% by 2010, compared with 1990 levels (UNECE 1999).

Table 2.1. Protocols relating to sulphur, nitrogen and ground-level ozone, entered into under the Convention on Long-Range Transboundary Air Pollution.

Protocol	Undertaking(s)	Base year	Target year	Ratified
First Sulphur Protocol 1985	30% reduction of sulphur emissions.	1980	1993	1987 (21 states)
NO_x Protocol 1988	Nitrogen oxide emissions to be frozen at base year level (12 countries declared in a separate agreement that they would reduce emissions by 30% by 1998 from a base year chosen from the period 1980–86).	1987	1994	1991 (26 states)
VOC Protocol 1991	30% reduction of emissions of volatile organic compounds.	1984–90, to be chosen by signatories	1999	1997 (17 states)
Second Sulphur Protocol 1994	Difference between actual sulphur deposition and critical loads to be reduced by 60%.	1990	2000	1998 (22 states)
Multi-Effect Protocol 1999	Emission ceilings for SO_2, NO_x, NH_x and VOCs.	1990	2010	

Marine environment conventions

The part played by nitrogen in marine eutrophication appeared on the agendas of the marine environment conventions at an early stage. Within both HELCOM and OSPAR, decisions were taken in the mid-1980s to halve anthropogenic inputs of nitrogen to the sea areas covered by these conventions by 1995. In principle, these commitments applied to all sources, i.e. atmospheric deposition as well as runoff and direct discharges. All the inventories and measurements carried out show that the 50% reduction target has definitely not been met, and, as the previous section made clear, the countries have fallen far short of it as far as ammonia and nitrogen oxides are concerned.

At a meeting of the OSPAR Commission in 1998, a Strategy to Combat Eutrophication was adopted, with the aim of eliminating all eutrophication due to human activities by the year 2010.

EU efforts to reduce emissions of nitrogen compounds

To date, European Community/European Union efforts to reduce emissions of nitrogen oxides have resulted in directives targeted on (new) large combustion plants and on cars and heavy vehicles.

As was mentioned above, a directive to limit emissions of nitrogen oxides from large combustion plants (with a rated thermal input of 50 MW or more) was adopted in 1988. The directive was aimed at new plants (built after 1987) and is expected to have reduced emissions from installations of this type by around 30% between 1980 and 1998. A proposal for a new directive, imposing more stringent standards on new plants, has been presented. The problem, however, is that it does not include standards for existing combustion plants.

The biggest source of nitrogen oxide emissions is the transport sector. In 1990, road transport was responsible for around half of EC emissions of this pollutant. The Community decided in 1989 to introduce emission standards for passenger cars, of the type that had long existed in the United States. These standards, which only became binding in 1993, will bring about a gradual reduction of emissions, as old vehicles are replaced with new. Their practical consequence was that all cars began to be fitted with catalytic converters. The standards have since been tightened up, chiefly by a decision taken in 1998, which will impose more rigorous re-

PHOTO: HANS WRETLING/TIOFOTO

quirements on vehicles from 2000 and 2005. For heavy vehicles, standards corresponding largely to those in place in the US were introduced in 1996.

Combined, the measures decided on will gradually reduce emissions of nitrogen oxides across the territory of the EU. There is considerable uncertainty, though, about the ultimate effect of the various standards.

In 1995 Sweden suggested that a special strategy should be developed to solve the problem of acidification – i.e. to reduce deposition to below critical loads – throughout the EU. Such a strategy was presented in spring 1997. A corresponding strategy has been drawn up for tropospheric ozone.

In June 1999, as a result of the strategies on acidification and ozone, the European Commission put forward a draft directive proposing 'national emission ceilings' for the year 2010 for sulphur dioxide, nitrogen oxides, ammonia and volatile organic compounds. The Commission's proposal will entail significant emission cuts for many countries. The aim is to promote cost-effective action that will reduce by at least 50%, in all parts of Europe, the area in which critical loads are exceeded. However, the proposed cuts will not be sufficient to bring deposition to below critical load levels in the most sensitive areas of south-west Sweden, for example.

Since the majority of nitrogen deposition in Sweden can be attributed to sources outside its borders, active efforts to achieve further progress within the EU and CLRTAP remain the most important line of attack on this problem.

National environmental objectives and measures

Although emissions in other countries account for a dominant share of nitrogen deposition in Sweden, further reductions of Swedish emissions are still important, not only with a view to reducing disturbance of the environment in this country, but also because a proportion of Sweden's emissions are exported.

To plan action that will lead in the direction of sustainable development, we need estimates of the changes that are required in our society. One way of achieving such estimates is to adopt national environmental objectives.

• NATIONAL ENVIRONMENTAL OBJECTIVES

In 1990, national emission targets for both nitrogen oxides and ammonia were adopted in Sweden (Government Bill 1990/91, p. 25, JoU 30, rskr 338):

> A 30% REDUCTION IN NITROGEN OXIDE EMISSIONS BY 1995, compared with 1980 levels.
>
> A 25% REDUCTION IN AMMONIA EMISSIONS BY 1995. In addition, the feasibility of halving emissions in southern and western Götaland (southern Sweden) was to be looked into.

The nitrogen oxides target was achieved in 1997, whereas ammonia emissions have not fallen, but in fact increased by 20%.

In April 1999 the Swedish Parliament adopted 15 new environmental quality objectives, including goals relating both to eutrophication and to acidification (Swedish Environmental Protection Agency 2000):

NO EUTROPHICATION: Nutrient levels in soil and water must not cause adverse effects on human health, the prerequisites for biological diversity or versatile land and water use.

NATURAL ACIDIFICATION ONLY: The acidifying effects of acid deposition and land use must not exceed limits that can be tolerated by land and water. In addition, deposition of acidifying substances must not accelerate the corrosion of technical materials or cultural artefacts and buildings.

The Government proposed a number of more specific intermediate goals, and in addition some twenty government agencies were commissioned to develop additional intermediate goals and sectoral targets, and to propose courses of action and specific measures to achieve them. In October 1999 the agencies' proposals were submitted to an all-party advisory committee, the Environmental Objectives Committee, which has the task of weighing together the various submissions and presenting a final set of recommendations on intermediate goals and action strategies to the Government in June 2000. The intermediate environmental quality objectives that are formulated are intended to guide the selection of appropriate measures.

• MEASURES

Action on nitrogen emissions will reduce the effects of this pollutant in terms of both acidification and eutrophication. Of Sweden's total emissions of *nitrogen oxides*, the majority come from various forms of transport.

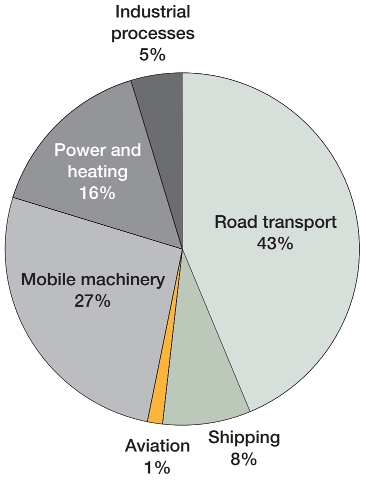

Figure 2.1. Swedish emissions of nitrogen oxides to air, 1998. The figures for shipping and aviation refer to emissions from fuels used in domestic traffic only.

Source: Statistiska meddelanden, Mi 18

The main focus of action in Sweden has been on achieving better exhaust gas treatment and cleaner fuels for road vehicles. All cars from 1989 models on are required to be fitted with catalytic converters. Emission standards for lorries and buses were introduced in 1993.

With the legislation and regulations already adopted, and on the basis of predicted trends, it is estimated that emissions of nitrogen oxides could be reduced by just over 40% between 1995 and 2010. Emissions from road transport are expected to fall by 70% and from shipping by 50%. The measures already decided on will bring about significant reductions in nitrogen oxide emissions, but will not be sufficient to meet the environmental objectives that have been set.

The most important source of *ammonia* emissions is livestock production, an area in which reductions have proved difficult to achieve. Almost 90% of Sweden's emissions of ammonia come from the farming sector.

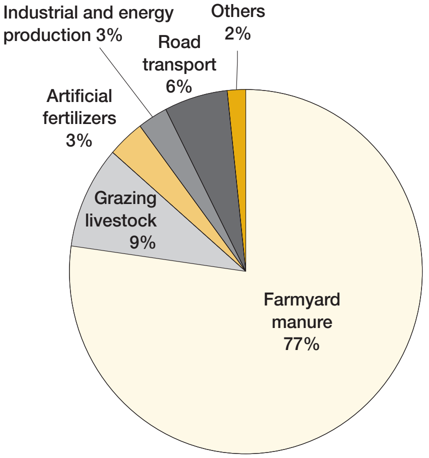

Figure 2.2. Swedish emissions of ammonia to air, 1997.

Source: Statistiska meddelanden, Mi 37

The main priority must therefore be to cut agricultural emissions of ammonia, particularly in the south of Sweden. The principal means of achieving reductions are expected to be improved methods for the storage and application of animal manure and urine.

The international negotiations in progress within the EU and CLRTAP and the current work on environmental objectives in Sweden will provide guidance as to what reductions in national nitrogen emissions are required and what action needs to be taken.

Information about protocols, emissions and deposition levels can be found at the following Web sites:
Convention on Long-Range Transboundary Air Pollution: www.unece.org/env/lrtap
Data on emissions, transport and deposition: www.emep.int
Models and estimates of measures required across Europe: www.iiasa.ac.at
Data on concentrations and deposition levels in Sweden: www.ivl.se/env_data.htm

QUESTIONS AND ANSWERS

Are critical loads for acidification the key determinant of the scale of action needed to combat nitrogen deposition?

No, not in general. The level of action required is determined, rather, by the eutrophication effects of nitrogen.

Will the measures already decided on or planned be sufficient to eliminate the effects of excessive nitrogen deposition?

If the national emission ceilings proposed in the EU are implemented, emissions of nitrogen oxides and ammonia in the EU area are expected to fall by 55% and 20%, respectively, compared with 1990 levels. The Multi-Effect Protocol (Protocol to Abate Acidification, Eutrophication and Ground-level Ozone) will cut deposition of oxidized nitrogen by just over 40% and of reduced nitrogen by just under 20%, for Europe as a whole. These measures will not be sufficient to eliminate the adverse effects of nitrogen deposition in Sweden.

NITROGEN DEPOSITION NOW AND IN THE FUTURE

GUN LÖVBLAD

Current deposition levels

Atmospheric deposition of nitrogen provides a significant nutrient input to both terrestrial and marine ecosystems, an input that has risen substantially since the 1950s. After the Second World War, strong economic growth resulted in an appreciable increase in the use of fossil fuels, while emissions from the transport sector spiralled. Figure 3.1 shows how emissions of nitrogen oxides and ammonia have developed in Sweden. Similar trends have been seen in all the countries of Europe, and the sum total of the resultant long-range transport of air pollutants is reflected, *inter alia*, in the field data that have been recorded as part of Sweden’s environmental monitoring programme.

Since the 1950s, emissions of nitrogen compounds, and above all nitrogen oxides, have increased in Sweden and the rest of Europe, with the result that deposition of both oxidized and reduced compounds of nitrogen in Sweden has shown a steady rise. In the last few years, however, a slight downward trend in wet deposition of nitrogen has been observed (see figure 3.2a). The same trend can be seen in concentrations in precipitation, and this is being investigated in more detail in a study in progress for the environmental monitoring programme (figure 3.2b) (K. Sjöberg, IVL, and others).

Data on current levels of nitrogen deposition in Sweden are now available on the Internet. The Web site of the Swedish Environmental Research Institute (IVL) (www.ivl.se) provides field data from the EMEP network, the precipitation chemistry network and regional forest plots. Deposition data calculated using the MATCH model (Persson *et al.* 1996, Robertson *et al.* 1999) can be found on the site maintained by the Swedish Meteorological and Hydrological Institute, SMHI (www.smhi.se). The maps presented on that site show a breakdown of estimated nitrogen deposition into oxidized and reduced nitrogen compounds, wet and total deposition of nitrogen, and dry deposition to land in different land use categories.

Figures 3.3 and 3.4 below show wet and total deposition of oxidized nitrogen (nitrate) and reduced nitrogen (ammonium) in Sweden. The maps illustrate the prevailing pattern of deposition across the country, which is affected on the one hand by gradients of pollutant concentrations in precipitation and air, on the other by climatic parameters, such as precipitation totals and prevailing wind directions.

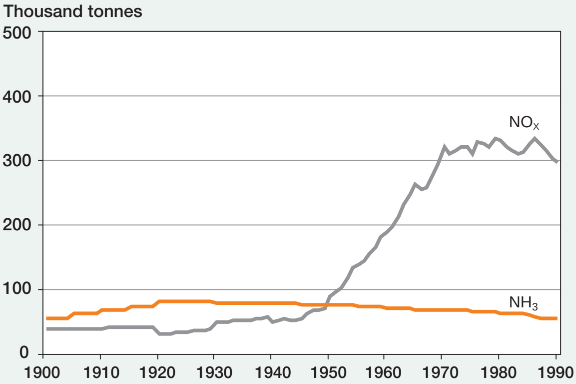

Figure 3.1. Emissions of nitrogen oxides and ammonia in Sweden (Kindbom *et al.* 1993).

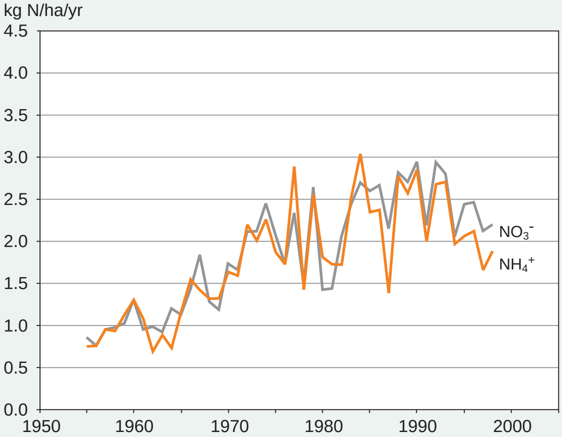

Figure 3.2a. Wet deposition of nitrate- and ammonium-nitrogen in southern central Sweden, 1955–98 (kg N/ha/yr). (Data from Department of Meteorology, Stockholm University, and IVL.)

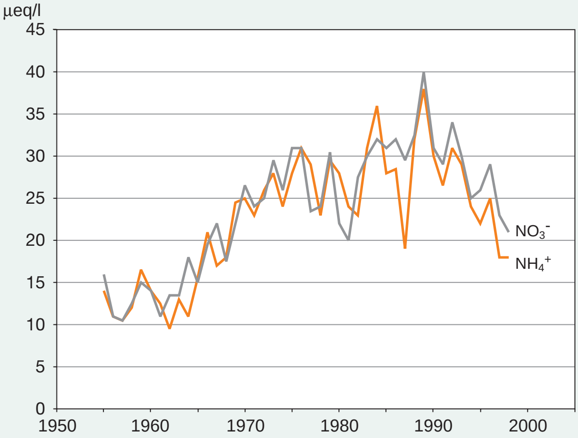

Figure 3.2b. Mean nitrate and ammonium concentrations (µeq/l) in precipitation over southern central Sweden, 1955–98.

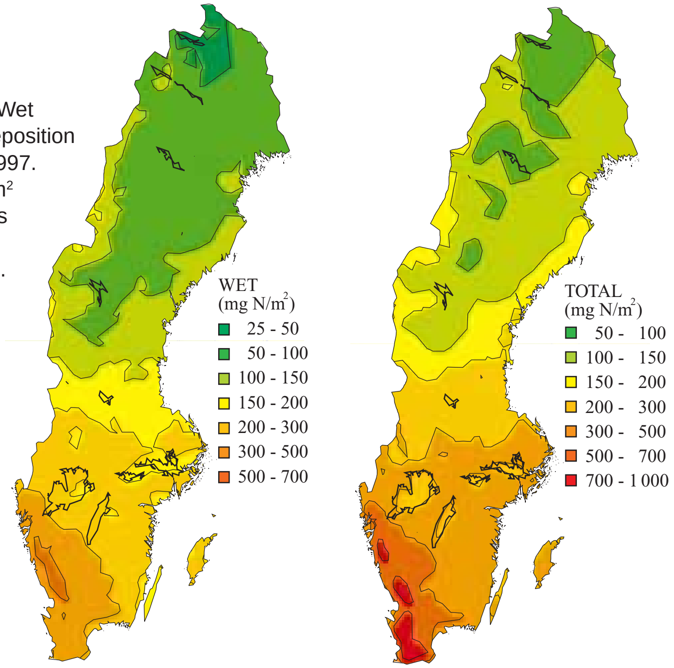

Figure 3.3. Wet and total deposition of nitrate, 1997. 100 mg N/m^2 corresponds to 1 kg/ha (SMHI, IVL).

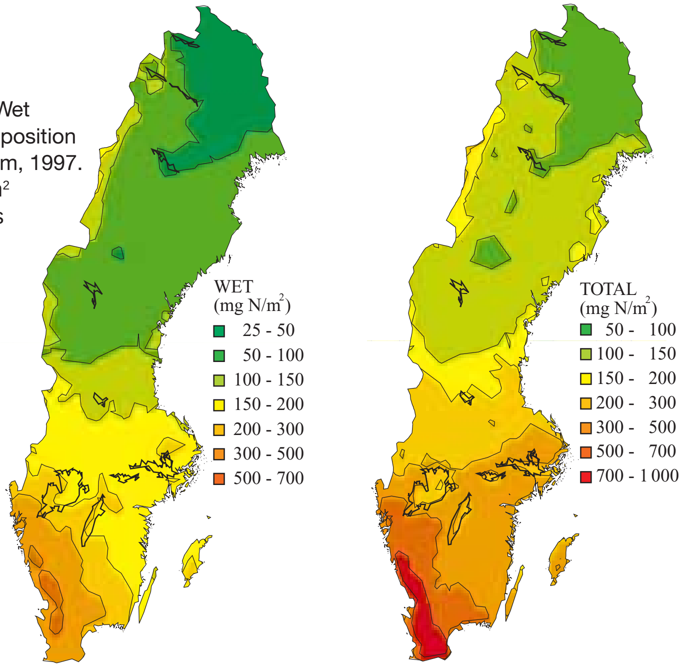

Figure 3.4. Wet and total deposition of ammonium, 1997. 100 mg N/m^2 corresponds to 1 kg/ha (SMHI, IVL).

The highest deposition levels occur in Skåne and the west coast region, primarily on higher ground, where total deposition, averaged over a large area, amounts to 5–7 kg of nitrate-nitrogen per hectare per year (0.5–0.7 g $N/m^2/yr$) and over 8 kg of ammonium-nitrogen per hectare per year (0.8 g $N/m^2/yr$). Deposition is high in the south-west of Sweden because the region is affected by the major emission sources in western Europe and because the prevailing precipitation-bearing winds here are south-westerly. A large proportion of deposition in upland areas occurs in rain and snow. Further north, total deposition of nitrogen decreases to around 2–3 kg per hectare per year. In southern Sweden as a whole, dry deposition makes up 25–50% of the total atmospheric input of nitrogen compounds, whereas in the north it accounts for an appreciably smaller proportion than wet deposition. However, there are wide variations between individual sites in the south of the country, and the highest levels of dry deposition occur on forest land exposed to heavy nitrogen loads.

The nitrogen deposited originates from emissions of nitrogen oxides and ammonia. Nitrogen oxide emissions are primarily produced by combustion processes in engines and boilers, as a result of atmospheric nitrogen and oxygen reacting at high temperatures. Ammonia is released in conjunction with livestock production, when manure is stored and applied to fields. In general, nitrogen oxides spread further than ammonia. This is because, once emitted, nitrogen oxides need to undergo further oxidation to nitrogen compounds with high deposition velocities before efficient deposition can take place. Reduced nitrogen already has a high deposition velocity in the form in which it is emitted (ammonia). However, any ammonia that is not deposited in the vicinity of its source reacts with acid gases and particles in the air to form very fine aerosols of ammonium salts. These aerosols disperse over large distances (more than 1000 km), together with nitrate and sulphate ions, and have a comparatively long atmospheric residence time.

On average, roughly equal quantities of nitrogen are deposited in the nitrate and ammonium forms in Sweden. In southern areas where ammonia emissions are high, deposition of reduced nitrogen predominates, while in northern parts of the country nitrate deposition prevails. The sources of the nitrogen deposition occurring in Sweden are shown in table 3.1.

In the case of nitrogen oxides, Sweden's own emissions account for between 10% and 20% of total deposition. Germany, Britain and other EU member states provide major contributions, together accounting for around 60% of the total in southern parts of the country and some 35% in the north. The EU countries are thus far and away the dominant source of

Table 3.1. Countries of origin of the nitrogen deposited in different areas of Sweden (from EMEP/MSC-W 1998).

Nitrogen oxides	Blekinge	Kronoberg	West coast	Stockholm	S Norrland	N Norrland
	%	%	%	%	%	%
Sweden	9	11	13	17	16	13
Baltic states	2	9	1	4	2	4
Norway	1	2	4	3	11	6
Germany	25	21	19	19	12	9
UK	11	15	19	8	9	6
Denmark	8	9	8	4	4	3
Other EU	14	15	15	14	12	16
Poland	10	6	4	9	6	4
Czech Republic	2	4	2	2	2	1
Other E Europe	4	3	2	6	4	6
Sea areas	5	4	4	4	3	2
Known origin	91	91	91	90	81	70
Unknown origin	9	9	9	10	19	30
Ammonia						
Sweden	44	34	25	22	17	10
Denmark	15	16	13	6	4	4
Norway	1	1	0	1	10	4
Baltic states	2	2	4	8	5	5
Germany	10	13	17	14	8	7
UK	4	4	2	3	3	2
Other EU	8	10	9	11	7	13
Poland	4	6	14	11	8	7
Other E Europe	4	5	6	10	6	8
Known origin	92	91	90	86	68	60
Unknown origin	8	9	10	14	32	40

inputs of oxidized nitrogen to Swedish ecosystems, and an EU strategy to reduce nitrogen oxide emissions should therefore be of great significance from Sweden's point of view.

As for ammonium deposition, domestic emissions make the largest contribution to the total, 25–45% in the south of the country and 10–20% in the north. Other countries accounting for large shares are Denmark, Germany and Poland, which are all neighbours of Sweden. Domestic measures to reduce emissions of ammonia will have a far greater effect in Sweden than corresponding efforts to curb nitrogen oxide emissions.

There are considerable variations in deposition across the country. The maps on p. 23 show mean deposition in 11x11 km squares with mixed land use. In reality, local variations are much greater than the maps indicate, since land use has such a marked impact on the scale of dry deposition. Over large areas of southern Sweden, the total deposition of nitrogen to forests is estimated to be 1.5 to 2 times the wet deposition. On open sites, total deposition is estimated to be roughly equal to wet deposition. To calculate deposition in particular areas, it is necessary to have data on concentrations of nitrogen compounds in both air and precipitation, local precipitation totals, and land use.

A more detailed account of temporal and spatial variations in deposition in Sweden, and of the contributions of different deposition processes, can be found in Lövblad *et al.* 1995.

Future deposition trends

Future trends in deposition will depend on the effectiveness of action to reduce air pollutant emissions. To assess how ecosystems will develop on a long time-scale, long-term forecasts of emission trends are needed. At present, however, reliable predictions cannot be made beyond the year 2010.

In the light of expected changes in emissions (see chapter 2), future deposition levels can be estimated using EMEP model calculations (EMEP/MSC-W 1998). The emission cuts that can be achieved in the framework of current plans and national objectives constitute the ‘reference scenario’ (REF J) for the pollution situation in 2010. The WGS scenario, drawn up in conjunction with the Multi-Effect Protocol, reflects the expected results of that protocol. Assuming the national emission ceilings planned by the EU are implemented, deposition in the year 2010 can be estimated on the basis of the EU H1 scenario.

Table 3.2 shows the changes in deposition that can be expected by 2010, compared with 1990, under the REF J, Multi Effect Protocol and EU H1 scenarios.

By the year 2010, under the three scenarios, deposition of oxidized nitrogen (nitrate) is expected to have fallen considerably, to around 2.5 kg of nitrogen per hectare per year in southern parts of the country and just under 1 kg in the north. This represents an overall decrease from 1990 levels of 50–60% in southern Sweden, and 40–50% in the north. Deposition of reduced nitrogen (ammonium) is expected to have decreased by 15–20% compared with 1990, to around 3 kg of nitrogen per hectare per year in the south of Sweden and roughly 0.5 kg in northern areas. These figures refer to mean deposition over large areas with mixed land use. In forested areas, deposition will be somewhat higher.

Provided that current reduction plans are implemented, the environmental situation will improve appreciably, creating a basis for ecosystem recovery.

Table 3.2. Estimated deposition levels (kg N/ha/yr) in different regions of Sweden in the year 2010: mean values over large areas and comparisons with 1990. Based on EMEP model calculations (EMEP/MSC-W 1998).

Scenario	Deposition	Blekinge	Kronoberg	West coast	Stockholm	S Norrland	N Norrland
Total N							
Ref. (J)	2010	5.55	5.93	5.18	3.78	1.54	1.31
	% of 1990	66	60	65	68	64	66
Multi-Effect Prot. (WGS 31b)	2010	5.73	5.92	5.18	3.80	1.56	1.31
	% of 1990	68	60	65	68	65	66
EU Ceilings Dir. (H1)	2010	5.20	5.36	4.80	3.54	1.47	1.25
	% of 1990	62	54	60	63	61	63
NO_x							
Ref. (J)	2010	2.35	2.69	2.54	2.08	0.89	0.84
	% of 1990	51	44	51	57	54	59
Multi-Effect Prot. (WGS 31b)	2010	2.35	2.56	2.54	2.08	0.89	0.84
	% of 1990	51	42	51	57	54	59
EU Ceilings Dir. (H1)	2010	2.44	2.35	2.35	1.94	0.85	0.80
	% of 1990	53	39	47	53	51	56
NH_3							
Ref. (J)	2010	3.20	3.24	2.64	1.70	0.65	0.47
	% of 1990	85	84	86	87	88	85
Multi-Effect Prot. (WGS 31b)	2010	3.38	3.36	2.64	1.72	0.67	0.47
	% of 1990	89	87	86	88	91	85
EU Ceilings Dir. (H1)	2010	2.76	3.01	2.45	1.60	0.62	0.45
	% of 1990	73	78	80	82	84	82

QUESTIONS AND ANSWERS

Is deposition of nitrogen decreasing in Sweden?

Yes, probably. Measurements of ammonium and nitrate concentrations in precipitation suggest a downward trend. An evaluation of trends is currently in progress within the environmental monitoring programme, and this will determine the statistical significance of observed trends. Measurements of Swedish urban air reveal an appreciable fall in concentrations of nitrogen dioxide, of the order of 30–50%, depending on the location, size and local emissions of the town or city concerned. Decreases can also be observed in other European countries, reflecting the emission reductions now being achieved, primarily thanks to rapidly increasing use of catalytic converters.

According to available inventory data, European emissions of nitrogen oxides fell by around 20% between 1990 and 1996. There are also data pointing to a similar reduction of ammonia emissions.

What proportions of oxidized and reduced nitrogen are present in deposition?

In Sweden, the ratio of nitrate to ammonium concentrations in precipitation is virtually 1:1. In the case of dry deposition, the proportions vary, with higher deposition of reduced nitrogen in the vicinity of agricultural areas.

How much of the nitrogen deposited in Sweden comes from other countries?

Non-Swedish sources account for around 85% of deposition of oxidized nitrogen compounds in Sweden. In the case of reduced nitrogen, domestic sources are more significant, accounting for some 35% of the total for the entire country. These figures, based on balances for 1998 calculated by EMEP, apply to Sweden as a whole.

Will current plans result in nitrogen deposition in Sweden falling below critical load levels?

No. In the areas currently exposed to the highest deposition levels, deposition will remain in excess of critical loads even when the measures now planned have been implemented. This is particularly true of forests, heaths and mires in Skåne, Halland, Blekinge, Bohuslän and adjacent areas of Småland (southern and south-west Sweden).

HOW ARE THE NITROGEN DYNAMICS OF FOREST SOILS AFFECTED?

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Nitrogen is the nutrient which plants need in the largest quantities, and in many ecosystems, such as temperate forests, its availability is normally the limiting factor for plant production. The supply of nitrogen also regulates many complex interactions within ecosystems, including interactions between different trophic levels. For this reason, a nitrogen-limited ecosystem differs radically from one that is nitrogen-saturated. The dynamics of nitrogen in the soil system are complex, but crucial to an understanding of this element's role in the ecosystem.

Increased availability of nitrogen, resulting for example from atmospheric deposition, can have a number of undesirable effects. Excess nitrogen is leached from the system, chiefly as nitrate, leading to pollution of groundwater and eutrophication of coastal sea areas. The nitrate leached out is accompanied by positively charged 'counter-ions', such as hydrogen and aluminium ions, which cause acidification of the receiving system, or the base cations calcium, potassium and magnesium, resulting in acidification of the leached soil. Nitrate can also be given off as nitrous oxide, N_2O, which can cause depletion of the ozone layer. Since nitrogen availability is generally the limiting factor for production, it also has a direct bearing on an ecosystem's ability to bind atmospheric carbon dioxide, and hence on the problem of climate change. In this chapter we discuss how nitrogen deposition provides an addition to the natural nitrogen cycle, and how this affects the soil system in particular. The chapter focuses to a large extent on the relationship between dose (level of nitrogen deposition) and response (ecosystem effects, chiefly in terms of leaching of nitrogen), and on differences between different forest ecosystems in this context.

NITROGEN SATURATION

A discussion is currently under way on how the concept of nitrogen saturation should be defined.

One alternative, based on the chemical notion of saturation, defines a nitrogen-saturated ecosystem as one where losses of nitrogen are equal in magnitude to inputs. The advantage of this definition is that it is strict and not open to different interpretations. A possible disadvantage is that it does not cover situations in which the supply of nitrogen is elevated (and harmful to certain organisms); however, such states can be described using other terms (Binkley & Högberg 1997).

Another definition broadens the concept to include systems in which an elevated level of nitrogen leaching can be observed, i.e. an increase compared with a given natural background level. This approach has the advantage that it draws attention to the effects of nitrogen deposition at an early stage. The disadvantages are that the chemical definition of saturation is abandoned, that it is difficult to establish an obvious limit value, and that transient and natural states (e.g. windthrow) may also fall within the scope of the definition.

Yet another possibility is to define nitrogen saturation as a state in which the supply of nitrogen exceeds the nitrogen needs of plants and micro-organisms. This definition focuses on the requirements of organisms in the ecosystem, but clearly says nothing about the extent to which nitrogen is being leached from the system (Aber *et al.* 1989).

We have chosen here to adopt the first definition, and to use expressions such as ‘an elevated supply of nitrogen’ to describe states in which nitrogen availability is above the natural background, but losses of nitrogen are not equal to inputs.

Deposition has increased nitrogen pools

Nitrogen rarely occurs in soil minerals and therefore, unlike calcium, phosphorus and other elements, it is not generally supplied to the soil by weathering. Historically (up to a hundred years ago), most nitrogen has been incorporated in ecosystems by biological fixation (nitrogen gas from the atmosphere, N_2, is reduced by certain bacteria, alone or in symbiosis with plants, to ammonia, which then binds to carbon chains to form amino acids). A small proportion of the nitrogen present in ecosystems is the result of fixation by lightning discharges. However, the current high output of artificial fertilizers and nitrogen fixation by combustion processes in industry and the transport sector have doubled the annual global supply of nitrogen (Vitousek *et al.* 1997). Analyses of the Greenland ice sheet confirm that a modest, more or less stable background level of nitrogen deposition has existed for thousands of years, but that a marked increase in deposition has occurred over the last few decades (Mayewski *et al.* 1986).

The store of nitrogen present in our forests is the net result of inputs and losses over the 9000–12 000 years that have elapsed since the last glaciation. Natural inputs of nitrogen (natural background deposition + biological fixation) have probably amounted to 1–2 kg per hectare per year. This could potentially mean an accumulated input of some 10–20 tonnes of nitrogen per hectare since the last ice age. Usually, however, the nitrogen pool is considerably smaller than this, probably mainly as a result of fires of varying frequency in coniferous forests (Zackrisson 1977), but also owing to leaching, chiefly of organic nitrogen compounds (Hedin *et al.* 1995).

The combined nitrogen pool of a forest ecosystem (in vegetation and in the soil down to a depth of 0.5 m) varies from roughly 1 tonne per hectare at low-fertility sites in northern Sweden to 10 tonnes per hectare in forests in the south of the country (Nohrstedt 1993). In exceptional cases, in pine forests on sites with extensive exposures of rock, the figure could probably be even lower, but no data are available for such sites. Higher values than 10 tonnes per hectare may also occur, chiefly in forests on drained peat (Holmen 1964), as a result of both smaller fire losses in these damp ecosystems and an influx of nitrogen from mineral soils at higher elevations. In general, stores (and turnover) of nitrogen increase below hill-slopes of significant size, owing both to a flux of nitrogen from groundwater recharge to groundwater discharge zones, and to increased cycling – and probably also fixation – of nitrogen with rising moisture levels and pH. This results in considerable variations in forest productivity and the composition of the flora (Giesler *et al.* 1998, Högberg 2000).

Over the last 100 years, in the most exposed areas of southern Sweden, anthropogenic deposition has added an estimated 500–1000 kg per hectare to the nitrogen capital of ecosystems. It thus follows that the man-made input of nitrogen to forests in the south of the country corresponds to an increase of, at most, some 50–100% (the latter figure an estimate for pine forests in areas of exposed rock in the south-west) and, as a minimum, less than 5%.

Most nitrogen in soil is bound to humus

The majority, often more than 80–90%, of the nitrogen capital of Swedish forests is to be found in the soil (Nykvist 1977, Nohrstedt 1993). A significant quantity of this nitrogen occurs in the mor horizon of the podzols on which the forests grow, but surprisingly large amounts are also found in humic substances in the upper layers of mineral soil, particularly the illuvial (enriched) horizon. In simplified terms, the nitrogen present in the soil can be divided into a number of component pools (figure 4.1), which vary in size and turnover time. The dominant pool consists of nitrogen bound to dead organic matter, chiefly humus, which is turned over very slowly, probably as slowly as the carbon to which it is bound – which would mean a turnover time of 20–100 years in the mor horizon and 200–500 or even 1000 years or more in the illuvial horizon (Tamm & Östlund 1960, Tamm & Holmen 1967). Another relatively large pool is more readily decomposed by micro-organisms and can be described as the slow-degrading pool, with turnover times of months to years (Binkley & Hart 1989). The nitrogen in micro-organisms such as bacteria and fungi is turned over more rapidly, on a time-scale of weeks to months (Binkley & Hart 1989). This pool makes up some 10% of the total store of nitrogen in the upper, biologically most active layers of the soil (table 4.1). The shortest turnover times of all, just a day or so, are found in the case of the inorganic pools of ammonium and nitrate ions (Davidson *et al.* 1992, Hart *et al.* 1994), and probably also the pool of free organic nitrogen compounds, such as amino acids and proteins. This is chiefly true of soils with a severe nitrogen limitation; turnover is probably appreciably slower in ecosystems with large pools of ammonium and nitrate. Table 4.1 shows, by way of illustration, the sizes of different nitrogen pools in the mor horizon of a nitrogen-limited coniferous forest in northern Sweden.

Plants
(years (leaves) – centuries (wood))
Soil

Microbial nitrogen	Free amino acids	Ammonium	Nitrate
(weeks–months)	(days–weeks)	(days–?)	(days–?)

More readily degradable organic nitrogen compounds
(months–years)

Very slow-degrading nitrogen compounds (e.g. nitrogen in humus)
(centuries–millennia?)

Figure 4.1. Nitrogen in plants and soil can be divided into different pools (fractions), which vary in size and turnover time (shown in parenthesis).

TABLE 4.1. Nitrogen pools in the mor horizon of a northern Swedish coniferous forest, expressed in kg N/ha (Näsholm *et al.* 1998).

Total store (mostly nitrogen bound to slow-degrading humus)	300
Nitrogen in micro-organisms	30
Extractable organic nitrogen (amino acids in the soil solution and loosely bound to soil particles)	1
Extractable inorganic nitrogen (ammonium + nitrate in the soil solution and loosely bound to soil particles)	0.3

Plants can also use organic nitrogen compounds

The cycling of nitrogen in soil is controlled to a large degree by biological processes. Traditionally, it has been held that plants can only take up inorganic forms of nitrogen (ammonium and nitrate), and that organic nitrogen compounds therefore only become available to them when they have been broken down into inorganic forms, i.e. mineralized. However, increasingly it has been discussed whether forest plants might in fact be able to assimilate simple organic nitrogen compounds, above all via their mycorrhizal fungi. This possibility is supported both by model experiments in the laboratory (Smith & Read 1997), and by the fact that, when samples of many acid forest soils with a high carbon/nitrogen (C/N) ratio are incubated in the laboratory, no *net* mineralization occurs for several weeks or months (Persson 1995). Rough model estimates based on data from laboratory experiments on such soils indicate a large shortfall in calculated net nitrogen mineralization in relation to uptake by forest trees (Persson 1995). Very recently, moreover, the uptake of an intact amino acid, glycine, was demonstrated in the field for the first time (Näsholm *et al.* 1998).

Ammonium and nitrate pools in soil can be turned over in a day

By adding small quantities of ammonium labelled with nitrogen-15 to a soil, it is possible to monitor how quickly the labelled ammonium is diluted with unlabelled ammonium. This *gross* mineralization of nitrogen can be very rapid, even in a coniferous forest soil (Davidson *et al.* 1992, Hart *et al.* 1994). Studies of net mineralization show only the net production of mineral nitrogen, and do not reveal that the newly produced mineral nitrogen is rapidly and constantly being taken up by micro-organisms (and, in the natural environment, also by mycorrhizal roots). Studies of gross turnover show that soil pools of ammonium and nitrate are turned over in the space of just a day or so in soils where these pools are small. With such short turnover times, it is possible that the mineralization process supplies trees with more inorganic nitrogen than net mineralization studies suggest. As yet, however, net and gross mineralization have not been compared in forest soils in which no net mineralization has been demonstrated. We are therefore unable to say anything very definite about the proportions of organic and inorganic nitrogen sources involved in nitrogen uptake by trees.

The uptake (assimilation) of inorganic nitrogen by micro-organisms, known as immobilization, is dependent on the micro-organisms having access to readily degradable carbon compounds (Hart *et al.* 1994, Kaye & Hart 1997). This is partly because the assimilation of inorganic nitrogen requires energy, and partly because this nitrogen has to be bound to a carbon compound to form an organic nitrogen compound (normally an amino acid). The carbon/nitrogen ratio of the soil is thus a key factor in the dynamics of nitrogen (see ‘Nitrogen retention and the carbon/nitrogen ratio’).

PROCESSES AND TERMS

Nitrogen mineralization (ammonification, nitrogen mobilization) is a process that takes place primarily inside the cells of micro-organisms and soil animals. It may, for example, involve an amino acid being split into ammonia and a fatty acid. The ammonia is given off through the cell membrane and, in an acid environment, forms ammonium. The following simplified formula sums up the process of mineralization:

$\text{Organic N} \rightarrow NH_4^+ + \text{carbon compound}$

Nitrification:

Autotrophic nitrification = ammonium is oxidized by micro-organisms (via nitrite) to nitrate in two steps (while the energy released by oxidation is used to assimilate CO_2):

$$2NH_4^+ + 3O_2 \rightarrow 2NO_2^- + 2H_2O + 4H^+$$

$$2NO_2^- + O_2 \text{ (from } H_2O) \rightarrow 2NO_3^-$$

Heterotrophic nitrification = oxidation of ammonium/ammonia or an organic nitrogen compound to nitrate (the oxidation providing no energy for the nitrifying organisms), according to the following simplified formula:

$\text{Organic N} \rightarrow NO_3^-$

Ion exchange:

Ions become bound to soil particles by electrostatic forces. These particles are usually negatively charged, and therefore ammonium (NH_4^+) is bound more strongly than nitrate (NO_3^-).

Denitrification:
Nitrate is reduced to nitrous oxide and/or nitrogen gas in the presence of a carbon source (which is oxidized), according to the following simplified formula:

$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$

Nitrate reduction (in plants or micro-organisms) is the reduction of nitrate to nitrite (followed by reduction to ammonium and subsequently assimilation into an amino acid).

Nitrogen immobilization:
Inorganic nitrogen is assimilated by soil micro-organisms. Inorganic nitrogen can also be immobilized chemically when nitrite binds to phenols or ammonia reacts with quinones.

Humus:
Collective term for highly decomposed and transformed organic matter, consisting of large molecules made up of combinations of aromatic rings and carbon chains of varying length.

Polyphenols:
Breakdown products of lignin, for example, consisting of aromatic rings, which do not degrade readily and which form part of humus molecules.

Quinones:
Aromatic rings formed from carbohydrates, polyphenols (lignin) and melanins (synthesized by micro-organisms), constituents of humus.

Mycorrhiza:
'Fungus root', symbiosis formed between plant roots and certain fungi. Most Swedish forest trees form ectomycorrhizas, consisting of a mantle of fungus around their roots and a network of hyphae penetrating both into the roots (between the cells) and out into the soil. The fungus obtains carbon from the tree, while enhancing the tree's supplies of water, nitrogen, phosphorus etc.

Nitrogen-15 (^{15}N):
Nitrogen atom with an extra neutron in its nucleus. Most nitrogen atoms (99.6%) have 7 protons and 7 neutrons in their nuclei (nitrogen-14), but nitrogen-15 has 8 neutrons. This stable (non-radioactive) isotope is widely used in biological and ecological research. Since nitrogen-14 has an overwhelming predominance in nature, it is relatively easy to track added nitrogen-15 as it passes through an ecosystem.

Relationship between soil acidity and nitrogen availability

A statistical relationship exists between the acidity (pH) of a soil and the productivity of the plant community, and not least the trees, growing on it (for references, see Giesler *et al.* 1998). Many researchers have interpreted this as evidence that trees need large quantities of base cations (high concentrations of base cations mean a high pH), and even that the supply of base cations (Ca, Mg, K) is a direct limiting factor for forest productivity (e.g. Sverdrup *et al.* 1992a, 1994). Acidification resulting from anthropogenic deposition would thus reduce forest production in a very direct way. However, with the exception of potassium, trees' base cation requirements are in fact relatively small (Linder 1995). Trees need considerably less calcium than nitrogen, but levels of calcium do have a major impact on soil pH, and hence on the activity of soil micro-organisms.

Experimental forest research shows that, in most parts of Sweden (with the exception of a number of sites in the south-west, see Binkley & Högberg 1997), additions of nitrogen increase forest productivity, despite the fact that they usually also lower the pH of the soil. At the same time, experiments involving liming (which raises soil pH) demonstrate that forest productivity can fall as a result of increased microbial immobilization of nitrogen (with the exception of a few cases in south-west Sweden). We can conclude from this that forest tree production is most commonly limited by a deficiency of nitrogen (once again, the exception being a small number of south-western sites). The strong correlation between soil pH and forest productivity can probably be attributed to the significance of pH for microbial turnover of nitrogen (Giesler *et al.* 1998), but it is not an effect that is achieved immediately after an application of lime (Högberg 1999). An interesting phenomenon in this context is that forest productivity increases in a regular manner with increasing distance down large hill-slopes. This rise in productivity parallels increases in pH and nitrogen availability that are linked to discharge of groundwater (Giesler *et al.* 1998, Högberg 2000).

Deposited nitrogen is first taken up by micro-organisms and plants

Some of the nitrogen in precipitation is taken up directly by tree crowns and by field- and ground-layer vegetation, and therefore does not reach the ground straightaway. The remainder reaches the soil surface, together with the portion of the previously dry deposited nitrogen which is washed from foliage by the rain. This nitrogen consists of a mixture of different forms: ammonium and nitrate ions, amino acids, proteins, and nitrogen bound in more complex compounds in particles. In forests in the south-west of Sweden, the dominant forms are ammonium and nitrate, the proportions of which depend on the importance of different pollutant sources (see chapter 3). In other words, air pollutant nitrogen mainly increases the nitrogen pools in the soil which both have a rapid turnover and are readily available to micro-organisms and plants. Nitrate ions, moreover, bind weakly to soil particles and are therefore potentially highly mobile in the soil.

Whether it is in the form of ammonium, nitrate or an amino acid, the nitrogen deposited will immediately become involved in cycles of microbial immobilization and mobilization, bind to cation or anion binding sites on soil particles, and possibly be taken up by plants. Depending primarily on the overall availability of nitrogen in the system, but also on the amount of precipitation and the initial moisture content, texture, structure etc. of the soil, nitrate will migrate down through the soil profile at a varying rate, but at all times it will be potentially exposed to biological uptake and conversion to other forms of nitrogen. There has been speculation as to whether rapid flow in larger 'macropores' might enable nitrate from deposition to pass rapidly through the soil profile and into groundwater without participating in biological processes. In most conditions, and in soils of normal depth (> 0.5 m), however, it takes many days or weeks for the water from a given precipitation event to reach groundwater, which is very probably long enough for relatively simple sources of nitrogen to be turned over biologically several times.

Depending on the time that has elapsed since a nitrogen input occurred, the nitrogen added will be found to varying degrees in different parts of the ecosystem. This is particularly apparent in studies in which nitrogen-15 is applied. A very large proportion of the nitrogen added rapidly turns up in micro-organisms, including the fungal hyphae that form part of the mycorrhizas of plants (Näsholm *et al.* 1998). Over relatively short periods, retention in the soil system is often close to 100% (e.g. Berggren *et al.* 1998, Sjöberg & Persson 1998). Eventually, the labelled nitrogen (nitrogen-15) spreads and mixes with older (and newer) unlabelled nitrogen in the system, and this provides a picture of what happens in the longer term. In conjunction with fertilizer applications to forests, studies have been made of where the nitrogen from the fertilizer ends up. Normally, less than 20% of the nitrogen applied is found in the trees two years after fertilization, while an estimated 50–60% is present in the soil. In a detailed investigation, in which nitrogen-15 was added with a fertilizer dose of 150 kg of nitrogen per hectare, a broadly similar breakdown was found (Melin 1986). In the same experiment, if the nitrogen was added as nitrate rather than ammonium, tree uptake and leaching were found to be higher and immobilization in the soil lower.

Nitrification and denitrification

The process of nitrification, i.e. microbial oxidation of ammonium to nitrate, is of particular importance in the biogeochemistry of nitrogen, owing to the mobility of nitrate in the soil system. Soil has a large capacity to bind cations, but not anions such as nitrate. Consequently, in the absence of a powerful biological sink (plants and micro-organisms with a high nitrogen demand), and in humid conditions, nitrate can easily be leached from the soil. In addition, when oxygen is in short supply, certain micro-organisms can use nitrate (rather than oxygen) as the terminal electron acceptor in the process of denitrification, resulting in nitrogen being lost from the system as nitrous oxide (N_2O, which is a greenhouse gas) and/or nitrogen gas (N_2).

Autotrophic and heterotrophic nitrification

A distinction is made between classical, chemoautotrophic nitrification and heterotrophic nitrification. Autotrophic nitrification (in which the organisms involved – plants and certain bacteria – obtain their carbon from CO_2 or HCO_3^-) is performed by at least two genera of bacteria (*Nitrosomonas* and *Nitrobacter*) and comprises two steps: first from ammonium to nitrite, and then oxidation of nitrite to nitrate. This process is pH-dependent, and only occurs to a limited extent at pH values below 5.5 (even though it is itself acidifying). Recently, however, increasing attention has focused on autotrophic nitrifying bacteria of the genus *Nitrosospira*, of which both acid-tolerant and acid-sensitive forms exist. Heterotrophic nitrification (in which the organisms concerned make use of organically bound carbon, rather than CO_2) is carried out primarily by certain fungi and bacteria. They use organic nitrogen compounds, such as amines or amides, directly as a substrate, but they also utilize ammonium. This process is not as markedly sensitive to soil acidity as autotrophic nitrification appears to be.

Denitrification is common in anoxic environments (although recently the possibility of it occurring at relatively high oxygen concentrations has been discussed; see Lloyd 1993), and it requires access to nitrate and sources of carbon. The process is performed by a relatively large number of species of bacteria. Many heterotrophic nitrifiers are also denitrifiers. In neutral conditions (around pH 7), the dominant product is nitrogen gas, but the proportion of nitrous oxide increases with rising acidity.

As has already been mentioned, the importance of nitrification in acid forest environments has probably been underestimated, since only net nitrification has been determined and the possibility of cycles of production followed by rapid consumption of nitrate thus overlooked. Elevated deposition of ammonium nitrate, for instance, increases the soil pool of nitrate both directly and indirectly, via increased nitrification. Eventually, the supply of this ion exceeds the biological demand, and more and more nitrate is leached from the soil.

Denitrification primarily takes place in oxygen-depleted environments, e.g. at sites with groundwater discharge. However, it can also be significant during short episodes of water saturation, even in normally drier soils. In most Swedish forest soils, though, losses of nitrogen due to denitrification probably do not exceed 1–2 kg per hectare per year (Nohrstedt 1988, Nohrstedt *et al.* 1994). The denitrification that occurs in groundwater at greater depths has an impact on surface water quality.

Nitrification and denitrification are examples of important dynamic processes that are difficult to model. Really successful modelling presupposes an understanding of the biochemistry and population biology of the organisms concerned, and of their interactions with other groups of organisms, e.g. with other organisms which utilize nitrate.

Trees immobilize significant amounts of nitrogen

It has been discussed whether studies involving large single applications of nitrogen can provide a realistic picture of what happens when nitrogen is supplied in smaller, more frequent doses (chapter 8). Johnson (1992) took the view that long-term immobilization in soil tended to be overestimated by nitrogen-15 budgets that were calculated too short a time after applications of nitrogen, and following unrealistically high doses. He believed that, in many cases, trees could account for a large proportion of long-term immobilization. In the rapid turnover of nitrogen, i.e. the rapid mobilization–immobilization cycle, mycorrhizal hyphae occupy a unique position, since they are constantly supplied with carbon from plant photosynthesis and thus do not need to compete with other micro-organisms for this element. Instead of releasing nitrogen again by mineralization (mobilization) when the supply of carbon runs low, as it can easily do for free-living micro-organisms, mycorrhizal fungi pass on considerable quantities of nitrogen to their host plants. Nitrogen immobilization in the biomass of micro-organisms other than mycorrhizal fungi entails only temporary storage, and some of this nitrogen may be liberated again within weeks to months (Sjöberg & Persson 1998) and thus once more become available for competitive uptake by plant roots (with their mycorrhizas) and free-living soil micro-organisms. In this regard, trees hold a special position, since they do not rapidly recycle nitrogen to the soil system. Johnson (1992) argued that levels of nitrogen deposition to many North American forests were low enough to allow all the nitrogen to be immobilized by growing wood alone. Productive Swedish forest sites have a stemwood growth rate of the order of 1–10 tonnes per hectare per year. Assuming that wood contains 0.06% nitrogen, this would mean immobilization of 0.6–6 kg of nitrogen per hectare per year. In addition, some growth of wood occurs in thick branches and roots (in more mature forests, the needle or leaf biomass may be expected to be constant over long periods). Altogether, this immobilization probably corresponds to around half the total deposition of nitrogen at many sites (see above). After felling, some of the nitrogen that has thus accumulated during the rotation is removed from the forest.

Younger middle-aged forests have the fastest growth rates, and also the highest rates of nitrogen retention (Vitousek & Reiners 1975, Reynolds *et al.* 1994). Not only is the growth of wood rapid; so too is the increase in the needle or leaf biomass, which also contributes to nitrogen retention. From this point of view, short forest rotations may be preferable, despite the problem of leaching of nitrogen after felling.

When air pollutant deposition is high, the capacity to retain nitrogen can fall appreciably, owing partly to direct damage to tree crowns (and potentially also to root systems), and partly to a lowering of the nitrogen uptake capacity of trees exposed to large inputs of nitrogen over a long period (Jones *et al.* 1994, Högberg *et al.* 1998). A similar reduction of the nitrogen uptake capacity occurs when some other element, such as phosphorus, becomes the limiting factor for growth (Stevens *et al.* 1993). For this reason, the capacity for ammonium uptake per gram of tree roots is three to four times lower in the forests of central Europe than in severely nitrogen-limited forests in northern Sweden (Högberg *et al.* 1998). At the same time, the opposite pattern can be observed when it comes to the nitrate reductase activity of roots, and the lower capacity to take up ammonium therefore cannot be seen as evidence of a general decline in root vigour in central European forests.

Studies of the capacity of tree roots to take up ammonium- or nitrate-nitrogen in solution show that they have a 20–30 times greater uptake capacity with regard to ammonium than with regard to nitrate (Kronzucker *et al.* 1997, Högberg *et al.* 1998). When both these forms of nitrogen are present at the same time, the majority of Swedish forest plants, not least trees, show a marked preference for ammonium. In an illustrative study of Norway spruce (Marschner *et al.* 1991), only ammonium was taken up from a solution of ammonium nitrate, up to the point at which the concentration of ammonium fell below 100 μmol per litre. Only then did any significant uptake of nitrate occur. This study was carried out in the field, but with (non-mycorrhizal) roots immersed in a container of synthetic soil solution, in which the measurements were performed. As a result, it underestimated the significance of the soil as an ion exchanger – in this context, particularly its ability to buffer movements of cations such as ammonium. Despite this preference for ammonium, nitrate may still be an important source of nitrogen, given that ammonium moves far more slowly through the soil system.

Only a small proportion of nitrogen is immobilized long-term in micro-organisms

Mycorrhizal fungal hyphae and many other micro-organisms also prefer ammonium to nitrate (Smith & Read 1997), but this preference probably only manifests itself when nitrogen is relatively abundant. This partly explains why nitrate leaches more readily than ammonium. Long-term immobilization of nitrogen in living micro-organisms is relatively limited, and normally total microbial immobilization probably does not exceed 50–100 kg of nitrogen per hectare (cf. the value for a nutrient-poor site in northern Sweden, in table 4.1). Micro-organisms are unable to store very significant quantities of nitrogen unless they are supplied at the same time with large amounts of readily available carbon, but any build-up of this nitrogen pool is counteracted to some extent by an accompanying increase in the consumption of micro-organisms by soil fauna and the subsequent release of the nitrogen in the animals' excretion. On the other hand, the fact that nitrogen compounds in dead micro-organisms constitute sources ('precursors') of slow-degrading nitrogen compounds, and that micro-organism activity itself can result in the production of carbon compounds to which nitrogen can bind, are factors of longer-term and considerable quantitative significance for nitrogen retention in the soil.

Nitrogen immobilization

Both inorganic and organic nitrogen can be immobilized and incorporated in humus abiotically, by spontaneous chemical and/or enzymatic reactions outside micro-organisms. Certain nitrogen compounds are reactive and therefore play an active part in building up humus. There are many different reactions of this type. For instance, nitrite (NO_2^-) can react with organic matter to form stable nitrogen complexes, such as aromatic nitroso compounds. At high pH, chemical fixation of ammonia (NH_3) in humus is possible. Elevated pH can occur locally in micro-environments, even in acidic forest soils, and can be particularly common in association with decomposition, e.g. of faeces, urine, fungal fruiting bodies or urea (from forest fertilizers). Ammonium and organic amino compounds can react with cyclic quinones, formed from carbohydrates, polyphenols (lignin) and melanins (synthesized by micro-organisms). Functional groups containing nitrogen can also be involved in the formation of strong complexes with metallic ions (McBride 1994).

Despite the fact that the majority of soil nitrogen is bound to slow-degrading organic compounds, humus, relatively few studies have been made of the binding mechanisms involved (see overviews by Stevenson & He 1990, Stevenson 1994, Schulten & Schnitzer 1998). The following are some of the ways in which nitrogen binds to humus: (1) nitrogen forms part of an amino acid, which is attached to an aromatic ring; (2) nitrogen acts as a bridge linking quinone rings; (3) nitrogen forms part of a heterocyclic ring; (4) nitrogen is included in a group in an open chain (–NH–, =N–), and (5) nitrogen forms part of peptides and proteins which bind to larger organic molecules (Stevenson 1994). Of these various nitrogen compounds, the ones described in (5) are probably much more readily available to micro-organisms than the others, and thus the first to become potentially available to plants again. Johnsson and colleagues (1999) have demonstrated that bound, hydrolysable amino acids (and amino sugars) are the form of nitrogen most available to micro-organisms in soil organic matter.

A special case of abiotic nitrogen immobilization is the fixation of ammonium in the crystal lattice of the clay mineral illite. Quantitatively, this is not an important process in the majority of Swedish forest sites on till soils, but may be of significance in clay soils. The nitrogen fixed in this way has very limited exchangeability with ammonium and potassium ions in the soil solution.

Nitrogen retention and the carbon/nitrogen ratio

The supply of carbon and the ratio of carbon to nitrogen (C/N) in a soil are of decisive significance for its potential to retain nitrogen. This can be explained by the strong correlation which generally exists between the C/N ratio of soil organic matter and the net mineralization rate of nitrogen, and which is most apparent in the mor horizon (figure 4.2). Nilsson and coworkers (1998a) showed that, in podzols, some 50% of net mineralization of nitrogen occurs in this particular horizon. An ecosystem with a high rate of internal nitrogen turnover (i.e. rapid cycling of this element between soil and vegetation) also has a high rate of net nitrogen mineralization. Such a system has a limited capacity to further accelerate the turnover of nitrogen, i.e. it has only a moderate potential for nitrogen retention in both soil and vegetation. All ecosystems presumably have an upper limit as regards the rate at which nitrogen can be turned over, varying according to such factors as climate, tree species and availability of other nutrients, e.g. phosphorus (Aber *et al.* 1997). When this ceiling is reached, the ecosystem is nitrogen-

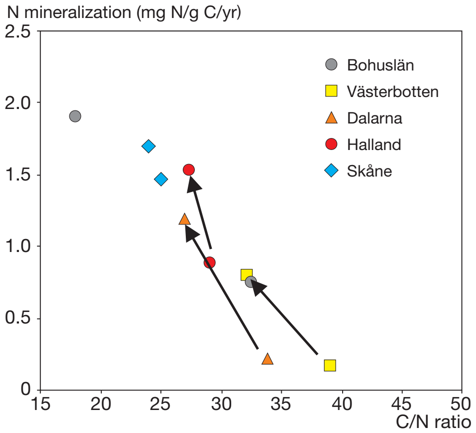

Figure 4.2. Relationship between net nitrogen mineralization rate and C/N ratio in mor horizons (F plus H horizons) at different sites in Sweden. The arrows show how the two variables changed as a result of fertilizer applications in Halland (Skogaby experiment: average of 100 kg N/ha/yr applied over 9 years), Dalarna (Stråsan experiment: average of 35 kg N/ha/yr over 30 years) and Västerbotten (Flakaliden: average of 83 kg N/ha/yr over 10 years). The plots in Bohuslän and Skåne were not fertilized. (P. Andersson *et al.*, manuscript.)

saturated, i.e. as much inorganic nitrogen leaches from the system as enters it. However, inorganic nitrogen (above all nitrate) will leach from the ecosystem long before it reaches this state.

Another interesting illustration of the significance of the C/N ratio is provided by studies of the interaction between liming and nitrogen turnover (Persson & Wirén 1996). Liming of soils with a low C/N ratio boosts nitrogen turnover, and in particular nitrification. When soils with a high C/N ratio are limed, on the other hand, immobilization of nitrogen increases, resulting in reduced turnover. Liming of sites of the latter type can thus reduce forest productivity for several decades to come.

In a study of Norway spruce forests in Halland in south-west Sweden, two sites had roughly the same high input of nitrogen from deposition, but one of them was found to be leaching considerably more nitrate than the other (Nohrstedt *et al.* 1996). The two stands were of the same age and had similar soils, and no other likely cause of the different rates of leaching was found than the lower soil C/N ratio (in turn probably a result of past land use) at the site with the higher nitrogen losses. Data from other parts of Europe reveal similar patterns. In Denmark and the Netherlands, for example, heavy leaching of nitrate was found at sites with C/N ratios of less than 25 in the mor horizon, whereas hardly any leaching at all was observed at sites where C/N > 30 (Gundersen *et al.* 1998a). In another, wider-ranging European study, it was emphasized that the C/N ratio made no difference to nitrate leaching at low levels of nitrogen deposition, but that it was negatively correlated to leaching when deposition exceeded 10 kg of nitrogen per hectare per year (Dise *et al.* 1998).

The effects of nitrogen deposition on the decomposition of plant litter are complex (Berg & Matzner 1997). Initially, a nitrogen-richer litter breaks down more rapidly than a nitrogen-poor one, but when ammonium and nitrate are added to humus its decomposition is suppressed. One explanation for the slower rate of decay at this later stage is believed to be that an input of nitrogen inhibits the breakdown of lignin. In addition, high nitrogen availability results in increased lignin formation in needles.

Immobilization of nitrogen in more or less slow-degrading nitrogen compounds is probably one reason for the marked decline in nitrogen availability in the soil–plant system that occurs when deposition decreases (chapter 8). When no new readily available nitrogen is supplied, the readily available pool is rapidly diminished by uptake and leaching, while the nitrogen immobilized on a longer-term basis remains in the system.

Risk of nitrogen leaching

Forest ecosystems often have a considerable capacity to take up deposited nitrogen. As a rule, therefore, the amount leached is much less than the amount supplied. According to Dise and Wright (1995), three different dose–response relationships can be discerned in European forests (figure 4.3): (1) at a nitrogen deposition level of less than 9 kg per hectare per year, leaching of nitrogen is insignificant; (2) where deposition is in the range 9–25 kg per hectare per year, sites with somewhat elevated leaching (> 5 kg of nitrogen per hectare per year) occur alongside sites with low rates of leaching; and finally (3) where deposition exceeds 25 kg per hectare per year, leaching is consistently high and several sites are nitrogen-saturated, in the sense that leaching is of the same magnitude as deposition. These dose–response relationships are confirmed by Swedish studies (Nohrstedt 1993, Nohrstedt *et al.* 1996, Nilsson *et al.* 1998a) and by studies in North America (Fenn *et al.* 1998), and thus appear to be fairly generally applicable to northern temperate forests.

The majority of Sweden's forests fall within the first group (1), while the sites exposed to the heaviest deposition, chiefly in the south-west, can generally be assigned to

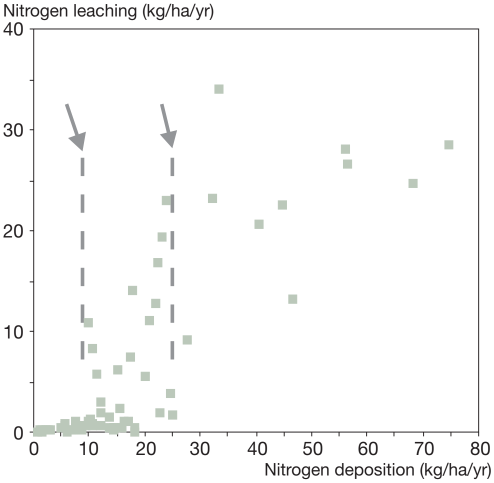

Figure 4.3. Relationship between deposition and leaching of nitrogen in European forests (data from Dise & Wright 1995).

the intermediate group (2) in dose–response terms. Exceptionally, however, there are sites, such as Harplinge in Halland, where leaching is on a par with deposition, i.e. the system is nitrogen-saturated (Nohrstedt *et al.* 1996). This saturated state is probably due largely to the high deposition and to past land use. There are, though, instances of natural nitrogen saturation in groundwater discharge zones, where iron and aluminium compounds of low solubility give the soil such a strong capacity to bind phosphate that phosphorus is the limiting factor for production (Giesler *et al.* 1998). Such sites can even be found in areas with low nitrogen deposition, e.g. in northern Sweden.

Some Swedish nitrogen experiments

Gårdsjön. The European NITREX project comprises ten experiments at eight different sites in seven countries, in which nitrogen deposition has either been increased by additional applications, or reduced by building roofs, with a view to simulating recovery. As part of NITREX, nitrogen has been added to a catchment in the Lake Gårdsjön area in Bohuslän (south-west Sweden). Here, deposition has been increased from a background level of 11 kg to 50 kg of nitrogen per hectare per year by applying a solution of ammonium nitrate to the soil via a sprinkler system. Most (> 95%) of the 'extra' nitrogen applied has been retained by the forest ecosystem (a mixed coniferous forest) during the eight years that have been studied. However, a slight episodic elevation of nitrate concentrations in runoff has been observed (Moldan & Wright 1998).

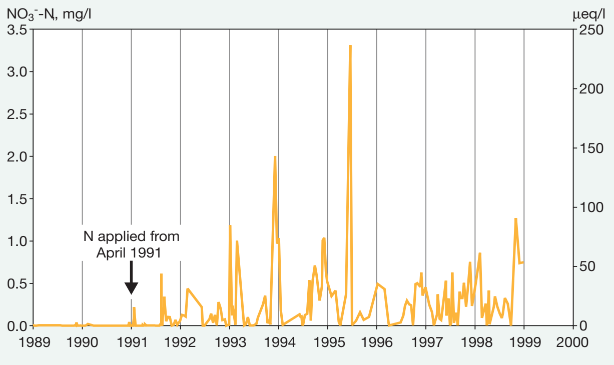

Figure 4.4. Nitrate concentrations in runoff from the NITREX experiment at Gårdsjön (after Moldan & Wright 1998; Moldan, unpublished).

Skogaby. At Skogaby in Halland (south-west Sweden), where atmospheric deposition of nitrogen is around 15 kg per hectare per year, a much larger quantity of nitrogen – 100 kg per hectare per year in addition to deposition – has been applied in the form of ammonium sulphate over a period of just over ten years. At the outset, many of those involved believed that this acidifying treatment would rapidly lead to substantial leaching of nitrogen and greatly reduced growth of the Norway spruce forest. For the first six years, however, the fertilized forest grew more rapidly than the untreated control, despite the drastic treatment (Nilsson & Wiklund 1995b), showing that forest growth had initially been nitrogen-limited. After eight years of treatment (the equivalent of 50 years of extra deposition), however, basal area growth was no higher on the fertilized plots than on the control plots (see chapter 5, figure 5.1). Subsequently, growth on the fertilized plots has declined further. The reasons for the recent decline in growth have still to be elucidated, but there could possibly be a link with falling needle concentrations of magnesium, potassium or micronutrients. During the first three years of treatment, most of the nitrogen added was retained in the ecosystem, partly thanks to surprisingly high retention by the trees themselves, but after that concentrations of inorganic nitrogen (chiefly nitrate) in runoff rose rapidly, reaching levels of tens of kilograms per hectare per year (Nilsson & Wiklund 1995b). At the same time, the soil became acidified, resulting in high concentrations of inorganic aluminium in the soil solution.

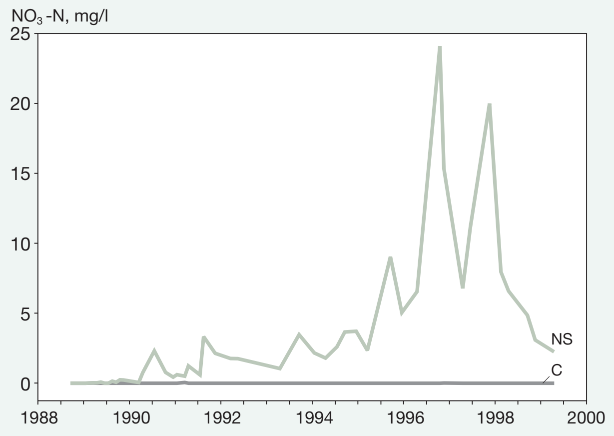

Figure 4.5. Nitrate concentrations in runoff from the ammonium sulphate (NS) and control (C) plots at Skogaby (Bergholm, unpublished).

Stråsan. In experiment E26A at Stråsan in Dalarna (north-east central Sweden), nitrogen has been applied to a Norway spruce forest, with or without additions of phosphorus and potassium (the latter applied together with other nutrients, such as magnesium and micronutrients). The nitrogen treatments began in 1967, nitrogen being applied as ammonium nitrate, at four different doses (N0–N3): 0, 36, 73 and 108 kg of nitrogen per hectare per year. Treatments N2 and N3 were discontinued in 1989 and 1992, respectively, while N1 is still in progress. The results show that tree growth was initially clearly nitrogen-limited. When this changed following a long-term input of nitrogen, a marked increase in growth was also achieved by the additions of phosphorus and potassium (Tamm 1985, 1991). The degree of nitrogen retention in the ecosystem is high (Berggren *et al.* 1998): in treatment N1, virtually all the nitrogen applied has been retained; in N2 plots, around 90% of it (table 4.2). The values for N3 are less certain, but suggest an appreciably lower level of retention (45%). Nitrogen is primarily retained in the soil, and chiefly in the mor horizon, which has become substantially deeper in treatments N1–N3, owing to both increased litter production and reduced decomposition (Berggren *et al.* 1998). In N0 plots, the insignificant amounts of nitrogen being leached consist predominantly of dissolved organic nitrogen compounds. In the N1 plots, which are still being fertilized, leaching of nitrate is clearly elevated, while in the N2 and N3 plots, where treatment has been discontinued, nitrate leaching is low and dissolved organic nitrogen compounds are once again the dominant form of nitrogen in the soil solution. In the analysis of the Stråsan experiment, an attempt has been made (Berggren *et al.* 1998) to use a biogeochemical model which is designed to calculate maximum theoretical rates of nitrogen turnover in forest ecosystems (Aber *et al.* 1997). Applying this model, the measured net turnover of nitrogen in N1 has been found to be 90% of the maximum possible. This would suggest that, if inputs to the N1 plots continue, more nitrogen will probably soon start to leach from the ecosystem.

Norrliden. Another nitrogen fertilization experiment that has been studied intensively is located in a Scots pine forest at Norrliden in Västerbotten (northern Sweden). Here, nitrogen was applied in the same four doses as at Stråsan (N0, N1, N2 and N3, involving 0, 36, 73 and 108 kg of nitrogen per hectare per year) every year between 1971 and 1990 (cf. table 4.2). The N1 and N2 treatments were resumed in 1992. Retention of the added nitrogen in the trees and in the soil down to 20 cm below the surface of the mineral soil (Tamm *et al.* 1995) was found to be considerably lower than in the Stråsan experiment (table 4.2), and in no case did the increase in the ecosystem nitrogen pool compared with the control plots exceed 600 kg per hectare. The highest dose of nitrogen, N3, quite clearly led rapidly to nitrogen saturation (in the sense that further nitrogen inputs did not increase tree growth), whereas this took appreciably longer in the N2 treatment (Tamm 1991, Tamm *et al.* 1995).

Data on nitrogen-15 retention from a study performed in 1993–94 show that nitrogen applied to the control (N0) remained in the uppermost layer of the soil, the mor horizon, whereas nitrogen added to already fertilized plots was transported down through the soil profile (Johannisson *et al.* 1999). When only the ammonium in the ammonium nitrate applied was labelled with nitrogen-15, the amounts of nitrogen-15 nitrate found in soil water at a depth of 20 cm were small in treatments N0 and N1, compared with N2. This suggests that long-term deposition of more than 30 kg of nitrogen per hectare per year is needed to bring about significant levels of nitrification and nitrate leaching at this site. These results tally well with observations of the variation in nitrogen retention in the mor horizon along deposition gradients in Europe (Tietema *et al.* 1998a).

Another interesting result found both at Stråsan and Norrliden and in an experiment at Mangskog, Värmland (western central Sweden), is that roughly the same total retention of added nitrogen can be observed at any given site, regardless of the quantity of nitrogen applied (Berggren *et al.* 1998, Tamm *et al.* 1995, Nohrstedt *et al.* 2000). Unlike the situation at Stråsan, however, at Norrliden applications of phosphorus and potassium did not increase forest productivity on nitrogen-fertilized plots. Nevertheless, there is a tendency towards increased retention of nitrogen in the soil in the phosphorus/potassium treatments at Norrliden, probably owing to greater accumulation of organic matter, due in turn to reduced decomposition (T. Persson and M. Sjöberg, unpublished; P. Högberg, C. Johannisson and A. Ekblad, unpublished).

TABLE 4.2. Nitrogen retention in trees and soil down to 20 cm below the mineral soil surface in plots subjected to nitrogen treatments N1–N3 in the experiments at Stråsan (Norway spruce) and Norrliden (Scots pine), expressed as the increase in the quantity of nitrogen (kg/ha) compared with the control N0, and as a percentage of the nitrogen applied (Stråsan: Berggren *et al.* 1998; Norrliden: Tamm *et al.* 1995).

SITE AND TREATMENT	NITROGEN APPLIED	NITROGEN RETAINED	
Stråsan	**kg N/ha**	**kg N/ha**	**% of amount applied**
N1	1060	1124	100
N2	1760	1584	90
N3	2820	1279	45
Norrliden			
N1	660	430	65
N2	1320	568	43
N3	1980	574	29

Nitrogen, acidification and leaching of metals

Nitrogen not only has a fertilizing effect, but can also give rise to acidification. Atmospheric deposition of nitrogen acidifies forest soils as a result of three processes. First, the uptake of ammonium by roots and/or micro-organisms. Second, the conversion of ammonium to nitrate – if this nitrate is leached from the soil, the acidifying effect is greater than if it is taken up by plants or micro-organisms. And third, increased forest productivity and an associated increase in the uptake of base cations, which is balanced by the release of protons.

On the basis of fluxes of protons, ammonium, nitrate and sulphate into and out of the ecosystem, it is possible to estimate the 'proton loading' to a soil (see for example Bergkvist & Folkeson 1995). In calculating the contribution of nitrogen to this loading, the processes listed above are taken into account. It can be shown that, if inputs of ammonium and nitrate from deposition are roughly equal and nitrogen leaching from the ecosystem is low, the acidifying effect of the nitrogen added is fairly small compared with that of strong acids (chiefly sulphuric acid). If the ecosystem begins to leach nitrate at a rate exceeding that of deposition, nitrogen's contribution to soil acidification increases appreciably. The acidifying effect of nitrogen is thus closely linked to the scale of leaching of this element.

Accelerated acidification of a forest soil increases the risk of leaching of certain toxic metals, such as aluminium and cadmium.

• ALUMINIUM

At the end of the 1970s, researchers discovered that large quantities of aluminium were being leached from forest soils in the north-eastern United States (Cronan & Schofield 1979) and western Germany (Ulrich *et al.* 1979). It soon became clear that this leaching was due to the deposition of strong acids in rain and snow. The solubility of aluminium is highly dependent on pH, increasing markedly when the pH of the soil solution falls below 4.5 (figure 4.6). Forest soils with a pH of less than 4.5 are common in Denmark, the Netherlands and Germany, for example, but also in southern and south-west Sweden (Westling *et al.* 1992). While it is still unclear to what extent high soil solution concentrations of aluminiumions (Al^{3+}) adversely affect forest growth and vigour, it has been established that runoff with high concentrations of these ions causes serious biological damage to streams and lakes.

Dissolving of solid phases containing aluminium (the most important being aluminium hydroxide and organically complexed aluminium) is as a rule the principal buffering mechanism in acidic forest soils (pH < approx. 4.5). If a strong acid, e.g. sulphuric or nitric acid, is added to a sample of mineral soil from such a site, most of the hydrogen ions added will be replaced by aluminium ions from the solid phase, leaving a solution in which the anions of the

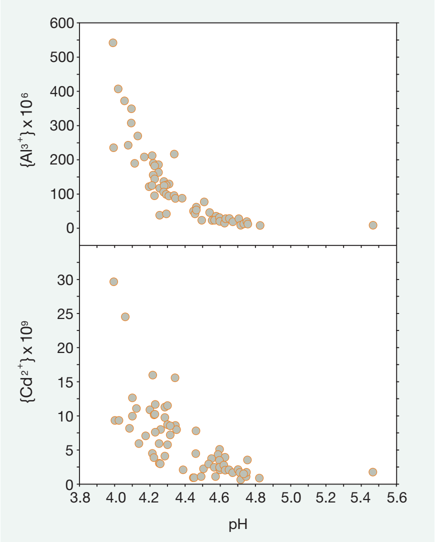

Figure 4.6.
Activity of aluminium (Al^{3+}) and cadmium (Cd^{2+}) ions in soil solutions collected at a depth of 50 cm in neighbouring Norway spruce, beech and birch stands at Rosenlund, north-east Skåne (southern Sweden). Activity is a measure of concentration, in this case roughly equal to the concentration expressed in moles per litre. Data from Berggren 1992.

strong acid are largely balanced by an equivalent quantity of aluminium ions (calculated on a charge basis). This is why there is often a strong correlation between concentrations of aluminium and sulphate, and/or aluminium and nitrate, in areas with leaching of nitrogen.

- **CADMIUM**

A declining soil solution pH is accompanied by increasing solubility, not only of aluminium, but also of the toxic heavy metal cadmium (figure 4.6). High cadmium solubility represents a clear threat to groundwater quality in areas where acidification has taken place. As figure 4.6 shows, aluminium and cadmium are pH-dependent to roughly the same extent, with a critical pH of about 4.5 below which their solubility increases dramatically. This is because, at these low pH values, the solubility of cadmium is linked to that of aluminium. The covariation of cadmium and aluminium ions at low pH is best explained by a 'simple' exchange of cations (Berggren 1992), i.e. electrostatically bound cadmium ions are replaced with aluminium ions from the soil solution.

Since nitrogen deposition is still high in the south and south-west of Sweden, the proportion of forest land with leaching of nitrate may be expected to increase. If this proves to be the case, nitrogen will assume greater significance in soil acidification, too, and hence in the leaching of metals – particularly given the fact that sulphur deposition is currently declining.

CONCLUSIONS

The dynamics of nitrogen in forest soils are controlled to a large degree by biological processes, with organisms linking the interacting cycles of nitrogen and carbon. If in the long term nitrogen deposition exceeds the biological demand of the ecosystem and its ability to bind nitrogen, primarily to humus, by means of biological and chemical reactions, the excess nitrogen will be lost by leaching or denitrification. The approximate quantitative relationships between deposition and leaching of nitrogen are relatively well known. Because of the high level of nitrogen deposition, particularly in south-west Sweden, nitrogen is accumulating in forests, and at some sites elevated leaching of nitrate can be observed. However, nitrogen saturation, in the sense that leaching of nitrogen is of the same magnitude as deposition, is probably only present at a small number of sites in the south-west of the country. If inputs of nitrogen continue, leaching of nitrate will increase. Because autotrophic nitrification is stimulated by elevated pH, and given the generally low capacity to immobilize nitrogen (low C/N ratios), there is a risk that, in south-west Sweden, liming will result in increased leaching of nitrate. We have a relatively good body of knowledge concerning the capacity of forest ecosystems to retain nitrogen, but the full picture regarding the mechanisms of long-term immobilization of this element in forest soils has yet to emerge. Above all, we lack a sufficient understanding of to what extent immobilized nitrogen is bound to very stable compounds, and we are therefore unable to predict with any accuracy how soil systems will respond to a continuing high level of nitrogen deposition, combined with disturbances such as certain forestry practices and soil liming. In addition, there is a need for models of the interactions between different groups of organisms, and of the effects of such interactions on the nitrogen dynamics of forest soils.

QUESTIONS AND ANSWERS

Is atmospheric deposition of nitrogen compounds having acidifying effects on forest soils in Sweden?

Yes. Deposition of ammonium acidifies forest soils in three ways: (1) release of protons (hydrogen ions) when ammonium is taken up by roots and/or micro-organisms; (2) production of protons when ammonium is nitrified to nitrate; and (3) increased uptake of base cations from the soil when forest productivity is boosted by increased availability of nitrogen. Acidification due to inputs of nitrogen has been documented in the experiments at Norrliden and Stråsan, where additions of ammonium nitrate have lowered the pH of the illuvial horizon by 1–1.5 units. At Norrliden, the pH reduction was in fact greater with ammonium nitrate (1760 kg of nitrogen per hectare) than with the highest dose of acid (Acid 3 = 18 kg of protons per hectare) in a parallel experiment.

Are large amounts of nitrogen leaching from Swedish forest soils?

No. In southern Sweden, leaching of nitrogen from forest soils generally amounts to less than 2 kg per hectare per year, compared with nitrogen deposition, which mostly varies between 8 kg and 20 kg per hectare per year. At a few sites, however, larger quantities of nitrogen are being leached.

How large a proportion of acidification can be ascribed to nitrogen?

This question is difficult to answer, since the breakdown of trees' nitrogen uptake between ammonium, ni-

→

trate and organic nitrogen sources is important. As a general rule, however, nitrogen begins to contribute to soil acidification when nitrate starts to leach from the soil system; the higher the level of leaching, the greater the contribution. At a few sites in southern Sweden, nitrogen thus makes a significant contribution to acidification of the soil. At Maglehem in western Skåne, for instance, nitrogen was found to account for around two-thirds of the proton loading to the soil (Bergkvist & Folkeson 1992). In areas with extremely high deposition of ammonium, above all around agricultural areas in the Netherlands, nitrogen deposition is responsible for most of the soil acidification occurring.

Does aluminium leaching increase with leaching of nitrogen?

Yes, in soils where base cation pools have been depleted there is a general link between the concentrations of dissolved inorganic aluminium and nitrate in the soil solution. This is because the hydrogen ions that are generated in particular by nitrification are mainly buffered by the dissolution of solid phases containing aluminium (e.g. aluminium hydroxide). It is well documented that losses of aluminium from nitrogen-rich forest soils co-vary with losses of nitrate.

Can the effects of excessive nitrogen deposition be counteracted by soil treatment and other measures in the field?

Yes, but only to a limited extent. It depends above all on what effects one wishes to remedy. If the problem is seen as leaching of nitrogen, the total pool of nitrogen can be reduced in conjunction with felling by also removing the green parts of the trees. However, this also removes a large proportion of the base cations which the trees have assimilated. In chapter 8 it will be shown that a very effective way of reducing nitrogen leaching is to reduce deposition. The acidifying effects of nitrogen can be diminished by applying lime or ash, but if this stimulates nitrification, the intended alkalinization is counteracted. As for nitrogen's effects on flora and fauna, there are no 'quick fixes' at present.

Does the rate of carbon accumulation in forest soils depend on nitrogen deposition?

Yes, increased nitrogen deposition means increased growth and hence increased accumulation (sequestration) of carbon in growing biomass and humus. Furthermore, binding of nitrogen to humus appears to result in slower decomposition of organic carbon.

Is it possible to design a strategy for an 'optimum' level of nitrogen deposition, i.e. one that will increase sequestration of carbon without having serious adverse effects on ecosystems?

No. Theoretically this is possible, but sources and dispersion of nitrogen compounds cannot be fine-tuned to ensure an optimal dose over large areas. Sweden's popular berry-producing dwarf shrubs are adapted to low nitrogen availability, and an increased supply of this nutrient would be highly unfavourable to them in the long term.

Will reduced deposition of nitrogen result in less carbon being sequestered in forests and forest soils?

Yes, probably. At the same time it must be realized that, in the long term, increased sequestration as a result of nitrogen inputs will have only marginal effects on the atmospheric concentration of carbon dioxide. After all, the latter has risen despite a doubling of nitrogen inputs to the earth's ecosystems in the last hundred years, and this is not only because nitrogen has been supplied to systems already saturated with this nutrient. In addition, the detrimental effects of nitrogen deposition must naturally be taken into account (see the answer above, for example).

HOW ARE FOREST TREES AFFECTED?

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MAARIT KYTÖ AND CHRISTER BJÖRKMAN

Atmospheric deposition of nitrogen quite clearly affects forest ecosystems in many different ways. Since trees are the most important primary producers in these ecosystems, how they are affected by deposited nitrogen will crucially determine what changes occur in many other parts of the systems. In the debate about the causes of the forest decline that has been observed, above all on the continent of Europe, the problem of nitrogen has attracted increasing attention. Several authors have highlighted the rise in nitrogen deposition as a likely cause of this decline (Nihlgård 1985, Van Dijk & Roelofs 1988, Aber *et al.* 1989). In certain circumstances, a more abundant supply of nitrogen can induce deficiencies of other nutrients, such as potassium and magnesium (e.g. Schulze *et al.* 1989), and it has been suggested that deficiencies of these or other mineral nutrients may affect trees and make them more susceptible to stresses of different types, both abiotic and biotic. Alongside these reports of nitrogen deposition having adverse effects, there is also evidence of increasing forest growth across large areas of Europe, including Scandinavia (see below). A number of studies have ascribed some of this increase to nitrogen deposition, while others have indicated that forests are also growing more rapidly in areas not exposed to significant amounts of deposition. In the Skogaby experiment, a major investigation of a young Norway spruce stand in an area with one of the highest pollutant levels in Sweden, it has been shown that a stand exposed to high deposition of nitrogen over a period of many years nevertheless responds with a very marked increase in growth when large doses of nitrogen and sulphur are applied, doses corresponding to several decades of deposition (figure 5.1; Nilsson & Wiklund 1992). The results of this and similar experiments indicate that nitrogen saturation – in the sense that inputs of nitrogen produce no additional growth – is not common in coniferous forests in Sweden. However, the Skogaby study, like many other experiments involving applications of nitrogen, has shown that the structure and functioning of the forest ecosystem change very substantially in response to such treatments. Clear effects of nitrogen include changes in growth patterns, nutrient composition and nutrient fluxes.

The Skogaby experiment in south-west Sweden has been set up in a young Norway spruce forest with sparse undergrowth (mostly forest bryophytes). This photograph, taken in May 1997, shows the tubing and sprinklers used to apply a nutrient solution in one of the seven experimental treatments. Photo: Tryggve Persson.

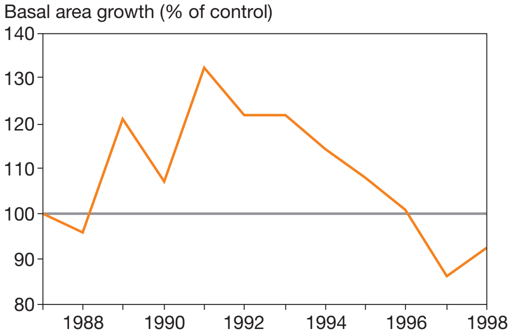


Figure 5.1.
Basal area growth of Norway spruce (*Picea abies*) in the NS treatment (100 kg N and S per hectare per year, applied as ammonium sulphate) in the Skogaby experiment, compared with the control (no N or S added) (L.-O. Nilsson, unpublished).

Nitrogen and forest decline

In the early 1980s, it was widely feared that the forest damage recorded on the continent of Europe, in the form of pronounced thinning of tree crowns, would spread across large areas of Sweden. However, studies of crown thinning in the framework of Sweden's National Forest Inventory have shown that the distribution of damage of this type across the country does not match that of air pollutant loads. On the contrary, the stands with the most severe crown thinning have been found in the least polluted regions. In an attempt to establish the causes of the forest decline observed in Sweden, Hägermark (1995) showed that stand age was the variable that best explained the variation in crown thinning: quite simply, older trees had thinner crowns than younger ones. A repeat analysis of the same data indicated fundamentally the same relationship between thinning and stand age, but at the same time it was emphasized that the explanatory power of each of the individual parameters considered was low and that it therefore could not be ruled out that other factors also had an impact on crown thinning (Rosengren-Brinck *et al.* 1998).

These studies, then, show that the crown thinning occurring in Sweden's coniferous forests is not directly linked to the nitrogen deposition now affecting southern parts of the country. At the same time, every experiment that includes applications of nitrogen shows that such treatments have major effects on both trees and other vegetation. These effects range from changes in plant biochemistry to altered patterns of growth and biomass allocation. So we know that inputs of nitrogen cause changes in forest trees, but that these changes do not directly give rise to visible damage. However, we cannot say for certain how such changes will affect the long-term survival and growth of trees. In this chapter, therefore, we have chosen to describe the changes that arise in conjunction with simulated (or real) nitrogen deposition, with a view to assessing their possible consequences for forests. The chapter is primarily concerned with the coniferous species Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), which are very common in Sweden, and most of the references cited relate to studies of these species. However, many of the changes caused by nitrogen, both chemical and structural, differ to only a small degree between coniferous and broad-leaved trees, and the discussion should therefore be partly applicable to the latter group as well.

Physiological changes

• Rate of nitrogen uptake by roots decreases

An increased supply of nitrogen normally results in trees taking up larger amounts of this nutrient. However, studies of experimental plots receiving different applications of nitrogen, and of sites exposed to varying loads of nitrogen deposition, show unequivocally that the *instantaneous* nitrogen uptake rate of tree roots – their ability to absorb nitrogen under *standardized* conditions – decreases when nitrogen availability increases (figure 5.2; Jones *et al.* 1994, Clemedsson-Lindell 1997, Rosengren-Brinck 1999, Quist *et al.* 1999). Tests on roots dipped in a solution containing labelled nitrogen show that roots from nitrogen-fertilized trees absorb less nitrogen than those from trees that have not received large amounts of this nutrient. The fact that trees usually increase their uptake of nitrogen, despite this decrease in the uptake rate, is probably attributable to increased soil concentrations of different nitrogen compounds. The reduced level of root activity in terms of nitrogen uptake enables the trees to avoid taking up excessive amounts of this element in relation to what they require for growth. It also means that the trees, as consumers of nitrogen, will not as effectively deplete the pools of inorganic nitrogen formed in the soil or added by deposition. In acidic forest soils, an important inorganic form of nitrogen is the ammonium ion. Reduced uptake of ammonium by trees can result in increasing concentrations of this ion in the soil solution, an important prerequisite for the activity of nitrifying bacteria. Nitrification, the process by which ammonium ions are converted to nitrate via nitrite, is also a key process with regard to both acidification of and leaching of nitrogen from forest soils. Its importance in the latter regard has to do with the fact that nitrate ions are the form of nitrogen most easily leached from forest soils by the water passing through them (see chapter 4). When nitrogen is in plentiful supply, rates of uptake of both nitrate and ammonium decline. What is more, at intermediate to high concentrations of ammonium, direct inhibition of nitrate uptake occurs in many plants. This has been noted in Norway spruce, for example (see e.g. Marschner 1991). However, there is some uncertainty as to whether this phenomenon really does manifest itself in field conditions, and in certain cases measurements have indicated that some uptake of nitrate does occur, despite very high ammonium concentrations in the soil solution (Högberg *et al.* 1998).

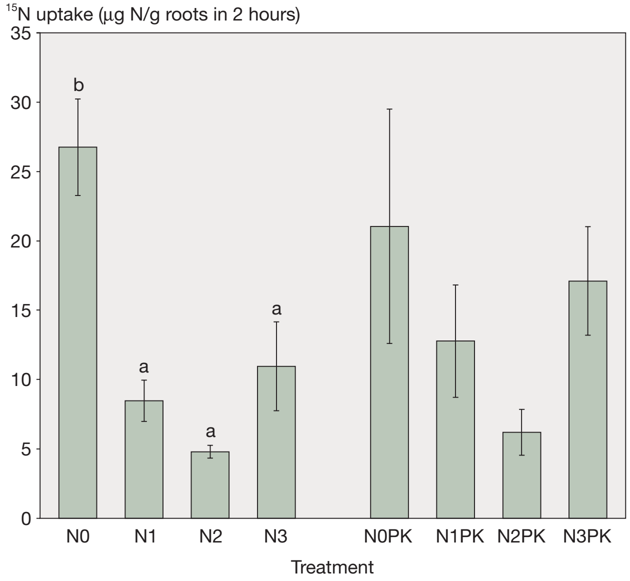


Figure 5.2. Instantaneous nitrogen uptake rate of Scots pine roots. Treatments: N0 = control, N1 = 30 kg N/ha/yr, N2 = 60 kg N/ha/yr, N3 = 90 kg N/ha/yr (but treatment ended eight years before sampling). The N0PK, N1PK, N2PK and N3PK treatments involved the same additions of nitrogen, combined with phosphorus (P) and potassium (K). Data from the Norrliden experiment (Quist *et al.* 1999). Different letters above bars indicate significant differences between treatments.

An increased supply of nitrogen, then, will probably lead to a decrease in the uptake of this nutrient by forest trees (i.e. in the instantaneous uptake rate) (see chapter 4). As a result, more nitrogen will be available in the soil system, creating a risk of increased leaching. The low uptake thus does not directly harm the trees themselves, but it could increase leaching of nitrogen, an effect which is of course detrimental both to forest soils and to surface and ground waters.

• Nitrogen concentrations in some plant parts increase

Despite the reduction in the rate of root uptake discussed above, additions of nitrogen, whether from deposition or fertilization, usually nevertheless result in an increased overall uptake of this nutrient by trees. Most of the inorganic nitrogen taken up by the roots is also assimilated into organic compounds in below-ground parts of the tree. When nitrogen becomes more readily available in the soil, concentrations of organic nitrogen compounds in the conducting tissues of the tree will increase (figure 5.3).

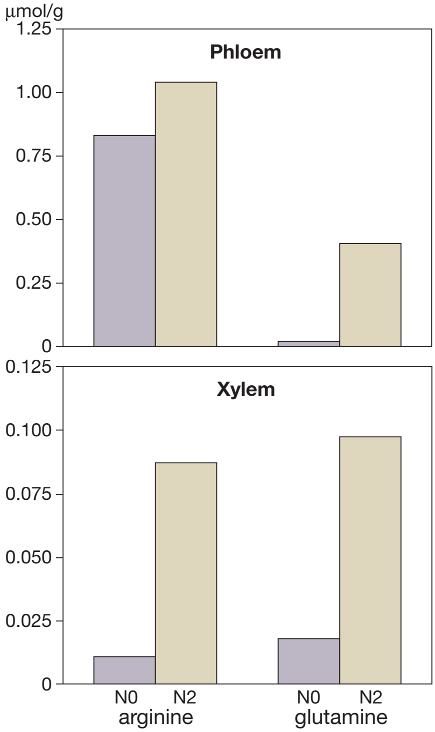


Figure 5.3.
Concentrations of the amino acids arginine and glutamine in the xylem and phloem of fertilized and non-fertilized trees in the Norrliden experiment. N0 = control; N2 = 60 kg N/ha/yr. N = 3. (Nordin *et al.*, in preparation.)

This increase can be observed in both the xylem and the phloem (Nordin *et al.*, in preparation), and results in enhanced transport of nitrogen to needles and leaves, as well as a higher turnover of nitrogen in the tree. Increased nitrogen transport can in turn make the tree more prone to attack by certain sap-sucking insects, such as aphids, as will be discussed in more detail below.

The increased transport of nitrogen also results in higher nitrogen concentrations in leaves/needles, due initially to accelerated synthesis of proteins, above all ‘soluble’ proteins (Näsholm & Ericsson 1990). Furthermore, the higher level of protein synthesis enables several of the vital functions of the tree, including photosynthesis, to operate at a higher rate. There is in other words a clear link between needle concentrations of nitrogen and the rate of photosynthesis (e.g. Strand 1997, Lambers *et al.* 1998). In many ways, the higher nitrogen concentrations that are associated with increased concentrations of proteins appear to be beneficial to the tree. At a certain level, however, the supply of nitrogen will exceed the maximum amount which the tree can utilize for growth. Any additional amounts taken up beyond that limit will consequently not be used for active growth, and may be regarded as excess nitrogen. Several studies have shown that this surplus is accumulated in needles in the form of the free amino acid arginine (Aronsson 1985, Näsholm & Ericsson 1990, Näsholm 1994, Pérez-Soba & de Visser 1994). Unlike increased protein concentrations, elevated concentrations of arginine do not appear to be associated with enhanced growth. On the contrary, certain studies suggest that high levels of this amino acid in coniferous trees can have an adverse effect. Lambert (1986), for example, observed increased attacks by parasitic fungi on trees with high arginine concentrations.

Forest trees can be exposed to two forms of nitrogen excess. An *absolute* excess of nitrogen means that there is more nitrogen than the tree is able to utilize at its maximum growth rate. A *relative* excess occurs when there is a deficiency of some other mineral nutrient, with the result that a surplus of nitrogen exists in relation to that nutrient. Whichever form is involved, it appears that a nitrogen excess always gives rise to increased arginine levels in conifers.

As well as causing the changes in nitrogen compounds described above, greater availability of nitrogen also affects carbohydrates. In general, there is a negative correlation between carbohydrate concentrations and nitrogen availability, i.e. levels of carbohydrates are lower when nitrogen is more abundant (Ericsson 1979). In the case of coniferous species, however, this relationship is less clear, since conifers only store carbohydrates in the early summer, and not in the autumn and winter as deciduous trees do (Ericsson 1979, Linder 1995). Elevated levels of nitrogen can also lead to lower concentrations of what are termed secondary metabolites: phenols, terpenes and resin acids. These substances are believed to play an important role in plant resistance to both insects and parasitic fungi (see below).

Concentrations of nitrogen in needles are consistently higher in the south of Sweden than in the north (Nohrstedt 1990a, Ericsson *et al.* 1993). This negative correlation between needle nitrogen concentrations and latitude is at the same time a positive correlation between these concentrations, on the one hand, and levels of nitrogen deposition and soil productivity, on the other.

For Sweden as a whole, no analyses of changes in needle nitrogen levels over time have been performed. Needle composition has not been systematically investigated as part of the environmental monitoring programme. However, three sets of data from southern areas of the country provide evidence of temporal changes in nitrogen concentrations in needles. Aronsson (1985), studying a number of sites in Halland, south-west Sweden, found an increase in nitrogen concentrations between the 1960s and the 1980s. Nohrstedt (1993) observed a rise during the 1980s, but not the 1970s, in a number of experiments located in the south of the country. For two different subsets of data, the average increases during the 1980s corresponded to 0.14% and 0.18% per decade. Thelin and co-workers (1998) analysed trends in needle chemistry in 42 coniferous forests in Skåne between 1985 and 1994, but were unable to discern any unequivocal change in nitrogen concentrations over that period. However, they did find a downward trend in the potassium/nitrogen ratio over the period in question. In several central European studies, increases in needle nitrogen concentrations have been found from the 1960s on (references in Hüttl & Schaaf 1995).

• Effects on other nutrients

Inputs of nitrogen affect the nutrient composition of needles. This has been shown both by studies in areas with clear nitrogen deposition gradients (Nohrstedt 1990a, Ericsson *et al.* 1993, 1995) and by fertilization experiments of several types. Where nitrogen is applied to nitrogen-limited stands in order to boost productivity, then of course an initial rise in nitrogen concentrations is one of the aims of the exercise. Following an application of 150 kg of nitrogen per hectare, the concentration of nitrogen in current-year needles has been found to increase by around 25% in the course of a couple of years, compared with control plots (Sikström 1992, Jacobson & Nohrstedt 1993, Nohrstedt *et al.* 1993). In the Skogaby experiment, needle nitrogen levels were considerably elevated after three and five years of treatment with 100 kg of nitrogen per hectare (Nilsson & Wiklund 1994, Rosengren-Brinck & Nihlgård 1995). The increase amounted to 25–100%, compared with controls, and was most pronounced in older age classes of needles (Rosengren-Brinck & Nihlgård 1995). Similar concentration increases were found in the experiment at Farabol (Andersson *et al.* 1994) and the 'optimum nutrition' experiments (Tamm 1991).

If the input of nitrogen declines, there will usually also be a relatively rapid decrease in needle concentrations of this nutrient. This has been demonstrated both in the Swedish experiments at Norrliden (see chapter 8; Quist *et al.* 1999) and Stråsan (Andersson 1997), a few years after programmes of annual fertilization had been completed, and in experiments in the Netherlands, in which deposition was excluded by roofs (Boxman *et al.* 1998b). In the Lisselbo experiment in Sweden, needle nitrogen levels fell fairly quickly, but were still relatively high several years after nitrogen fertilization had ended (Edfast *et al.* 1996).

Additions of nitrogen also affect needle concentrations of other nutrients. In one study, in which nitrogen was applied several times at a dose of about 150 kg per hectare per application, the only other macronutrient that appeared to be affected a couple of years later was magnesium, concentrations of which had fallen by an average of around 10% (Jacobson & Nohrstedt 1993). At Skogaby, annual additions of 100 kg of nitrogen per hectare in the form of ammonium sulphate did not, over the following three or five years, give rise to any statistically significant changes in needle concentrations of other macronutrients than nitrogen, apart from a rise in levels of sulphur, which was added with the fertilizer (Nilsson & Wiklund 1995a, Rosengren-Brinck & Nihlgård 1995). Similarly, in the Farabol experiment, few effects of nitrogen inputs on other macronutrients were observed (Andersson *et al.* 1994).

Of the micronutrients, several show reduced levels after repeated applications of nitrogen (Jacobson & Nohrstedt 1993). In the case of manganese, zinc and copper, needle concentrations are 20–30% lower after repeated fertilization at the intervals normal in forestry practice. However, the concentrations of manganese and zinc are above the proposed limit values for nutrient deficiency (Braekke 1994). Nitrogen fertilization can give rise to a deficiency of boron (Aronsson 1984, Möller 1984). This is particularly true in inland areas of northern Sweden, where, owing to low atmospheric deposition of marine salts, little boron is available in the soil.

Since additions of nitrogen result in higher concentrations of that element, while those of the other macronutrients are unaffected or decrease, the ratios of other macronutrients to nitrogen will fall (Aronsson 1984, Jacobson & Nohrstedt 1993, Rosengren-Brinck & Nihlgård 1995). Following repeated nitrogen applications, the ratios of phosphorus and potassium to nitrogen are often below the values that indicate an optimum nutrient composition (cf. Braekke 1994). In areas with heavy deposition of nitrogen (The Netherlands, Germany), the construction of roofs to reduce nitrogen inputs resulted in higher ratios of potassium and magnesium to nitrogen (Boxman *et al.* 1998b, Bredemeier *et al.* 1998a). The increased potassium/nitrogen ratio, however, does not necessarily indicate that the trees were suffering a potassium deficiency before the experiments began, since it could also be due to a reduced needle concentration of nitrogen.

Effects on growth

• Additional nitrogen favours above-ground growth

During the first year after nitrogen has been applied to a forest stand, growth in both tree crowns and the radius and height of stems begins to increase. A slight upward shift in crown growth can be observed in fertilized trees, compared with unfertilized ones, and, as regards the above-ground biomass as a whole, a greater proportion of growth occurs in branches (Valinger 1990, Nilsson & Wiklund 1992). A few years after the onset of fertilization, trees allocate relatively more growth to their needles, but subsequently the relative allocation to needles tends to decrease, while the allocation to the stem increases (Axelsson 1985, Valinger 1990, Nilsson & Wiklund 1992). The height on the stem at which the stem growth increase occurs varies, and can probably be affected by both tree species and age (Friberg 1974, Tuimala 1989, Valinger 1990).

In one field experiment involving annual fertilizer applications, Axelsson (1985) found that growth of coarse roots increased somewhat in fertilized trees, compared with trees that were not fertilized. At the same time, though, their biomass decreased in relation to the above-ground biomass. Production and biomass of fine roots generally tend to be unaffected by nitrogen inputs, although results vary considerably (Persson & Ahlström 1990, Andersson *et al.* 1994, Majdi & Persson 1995, Majdi & Kangas 1997). In the Skogaby experiment, two years of fertilization with ammonium sulphate (100 kg N/ha) are reported to have resulted in a redistribution of roots in the soil profile, with a larger proportion of roots in the litter and mor horizons than was the case in the control plots (Persson 1994, Persson *et al.* 1994). If this is a widespread effect of additions of nitrogen, it could render trees more sensitive to drought (see below).

• Forest growth often increases

Several studies point to an increase in forest growth in the course of the 20th century, both in Sweden and in Europe generally (Spiecker *et al.* 1996), and atmospheric deposition of inorganic nitrogen may be a contributory factor (cf. Cannell *et al.* 1998). Such an increase in growth is to be expected in a situation where nitrogen is a growth-limiting factor, as is the case for the majority of forest land in Sweden (cf. Nohrstedt 1993).

Numerous field experiments in the Nordic countries have shown that additions of inorganic nitrogen often boost forest growth (Sikström & Nohrstedt 1995). This effect has mainly been noted on mineral soil sites, since peatland sites are generally deficient in other nutrients than nitrogen, primarily phosphorus and potassium (Clymo 1983). Sometimes, however, an added effect is obtained on peatlands if nitrogen is applied together with these nutrients (Almqvist 1989).

On mineral soils, the relative increase in growth following an application of nitrogen depends on the fertility of the site, with the largest relative response occurring on poor soils and the smallest on nutrient-rich soils (Mälkönen *et al.* 1990, Pettersson 1994a). The average relative increase in growth achieved over a five-year period following a single application of 140–150 kg of nitrogen per hectare (a normal dose in forestry) is of the order of 20–50% (Pettersson 1994b). This corresponds to an additional roughly 10 cubic metres of stem wood with bark per hectare, a value that is relatively independent of geographical location in Sweden. Much larger growth increases, in both relative and absolute terms, are often, but not always, obtained with annual applications of nitrogen (Tamm 1985, 1991, Nilsson & Wiklund 1992, Linder & Bergh 1996).

• Growth response sometimes absent on fertile sites

Although in the Nordic countries nitrogen fertilization frequently results in enhanced forest growth on mineral soil sites, this is not always the case. In several experiments conducted in Norway spruce stands on relatively fertile soils, no increase in growth was obtained (Mälkönen *et al.* 1990, Sikström & Nohrstedt 1995, Persson *et al.* 1994). As a rule, the stands concerned have a relatively high site index: around 30 or higher for Norway spruce (i.e. trees of this species are expected to reach a height of 30 m or more at the age of 100 years). On fertile land, however, there have also been experiments in which growth did increase after applications of nitrogen (Sikström & Nohrstedt 1995). What stand or site properties determine whether or not an increase in growth occurs is still unclear.

• Adverse effects on growth?

There are few clear instances of additions of nitrogen resulting in reduced growth or evident damage. When applied research into forest fertilization began to gather momentum in the mid-1960s, one of the first concerns was to determine suitable fertilizer doses, and as a rule 600 kg of nitrogen per hectare was the largest single dose that was tested. At this high dose, favourable effects on growth were generally obtained, and no damage was observed. However, in a supplementary study it was found that a single dose of 840 kg of nitrogen per hectare caused considerable damage and killed a number of trees (Möller 1984). From Germany and Britain it has been reported that not even one-off applications of 1 tonne per hectare, and occasionally even higher doses, have produced damage symptoms or adverse effects on growth (Kenk & Fischer 1988, Miller & Miller 1988).

In one study, though, even a relatively low input of nitrogen led to reduced forest growth (Nys 1990, Bonneau *et al.* 1990). The site in question was a spruce stand with marked crown thinning and low needle concentrations of calcium and magnesium, situated in the French Ardennes, where nitrogen deposition was around 30 kg per hectare per year. Over a period of roughly 10 years following two applications of 100 kg of nitrogen per hectare, basal area growth decreased by more than 10%. As a result of the extra nitrogen, the already low levels of calcium and magnesium fell still further and crown thinning became more pronounced. In the experiment at Skogaby, after some 10 years of annual applications of 100 kg of nitrogen per hectare, forest growth has fallen below the level of the control, having previously been some 30% above that level (L.-O. Nilsson, Swedish University of Agricultural Sciences, personal communication; figure 5.1). The reason for this decline has not been established.

In experiments on the continent, in which inputs of nitrogen and other air pollutants have been substantially reduced by building roofs and irrigating the soil with water with a more natural composition, increases in growth have been observed (Boxman *et al.* 1998b, Bredemeier *et al.* 1998a). One of several possible explanations for this is that nitrogen deposition had previously had an adverse effect on the growth of these forests and that this adverse effect was alleviated by the deposition reduction resulting from the construction of the roofs. In the first of the studies referred to, involving a Scots pine stand in the Netherlands, the increase in growth was linked to a higher potassium/nitrogen ratio in needles.

• NITROGEN STATUS OF TREES IMPORTANT

The ability of a forest soil to supply nitrogen in a plant-available form and the internal nitrogen status of the trees growing there probably make a decisive difference to whether the trees can utilize even more nitrogen in the event of a higher input. The soil's ability to supply nitrogen is difficult to estimate. The internal nitrogen status of the trees, on the other hand, can be described relatively simply, by sampling and analysing needles or leaves. Usually, needles are sampled in winter, when nutrient levels are stable in relation to dry weight. An analysis by Sikström and co-workers (1998) showed that, in middle-aged stands, nitrogen concentrations in current-year needles from non-fertilized control plots were of some predictive value for estimating the relative growth increase that would occur following applications of nitrogen (figure 5.4). The relative increase in growth fell with increasing nitrogen concentrations, and the study suggested a threshold concentration of 15–16 milligrams per gram, above which an enhancement of growth seemed unlikely. Roughly the same concentration has proved to be the one at which stable maximum growth can be maintained (Tamm *et al.* 1995), provided that water and other nutrients are available in excess. Linder (1995) used somewhat higher 'target concentrations' of nitrogen, 18–20 mg/g, with a view to achieving optimum growth.

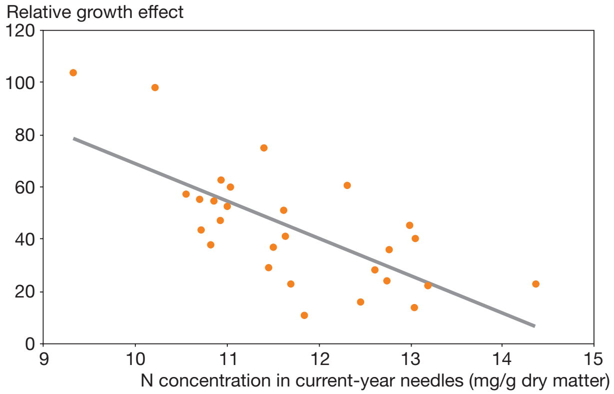


Figure 5.4. Relationship between nitrogen concentrations in current-year needles and relative growth effect (over a five-year period). Data have been obtained from some of the nitrogen fertilization experiments carried out in Swedish Scots pine stands by the Forestry Research Institute of Sweden. The nitrogen concentrations shown are means for control plots, while growth effect values are means for all fertilized plots within each experimental site (after Sikström *et al.* 1998).

• DEVELOPMENT OF GROWTH RESPONSE OVER TIME

Since nitrogen accumulates in the soil on most conventionally managed forest land (see chapter 4; Nohrstedt 1993, Egnell *et al.* 1998), the increase in growth achieved by fertilization could possibly be expected to diminish over time. Such an effect would be expected to be most marked in southern Sweden, where the highest levels of nitrogen deposition and accumulation are found. However, Pettersson (1994a), in an analysis of experimental data from three decades (1960s, 1970s and 1980s), found no clear temporal trend in growth responses following additions of nitrogen, even in the data for the south of the country.

The fact that trees' needle concentrations of nitrogen appear to have risen over time, together with the earlier mentioned negative correlation between those concentrations and the relative increase in growth, should in theory imply that the growth effect of nitrogen inputs declines with the passing of time. Analysed using the regression equations presented by Sikström and co-workers (1998), the increase in needle nitrogen levels found by Nohrstedt (1993) would appear to suggest a decrease in the effect on growth of some 10–20% per decade. However, this does not appear to have happened. How can these clearly contradictory results be explained?

Pettersson's (1994a) study suggests that the increase in growth achieved is relatively constant across different degrees of soil fertility, up to a point at which no further increase is obtained. Thus, the growth response as such provides no information as to how close to nitrogen saturation a given stand is. Only a small proportion of Sweden's forested mineral soil sites have an excess of nitrogen in the sense discussed here (Nohrstedt 1993). It is therefore probably very difficult to discover by means of fertilization experiments whether the area of nitrogen-saturated stands has increased over time.

In both the analyses referred to (Pettersson 1994a, Sikström *et al.* 1998), generally less than 50% of the variation observed is accounted for. This naturally makes it more difficult to establish, on the basis of the results of fertilization experiments, whether nitrogen-related increases in growth have changed in magnitude over time.

From Denmark, which for a long time has had higher levels of nitrogen deposition than Sweden, Dralle and Larsen (1995) have reported that growth responses to nitrogen fertilization decreased considerably between the 1950s/1960s and the 1980s. On the basis of a large body of experimental data relating to Norway spruce plantations in Jylland, they found that the post-fertilization increase in growth declined from some 3–4 to less than 1 cubic metre per hectare per year.

Tools to study the impact of nitrogen on forests

The biochemical changes observed in experiments of various kinds can be used as tools to study how nitrogen deposition is affecting forest trees in different regions. It has for example been found that, in stands where nitrogen is leaching from the soil, needle concentrations of arginine are elevated (Nohrstedt *et al.* 1996, Näsholm *et al.* 1997; figure 5.5). Such stands also show changes in the proportions of the stable isotopes ^{14}N and ^{15}N present, as well as elevated total nitrogen concentrations in needles. Unlike biochemical changes, an altered isotopic composition does not affect a tree's vital functions, but it does say something about the processes the tree is exposed to in its environment. In forest fertilization experiments, changes in isotopic composition have shown a strong correlation with leaching of nitrogen from the soil (Högberg 1990, Högberg & Johannisson 1991). Accumulation of arginine in needles and changes in nitrogen isotope composition are indicative of two aspects of a forest stand enriched in nitrogen. An elevated arginine concentration shows that 'luxury' consumption of nitrogen is occurring, i.e. that more nitrogen is available than the trees need for their growth. A higher $^{15}N/^{14}N$ ratio (a higher $\delta^{15}N$ value) in needles indicates that the trees are growing on a soil which could potentially leach nitrogen.

Which of these parameters is (or are) of most diagnostic value in terms of identifying forest stands that are leaching nitrogen is uncertain. In the studies cited, total nitrogen concentration, arginine concentration and $\delta^{15}N$ follow the same pattern, and all of these parameters can therefore be used as diagnostic tools. The advantage of using total nitrogen as an indicator is

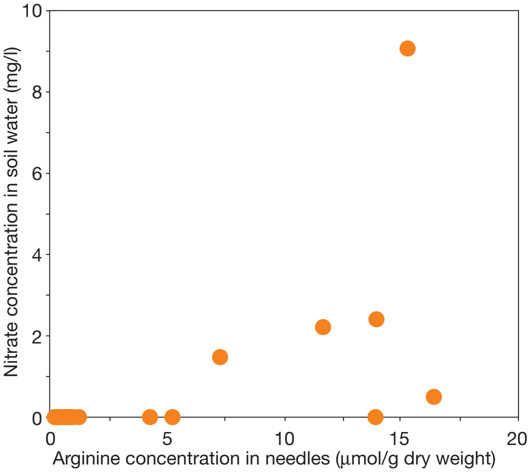


Figure 5.5.
Relationship between nitrate concentrations in soil water and arginine concentrations in current-year needles of Norway spruce. Each point corresponds to one stand. Data from the National Board of Forestry's permanent sample plots in southern Sweden.
After Näsholm *et al.* 1997.

that techniques for determining it are well established in many laboratories. The disadvantage, perhaps, is that the difference in levels of total nitrogen between leaching and non-leaching stands is relatively small. In addition, stands which are deficient in other nutrients than nitrogen (i.e. where there is a relative excess of the latter) could conceivably be leaching nitrogen, but still have relatively low needle concentrations of total nitrogen. Analyses of both arginine and $\delta^{15}N$ require equipment that is less widely available than that needed for total nitrogen analysis. The advantage of using arginine levels to identify nitrogen-enriched stands, though, is that there is a large difference in this variable between such stands and those that are not enriched in nitrogen. For different types of monitoring or inventory work, therefore, it makes sense to employ a combination of these techniques.

The Swedish Environmental Protection Agency's environmental quality criteria for the forest landscape (Naturvårdsverket 1999) propose that the risk of nitrogen leaching should be assessed on the basis of nitrogen deposition, nitrogen and arginine concentrations in current-year needles, and nitrogen concentrations in the soil solution. The risk of leaching is to be considered high if the needle concentration of nitrogen exceeds 15 mg per gram of dry matter and/or the concentration of arginine exceeds 5 µmol per gram of dry matter.

Sensitivity to drought and frost may increase

• Greater risk of drought stress?

When nitrogen availability increases, the appearance of a tree changes and, to begin with at least, growth also shifts towards the crown, as more needles and branches develop. These changes could possibly make trees more sensitive to drought (Lindroth 1987) and storms (Laiho 1989). According to Lindroth (1987), greater drought sensitivity would be expected to manifest itself in increased needle litterfall, among other things. However, no abnormal increase in needle fall or particularly marked temporary reduction in the growth response has been observed in different nitrogen fertilization experiments, not even during years of severe drought (Nohrstedt *et al.* 1993; L.-O. Nilsson, Swedish University of Agricultural Sciences, personal communication).

• Greater frost sensitivity?

The nitrogen status of a tree can affect its frost-hardiness, a question addressed by Skre (1988) in a review of the literature. If needle concentrations of nitrogen are high, frost sensitivity may increase. Frost damage during the growing season may become more common, as a result of budbreak occurring earlier and onset of winter dormancy later when nitrogen is in plentiful supply. In addition, there may be some increase in the incidence of frost injury in the winter months. Low nitrogen levels, too, are believed to entail an increased risk of frost damage. The risk of damage is believed to be lowest at a nitrogen concentration of 13–15 milligrams per gram. Potassium is an important factor in frost-hardiness. However, it appears that not even repeated applications of nitrogen reduce the potassium levels in needles (Jacobson & Nohrstedt 1993, Nilsson & Wiklund 1995a).


Photo: Jan Grahn/N

Incidence of pathogens and pests may increase

• Fungi

Scleroderris canker, a disease caused by the fungus *Gremmeniella abietina*, appears to be promoted by a plentiful nutrient supply (Annila & Kurkela 1989): Scots pines growing on fertile soils are often infected. Nitrogen is probably a key factor, and a higher input of it may therefore increase the incidence of this disease. Finnish researchers report that *Lophodermella sulcigena* needle cast may be favoured if one-sided applications of nitrogen result in a deficiency of trace elements (Annila & Kurkela 1989). It has also been claimed in Finland, though with no research results to support the view, that nitrogen fertilization could lead to a higher incidence of *Heterobasidion annosum* root rot in Norway spruce and Scots pine. On the other hand, an American experimental study of mountain hemlock *(Tsuga mertensiana)* showed that a good supply of nitrogen made the trees more resistant to laminated root rot (Matson & Waring 1984). Measures which enhance tree growth, such as nitrogen fertilization of forests where nitrogen is the limiting factor, are believed to render trees more susceptible to rust diseases, such as resin top of pine (Scots pine blister) (Annila & Kurkela 1989). High nitrogen levels have also been shown to favour infection of conifers by the pathogenic fungus *Sphaeropsis sapinea* (Roelofs *et al.* 1985).

• INSECTS

As has already been noted, increased availability of nitrogen, due to fertilization or atmospheric deposition, results in higher concentrations of nitrogen in coniferous trees, which usually have relatively low levels of this nutrient compared with many other plants. Some insects are specialists with respect to host plants, but generalists with respect to nitrogen, i.e. they can make use of all forms of nitrogen; others are host generalists and nitrogen specialists. Nitrogen generalists are not as sensitive to changes in the nitrogen content of the host plant (Prestidge & McNeill 1983). Most of the insects found on Swedish forest trees specialize in one or just a few tree species, which they feed on regardless of their nutritional quality. However, it is very important to all insect species how nutrient-rich and easily digested their food is, with both quality and quantity determining the effort they have to invest in order to obtain sufficient nutrition. Well-nourished insects produce more offspring, and their offspring develop more rapidly on readily accessible and nutritious food. The shorter an insect's period of development is, the better are its chances of surviving and itself reproducing. However, competition is also of some significance in this context: insects which are weak competitors in other respects can do well if they live on plants or plant parts of 'poor' quality, which most other species are unable to utilize.

Plants not only contain nutrients, but also varying quantities of harmful or even toxic substances which protect them from being consumed by herbivores. In forest trees, especially conifers, the majority of such 'secondary metabolites' are carbon compounds of various kinds, e.g. phenols and terpenes. The higher the levels of these defensive agents in a tree, the better is its resistance to pests (Rhoades 1979). The production of secondary metabolites costs energy and reduces the available quantities of carbohydrates, which trees also need for more basic functions such as respiration and growth. As the word 'secondary' implies, basic metabolism and growth are regarded as primary uses of the products of photosynthesis, secondary metabolites being manufactured from anything that is left over (Waring & Pitman 1985). Several theories have been put forward to explain the relationship between growth and herbivore resistance in plants (see Herms & Mattson 1992). A moderate nitrogen deficiency in a forest soil is assumed to limit growth more than it limits photosynthesis, thereby giving rise to high levels of secondary metabolites. An increased supply of nitrogen boosts growth, which may in turn result in poorer resistance if photosynthesis does not also increase (Herms & Mattson 1992).

In view of how different insect species are in many respects, it would be unreasonable to expect all insects to be affected in the same way by an enhanced supply of nitrogen. One group of insects which almost always seem to be favoured by higher nitrogen levels in plants are the sap-sucking species, above all aphids (Waring & Cobb 1992). The causal factor here may be an elevated concentration of nitrogen, or alternatively a change in amino acid composition (see figure 5.3), since certain amino acids are more necessary to aphids than others. What is more, aphids, which extract fluid from the cells of plant tissues, presumably ingest smaller quantities of secondary metabolites than insects which feed on needles or phloem. Carrow and Betts (1973) showed that different fertilizers produced different responses in trees' amino acid compositions and that sucking adelgids (balsam woolly aphids) were strongly favoured by urea fertilization, while ammonium-nitrogen reduced adelgid numbers compared with control trees. Nitrogen fertilization has been shown to increase not only nitrogen concentrations in plant tissues, but also levels of other necessary substances, such as sugars, lipids and water (Shaw & Little 1972, Baylis & Pierce 1991, McCullough & Kulman 1991). As far as secondary metabolites are concerned, insects are favoured by a reduction of phenol and tannin levels following fertilization (Bryant *et al.* 1987, 1993, Waring & Price 1988).)On the other hand, they are adversely affected by the increased resin fluxes (Oldiges 1959, Mopper & Whitham 1992) and higher concentrations of resin acids and monoterpenes (Björkman *et al.* 1991, McCullough & Kulman 1991) found in fertilized plants. The reason fertilization can raise concentrations of some secondary metabolites, while reducing levels of others, may be that different substances are synthesized and stored in different ways and therefore affected differently by inputs of nitrogen (Björkman *et al.* 1991, 1998).

In laboratory experiments and other controlled situations, nitrogen fertilization has beneficial effects on the majority of insects (Waring & Cobb 1992). In studies of effects at the population level over a long period and under natural conditions, on the other hand, insect damage to forest trees has usually been found to be unaffected or, in certain cases, even to have decreased (Stark 1965, Kytö *et al.* 1996). Where a decrease is observed, it may be partly due to the fact that the total biomass of trees normally increases when more nitrogen becomes available, with the result that an unchanged quantity of damaged needles may look like a reduced level of damage, since the damaged needles then constitute a smaller proportion of the total needle mass (Wickman *et al.* 1992). The reason populations are not favoured in the same way as individuals may be that other ecosystem factors, such as predation and parasitism, overshadow the nutritional effect in fertilized stands (Strauss 1987, Kytö *et al.* 1996). In long-term experiments involving repeated fertilizer applications, no increases in infestation by insects have been found. It therefore seems unlikely that moderate deposition of nitrogen causes large-scale insect damage.

Mycorrhizas change

A mycorrhiza is a symbiosis between a fungus and the roots of a plant, whereby the fungus helps the plant to increase its uptake of mineral nutrients and water and, in return, is supplied with carbohydrates. The fruiting body, i.e. what is commonly referred to as a mushroom or toadstool, constitutes only a small part of the fungus, at most a few per cent of its total weight. The rest consists of micrometre-thin filaments, or hyphae, which can be found on and in the root tips of plants or growing in the soil. In Sweden, around 1000 species of fungi form mycorrhizas with coniferous or deciduous trees. Predominantly mycorrhizal groups include *Amanita*, *Russula*, *Lactarius* (milkcaps), *Cortinarius* and *Inocybe* species and Boletaceae (boletes).

• FEWER MUSHROOMS TO PICK, BUT FUNGI STILL GROWING ON TREE ROOTS

In the late 1980s, there were alarming reports from Dutch and other researchers about a declining abundance of mycorrhizal fruiting bodies. A comparison of inventories of fruiting bodies at the beginning of the century with recent surveys indicated that the number of species of mycorrhizal fungi had decreased dramatically in several areas of central and western Europe. Nitrogen, which is in short supply in forests undisturbed by human activities, was suggested as one reason, since atmospheric deposition of this nutrient had risen sharply since the middle of the century (Arnolds 1991). What is more, several nitrogen fertilization experiments pointed to similar effects on the formation of fruiting bodies (Romell 1938, Wästerlund 1982, Rühling & Tyler 1991, Brandrud 1995). At Skogaby, Wiklund and co-workers (1995) showed that an annual fertilizer dose of 100 kg of nitrogen per hectare resulted in a virtual cessation of fruiting body production within a couple of years of the treatment starting.

Studies by Kårén and Nylund (1996) showed that the *proportion* of roots colonized by mycorrhizas did not decrease in any of the experiments at Skogaby or Norrliden. The latter included an 'N1' treatment, involving applications of an average of 36 kg of nitrogen per hectare per year (Holmen *et al.* 1976), which corresponds to roughly twice the nitrogen deposition recorded in south-west Sweden. Virtually all the fine root tips present (around 25 billion in a 100 x 100 m plot at Skogaby) were colonized by fungi within a short time of being formed. On the other hand, the *number* of mycorrhizal root tips was reduced as a result of the nitrogen treatment, which may partly explain the radical decrease in mycorrhizal fruiting bodies. Another conceivable reason is that fertilization led to changes in the species composition, so that nitrogen-sensitive, fruit body-forming species became less abundant on the roots.

• Nitrogen changes species composition

To investigate in greater detail the effects of nitrogen inputs at Skogaby and Norrliden, a DNA technique was used (Kårén & Nylund 1997, Kårén 1997). A comparison of fungal DNA from mycorrhizal root tips with DNA from fruiting bodies allowed the frequency of different species on root tips to be determined (Kårén *et al.* 1997). On plots fertilized with nitrogen, basically only fruiting bodies of *Lactarius rufus* (rufous milk-cap) were found, while on control plots those of *Cortinarius* species predominated. The DNA analyses of mycorrhizas revealed marked changes in species composition. The proportion of root tips colonized, for example, by *L. rufus* and the crust fungus *Tylospora fibrillosa* was higher in nitrogen-treated than in untreated plots. A corresponding decrease in the proportion of mycorrhizal root tips in the nitrogen plots was noted for *Cortinarius* species, *Piloderma croceum*, *Suillus variegatus* (variegated boletus), and a few as yet unidentified fungi which are believed to belong to the genus *Piloderma* (figure 5.6).

• Does greater nitrogen availability result in a reallocation of resources?

Another reason why certain fungi stop producing fruiting bodies after nitrogen fertilization could be that they allocate their resources differently when more nitrogen is available. For example, they might give nutrient

Lactarius rufus
Photo: Ulf Risberg/N

uptake and growth on tree roots priority over the formation of fruiting bodies (Wallander 1995). Thus, although the fruiting bodies of a species may become less numerous or disappear altogether, the species may still be present on root tips in the soil. This is illustrated by the results for *Lactarius rufus* in the Norrliden experiment. Despite its greater abundance on root tips in nitrogen-treated plots (roughly 15 times higher than in control plots), this species produced fewer fruiting bodies (less than 10% of the number found on the control plots).

All in all, the research results from Skogaby and Norrliden (Kårén 1997) suggest that nitrogen deposition or nitrogen fertilization of forest soils does not lead to the disappearance of the mycorrhizal fungi associated with tree roots. However, the species composition of these fungi does change dramatically, and many species probably disappear, at least locally where fertilization has taken place, or in areas with high deposition of nitrogen (figure 5.6). It is still unclear what consequences this has for the functioning of mycorrhizal fungi in forest ecosystems. If the activity of the mycelium (i.e. the network of hyphae) in the soil is affected – either by a decrease in abundance, physiological changes, or indirectly by a reduced abundance of species important for the uptake of nutrients other than nitrogen – adverse effects on nutrient uptake by forest trees could ensue. The species changes observed may perhaps involve a shift from species specializing in the uptake of organic nitrogen compounds to others with a high capacity to take up inorganic nitrogen. Initially, this would increase tree uptake of nitrogen. If a forest ecosystem develops from a dominance of inorganic to a dominance of organic forms of nitrogen (e.g. some time after heavy fertilization with nitrogen, or after a decrease in nitrogen deposition), it could be detrimentally affected if it has lost the mycorrhizal species that specialize in organic nitrogen. There is thus a need for further research to explore the long-term effects of nitrogen on mycorrhizal fungi on tree roots and their mycelia in the soil, and on the functioning of the latter.

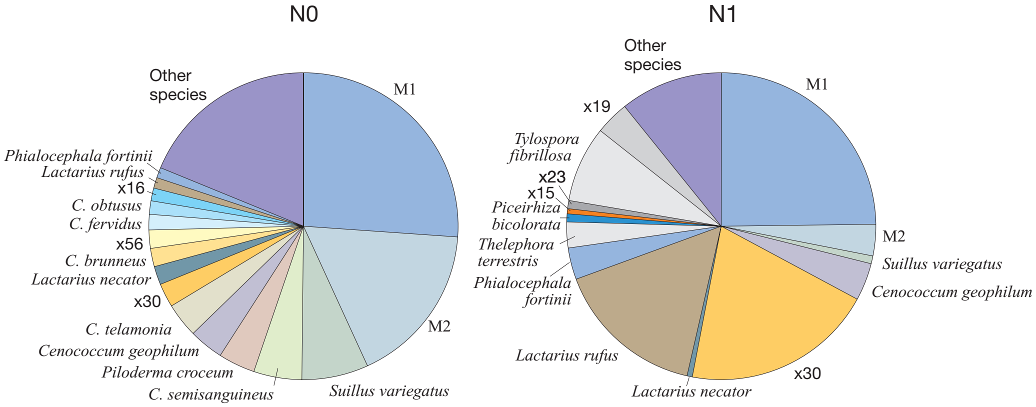


Figure 5.6. Changes in the species composition of mycorrhizal fungi on fine roots of Scots pine in the Norrliden experiment. N0 = control; N1 = 30 kg of nitrogen per hectare per year. C. = *Cortinarus*. M1 and M2 are probably *Piloderma* species (E. Larsson, A. Dahlberg *et al.*). Species designated x followed by a number are unidentified.

CONCLUSIONS

Atmospheric deposition of nitrogen affects forest trees in many different ways. Increased nitrogen availability results in higher levels of the nutrient in needles or leaves, higher concentrations of certain nitrogen compounds, and altered patterns of growth. These changes can, particularly if inputs of nitrogen are high, render trees more susceptible to frost, drought, fungal infection or insect attack. However, reports of forest trees actually suffering damage as a result of large additions of nitrogen are rare.

Nitrogen saturation is a state in which the supply of nitrogen exceeds the needs of plants and micro-organisms. Nitrogen-saturated trees are unable to make efficient use of the nitrogen available, resulting in higher levels of inorganic nitrogen in the soil and hence a greater risk of leaching. The majority of forest ecosystems are nitrogen-limited. Nitrogen deposition should therefore alleviate this limitation, allowing trees to grow better. However, studies of temporal trends in forest growth have shown that growth has also increased in areas not exposed to significant deposition, and the impact of nitrogen deposition on growth therefore remains unclear.

Of the changes that occur in the wake of nitrogen deposition, the effects on mycorrhizal fungi are particularly striking. These organisms exhibit a high species diversity and play an important part in nutrient cycling in forests. Inputs of nitrogen do not result in the disappearance of mycorrhizas, but do cause major changes in their species composition, which could conceivably affect cycling of nutrients.

The highest levels of nitrogen deposition are found in southern and south-western areas of Sweden. In certain parts of these regions, deposition is probably so high that forest trees will end up with (and in certain cases already have) an excess of nitrogen. In other areas of the country, nitrogen deposition is lower and will probably not result in nitrogen availability exceeding what trees require for their growth.

QUESTIONS AND ANSWERS

Has nitrogen deposition resulted in increased forest growth in Sweden?

Studies have revealed a higher than predicted rate of forest growth. Various factors, including forestry practices, genetic selection, increased nitrogen deposition and an elevated atmospheric concentration of carbon dioxide, may have contributed to this increase. Clear-cut evidence of the part played by nitrogen deposition in this context is not available. Both Swedish (Elfving & Tegnhammar 1996) and European studies (Spiecker *et al.* 1996) show that forest growth is also increasing in areas with low deposition of nitrogen, indicating that factors other than nitrogen have been of significance.

Are there any signs of forest trees being adversely affected by current levels of nitrogen deposition?

There is no evidence of direct damage to trees attributable to the levels of nitrogen deposition currently occurring in Sweden.

Are the effects of nitrogen deposition predominantly beneficial or detrimental?

Detrimental effects predominate. A possible increase in forest growth due to nitrogen deposition cannot offset the changes to forest and other ecosystems which this deposition causes. The argument that nitrogen deposition can be compared to large-scale nitrogen fertilization is a superficial one. Fertilizers can be targeted on particular stands and applied in such a way as to minimize the effects on the surrounding environment. Nitrogen deposition strikes indiscriminately.

Does nitrogen have different effects, depending on its chemical form or the route of exposure?

Yes, there are a number of differences between ammonia/ammonium and nitrogen oxides/nitrate, among other things in terms of deposition and uptake processes. However, we do not know whether these differences result in differing ecological effects. As for different exposure routes, direct uptake versus uptake via the soil, there is reason to believe that direct uptake produces more marked effects in vegetation.

DOES NITROGEN DEPOSITION CHANGE THE FLORA?

URSULA FALKENGREN-GRERUP, LARS ERICSON, URBAN GUNNARSSON,
ANNIKA NORDIN, HÅKAN RYDIN AND BO WALLÉN

For many plant species, either nitrogen or phosphorus is generally considered to be the limiting factor for growth. Forests in northern regions are regarded as nitrogen-limited (Tamm 1991), but on calcareous soils phosphorus is usually the limiting factor. Increased atmospheric deposition of nitrogen can thus be expected to have very different effects, depending on the types of vegetation and soil involved. The earlier more or less one-sided focus on nitrogen as a production-enhancing factor meant that many of the experiments established to study its effects were concerned primarily with production, and paid far less attention to effects on groups of organisms other than those of commercial interest. In many areas, however, the eutrophication (nutrient enrichment) caused by nitrogen deposition has given rise to changes in the flora. Forbs (i.e. non-grassy herbs), grasses, bryophytes (mosses and liverworts) and lichens may in many respects be more sensitive to different forms of disturbance than forest trees and therefore respond more rapidly and more specifically. For this reason, the effects of nitrogen deposition on flora are among the factors that can be used to determine critical loads of nitrogen (see chapter 7). This chapter describes the effects of nitrogen deposition on the flora of deciduous and coniferous forests and of mires. It includes both an account of the floristic changes which we believe have resulted from nitrogen deposition, and a description and discussion of the different methods available to study the effects of nitrogen on different plant species and communities.

Geology, climate and land use modify the effects of nitrogen deposition

• DEPOSITION GRADIENT

Deposition of nitrogen is highest in the far south-west of Sweden and decreases towards the north-east (see chapter 3). In the far south of the country, forest areas receive an annual input of roughly 20 kg of nitrogen per hectare, whereas in the north the input is just 1 kg per hectare. Nitrogen enters ecosystems both in precipitation and by the filtration of particles and gases from the air by vegetation. The nitrogen load varies at both a local and a regional level (see chapter 3). Deposition to forests is roughly twice as high as deposition to open sites, since the leaves and needles of trees are efficient filters for gases and particles containing nitrogen (Westling *et al.* 1995). Forest edges represent an even more powerful filter, which can in addition efficiently intercept local emissions of ammonia from farmland and livestock buildings. At Söderåsen in Skåne, for example, nitrogen deposition to a Norway spruce forest, exposed to south-westerly winds bearing pollutants from other parts of Europe as well as Sweden, was found to be 30 kg per hectare per year in the heart of the forest and 75 kg at its edge (Balsberg-Påhlsson & Bergkvist 1995). It is thus evident that nitrogen loads to specific ecosystems and sites can differ considerably and that the effects may therefore also be expected to vary widely.

Deposition of acidifying compounds and nutrients is appreciably higher in central Europe than in the Nordic countries, an important point to bear in mind when we compare changes in different polluted areas. In the Netherlands, for example, nitrogen deposition was 20 kg per hectare per year as early as the 1950s, i.e. the level currently found in the far south of Sweden, and today it can approach 100 kg per hectare locally, in forests situated close to livestock farms.

• Geology, climate and vegetation

The bedrock and soil of an area are major factors in determining what flora and fauna become established there, and the impacts of air pollutants vary according to these basic parameters. In the Precambrian regions that make up a large part of Sweden, the soil had only limited stores of easily weathered materials from the outset, and these reserves have subsequently been drained as a result of both natural depletion and deposition of acidifying pollutants. However, scattered across Sweden there are also areas with readily weatherable rock types, and here both pH and nutrient supplies are more favourable for many species. Such areas exist above all on Öland and Gotland, where limestone formations predominate, but calcareous soils can also be found in Skåne, Östergötland, Västergötland, Uppland and the Scandinavian mountain range and around Lakes Siljan and Storsjön.

Climate often defines the limits of species' ranges. Several vegetation zones are to be found within Sweden's borders: the nemoral (deciduous forest) zone in Skåne and parts of the west coast region, the boreo-nemoral (mixed forest) zone in the rest of southern and most of central Sweden, and the boreal (coniferous forest) zone in the remainder of the country. The mountain region falls within the subalpine or alpine vegetation zone. Given the variation in soils, climate, deposition levels and vegetation across the country, air pollutants may be expected to have widely varying effects.

Forests cover two-thirds of Sweden's land surface (40–45% Scots pine and Norway spruce, 10% birch and 5% other deciduous species). Their distribution varies considerably within the country, in terms of both area and dominant species. Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are found throughout Sweden, but occur sparsely in the far south. A characteristic of the latter region is beech (*Fagus sylvatica*), which in southern Skåne achieves a cover of as much as 30%. Birch (*Betula* spp.), alder (*Alnus* spp.) and willow (*Salix* spp.) occur throughout the country, while species such as oak (*Quercus* spp.), ash (*Fraxinus excelsior*), elm (*Ulmus* spp.), lime (*Tilia* spp.) and maple (*Acer* spp.) by and large have the *limes norrlandicus* as the limit of their range, i.e. are found to the south of the River Dalälven. In Sweden, a relatively large amount of research has been done on deciduous forests, in proportion to their distribution. This is partly because the range of deciduous woodlands coincides with the area affected by substantial deposition of air pollutants, and also because they are home to a large proportion of Sweden's forest flora.

• LAND USE

The use of land by human beings has impacts from the landscape level down to individual groups of trees. For thousands of years, before agriculture and other human activities began to modify the landscape, most of Sweden was covered with vast forests, in which change was above all brought about by fires, storms, and grazing and browsing wild animals. People exerted an influence on these forests by grazing their livestock there, clearing land, and extracting timber and firewood for their domestic needs. Industrialization brought a rapid increase in the amounts of timber removed, not least in northern Sweden, and large areas of forest were felled, beginning along the coast and gradually moving further inland. In southern Sweden, extensive plantations were established on heaths and in other open countryside, leading to an expansion of the forest industry in that part of the country, too. In the 20th century, the practice of grazing livestock in forests was abandoned, forestry was mechanized, and new forest roads provided access to areas not previously opened up for forestry.

All these changes occurred in parallel with a rise in nitrogen deposition. It is therefore not always very easy to say to what extent observed changes in the composition of the flora are due to a modified chemical environment. Since the Second World War, for example, traditional management regimes, such as mowing, grazing and controlled burning of meadows and heaths, have fallen into disuse. This has led to more rapid scrub invasion of once open land, with the result that low, slow-growing species favoured by disturbance have been replaced by tall, fast-growing species –

changes similar to those that occur when nitrogen deposition increases. Studies which take account of changes at the landscape level provide a comprehensive picture of floristic change (Oredsson 1990, Tyler & Olsson 1997), but can often produce different results to studies confined to individual ecosystems (Falkengren-Grerup 1995a).

There have also been changes in the way the deciduous forests of southern Sweden are managed. At the beginning of the 20th century, livestock were put out to graze in these woodlands, but this practice was gradually abandoned and it was not until the later part of the century that grazing and browsing once again had an effect on the vegetation, although now the rapidly growing populations of elk (moose, *Alces alces*) and roe deer (*Capreolus capreolus*) were responsible. Around the middle of the 20th century, deciduous forests were used to a far lesser extent, and they became denser and darker. Since the 1980s, harvesting of timber from these forests has increased markedly, and the use of heavy machinery for this purpose is a new factor affecting forest land, involving the felling of larger areas and the possibility of soil compaction. Intensified management is increasing the biodiversity of beech forests, by allowing more light to reach the ground (Brunet *et al.* 1996, Diekmann & Falkengren-Grerup 1998), and of oak forests, although the latter are not limited by light availability to the same extent as beech forests (table 6.1).

TABLE 6.1. Changes in the numbers of forb and grass species in oak and beech forests in Skåne between the 1980s and 1990s.

INTENSITY OF MANAGEMENT	LOW	INTERMEDIATE	HIGH
OAK			
No. of species 1983	27	25	21
No. of species 1993	29	30	34
BEECH			
No. of species 1980	8	15	15
No. of species 1990	8	17	23

The forests were subject to differing intensities of management (low = no or little disturbance; intermediate = regular thinning and less than half the trees removed; high = over half the trees removed and some disturbance of the ground) (Brunet *et al.* 1996). The increase over the 10-year period was statistically significant ($p<0.05$) for all the management intensity classes apart from the lowest one in the case of the beech forests. The greater the intensity of management, the greater was the increase in the number of species.

Difficult to prove direct effects of nitrogen deposition

Although we can describe vegetation changes in time and space, then, it may be difficult to determine to what extent they are due to nitrogen deposition, changes in land use or other factors. On the basis of correlative studies, earlier vegetation data and experiments of various kinds, however, it is possible to get closer to an answer. Species can be classified on the basis of their abundance in relation to nitrogen availability and their response to inputs of nitrogen. Various types of index characterizing nutrient availability and soil acidity can also be employed.

Experiments can be used to simulate the effects of nitrogen deposition on vegetation, although it is difficult to interpret the results and apply them more generally to natural conditions and larger areas. This is particularly true of indoor experiments, which can provide valuable information about how particular species react under controlled conditions, but can yield results at the individual plant level which differ considerably from the situation at the population level. A great deal of work therefore remains to be done to explore how increased deposition of nitrogen affects the species composition of different ecosystems and the distribution of different vegetation types on a landscape scale. Nitrogen deposition also affects interactions within and between species, producing effects which in turn may be of great significance for the structure and dynamics of plant communities. Field experiments may provide information which can more easily be generalized, since they take into account not only individual species' responses to changes in nitrogen availability, but also interactions within and between plant species, and between plants and organisms at other trophic levels (i.e. levels in the food chain). It is important, however, that the amounts of nitrogen applied in such studies are sufficiently small, that a large enough scale is used, and that the experiments are allowed to continue over a relatively long period.

• NITROGEN INDICES FOR INDIVIDUAL SPECIES

To uncover the causes of floral changes, various information concerning the environmental demands of different species can be used. Relevant and sufficiently comprehensive information is hard to come by, and there is much debate about how applicable different data are. One frequently used index is Ellenberg's (1992) indicator values, which have been assigned to a very large number of central European vascular plants, bryophytes and lichens. These values characterize species in terms of various properties of the sites where they are found, including nitrogen availability (N), soil acidity (R), soil moisture (F), light (L) and temperature (T). Scores of between 1 and 9 are used. Low scores for the different factors mentioned mean that the species concerned grows on soils with a limited supply of nitrogen, at low pH and moisture levels, on dark sites and at low temperatures. High scores mean the opposite (see table 6.2, p. 89). Indicator values are based to a large extent on measurements, but also on expert assessments.

Another index is FNIS, which characterizes forest species on the basis of their occurrence in relation to the rates of production of ammonium and nitrate in the soil (Diekmann & Falkengren-Grerup 1998). FNIS is based on soil and vegetation measurements from 600 deciduous forest plots in Sweden, and on the potential net mineralization both of total nitrogen and of ammonium and nitrate separately. The scale is from 1 to 9, a low value meaning that a species occurs mainly on ammonium-producing soils and a high value that it is found on soils with high production of nitrate (see table 6.2). This index is based on measurements, rather than subjective, experience-based estimates of nitrogen availability. It therefore has the potential to gain acceptance as a source of evidence of floristic change – in contrast to Ellenberg's nitrogen scores, whose value in this respect has often been questioned. Fortunately, the FNIS index lends support to the Ellenberg indicator values for nitrogen.

• Amino acid levels in plants

Changes in the species composition of an ecosystem are preceded by a number of other changes. When vegetation is exposed to nitrogen deposition, the initial effect is an increased uptake of nitrogen by the plants already established. This increased uptake is accompanied by various biochemical changes. One of the early changes of this kind has to do with the ability of plants to store nitrogen.

Many perennial plants store nitrogen in their roots or rhizomes (underground stems). This storage, which varies on a seasonal basis, ensures that the plant has a supply of nitrogen for its intense growth of shoots the following spring, when the uptake from the soil is often insufficient to meet the plant's needs (Jaeger & Monson 1992). As a result, growth is not directly dependent on nitrogen availability, but can be adjusted to the aggregate supply of nitrogen over several years (Chapin 1980, Chapin *et al.* 1990). Many plants in Swedish forest ecosystems, which have adapted to a limited and irregular supply of nitrogen, can take advantage of sudden nitrogen pulses, and what is more they do not limit their uptake of nitrogen when its availability improves (Chapin 1980). With increasing eutrophication, therefore, plants store more nitrogen (Chapin *et al.* 1986, Ohlson *et al.* 1995, Lipson *et al.* 1996, Nordin *et al.* 1998).

In wild forbs and grasses, nitrogen is primarily stored as free amino acids, whereas certain agricultural crops and trees also make use of soluble proteins (Chapin *et al.* 1986, Lähdesmäki *et al.* 1990, Volenec *et al.* 1996, Nordin & Näsholm 1997). It seems that only a handful of amino acids are of importance in Swedish forest ecosystems, e.g. arginine, asparagine and glutamine, and the choice of amino acid seems to be specific to individual species. In nitrogen-poor ecosystems, arginine is virtually the only amino acid used (Chapin *et al.* 1986, Lipson *et al.* 1996, Nordin & Näsholm 1997), while in nitrogen-rich ecosystems many species chiefly use asparagine (Rosnitschek-Schimmel 1985, Ohlson *et al.* 1995). Amino acids are used both for seasonal storage of nitrogen and for nitrogen taken up in excess of plants' basic needs.

By measuring the quantities of amino acids in plants it is possible to determine whether the supply of nitrogen exceeds their basic requirements, and the amino acid composition (a switch from arginine to asparagine) can indicate whether growth is being favoured. These biochemical responses occur at an early stage and can be discerned at low doses of nitrogen (Nordin *et al.* 1998), and are therefore a sensitive measure of enhanced nitrogen availability.

Vegetation changes

• Effects on forest and other land outside Sweden

In contrast to the rest of Europe, the majority of studies in the Nordic countries have been carried out in forests – a result of the large areas of forest in this region. The changes observed naturally depend on the types of vegetation and soil studied, but it can be said that certain changes which are now beginning to be discerned in Sweden are already fully visible in countries with high nitrogen deposition. In the Netherlands, lichens that once grew on trees have disappeared and wavy hair-grass (*Deschampsia flexuosa)* and a few other grass species, together with raspberry (*Rubus idaeus)*, stinging nettle (*Urtica dioica)* and narrow buckler fern *(Dryopteris carthusiana)*, have become more abundant (Bobbink *et al.* 1996). A study in north-eastern France (Thimonier *et al.* 1994) revealed an increase in the abundance of nitrophilous (nitrogen-demanding) species, whereas such tendencies were less clear in Norway (Bjørnstad 1991) and Finland (Nieppola 1992). Certain experiments also suggest that vegetation recovers when nitrogen deposition decreases, e.g. raspberry was found to grow less profusely when the input of nitrogen was reduced (Boxman *et al.* 1998a).

Heaths and grasslands in the Netherlands have been studied in detail (Bobbink *et al.* 1996). Many of the country's *Calluna* heaths have been transformed into grass-dominated habitats, owing to the greater competitiveness of grasses at higher nitrogen levels. However, for this transformation to take place, the heather's foliage must first be attacked by insects, to expose the soil and enable grasses to establish themselves. Similar interaction between natural enemies and vegetation changes has been observed in the case of bilberry (*Vaccinium myrtillus*) in northern coniferous forests, where increased supplies of nitrogen result in more widespread infection by parasitic fungi, allowing wavy hair-grass to expand. In the case of heather, another contributory factor may be greater sensitivity to frost when plants take up large amounts of nitrogen. Species-richer heaths and grasslands, like forests, experience a shift towards more nitrophilous vegetation that can also cope with acidified soil. In the Netherlands, the high soil concentrations of ammonium in relation to nitrate that have resulted from large emissions of ammonia from intensive arable and livestock production may be toxic to certain species. Calcareous soils are buffered against acidification, but an input of nitrogen can result in appreciable changes in their vegetation. The high species diversity that is characteristic of such soils cannot be maintained when there is a dramatic increase in the cover of other species, such as tor grass (*Brachypodium pinnatum*).

In British nitrogen experiments on heaths and grasslands, involving annual additions of 40–140 kg of nitrogen per hectare between 1991 and 1996, heather (*Calluna vulgaris*) initially grew better, but then suffered climate-related damage during the colder half of the year (Lee & Caporn 1998). However, higher plants became less abundant on both the acidic and the calcareous grasslands studied, and growth was not stimulated. These results are of particular interest in that, despite relatively high deposition of nitrogen over a long period, the heaths initially responded positively to nitrogen fertilization (increased growth), while the grasslands responded negatively. In other studies of grasslands in Britain, it was concluded that the ecosystem was not sensitive to nitrogen inputs (Wilson *et al.* 1995), but most researchers take the results to indicate, rather, that the changes attributable to nitrogen have already occurred. Lee and Caporn's (1998) study also showed that the applications of nitrogen affected soil micro-organisms and stimulated nitrogen mineralization – the same results as were found for a natural deposition gradient with more moderate inputs of 5–20 kg of nitrogen per hectare per year (Falkengren-Grerup *et al.* 1998).

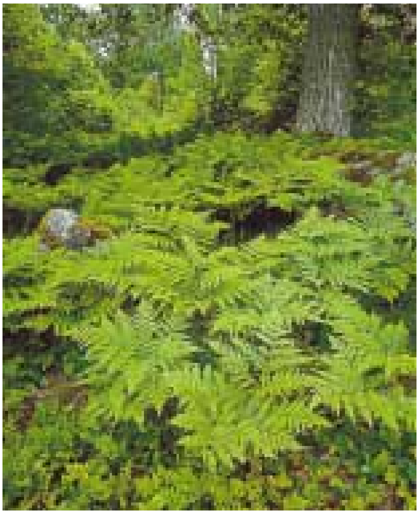
• DECIDUOUS FORESTS IN SOUTHERN SWEDEN

There are some 2000 vascular plant species in Sweden, and 370 of these are found in forests, particularly deciduous forests. Threatened (i.e. endangered, vulnerable, rare or care-demanding) species make up just over 15% of this number, and they occur mainly in deciduous woodland in the far south of the country, on soils with higher nutrient levels and lower acidity than those on which non-threatened species are found (Gustafsson 1994). They also appear to be associated with land that has been forested for a long time. In Germany, Switzerland and France, threatened species have a different distribution, occurring primarily on nitrogen-poor soils. The threats to plant diversity thus differ: increased nitrogen deposition constitutes a greater risk factor in the rest of Europe than in Sweden, where soil acidification may be more critical.

Vegetation changes take longer on acid soils

Several studies have been undertaken which shed light on the impact of nitrogen on the flora of southern Swedish deciduous forests. One of them incorporates both a spatial and a temporal dimension: a study of oak forests in Skåne and eastern Småland, carried out at the beginning of the 1980s and repeated 10 years later (Diekmann *et al.* 1999). In this study, Ellenberg's indicator values were used to characterize species' tolerance of or preference for nitrogen (N) and acidity (R). A comparison between the two provinces showed Skåne to have a larger proportion of nitrophilous species (higher N scores) than Småland (figure 6.1). This was true both of acidic (low R) and nutrient-poor soils, supporting a small number of species, and of richer soils with higher pH and species diversity. As for changes over time, the sites with acid soils responded very slowly, with little change observable over the relatively short period of the study. On the less acidic soils, on the other hand, the proportion of nitrophilous species increased considerably, in both Skåne and Småland. This study shows that nitrophilous species take a long time to establish themselves on acid soils, but that on less acidic sites the rate of change can be high, both in a region exposed over several decades to what by Swedish standards is a high level of nitrogen deposition, and in a region subjected to roughly half that deposition pressure.

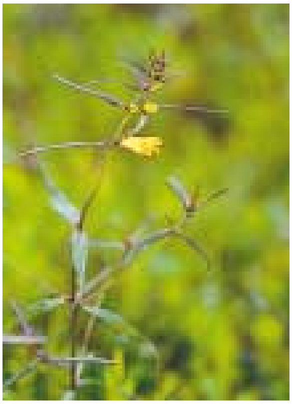
Figure 6.1. Indicator values with respect to acidity (R) and nitrogen (N) (Ellenberg 1992) of the vegetation of oak forests in Skåne and Småland in 1983 and 1993 (adapted from Diekmann *et al.* 1999). A low R score indicates that the vegetation is characterized by species that occur on acid soils (low pH), a low N score that it has a preponderance of species growing on soils with low levels of nitrogen. The regression lines are based on around 100 sites for each region and are statistically significant ($p<0.001$; r^2 values for the regression lines are 0.58 (Skåne 1983), 0.86 (Skåne 1993), 0.58 (Småland 1983) and 0.64 (Småland 1993)).



BRACKEN PHOTO: PER-OLOV ERIKSSON

Why does it take so much longer for changes to occur on the most acidic soils? The few species that grow on such sites usually have modest demands in terms of nitrogen and other nutrients and are tolerant of hydrogen and aluminium ions, which, can be toxic to plants. Nitrophilous species have not had time or been able to establish themselves (Brunet *et al.* 1996, 1997, 1998). Species found on soils with low pH include bracken (*Pteridium aquilinum*), bilberry (*Vaccinium myrtillus*), chickweed wintergreen (*Trientalis europaea*), common cow-wheat (*Melampyrum pratense*) and heath bedstraw (*Galium saxatile*), on the most acidic soils; and narrow buckler fern (*Dryopteris carthusiana*), pill sedge (*Carex pilulifera*), hairy wood-rush (*Luzula pilosa*), wavy hair-grass (*Deschampsia flexuosa*) and may lily (*Maianthemum bifolium*), which have somewhat wider distributions. The first group has an average FNIS value of 2.2, the second 2.8. Both these scores are low on a scale from 1 to 9. The groups' Ellenberg N values are also low, namely 2.6 and 3.2. Another point to be borne in mind is that something other than nitrogen may be the limiting factor in these systems, such as toxic levels of hydrogen or aluminium ions, or a deficiency of some other nutrient (Falkengren-Grerup 1995a).

The study of Skåne and Småland oak forests is also of interest in that estimates of the nitrogen-forming capacity of the soil are available for all the sites investigated (Falkengren-Grerup *et al.* 1998). Since the formation of plant-available nitrogen in the soil has to be studied over an extended period, and therefore cannot be measured by simple soil sampling methods, such analyses are not common in vegetation studies. In the great majority of cases, moreover, a simplified laboratory approach has to be used, since field measurements are extremely labour-intensive. The simplification involves storing soil samples at standardized moisture levels and temperatures. In this study, therefore, it was possible to test the hypothesis that the effects of nitrogen inputs depend on how high deposition is in relation to the estimated production of inorganic nitrogen in the soil. When nitrogen deposition amounted to around a third or more of the amount produced in the soil, the vegetation tended to change more in the direction of nitrophilous species than if deposition was lower in relation to the nitrogen available in the soil (Diekmann *et al.* 1999).


Common cow-wheat
Photo: Ulf Risberg/N

The main weakness of studies of this kind is that they encompass a relatively short period, and that nitrogen deposition has already been in progress for several decades. This is a particular problem in the studies carried out in central Europe, whereas those undertaken in the north of Sweden, for example, produce results relating to unpolluted land (see under 'Coniferous forests'). Skåne, the region of Sweden with the highest nitrogen load, may have passed the points at which breaks in linear trends have occurred, and we can therefore find out little about the earlier impacts of nitrogen inputs (figure 6.2). If a study were carried out between dates 1 and 2 in the diagram, the results would suggest that all three species had become more abundant, whereas a comparison between dates 2 and 3 would show that one species had increased, one remained unchanged, and one declined. Unfortunately, there is no choice but to rely on the approach described, since it is not possible to generalize from results relating to other vegetation types and climatic zones.

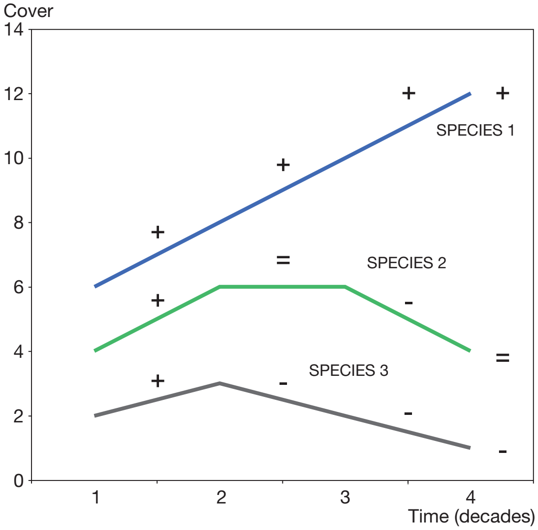


Figure 6.2. Possible trends in the cover of a number of species during a period of increasing nitrogen deposition, based on studies of how the vegetation of deciduous forests has developed over one to four decades in southern Sweden (Falkengren-Grerup 1995a). The diagram illustrates how the study period chosen will determine what changes are observed. Over the period as a whole, species 1 shows an increase, species 2 is unchanged and species 3 declines. Over different parts of the period, the opposite changes may occur, as is illustrated by the plus, minus and equals signs. Examples of species showing different trends are rosebay willowherb (*Epilobium angustifolium,* species 1), yellow archangel (*Lamium galeobdolon*, species 2) and common and early dog violet (*Viola riviniana* and *V. reichenbachiana,* species 3).

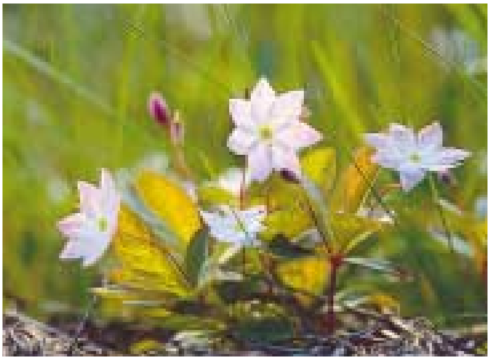
Composition of vegetation can be linked to deposition and nitrogen status of soil

The deciduous forests of southern and central Sweden are exposed to widely varying levels of nitrogen deposition (approx. 5–20 kg per hectare per year) and therefore permit investigations of deposition effects within a region with a relatively similar climate, especially compared with other gradient studies that extend across several countries of Europe (Wright & Rasmussen 1998). Studies of such forests – chiefly oak, but also elm, ash, lime and maple – from Västergötland–Uppland to Skåne provide a basis for distinguishing the effects of nitrogen deposition from variations due to other factors. In one such investigation (Falkengren-Grerup *et al.* 1998), (net) mineralization of nitrogen in the soil has been found to be twice as high in Skåne as in the provinces around Lake Mälaren, central Sweden, a remarkable difference that is probably due to the higher accumulation of deposited nitrogen in the far south of the country. This study shows that the vegetational composition of these forests can largely be explained by the production of plant-avalaible nitrogen in the soil, which is dependent on both the general nutrient status of the soil and, probably, the effects of accumulated nitrogen deposition. When soil organic matter is broken down, ammonium ions are the first inorganic form of nitrogen to be produced. In most deciduous forest soils, these are then converted to nitrate ions, although not where soil pH is very low. At a pH of less than 3.5 (pH measured in 0.2 M KCl), 10% of mineralized nitrogen was found to consist of nitrate and the rest of ammonium. Between pH 3.5 and 4.0, the proportion of nitrate was 50%. These figures refer to Skåne; in other regions, the percentages of nitrate were only half as high. The reasons for this have still to be investigated. Both the total amount and the dominant form of plant-available nitrogen produced in a soil can thus vary. The proportions and quantities of the different forms of nitrogen produced in the soil, as reflected in the FNIS index, are the factor which best explains the composition of the forest flora (table 6.2).

Nitrogen deposition, too, explains a considerable proportion of the variation in the flora of southern Swedish deciduous forests (Brunet *et al.* 1998). Species which were found to co-vary with deposition included raspberry, lady fern (*Athyrium filix-femina*), stinging nettle, common hemp-nettle *(Galeopsis tetrahit)* and three-veined sandwort (*Moehringia trinervia*). These species have high FNIS values, i.e. they are favoured by a good supply of nitrate. Several of them establish themselves in forests where there has been some form of ground disturbance, and they rarely achieve a very high cover.

Table 6.2. Indicator values with respect to nitrogen for species analysed in at least 100 deciduous forests in southern Sweden (Diekmann & Falkengren-Grerup 1998). Values, which can range from 1 to 9, are based on the cover of each species in relation to production of ammonium and nitrate in the soil (FNIS), and on assessments guided by experience (Ellenberg 1992). A low FNIS score means that the species occurs on soils in which nitrogen is present mainly as ammonium, a high score that it occurs where nitrogen is present primarily in the nitrate form. Ellenberg N values refer to low to good nitrogen availability.

FNIS class	Ellenberg N value (mean)	Scientific name	English name
2	3	*Vaccinium myrtillus, Deschampsia flexuosa*	bilberry, wavy hair-grass
3	4	*Luzula pilosa*	hairy wood-rush
4	2.6	*Agrostis capillaris Anthoxanthum odoratum, Festuca ovina, Maianthemum bifolium, Melampyrum pratense*	common bent, sweet vernal grass, sheep's fescue, may lily, common cow-wheat
5	3.6	*Campanula persicifolia, Hieracium murorum, Lathyrus linifolius, Poa angustifolia, Rubus idaeus*	peach-leaved bellflower, few-leaved hawkweed, bitter-vetch, narrow-leaved meadow-grass raspberry
6	5.5	*Convallaria majalis, Dactylis glomerata, Dryopteris filix-mas, Fragaria vesca, Galeopsis bifida/tetrahit, Melica nutans, Melica uniflora, Oxalis acetosella, Poa nemoralis, Stellaria holostea, Stellaria media, Veronica chamaedrys*	lily of the valley, cocksfoot, male fern, wild strawberry, common hemp-nettle, mountain melick, wood melick, wood sorrel, wood meadow-grass, greater stichwort, common chickweed, germander speedwell
7	7.4	*Anthriscus sylvestris, Cardamine bulbifera, Hepatica nobilis, Milium effusum, Primula veris, Rubus saxatilis, Vicia sepium*	cow parsley, coralroot bittercress, hepatica, wood millet, cowslip, stone bramble, bush vetch
8	6.7	*Galium aparine, Geranium sylvaticum, Geum rivale, Geum urbanum, Mercurialis perennis, Taraxacum officinale* agg.	common cleavers, wood cranesbill, water avens, herb bennet, dog's mercury, dandelions
9	7	*Paris quadrifolia*	herb Paris



Chickweed wintergreen
Photo: Torbjörn Lilja/N

Other species that co-varied with nitrogen deposition were may lily, wavy hair-grass, pill sedge and chickweed wintergreen. These species have low FNIS scores, i.e. are favoured by a relative abundance of ammonium. An alternative explanation is that they do not depend on nitrate to retain their niche in deciduous forests in the face of competition from other species. The species mentioned are not usually regarded as nitrophilous, which only goes to demonstrate the complexity of that concept. All changes in species composition and abundance that are caused by an increased supply of nitrogen should of course be regarded as an effect of nitrogen, even if the species concerned are not extremely nitrogen-demanding, with high nitrogen scores in terms of one index or another. Naturally, nitrogen deposition promotes the growth of most species, but the crucial factor is competition with other species for nitrogen and for space. The fact that the second group of species mentioned here occur where nitrogen deposition is high shows that they too are favoured by nitrogen, but they grow on poorer soils where species traditionally regarded as nitrophilous do not occur. Apart from co-varying with nitrogen deposition, the species mentioned have, in several other studies, shown a more or less clear tendency to become more abundant over the last few decades (Falkengren-Grerup 1995a, Brunet *et al.* 1997, Tyler & Olsson 1997).

Deposition of nitrogen appears to result in increased abundance of several forest ferns, such as lady fern and broad buckler fern (*Dryopteris dilatata*), and many forbs have also become more common. Table 6.3 shows species which, in one or more studies (including Brunet *et al.* 1998), have shown a positive correlation between nitrogen deposition and abundance. There are of course also species that have become less abundant, but this is probably an effect of deposition of acidifying compounds, which reduces the pH and nutrient content of the soil (Falkengren-Grerup 1995a). Common hemp-nettle, raspberry, three-veined sandwort and small balsam are nitrophilous species that showed increases in all the studies compared. Forbs found to become more abundant in at least half the studies included both species requiring more fertile soils and species that grow on poorer soils with low pH. Enchanter's nightshade, red campion, the stitchworts and stinging nettle are examples of the first group, while rosebay willowherb, may lily and chickweed wintergreen can tolerate less fertile soils. Grasses, sedges and rushes also appear to increase in abundance with nitrogen deposition, although according to the study by Brunet and co-workers (1998) the correlation is weaker. Pill sedge and soft rush show the clearest increase, while wavy hair-grass has been found to increase in fewer studies of deciduous forests than in coniferous forest studies (see table 6.3).

MAY LILY
PHOTO: LARS JARNEMO/N

Do nitrogen inputs favour grasses?

A study of forest land in Sweden demonstrated an increase in the abundance of narrow-leaved grasses at the expense of cowberry (*Vaccinium vitis-idaea*) and bilberry, and this was interpreted as an effect of nitrogen deposition (Rosén *et al.* 1992). These dwarf shrubs are not very abundant in the deciduous forests of southern Sweden, and increased cover of narrow-leaved grasses in proportion to other species has not been found in studies of these forests (Diekmann *et al.* 1999). However, the competitive potential of grasses appears to be confirmed by greenhouse experiments in which 15 forbs and 13 grasses and sedges (graminoids) were grown at three different nitrogen concentrations (50, 250 and 1250 μM)

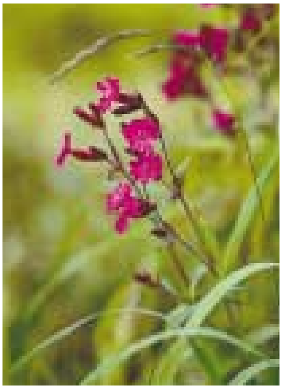
Table 6.3. The abundance of the species in this table in southern Swedish oak forests is positively correlated with nitrogen deposition (Brunet *et al.* 1998). The more studies there are which show that a species has become more abundant during a period of increasing nitrogen deposition, the greater is the probability that nitrogen has been a factor in the success of that species. Here Brunet *et al.* 1998 is compared with between two and five retrospective studies relating to Skåne, covering periods of 10–60 years (Falkengren-Grerup 1995a, Brunet *et al.* 1997, Tyler & Olsson 1997). The percentages indicate in what proportion of the studies the species were found to have increased in abundance.

%	Forbs	Grasses, sedges and rushes	Ferns and horsetails
100	Common hemp-nettle (*Galeopsis tetrahit*) Small balsam (*Impatiens parviflora*) Three-veined sandwort (*Moehringia trinervia*) Raspberry (*Rubus idaeus*)	Pill sedge (*Carex pilulifera*)	
40-75	Enchanter's nightshade (*Circaea lutetiana*) Rosebay willowherb (*Epilobium angustifolium*) Ground ivy (*Glechoma hederacea*) May lily (*Maianthemum bifolium*) Red campion (*Silene dioica*) Lesser stichwort (*Stellaria graminea*) Common chickweed (*Stellaria media*) Wood stitchwort (*Stellaria nemorum*) Chickweed wintergreen (*Trientalis europaea*) Stinging nettle (*Urtica dioica*)	Soft rush (*Juncus effusus*)	Lady fern (*Athyrium filix-femina*) Broad buckler fern (*Dryopteris dilatata*)
0-25	Broad-leaved willowherb (*Epilobium montanum*) Heath bedstraw (*Galium saxatile*) Yellow archangel (*Lamium galeobdolon*) Common Solomon's seal (*Polygonatum multiflorum*) Tormentil (*Potentilla erecta*) Common sorrel (*Rumex acetosa*)	Wavy hair-grass (*Deschampsia flexuosa*) Creeping soft-grass (*Holcus mollis*) Purple moor-grass (*Molinia caerulea*)	Narrow buckler fern (*Dryopteris carthusiana*) Wood horsetail (*Equisetum sylvaticum*)

and low levels of other nutrients, resembling the nutrient status of acid forest soils (Falkengren-Grerup 1998). At these low nutrient levels, the grass species were able to make far more use of an increased supply of nitrogen (though not the highest concentration) and increase their growth. If these results are applicable to field conditions, they imply that grasses could expand at the expense of forbs. Roughly half of the graminoids had more than 50% higher growth at 250 µM than at 50 µM nitrogen, the species concerned being Yorkshire fog (*Holcus lanatus*), common bent (*Agrostis capillaris*), cocksfoot (*Dactylis glomerata*), annual meadow-grass (*Poa annua*), pill sedge (*Carex pilulifera*) and bearded couch (*Roegneria canina*). Of the forbs, only common sorrel (*Rumex acetosa*) increased to a corresponding degree.

Plants affected by whether nitrogen is present as nitrate or ammonium

Several indoor studies have shown, and the FNIS index has confirmed, that the form in which nitrogen is available affects how well species grow. Only a few species – such as ground elder (*Aegopodium podagraria*) – are favoured by nitrate as the only nitrogen source (Falkengren-Grerup & Lakkenborg-Kristensen 1994), whereas species occurring on acid soils, where ammonium is the dominant inorganic form of nitrogen, grow well (though rarely better) on ammonium alone (Falkengren-Grerup 1995b). The latter group includes wood sorrel (*Oxalis acetosella*), pill sedge, giant fescue (*Festuca gigantea*), wood meadow-grass (*Poa nemoralis*), wavy hair-grass, lesser stitchwort (*Stellaria graminea*) and lily of the valley (*Convallaria majalis*). Many species that grow on less acidic soils, in which nitrate is often formed, are favoured when both ammonium and nitrate are available. Examples of this group are lesser hairy brome (*Bromus benekenii*), herb bennet (*Geum urbanum*), ground elder and red campion (*Silene dioica*).



Red campion
Photo: Jan Töve/N

Many forbs favoured by nitrogen

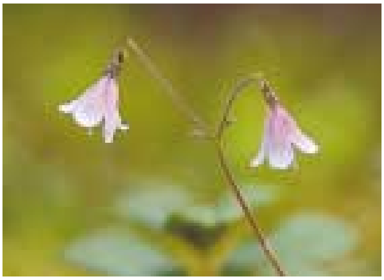
The effects of nitrogen deposition on the flora of deciduous forests are summarized in table 6.3, which is based on several studies of common species. In the table, species which a gradient study (Brunet *et al.* 1998) showed to have a positive correlation with nitrogen deposition in southern Sweden are compared with the same species in studies of vegetation changes over different periods of time. The fact that most of the species are forbs is due to such species being more numerous than grasses, which in turn are more numerous than ferns. All three groups include species which appear to be favoured by nitrogen. Some of the species, apart from showing a positive correlation with nitrogen deposition in the gradient study, were found to have increased in abundance in 100% of the retrospective studies, while others had become more abundant only under certain conditions. Relevant factors may include the characteristics of the soil and other vegetation at the sites studied, but another explanation could be that the species concerned are not unequivocally favoured by nitrogen. Four forbs and one sedge increased in all the studies. Ten forbs, one rush and two ferns became more abundant in around half of them. Six forbs, three grasses, one horsetail and one fern increased in a smaller number of studies. The forbs which increased in abundance included species that grow at highly varying pH and nutrient levels, among them both genuine forest species and more weed-like species. Grasses and sedges most commonly grow on intermediate to acid soils, and the table includes pill sedge and wavy hair-grass, which are typical acid soil plants. The ferns appear to be a group that becomes more abundant with an increasing supply of nitrogen, but the reasons for this are not known.

• CONIFEROUS FORESTS

Dwarf shrubs and bryophytes adversely affected

The availability of nitrogen is a key factor influencing the structure and functioning of boreal forests (Tamm 1991). A number of forest experiments involving applications of nitrogen have shown that the extra nitrogen affects both forest productivity and ground- and field-layer vegetation. The results were fairly consistent, showing that dwarf shrubs (bilberry, cowberry) and forest bryophytes (stair-step moss (*Hylocomium splendens*), *Pleurozium schreberi*, *Dicranum* spp.) had been adversely affected, while various grasses (e.g. wavy hair-grass), forbs (e.g. rosebay willowherb), and mosses of the genus *Brachythecium* had been favoured. This is in line with the changes that can be expected when a forest of a nutrient-poor dwarf shrub type shifts towards a nutrient-richer herb/dwarf shrub or herb type. However, most of these experiments were conducted on a relatively small scale, with high doses of nitrogen.

Moderate nitrogen doses (4–40 kg per hectare) were found to have limited effects in coniferous forests in southern central Sweden. Wavy hair-grass and chickweed wintergreen became more abundant, the greater the dose of nitrogen, but the changes were gradual and it was only thanks to the fact that the experiments went on for as long as 5 years that the results were statistically significant (Kellner & Redbo-Torstensson 1995). Of the other species studied, neither bilberry, cowberry, twinflower (*Linnaea borealis*) nor hairy wood-rush (*Luzula pilosa*) responded to the addition of nitrogen.


TWINFLOWER
PHOTO: TORBJÖRN LILJA/N

Insect and fungal attacks on bilberry increase

In an experiment at Svartberget in northern Sweden, involving applications of 0–50 kg of nitrogen per hectare, populations of the natural enemies of bilberry (*Vaccinium myrtillus*) increased within two months. Herbivorous insects, the powdery mildew fungus *Podosphaera myrtillina* and the parasitic fungus *Valdensia heterodoxa*, which causes premature leaf fall in the host plant, became more abundant when nitrogen was applied (Nordin *et al.* 1998; Strengbom, unpublished). Infection of the bilberry plants by the parasitic fungus enabled wavy hair-grass to expand (figure 6.3). This experiment shows that several natural enemies can respond very rapidly to an increased, but still low dose of nitrogen, even in a strongly nitrogen-limited coniferous forest. Bilberry shoots and leaves showed elevated concentrations of both glutamine and arginine throughout the growing season. This could have serious ecological consequences, since the growth and reproduction of most herbivores and microorganisms which attack plants are regulated by levels of readily available nitrogen compounds (Mattson 1980, Hatcher 1995). How an increased supply of nitrogen leads to a greater abundance of these natural enemies is unclear, but in the case of the parasitic fungus, since distinct biochemical changes occur and the fungus is also nitrogen-limited, it seems natural to assume that the causal mechanism is the increase in readily available nitrogen.


WAVY HAIR-GRASS
PHOTO: KJELL-ARNE LARSSON

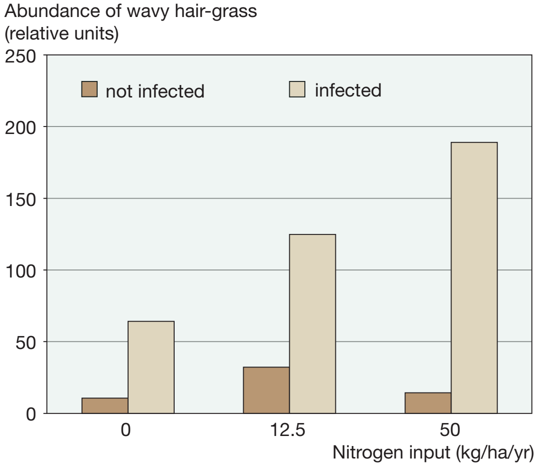


Figure 6.3.
Abundance of wavy hair-grass *(Deschampsia flexuosa)* in sample plots in which bilberry *(Vaccinium myrtillus)* was or was not infected by the parasitic fungus *Valdensia heterodoxa* (Strengbom *et al.*, unpublished).

Small plots may underestimate effects of nitrogen

The design of a study is a key factor in determining the interpretability of its results. This was made clear by the Svartberget study just mentioned, in which quadrats of between 1 m^2 and 5000 m^2 were used. The increases in the abundance of wavy hair-grass and in infection by the parasitic fungus, for example, were only statistically significant in the case of the largest plots (1000 m^2 and 5000 m^2). Such an effect is to be expected in a heterogeneous environment and when a disturbance occurs in a patchy manner, as with the parasitic fungus in question, but it rarely stands out as clearly as in this experiment. Because of this effect of scale, it is important to know and use the relevant scale for the characteristics being studied. In this case, the effects would have been underestimated if the smaller plots had been used, and small quadrats are common in studies of this type.

Amino acid levels reflect nitrogen status of plants

In the Svartberget experiment, involving doses of 0–50 kg of nitrogen per hectare, increased amino acid concentrations were observed in bilberry, wavy hair-grass and bryophytes after only one growing season, whereas the effect on cowberry at that time was comparatively small (figure 6.4). Over a longer period, however, nitrogen fertilization raised the concentration of amino acids in below-ground parts of cowberry, too (Nordin & Näsholm 1997). Amino acid levels often rise more in roots or rhizomes than in shoots, presumably because winter storage of nitrogen primarily occurs in these plant parts (figure 6.4). Elevated amino acid concentrations were also found in rosebay willowherb (*Epilobium angustifolium*), wood cranesbill (*Geranium sylvaticum*), goldenrod (*Solidago virgaurea*), may lily (*Maianthemum bifolium*) and chickweed wintergreen (*Trientalis europaea*) when they were

Figure 6.4. Concentrations of amino acids (sum of asparagine, glutamine and arginine) in different parts of plants treated with nitrogen (0–50 kg/ha). The nitrogen applications were performed in the summer of 1995 and the plant material was collected in the late autumn of the same year. (Nordin *et al.,* unpublished.)

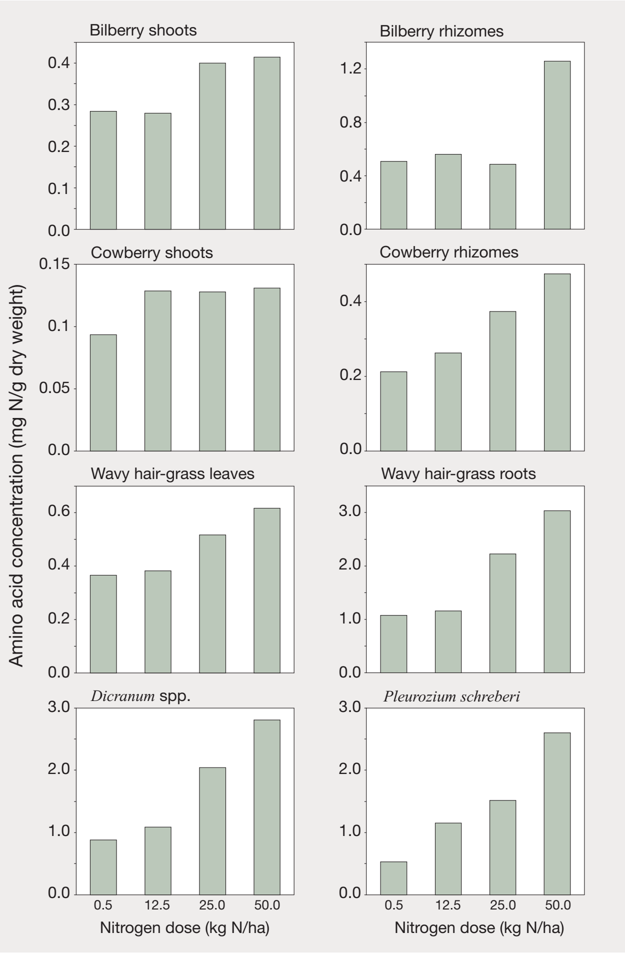
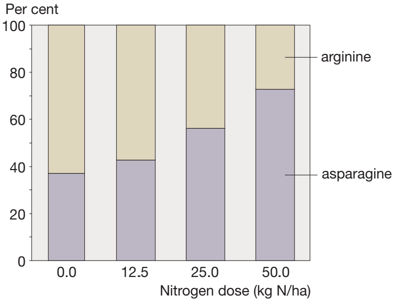


Figure 6.5. Percentages of asparagine and arginine in roots of wavy hair-grass (*Deschampsia flexuosa*) collected in autumn 1996. Nitrogen treatments were started in spring 1995. (Nordin *et al.,* unpublished.)



exposed to increased inputs of nitrogen over several years (Nordin & Näsholm 1997). Concentrations of amino acids are thus a sensitive measure of a plant's nitrogen status.

In some species, increased nitrogen availability can alter the composition of the amino acids present. For example, in wavy hair-grass, arginine was found to predominate when nitrogen levels were low, asparagine when more nitrogen was available (Näsholm *et al.* 1994, Ohlson *et al.* 1995, Nordin *et al.* 1998; figure 6.5).

This change in the amino acid composition of wavy hair-grass coincides with increased growth (Högbom 1992; J. Strengbom, unpublished data). Levels of different amino acids can thus be used to assess whether the prevailing supply of nitrogen is promoting the growth of this species. Certain species use the same amino acids for seasonal storage and for accumulation in conjunction with luxury uptake of nitrogen. In Swedish forests, wavy hair-grass often occurs alongside bilberry. Bilberry plants use arginine for seasonal nitrogen storage, and the arginine concentration also rises when the supply of nitrogen increases (Lähdesmäki *et al.* 1990, Nordin & Näsholm 1997, Nordin *et al.* 1998). However, unlike wavy hair-grass, bilberry does not become more abundant when more nitrogen becomes available; on the contrary, in nitrogen fertilization experiments its abundance has been found to decline or remain unchanged (Parsons *et al.* 1994, Nohlgren & Nohrstedt 1995, Press *et al.* 1998). Furthermore, in other species which, like bilberry, are slow-growing and adapted to nutrient-poor ecosystems, it has been found that excess nitrogen taken up and stored as arginine cannot be used for growth, even when the input of nitrogen to the system has ceased (Lipson *et al.* 1996). Since synthesis and storage of arginine require a supply of organic carbon and tie up storage capacity that could be put to other uses, long-term storage of nitrogen which does not promote growth may be expected to have a detrimental impact on plant survival.

BILBERRY
DRAWING: GUN LÖVDAHL

Bilberry and cowberry declining

Coniferous forests usually have more acidic soils and a smaller number of species than deciduous forests. In forests of the dwarf shrub type, several studies show that bilberry and cowberry are declining in the face of competition from wavy hair-grass, and this is assumed to be an effect of nitrogen. An increased abundance of bryophytes observed in Norwegian coniferous forests, on the other hand, has been attributed to a wetter, more favourable climate (Økland 1995). Table 6.4 presents vegetation changes that have been observed in retrospective studies and nitrogen fertilization experiments carried out in Norway and Sweden. Since numerous factors vary between these studies, individual species cannot be expected to change unequivocally in a given direction, but the results support the conclusion that wavy hair-grass has become more abundant, while cowberry and bilberry have declined. Raspberry is the species that has increased most consistently, in both deciduous and coniferous forests. The tendency for ferns to do better, which has been observed in deciduous woodlands, applies to one species growing in both types of forest (lady fern), but apart from that the ferns of coniferous forests show no change.

Cowberry
Photo: Jan Töve/N

TABLE 6.4. Changes in the abundance of coniferous forest species observed in two time series studies and in response to nitrogen fertilization in seven studies, according to Økland 1995 (parts of table 12), supplemented by data from Kellner & Redbo-Torstensson 1995 and Nordin *et al.* 1998. Only species included in two or more studies are shown. The percentages indicate in how large a proportion of the studies the species concerned increased (+) or decreased (-) in abundance.

%	FORBS	GRASSES AND RUSHES	FERNS AND CLUBMOSSES
+100	Raspberry (*Rubus idaeus*)		Lady fern (*Athyrium filix-femina*)
+80 to +40	Rosebay willowherb (*Epilobium angustifolium*) Chickweed wintergreen (*Trientalis europaea*)	Wavy hair-grass (*Deschampsia flexuosa*)	
+40 to -40	Wood anemone *(Anemone nemorosa)* Lily of the valley *(Convallaria majalis)* May lily *(Maianthemum bifolium)* Common cow-wheat *(Melampyrum pratense)* Toothed wintergreen *(Orthilia secunda)* Wood sorrel *(Oxalis acetosella)*		Northern buckler fern (*Dryopteris expansa* agg.) Oak fern *(Gymnocarpium dryopteris)* Interrupted clubmoss *(Lycopodium annotinum)* Beech fern *(Thelypteris phegopteris)*
-40 to -80	Twinflower *(Linnaea borealis)* Bilberry *(Vaccinium myrtillus)* Cowberry *(Vaccinium vitis-idaea)*	Hairy wood-rush *(Luzula pilosa)*	
-100	Stone bramble *(Rubus saxatilis)*		

• MIRES

In general, mires are nutrient-poor environments, and it can therefore be assumed that they will be appreciably affected by additions of nitrogen. This is particularly true of bogs (ombrotrophic mires), which depend for their nutrients on precipitation and are isolated from the surrounding mineral soil. Bogs have a naturally low pH (often below 4), whereas fens have a pH in the range 4–8, depending on the properties of the mineral soil in their vicinity. The vegetation of a fen depends crucially on its pH. Low pH values are associated with poor fens, dominated by bog mosses (*Sphagnum* spp.), and high pH with rich fens, dominated by 'brown mosses' (chiefly *Amblystegium* and *Drepanocladus* spp.). If acid precipitation were to alter the pH of the peat, therefore, appreciable changes in species composition could be expected, in the direction of a floristically poorer type.

In the 1940s, Sjörs (1948) carried out both pH measurements and extremely detailed mapping of the fine-scale distribution of over 100 species in an area of Skattlösbergs Stormosse, a mire in Dalarna, central Sweden, and in the 1950s a similar study was performed by Malmer (1962) on Åkhultmyren, a mire in the southern province of Småland. Recent repeat studies of these sites reflect long-term changes in parts of Sweden with different atmospheric loadings of nitrogen and acidifying compounds. Annual nitrogen deposition is about 8 kg per hectare at Skattlösbergs Stormosse and around 15 kg per hectare at Åkhultmyren.

Acidification more important than nitrogen deposition in central Sweden

Large areas of Skattlösbergs Stormosse have experienced a fall in pH (Gunnarsson *et al.*, in preparation) (figure 6.6). The biggest decreases – more than 1.5 pH units in certain cases – have occurred in the areas with the highest pH values in the 1940s .

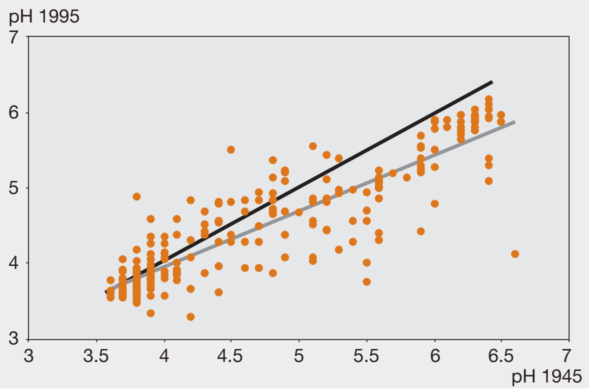


Figure 6.6.
pH values at 245 sampling points on Skattlösbergs Stormosse in 1945 and 1995. The slope of the grey regression line shows that pH was higher overall in 1945 than in 1995. $pH_{1995} = 1.03 + 0.73\ pH_{1945}$ ($R^2 = 0.78$). The black line shows unchanged pH.

The purely ombrotrophic areas of the mire have more or less unchanged pH values. The total number of species in the area sampled has decreased: six bryophyte and eight vascular plant species have disappeared, while two new vascular plant species have appeared. In general, bog mosses have increased and brown mosses decreased in abundance. The vegetation types that have lost most species are not the richest areas, but fen areas with an intermediate species number and pH. The poorest parts of the mire, i.e. the bog areas, have a largely unchanged species composition.

In terms of Ellenberg's indicator values (see under 'Nitrogen indices for individual species' in this chapter), the species that have declined or disappeared have higher R values (i.e. are more often found at higher pH) than those that have remained unchanged or increased. The declining or lost species have an average R value of 4.5, while unchanged or increasing species have an R score of 3.0. This also tallies with the pH measurements. In 1945, the now declining or lost species grew at pH 5.7, whereas the unchanged or expanding ones grew at pH 5.3. By contrast, there are no clear tendencies in terms of Ellenberg nitrogen (N) values. This suggests that acidification has had a greater impact than nitrogen deposition on mires in this part of the country. That acidification is affecting the mire vegetation of Sweden is also suggested by the dramatic changes observed in rich fens in Västergötland, where a large number of brown moss species have disappeared (Hedenäs & Kooijman 1996).

• INCREASED NITROGEN DEPOSITION MAY AFFECT THE RELEASE OF CARBON FROM BOGS

Ombrotrophic bogs are entirely dependent on atmospheric deposition for their nutrient supplies. Bogs have been regarded as nitrogen-limited, and still are in northern Sweden (Malmer 1993, Aerts *et al.* 1992). In the south of the country, increasing deposition has meant that the nitrogen requirements of the dominant *Sphagnum* species are now fully met, and in areas with an estimated annual wet deposition of 7–10 kg of nitrogen per hectare, phosphorus is considered to be the growth-limiting factor (Aerts *et al.* 1992; Aerts *et al.*, submitted). However, different *Sphagnum* species have been shown to have widely differing abilities to take up and make use of both ammonium and nitrate: hummock-forming species have a high potential capacity for nitrogen uptake per unit area, compared with species growing in wetter conditions (Jauhiainen *et al.* 1998). This means that, at least in areas with comparatively low nitrogen deposition, an increase in deposition will affect competition between functionally different *Sphagnum* species and thus shift the balance between hummocks and hollows, which will have far-reaching consequences for the carbon balance of mires (Malmer & Wallén 1996, Malmer *et al.* 1994, 1997), and hence for emissions of greenhouse gases (Joabsson *et al.* 1999). More efficient use of nitrogen and higher productivity in *Sphagnum* hummocks reinforce the micro-relief of the mire surface, and constitute the primary factor regulating the water table and hence the total accumulation of peat in a bog (Malmer & Wallén 1999).

Total peat accumulation (the peat formation rate) in the mires of southern Sweden has fallen from about 150 to around 50 grams per square metre per year, above all as a result of accelerated degradation of surface layers of peat (Malmer & Wallén 1999). The increase in nitrogen deposition in this region is probably partly responsible for this trend. A correlative study of the potential decay rate of *Sphagnum* litter along a nitrogen gradient in southern Sweden has shown decomposition of *Sphagnum* mosses to be more strongly correlated with their phosphorus content than with their nitrogen content (Hogg *et al.* 1994). In an experimental follow-up study, the decay rate appeared to be higher in a phosphorus-limited area (with high nitrogen deposition) than in a nitrogen-limited area, and showed a positive correlation with phosphorus and nitrogen levels in the litter (Aerts *et al.*, submitted).

On the Åkhultmyren mire in Småland, a study has been made of changes since the 1950s in the distribution of certain dominant species and of species which are good indicators of the chemical environment (Gunnarsson, Malmer & Rydin, in preparation). Some of the changes have been appreciable. Common cotton-grass (*Eriophorum angustifolium)*, a fen species, has spread onto what used to be purely ombrotrophic parts of the mire. Rannoch rush (*Scheuchzeria palustris*), a species of poor fens and bogs, was relatively widespread in the 1950s, but now seems to have disappeared altogether. These changes are the opposite of what would be expected following acidification, and greater nitrogen availability is a likely causal factor. An increase in the proportion of vascular plants on a bog means that less carbon is sequestered there, since litter from such plants breaks down far more rapidly than that from bryophytes (Malmer & Wallén 1993). Both increased abundance of vascular plants and changes in the composition of *Sphagnum* species could result in a release of carbon from bogs, further increasing greenhouse gas concentrations in the atmosphere.

CONCLUSIONS

Nitrogen deposition can have both a fertilizing (nutrient-enriching) and an acidifying effect, depending on the soil chemistry and vegetation of the areas exposed to it. Forbs, grasses, bryophytes and lichens are often more sensitive than forest trees, and effects on flora are therefore one of several criteria used in determining critical loads of nitrogen to different ecosystems. To what extent changes in the abundance of particular species are also due to changes in land use is not always very easy to decide.

Floristic changes can be described by means of retrospective studies and studies of responses to nitrogen fertilization, or by biochemical and physiological measurements, which can also indicate changes that have not yet had an impact on species composition. Concentrations of amino acids in plants increase with the supply of nitrogen, as do ratios of nitrogen to other nutrients. The causes of the vegetation changes that occur are competition between species that are favoured to differing degrees by nitrogen; elimination of species by soil acidification and the resultant higher concentrations of toxic substances or declining levels of nutrients; and increased parasite and herbivore attacks on plants.

Clearly, increased availability of nitrogen is affecting vegetation, particularly on soils that do not have a very low pH. Changes due to competition are usually slow and may be difficult to discover, but the research carried out, taken as a whole, shows nitrogen to be a significant factor. The vegetation changes, and the importance of nitrogen, are probably greater than has hitherto been appreciated, since little of the research undertaken covers the changes that took place in the middle of the 20th century, when nitrogen deposition was already high in many countries of Europe.

QUESTIONS AND ANSWERS

Does nitrogen deposition represent a threat to biodiversity?

Yes, if we are talking about the composition of the vegetation. Deposition of nitrogen alters the relative dominance of different species, with nitrophilous species becoming more abundant at the expense of those less favoured by nitrogen, partly because nitrophilous species are fast-growing and can compete successfully with smaller, slow-growing species. Species that can grow at low nitrogen levels, or produce their own nitrogen (nitrogen-fixing species), and species that are sensitive to parasite attack are put at a disadvantage by nitrogen deposition.

No, if we are talking about the number of species. If the soil is originally poor in nitrogen, an increased supply often enables more forest species to establish themselves. However, there is also a considerable risk of species not typical of the ecosystem beginning to grow in forests, in which case it is doubtful whether the larger number of species is to be welcomed.

Does nitrogen deposition pose a risk in terms of the abundance and range of threatened species in Sweden?

Yes, it represents a risk because of both its acidifying and its fertilizing effects. In Sweden, the largest numbers of threatened species are found in forests with relatively high pH and nutrient levels. The biggest threat therefore is probably the acidification caused by both nitrogen and sulphur deposition, rather than the additional input of nitrogen. In other parts of Europe, threatened species are often to be found on nitrogen-poor soils, where there is a danger of their being outcompeted by other, nitrophilous vegetation.

CRITICAL LOADS

HANS-ÖRJAN NOHRSTEDT AND ULLA BERTILLS

The concept of critical loads is being used at the international level to develop strategies aimed at reducing transboundary air pollution, the intention being to establish emission levels which the natural environment can withstand in the longer term. At a scientific workshop at Skokloster, Sweden, ‘critical load’ was defined as ‘a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge’ (Nilsson & Grennfelt 1988).

The concept is by no means simple or unambiguous. What, for example, constitutes a ‘harmful effect’? The effect concerned might conceivably be at the level of an entire ecosystem, or at the level of individual organisms or processes. If defined in relation to the most sensitive organisms of all, a critical load could be close to zero. In the case of nitrogen deposition, the basic principle is normally that critical loads should be set so as to avoid nitrogen-related acidification of the soil (Schulze *et al.* 1989, Sverdrup *et al.* 1992b), or leaching of nitrogen above a certain level (Johnson 1992, Rosén *et al.* 1992). Another guiding principle might be that there should be no enduring change in the composition of the flora. For terrestrial ecosystems, critical loads of nitrogen with respect to eutrophication are usually defined as the input per unit time that does not result in a long-term increase in nitrogen leaching or appreciably change the fauna and flora.

In the framework of the Convention on Long-Range Transboundary Air Pollution (CLRTAP), critical loads for nitrogen have been calculated from the point of view of eutrophication (nutrient enrichment). In Sweden, the calculations have been based on a relatively simple mass balance model and a philosophy of preventing elevated leaching of nitrogen and eutrophication effects on vegetation. The most important variables in such calculations are uptake of nitrogen by vegetation, leaching, immobilization and denitrification (Umweltbundesamt 1996).

A simplified formula for calculating the critical load of nutrient nitrogen is:

$$CL_{nut}(N) = N_i + N_u + N_{de} + N_{le}$$

where

N_i = immobilization of nitrogen in soil, N_u = net uptake of nitrogen into plants

N_{de} = denitrification, N_{le} = highest acceptable level of nitrogen leaching from the root zone

Critical loads of nutrient nitrogen are lower in the north of Sweden than in the south, but they are still exceeded to a greater degree in the south (see Bertills & Lövblad 2000 for further discussion).

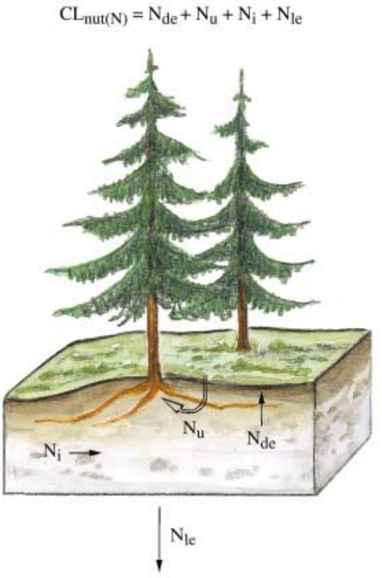


Figure 7.1.
Critical load of nutrient nitrogen – basic principles.
Illustration: Gun Lövdahl.

Critical loads with respect to leaching of nitrogen

Critical loads can be calculated by empirical methods, based on either field observations or experimental results, or by means of mass balance or process models.

Several theoretical estimates of critical loads have been made. Using a mass balance model, Rosén and co-workers (1992) arrived at values of 2–10 kg of nitrogen per hectare per year for Sweden/the Nordic countries. The results of calculations of this kind are determined to a large extent by the figures used for the net uptake of nitrogen into trees, and in the study just mentioned this parameter was computed as the net accumulation of nitrogen in stems, branches and needles during a forest rotation, which is equivalent to the amount removed when whole-tree harvesting is practised. The model used takes no account of the post-felling phase, or of the method of harvesting. Since branches and in particular needles contain large amounts of nitrogen, the felling method employed will crucially affect the critical load value derived on the basis of this model (Lundborg 1997).

In an analysis of the Nitrogen Saturation Experiments (NITREX), Reynolds and colleagues (1998) arrived by a similar method at a critical load of 3–8 kg of nitrogen per hectare per year for coniferous forests on acid soils, with no allowance made for the nitrogen removed by felling. If the nitrogen taken from forests with tree stems was taken into account, the critical load was 11–15 kg per hectare per year. These values are appreciably higher than those presented for the Nordic region by Rosén and co-workers (1992). This is because site fertility and hence immobilization of nitrogen in biomass have a substantial influence on critical load estimates. Soil fertility is higher further south, and all but one of the NITREX sites (Gårdsjön) were in central Europe. In the NITREX experiments, increased leaching of nitrogen was only observed when deposition exceeded the critical load by around 15 kg per hectare per year.

One weakness of mass balance models is that several of the quantities included, which are in fact dynamic variables, are treated as constants (Nohrstedt 1992). This is true both of uptake by vegetation, which can of course increase when more nitrogen is supplied to a nitrogen-limited system, and of the soil's capacity to retain nitrogen. The nitrogen retention capacity of the soil has often been overlooked (Skeffington & Wilson 1988), and is regarded as the most uncertain item in mass balance estimates (Aber 1992, Grennfelt & Thörnelöf 1992). On the basis of the nitrogen content of the soil at a number of Swedish mineral soil sites, Rosén and co-workers (1992) assumed a retention capacity of 0.5 kg of nitrogen per hectare per year, which tallies with the quantity of nitrogen that has accumulated in illuvial horizons since the last ice age. A study of 37 coniferous forest sites in southern Sweden suggests a mean rate of nitrogen accumulation in soil of 8.5 kg per hectare per year (Nilsson *et al.* 1998a). A status report from the Coordination Centre for Effects (CCE) proposes a figure of 2–5 kg per hectare per year (Posch *et al.* 1995). In none of the cases mentioned is any account taken of the fact that many of these forests used to burn at intervals of 50–150 years (Zackrisson 1977), which must have resulted in substantial losses of nitrogen (Ring 1997). The maximum retention capacity could possibly be appreciably higher, as many fertilization experiments in fact suggest.

Dynamic theoretical models have also been used to analyse under what conditions nitrogen leaching from forest ecosystems will increase and gradually approach the level of the input, i.e. when a 'saturated' state is reached (Ågren & Bosatta 1988, Aber *et al.* 1991; see box on nitrogen saturation in chapter 4 for further discussion). In these models, nitrogen has been linked to the cycling of carbon. According to the analyses performed using such models, only a very small input of nitrogen is possible if saturation is to be avoided in the long term. Ågren and Bosatta (1988) proposed, for the foreseeable future, a critical load of 10–20 kg nitrogen per hectare, which accords well with more empirically based analyses.

Empirical studies of critical loads, both in Sweden (IVL 1991, Nilsson *et al.* 1998a) and in Europe generally (Grennfelt & Hultberg 1986, Dise & Wright 1995, Tietema & Beijer 1995), show that clearly elevated leaching of nitrogen normally only occurs at deposition levels of more than 10–15 kg of nitrogen per hectare per year. A complication in this context is that leaching usually varies very widely, despite similar deposition levels (Grennfelt & Hultberg 1986, Dise & Wright 1995, Nohrstedt *et al.* 1996). Other factors, such as past land use and soil type, may be of great significance, as is discussed below. The low values for soil retention of nitrogen that are most commonly used in budget studies, as previously reported by Johnson (1992) for example, contrast to some extent with the results presented by Tietema and co-workers (1998b). Using a stable isotope technique (nitrogen-15), the latter studied retention at four central European sites used for NITREX experiments. These experiments were established in 35- to 75-year-old coniferous forests and involved nitrogen inputs, measured as throughfall, of 15–60 kg per hectare per year. At each site, inputs to individual plots were varied: either increased by supplying additional nitrogen, or reduced by constructing roofs. This provided, over the series as a whole, a gradient of nitrogen inputs from 4 to 91 kg per hectare per year. Sampling began when the treatments had been in progress for a year. This study demonstrated a not insignificant degree of soil retention of nitrogen. Anything from around 25% to 60% of the nitrogen supplied was retained in the soil, one- to two-thirds of it in the humus layer. The rate of retention in the soil was 2–24 kg per hectare per year, and showed a positive correlation with nitrogen inputs at three of the four sites.

Another NITREX experiment is in progress in the Lake Gårdsjön area in south-west Sweden. There, an extra 40 kg of nitrogen (ammonium nitrate) per hectare per year was applied by irrigation over five years. The increase in annual leaching corresponded to, at most, 6% of the nitrogen added (Hultberg *et al.* 1994, Wright *et al.* 1995, Moldan & Wright 1998). The great majority of the nitrogen entering the ecosystem thus remained there. From data reported by Kjønaas and co-workers (1998), it can be calculated that all this nitrogen was immobilized in the soil, with retention increasing from –2 kg per hectare per year in the control plot to 42 kg per hectare per year in the fertilized plot. This shows that soil has a large capacity to retain nitrogen in the short term, and that heavy deposition of this element results in its rapid accumulation in the soil.

Critical loads with respect to vegetation

In 1992, empirical critical load values were calculated under the auspices of CLRTAP (Bobbink *et al.* 1992), and this work was followed up four years later (Bobbink *et al.* 1996). Critical loads of nitrogen were determined on the basis of observed and published changes to different ecosystems, brought to light by experimental data, field observations or dynamic ecosystem models. As new data are produced and our understanding of the complex biological processes regulating the nitrogen cycle improves, these values may be revised. In some countries, critical nitrogen loads are estimated on the basis of empirical data relating to vegetation. Normally, such values are higher than those calculated with respect to the risk of nitrogen leaching. One explanation for this is that the data used relate to areas that have been exposed to large inputs of nitrogen over long periods. The following critical loads have been proposed, in kilograms of nitrogen per hectare per year (Bobbink *et al.* 1996):

Critical loads (kg N/ha/yr) with respect to vegetation changes

Forests: Coniferous forests on acid soils (7–20), deciduous forests on acid soils (10–20), forests on calcareous soils (15–20), unmanaged forests on acid soils (7–15). Heathlands: Dry lowland heaths (15–20), wet lowland heaths (17–22), species-rich heaths (10–15), upland *Calluna* heaths (10–20), Arctic and alpine heaths (5–15). Species-rich grasslands: Species-rich calcareous grasslands (15–35), neutral to acid grasslands (20–30), montane and subalpine grasslands (10–15). Wetlands: Mesotrophic fens (20–35), ombrotrophic bogs (5–10), shallow lakes (5–10).

Do fertilization experiments and budget studies result in different critical loads?

Different values for the nitrogen retention capacity of soils, for use in estimating critical loads, have previously been reported from budget studies of untreated sites and nitrogen fertilization experiments. As a rule, the latter have yielded considerably higher critical loads. There are a number of possible reasons why this could represent a systematic difference between the two approaches. The usefulness of results of fertilization experiments in predicting the effects of nitrogen deposition has previously been discussed by Miller and Miller (1988), Skeffington and Wilson (1988) and Johnson (1992), among others.

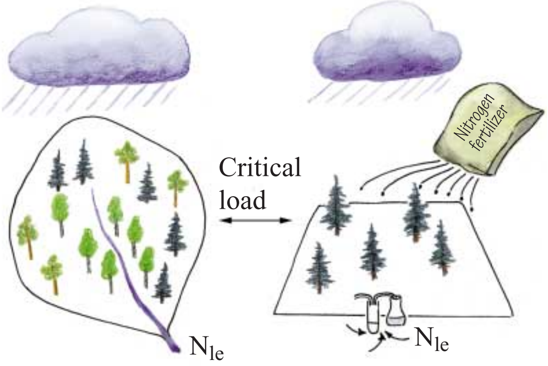


Figure 7.2.
Two ways of calculating critical loads: budget studies and fertilization experiments.
Illustration:
Gun Lövdahl

• DISTRIBUTION OF NITROGEN INPUTS OVER TIME

The distribution of additions of nitrogen over time can decisively influence the effects to which they give rise. It can for example affect how much nitrogen leaches from the soil, and how plants respond. Atmospheric deposition has a temporal distribution which matches fairly closely that of precipitation, with a relatively large proportion occurring during the colder half of the year, i.e. outside the growing season proper (Naturvårdsverket 1981). In fertilization experiments, nitrogen is usually applied within more limited periods – as a rule, during the growing season. Some experiments involve annual applications, in others fertilization is less frequent. Nitrogen additions affect the abundance of different plant species, causing some to expand and others to decline (for references, see Nohrstedt & Westling 1995). Within a few years of a single dose of nitrogen, plant communities often, although not always, return to their original state. It seems that the effects on cryptogams, especially lichens, may be more enduring than the effects on other groups of species. If nitrogen inputs are frequent, rather than confined to a single occasion, there is probably less chance of recovery. However, few systematic studies of this question have been undertaken. In many cases, data from fertilization experiments tend to overestimate critical loads and the soil's capacity to retain nitrogen.

• SITE CHARACTERISTICS

The characteristics of the site concerned may be assumed to significantly influence the effects of an input of nitrogen. Natural conditions and earlier anthropogenic perturbations can probably make a difference. Many Swedish fertilization experiments have been carried out at sites which are relatively northerly by European standards, and which were clearly deficient in nitrogen from the outset. In contrast, many budget studies which have shown low or zero retention of nitrogen in the soil have been undertaken at relatively southerly sites. Regarding the effects of past nitrogen inputs on leaching after a forest stand has been felled, a number of current Swedish studies (Ring 1996; Eva Ring, Forestry Research Institute of Sweden, personal communication; Nohrstedt *et al.* 1998b) suggest that leaching increases to a considerably lesser degree at originally nitrogen-rich sites than at previously nitrogen-poor sites. This is borne out by a Finnish study of a spruce forest growing on a fertile soil (Smolander *et al.* 1998). The results of fertilizer experiments at nitrogen-poor northern sites can scarcely be used generally as a basis for assessing the effects of nitrogen deposition at nitrogen-rich southern locations. However, in many southern Swedish forest ecosystems (Nilsson *et al.* 1998a) the soil appears to have a retention capacity almost on a par with those found in a number of northern fertilization experiments.

• Significance of stand age

A forest stand's ability to take up and store nitrogen affects how much nitrogen becomes available for leaching. Many fertilization experiments have been conducted in relatively mature stands, while deposition of course affects stands of all ages. Miller and Miller (1988), Johnson (1992) and Miller (1995) have argued that the age of a stand is of great significance for its nitrogen uptake, which decreases dramatically once the forest canopy has closed. Miller and Miller (1988) took the view that, for this reason, the absence of a response to nitrogen inputs to a stand could not be regarded as a meaningful definition of 'nitrogen saturation'. In forests in the south of Sweden, Nilsson and co-workers (1998a) found stand age to be negatively correlated to retention in the trees and the ecosystem as a whole. Possibly in contradiction to what has just been said, Kenk and Fischer (1988) and Pettersson (1994a) reported that stand age (over a range of approx. 20–220 years) had no influence on growth response following nitrogen fertilization.

• Composition of the nitrogen supplied

The form in which nitrogen is supplied to a forest can also influence the effects that arise. Different inorganic forms of nitrogen have differing propensities to evaporate, cause acute damage to vegetation, be taken up by plants, bind to soil particles and be leached from the soil. Atmospheric deposition supplies roughly equal quantities of ammonium and nitrate ions (Lövblad *et al.* 1995; chapter 3). The same is true of experimental applications of ammonium nitrate, but there are also many experiments in which plots have been treated with urea. Another difference between deposition and fertilization is that, in the first case, a large proportion of the nitrogen added is in a dissolved form, while in the second case solid forms predominate. The results of many fertilization experiments, especially those in which urea is applied at infrequent intervals, probably overestimate the retention capacity of the soil and the critical load. This is primarily because urea tends to be fixed chemically in organic matter and, in addition, to stimulate microbial immobilization to a greater extent than deposited ammonium and nitrate.

- **SIGNIFICANCE OF SCALE**

Although nitrogen deposition does vary spatially, on both a large and a small scale, it is fairly evenly spread over the landscape. In experiments, nitrogen is generally applied to plots of a few tenths of a hectare or less. Certain types of studies, e.g. of ground vegetation or soil water responses, sometimes make use of very small areas (just a few square metres). For various reasons, the effects of nitrogen inputs that emerge when small plots are used may differ from those observed when the nitrogen is supplied simultaneously to large stretches of countryside. In all likelihood, the results of fertilization experiments based on small areas overestimate the ecosystem's ability to absorb nitrogen. Ground- and especially field-layer vegetation is probably favoured more by applications of fertilizer nitrogen to small plots than by atmospheric deposition of nitrogen over larger areas. If this is indeed the case, possible reasons include edge effects, a lack of competition for light from the tree layer, and less pronounced herbivory and parasite attack.

- **SIGNIFICANCE OF ACCUMULATED NITROGEN**

Empirical models, which express the critical load as the present level of deposition in areas where leaching is elevated, have the weakness that historical nitrogen inputs are unknown (cf. Andersson 1997). Differences in historical inputs may partly explain the large variations in leaching that are observed at similar current deposition levels. Obviously, it is difficult to reconstruct historical inputs of nitrogen to individual forest plots. There is no clear correlation between the amount of nitrogen that has accumulated at a site and the rate of leaching (cf. Ågren & Bosatta 1988). By contrast, the ratio of carbon to nitrogen in the soil, which reflects the aggregate result of many external and internal ecosystem processes, has proved to be clearly correlated to leaching of nitrogen. Nitrogen inputs tend to reduce the C/N ratio of the soil (Nohrstedt 1990b, Andersson 1997), and it therefore seems likely that a continuous input of nitrogen will sooner or later result in increased leaching, above all of nitrate. This has in fact been verified experimentally (Nilsson *et al.* 1988a, Nohrstedt 1990b, Ring

1996, Berdén *et al.* 1997). However, nitrogen inputs in the form of fertilizer applications, and probably also in the form of deposition, do not produce an easily predictable change in the C/N ratio, since the nitrogen affects cycling of carbon in a way that varies from one site to another (Nohrstedt *et al.* 1989, Martikainen *et al.* 1989, Arnebrant *et al.* 1995).

CONCLUSIONS

Retention of nitrogen in the soil is currently the biggest source of uncertainty in the calculation of critical loads. New budget studies and also new fertilization experiments involving relatively small additions of nitrogen labelled with stable isotopes have partly modified our understanding of the capacity of forest soils to retain nitrogen. In southern Sweden, such soils appear to have a high retention capacity for nitrogen and, what is more, retention increases with deposition. There is also much to suggest that both tree species and soil type are factors of major significance. In addition, the isotope studies, carried out primarily as part of the NITREX project at sites in central Europe, have indicated a higher level of retention than expected. In budget studies, retention of nitrogen in the soil is calculated as the difference between other measured fluxes. The reliability of the values arrived at therefore depends entirely on how accurately those other fluxes have been determined. Several of the earliest budget studies only took wet deposition into account, presumably resulting in an underestimation of retention in soil at many sites. While the new budget studies have revised upwards such earlier estimates of retention capacity and critical loads, some new evaluations of fertilization experiments which have included the regeneration phase have tended to produce lower estimates than earlier experimental studies. The gap between the values obtained by these two empirical methods of calculating critical loads has thus narrowed, and the results of both are now closer to theoretical estimates of critical loads with respect to nitrogen saturation, which are of the order of 10–20 kg of nitrogen per hectare per year. Neither of the two empirical approaches takes account of historical inputs of nitrogen; they merely analyse whether there is a surplus in relation to current inputs. This often results in values that are below the present level of deposition. The ratio of carbon to nitrogen in the soil reflects past cycling of nutrients and, in various collations of data, has proved to co-vary closely with leaching of nitrogen. Increased leaching occurs at ratios below about 25, and this tallies closely with theoretical analyses. An analysis of soil carbon/nitrogen ratios is therefore probably important in the context of environmental monitoring.

QUESTIONS AND ANSWERS

Is it possible to identify forest soils with elevated leaching of nitrogen?

Yes, with a reasonable degree of probability. If nitrogen inputs in throughfall to a forest soil exceed 10 kg per hectare per year and the C/N ratio of the soil is lower than 25, the risk of leaching is appreciably increased. Such conditions only occur locally in the south of Sweden, in the vicinity of areas with intensive agriculture. Nitrogen concentrations in current-year needles of forest trees may also be a good indicator of an excess of this nutrient. The threshold value appears to be around 15–16 mg of nitrogen per gram dry weight.

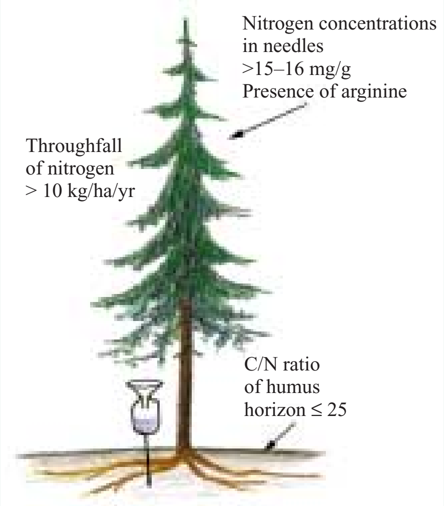


Figure 7.3. A forest at risk of increased leaching of nitrogen. Illustration: Gun Lövdahl.

Will leaching of nitrogen increase substantially over the next few decades (i.e. is there a risk of nitrogen saturation)?

There is nothing to suggest this. Experiments involving increased inputs of nitrogen (NITREX and other projects) show that leaching from acidified soils remains low even after long periods with high doses (40 kg of nitrogen per hectare per year). However, leaching may increase after final felling, or following applications of lime or ash to particularly nitrogen-rich soils.

Is nitrogen deposition contributing to the exceedance of critical loads with respect to acidification?

Yes, deposition of nitrogen is a significant factor behind the exceedance of critical loads. However, in most areas it is currently making only a small contribution to short-term acidification. In almost all areas of Sweden, nitrate accounts for less than 5% of the total concentration of nitrate + sulphate (in equivalent terms) in runoff from forest soils. The fact that critical loads are being exceeded means that, if nitrogen deposition remains at its present level, increased leaching of nitrogen may be expected in the future. It is uncertain, though, *when* a substantial increase in leaching will occur. What is more, critical loads have been set ‘on the safe side’: forest ecosystems probably have a greater long-term capacity to immobilize deposited nitrogen than the current critical load figures indicate.

WHAT HAPPENS WHEN NITROGEN DEPOSITION DECREASES?

MAUD QUIST, DAN BERGGREN,
TRYGGVE PERSSON AND RICHARD WRIGHT

Aware as we now are of the adverse effects of high levels of nitrogen in the environment, it is imperative to reduce the emissions that give rise to them. Major efforts are currently being made to adopt and implement international protocols to regulate these emissions (see chapter 2). A question that merits investigation, therefore, is what happens when nitrogen loads decrease. How is the nitrogen status of forest ecosystems affected? Can pre-industrial nitrogen levels be restored in systems that are currently saturated with this nutrient? How rapid is the recovery process? How are the organisms inhabiting forest ecosystems affected?

There are two possible ways of finding answers to these questions. One is to carry out field experiments in which large doses of nitrogen are applied over a long period and subsequently discontinued. Another is to build roofs to exclude nitrogen deposition and to irrigate the covered areas with nitrogen-free water. The first approach works best in areas with low nitrogen deposition, the second in regions where deposition is high. The experiments referred to in this chapter are outlined in table 8.1.

Nitrogen leaching decreases

• ROOF EXPERIMENTS

Far less nitrogen is leached from a nitrogen-saturated forest ecosystem when the input of nitrogen ceases or is appreciably reduced. This has been shown by experiments in which heavy deposition of nitrogen was reduced by the building of roofs (Wright *et al.* 1995, Bredemeier *et al.* 1998b).

At Ysselsteyn in the Netherlands, nitrogen deposition was reduced from 60 kg to less than 5 kg per hectare per year. As a result, leaching of nitrate from the soil was halved (from about 1 to around 0.5 mmol per litre) in one year. After a further three years of treatment with ‘clean rain’, nitrate leaching was down to a quarter of its original level (around 0.25 mmol per litre) (Boxman *et al.* 1995).

In the Solling Mountains in Germany, too, where annual nitrogen deposition is around 35 kg per hectare, a year’s treatment with clean rain resulted in a halving of nitrate leaching from the soil. After two years, leaching had fallen to a quarter of what it was before the roof was erected (Xu *et al.* 1998).

At Risdalsheia in Norway, which is exposed to nitrogen deposition of some 20 kg per hectare per year, leaching of nitrate from the catchment fell markedly after just two weeks of treatment with nitrate-free rain (Wright *et al.* 1993), and remained at a low level during the years that followed.

• OLD FERTILIZATION EXPERIMENTS

Long-term nitrogen fertilization experiments in Sweden, completed some time ago, also show that leaching of nitrogen declines rapidly when fertilization ceases.

In the fertilization experiment at Norrliden in Västerbotten, northern Sweden, leaching of nitrate abated when applications of the highest nitrogen dose, 90 kg per hectare per year (N3), were discontinued. After three years, nitrate leaching was at the same level as in the 30 kg treatment (N1), which was still in progress, and roughly a third of the level observed in the ongoing 60 kg treatment (N2) (Johannisson *et al.* 1999). In the N3 plots (with or without phosphorus and potassium), quantities of exchangeable nitrogen (ammonium + nitrate) in the humus layer and the top 20 cm of the mineral soil fell from about 40 kg per hectare (in 1988, when fertilization was still in progress; Tamm 1991) to barely measurable amounts seven years after the last fertilizer application, despite the fact that as much as 2160 kg of nitrogen per hectare had been applied over a period of 20 years (Quist *et al.* 1999). In other words, there is no build-up of a lasting pool of exchangeable nitrogen on colloid surfaces; instead, the nitrogen is immobilized in soil organic matter, living soil organisms and vegetation or, to some extent, leached out or possibly given off in gaseous form following denitrification.

In the optimum nutrition experiment at Stråsan in Dalarna, northern central Sweden, budget estimates show that roughly half the nitrogen added in the N3 treatment (90 kg per hectare per year) has leached from the system (Berggren *et al.* 1998). Three years after fertilization ended, leaching of inorganic nitrogen (ammonium + nitrate) from the soil system was as low as in the control plots (< 0.1 kg per hectare per year). Most of the nitrogen leached (0.3 kg per hectare per year) consisted of organic forms, a characteristic of undisturbed forest ecosystems, where nitrogen is a sought-after nutrient which is available in limited amounts and which is rapidly taken up and incorporated in organic compounds.

Table 8.1. Overview of the fertilization and roof experiments mentioned in the text. AN = ammonium nitrate, U = urea, LAN = ammonium nitrate with dolomite lime, Fertig = fertigation (irrigation with nutrient solution), ±PK = with or without phosphorus and/or potassium, DEP = deposition, ROOF = nitrogen applied under roof.

Fertilization experiment	Species	Form of nitrogen	Total dose (kg N/ha)	No./freq. of appl.	Period fertilized
Billingsjön, Härjedalen	Scots pine	AN and U	360–1800	3	1967–81
Hagfors, Värmland	Scots pine	LAN	300–600	2–4	1981–93
Jädraås, Gästrikland	Scots pine	AN Fertig	1790	Annual	1974–90
Lisselbo, Gästrikland	Scots pine	AN	540–1620	Annual	1969–88
Mangskog, Värmland	Norway spruce	U	480–2400	4	1967–82
Norrliden, Västerbotten	Scots pine	AN±PK	930 (N1)	Annual	1971–
		AN±PK	1860 (N2)	Annual	1971–
		AN±PK	2160 (N3)	Annual	1971–90
Stråsan, Dalarna	Norway spruce	AN	1060 (N1)	Annual	1967–
		AN	1760 (N2)	Annual	1967–90
		AN	2820 (N3)	Annual	1967–92
		AN+P	730 (N1)	Annual	1967–85
		AN+P	1700 (N2)	Annual	1967–89

Roof experiment	Species		Total dose (kg N/ha)
Ysselsteyn, Netherlands	Norway spruce	DEP	60/year
		ROOF	<5/year
Solling, Germany	Norway spruce	DEP	35/year
		ROOF	7/year
Risdalsheia, Norway	Norway spruce	DEP	20/year
		ROOF	2/year

Levels of plant-available nitrogen fall

When an input of nitrogen ceases, concentrations of the nutrient in plants fall, showing that the amounts of plant-available nitrogen in the soil are decreasing.

• Concentrations in needles

At Norrliden, a downward trend in nitrogen concentrations in Scots pine needles was observed only two years after the N3 treatment ended. Where phosphorus and potassium had been applied at the same time as the nitrogen, however, the effect of stopping the nitrogen applications appears to have been delayed by a year or so (Quist *et al.* 1999). Seven years after the N3 treatment had been stopped, needle nitrogen levels had fallen from about 1.8% to 1.5% (figures 8.1a and b), which was comparable to the levels observed in N1 and significantly lower than those recorded in the N2 plots (about 1.8%). Concentrations were still higher than in the control plots, however, where they were around 1.2%. Seven years after completion of the N3 treatment, nitrogen concentrations in pine roots and in leaves of wavy hair-grass (*Deschampsia flexuosa*) were at the same level as in N1 and hence lower than in N2, but still higher than in the unfertilized control plots (Quist *et al.* 1999).

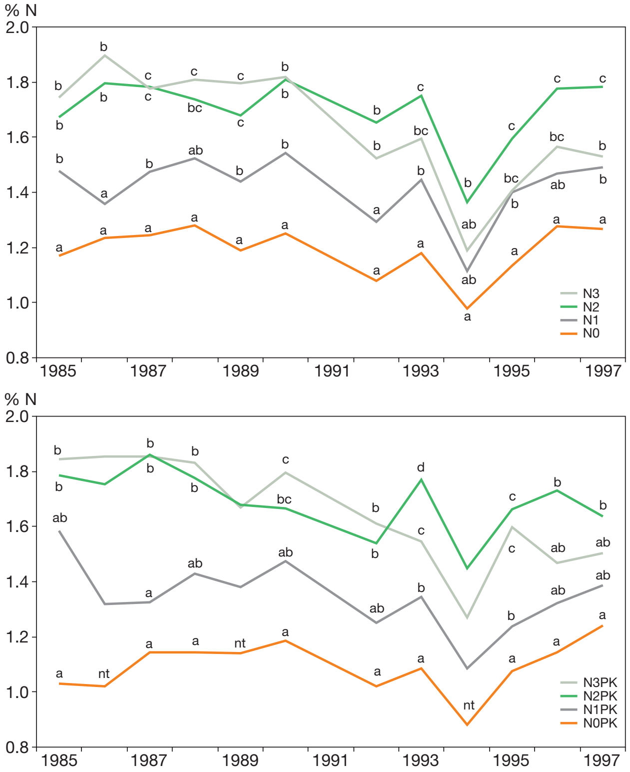


Figure 8.1, a and b. Average nitrogen concentrations (% dry weight) in current-year pine needles in the Norrliden fertilization experiment. The last N3 and N3PK applications were performed in 1990, while the others are continuing. Differences between treatments are significant if the points representing them have no letter in common within a given year (nt = not testable as n = 1 in some treatments) (Quist *et al.* 1999).

At Stråsan, four and six years after the last application of nitrogen in N3 and N2, respectively, nitrogen concentrations in Norway spruce needles had fallen to the same level as in needles from the N1 plots (where fertilization was still in progress) (Andersson 1997).

At Lisselbo in Gästrikland, on the other hand, concentrations of nitrogen in Scots pine needles remained at a more or less constant level of around 1.6% throughout the five-year period after the N3 treatment had ended (Edfast *et al.* 1996).

In the roof project at Ysselsteyn, nitrogen levels in pine needles were found to have declined and ratios of magnesium and potassium to nitrogen to have increased two to three years after the nitrogen input had been reduced. However, nitrogen concentrations were still over 2%, which is high compared with what is regarded as the optimum level of around 1.4–1.8% (Boxman *et al.* 1998b).

• INDIRECT MEASURES OF PLANT-AVAILABLE NITROGEN

There are several useful indirect measures of the amounts of plant-available nitrogen in the soil, for example arginine concentrations, ^{15}N bioassay and nitrate reductase activity (NRA), which are explained below.

If nitrogen is available in excess in relation to other nutrients, plants can store it in the form of the amino acid arginine. In needles collected from N3 plots at Norrliden seven years after the treatment had ended, arginine levels were roughly comparable to those found in needles from N1 plots, but still high compared with the unfertilized control. Two or three years without nitrogen inputs were sufficient to reduce the concentration of this amino acid to below the level found in the N2 plots (Quist *et al.* 1999). At Lisselbo, needle arginine fell appreciably three years after termination of the N3 treatment, suggesting that the nutrient imbalance that had been caused by fertilization could be corrected by stopping the supply of nitrogen. The same decrease in arginine levels was obtained if supplementary doses of phosphorus, potassium and magnesium were applied after nitrogen fertilization was discontinued (Edfast *et al.* 1996). At Ysselsteyn, a decline in arginine concentrations was observed within just a year of nitrogen inputs being reduced. However, even after five years, they were still considerably higher than in unpolluted areas of northern Sweden, for example (Boxman *et al.* 1998b).

Measurements of root uptake of ^{15}N-labelled ammonium provide an indication of how ‘starved’ of nitrogen plants are. A high uptake shows that there is a deficiency of plant-available nitrogen in the soil. Two years after the final N3 treatment at Norrliden, uptake of nitrogen had risen to the level found in N2 plots, or somewhat higher (Jones *et al.* 1994). After a further five years this trend had been reinforced, nitrogen uptake in the N3 plots then being at the same level as in N1 plots or even higher, pointing to an appreciable decrease in the amount of plant-available nitrogen after fertilization had ceased (see figure 5.2; Quist *et al.* 1999). When ^{15}N-labelled ammonium-nitrogen was added to humus samples from Jädraås, it was taken up equally effectively in samples from plots previously fertilized with nitrogen and in those from the unfertilized control (Sjöberg & Persson 1998). In other words, nitrogen availability now appeared to be the limiting factor for assimilation in both treatments. However, immobilization was more rapid in the control plots: one hour after the ammonium-nitrogen had been added, a larger quantity of ^{15}N was found in organic matter in samples from those plots than in the samples from previously fertilized plots.

The activity of the enzyme nitrate reductase (NRA) provides a measure of the availability of nitrate in the soil. When fertilization was still in progress in all the treatments at Norrliden, the highest NRA in wavy hair-grass was found in N3. Two years after the final fertilizer applications in the N3 plots, NRA in this species had fallen to the level found in the N2 treatment, and after a total of seven years it had decreased further, reaching a value between those recorded in the N1 and control plots (figure 8.2). This means that levels of plant-available nitrate had declined (Quist *et al.* 1999). It should be noted, however, that the fertilizer used included nitrate.

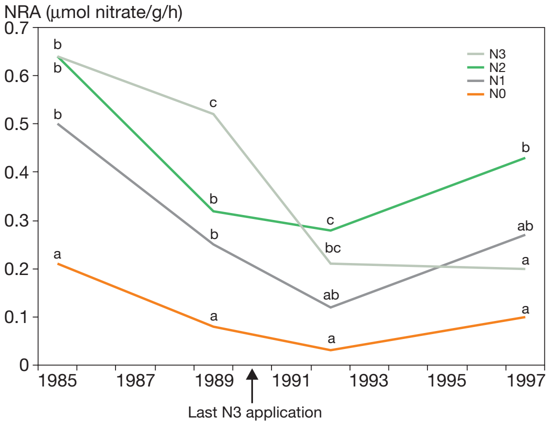


Figure 8.2.
Average nitrate reductase activity (NRA) in leaves of wavy hair-grass (*Deschampsia flexuosa*) at Norrliden. Nitrate availability decreased appreciably when nitrogen fertilization was discontinued. The last N3 application was performed in 1990 (Quist *et al.* 1999).

Soil pool of organic nitrogen changes slowly

The rapid and marked reduction of nitrogen leaching and plant-available nitrogen is not matched by a similarly rapid decrease in the internal cycling of this element. When a high input of nitrogen persists over a long period, a large proportion of the nitrogen is immobilized in organic matter in the soil. This is achieved by an increase in forest growth and hence in litter production, on the one hand, and by immobilization in soil organic matter by micro-organisms, on the other. Budget estimates at Stråsan, for example, showed that between 65% and 88% of the nitrogen that had accumulated in the forest ecosystem was to be found in the soil (litter and mor horizons), the rest in the trees (Andersson 1997).

A higher input of nitrogen results in an increase not only in the amount of nitrogen in the soil, but also in the ratio of nitrogen to organic carbon (i.e. a reduction of the C/N ratio). This means that the organic matter present becomes richer in nitrogen, which in turn increases internal cycling of this element. Changes in the C/N ratio of organic matter have been demonstrated in a number of fertilization experiments in Sweden. At Stråsan, the C/N ratio of the organic soil horizons was found to be considerably lower in fertilized and previously fertilized plots (C/N = 25–30) than in control plots (C/N = approx. 40) (Andersson 1997). Similarly, in an experiment at Mangskog in Värmland, western central Sweden, which was followed up 13 years after the final fertilizer application, the C/N ratio of the humus horizon was lower when the nitrogen dose was higher (Nohrstedt *et al.* 1998a). In the Jädraås experiment in Gästrikland (Sjöberg & Persson 1998), too, a lower C/N ratio was found in previously fertilized plots (approx. 24) than in control plots (approx. 37). Within the EU NITREX project, low C/N ratios in the humus layer were shown to be associated with high deposition of nitrogen, and vice versa (Gundersen *et al.* 1998b).

While fertilization was still in progress at Jädraås, the input of nitrogen was found to inhibit mineralization of carbon in the humus horizon (Persson *et al.* 1989). At that time, carbon mineralization was roughly three times lower in nitrogen-fertilized than in non-fertilized plots. This difference could no longer be observed four years after the fertilizer treatment had ended, suggesting that the sites had recovered. No difference in microbial activity (measured as release of carbon dioxide) could be detected, although the microbial biomass was greater in the control than in the plots previously fertilized with nitrogen (Sjöberg & Persson 1998). At Ysselsteyn, both microbial biomass and respiration were higher four years after nitrogen deposition had been substantially reduced, compared with plots still exposed to the prevailing level of deposition (Tietema & van

Dam 1996). Nilsson and co-workers (1998b) recently showed there to be a strong correlation between the net mineralization rate and the C/N ratio of the mor horizon at several locations in Sweden, including the NITREX sites and sites that had been fertilized with nitrogen over a long period (Stråsan, Flakaliden and Skogaby).

Felling of nitrogen-enriched forest stands may cause nitrogen leaching

A high input of nitrogen over a long period thus increases both the nitrogen content of organic matter and internal cycling of nitrogen. Turnover of nitrogen increases long before any inorganic nitrogen is leached from the system. It takes far longer to lower the nitrogen status of a system than it does to reduce leaching of nitrogen from it. This is because the availability of the nitrogen added is probably only reduced as the soil store of nitrogen is 'diluted' with carbon assimilated by vegetation and then added to the soil in litter (giving a higher C/N ratio), or as the bioavailability of the organic nitrogen compounds in the soil decreases over time. Both these processes are relatively slow. Nitrogen cycling thus remains high for a long time after leaching has been reduced. This means that nitrate can still be leached several years after the input of nitrogen has ceased, if the system is disturbed in any way.

One year after the previously fertilized spruce stands in plots N1P1 and N2P2 at Stråsan in Dalarna had been felled, significant leaching of nitrate from the soil was recorded (Berdén *et al.* 1997). By that time, six years (N1P1) and two years (N2P2) had elapsed since the last fertilizer application. In the case of the N1P1 plots, leaching increased from 0 to about 7 kg of nitrate-nitrogen per hectare after felling; from the N2P2 plots, it rose from about 5 kg of nitrate-nitrogen per hectare before to some 34 kg after felling. In addition, soil water from the previously nitrogen-fertilized plots had a lower pH and a higher concentration of inorganic monomeric aluminium (a toxic form) than water from the control plots.

Similarly, when a Scots pine stand previously fertilized with nitrogen at Billingsjön in Härjedalen (northern Sweden) was harvested, elevated leaching of nitrate was observed three to six years after felling, which was ten years after the last application of fertilizer (Ring 1995, 1996). Nitrate leaching was significantly higher from the plots given the largest nitrogen doses than from those that had not been fertilized; this was due to increased nitrification, which also resulted in a lower pH in the soil solution. Even before the stand was felled, some leaching of nitrate occurred from the most heavily fertilized plots, but during the first two years after felling no increase in leaching was recorded (Nohrstedt *et al.* 1994).

Unclear effect on growth

The diameter growth of Scots pine at Ysselsteyn (Boxman *et al.* 1998b) and of spruce in the Solling area (Bredemeier *et al.* 1998a) increased after atmospheric deposition had been excluded. This may have been because the nitrogen input had previously been supraoptimal. It should be remembered, though, that the deposition of sulphur and protons was also reduced, and this could equally well have been responsible for the higher growth rate. The diameter growth of pine on N3 plots at Norrliden between 1989 and 1998 (the N3 treatment ended in 1990) was comparable to that observed on control plots and lower than the growth recorded on N1 and N2 plots (M. Quist and B. Elfving, unpublished). Whether this was due to a lingering adverse effect of earlier supraoptimal nitrogen inputs, or to nitrogen supplies having been suboptimal for the last eight years, is unclear. Seven years after the final fertilizer application, the length of current-year shoots on N3 plots was roughly comparable to shoot length on N2 plots and significantly greater than that recorded on the control plots.

Recovery of vegetation can take a long time

Increased availability of nitrogen results in changes in the species composition of the field-layer vegetation (see chapter 6; Bobbink *et al.* 1998, Brunet *et al.* 1998). At Norrliden, species such as wavy hair-grass (*Deschampsia flexuosa*), narrow buckler fern (*Dryopteris carthusiana*), rosebay willowherb (*Epilobium angustifolium*) and hairy wood-rush (*Luzula pilosa*) became more abundant, at the expense of cowberry (*Vaccinium vitis-idaea*), bilberry (*Vaccinium myrtillus*) and lichens. Eight years after nitrogen fertilization was discontinued, there are no signs of the vegetation reverting to its unfertilized state (Quist *et al.* 1999). At Hagfors, too, lichens were adversely affected by nitrogen fertilization, an effect that was still in evidence eight years

ROSEBAY WILLOWHERB
PHOTO: PER-OLOV ERIKSSON/N

after the final fertilizer treatment (Nohrstedt 1998). Vegetation changes probably take considerably longer than this, since they are dependent on the ability of species to establish themselves and on their relative competitiveness. We do not know how species composition will develop over time. In the Norway spruce forest at Stråsan, there is still no undergrowth, four and six years after fertilization with nitrogen ended. In this case, the reason may be that the closed stands are effectively preventing light reaching the ground (Andersson 1997). At Ysselsteyn, six years after nitrogen inputs were reduced, the field-layer species that had previously declined as a result of the abundant supply of nitrogen have yet to re-establish themselves, even though the dominant nitrophilous species, raspberry (*Rubus idaeus*) and broad buckler fern (*Dryopteris dilatata*), are cut back every year (Boxman *et al.* 1998b).

Increased availability of nitrogen also results in changes in the species composition of mycorrhizal fungi (Kårén 1997). There are signs that the macrofungal flora at Ysselsteyn is recovering. The number of fruiting bodies increased from 0 to 70 per 100 m^2 in four years, but they were confined to just one or two species (Boxman *et al.* 1998b). The frequency of mycorrhizal fine roots increased at both Ysselsteyn and Solling when the roofs were constructed (Boxman *et al.* 1998a). In general, though, the roof projects show that it takes more than six years of substantially reduced nitrogen deposition to bring about any clear response in the majority of the organisms studied (Boxman *et al.* 1998a).

CONCLUSIONS

Nitrogen saturation of forest ecosystems appears to be a reversible condition. Only a couple of years after inputs of nitrogen have been reduced, leaching of nitrogen and levels of plant-available forms of the nutrient in the soil decrease. This can be seen both from roof experiments, in which nitrogen deposition was excluded, and from completed fertilization experiments. The reversal process probably occurs at different rates in different systems, depending on such factors as initial nitrogen status and climate. The rapid and marked decrease in nitrogen leaching and the quantity of plant-available nitrogen is not, however, matched by an equally rapid reduction of internal cycling of this nutrient, nor does it mean that pre-industrial nitrogen levels are restored. We still have an inadequate understanding of what happens to nitrogen cycling in systems that have accumulated large quantities of this element, particularly if they are disturbed in various ways. Soils previously fertilized with nitrogen have for example been found to leach considerable amounts of nitrate following felling. However, a period of eight years after nitrogen applications have ceased does not appear to be long enough for the species composition of the vegetation to change in the direction of a nitrogen-limited community. Vegetation changes probably take longer than this, and we do not know how species composition will develop over time.

QUESTIONS AND ANSWERS

How rapidly do ecosystems damaged by nitrogen deposition recover when the load is reduced?

In experiments, when inputs of nitrogen are reduced almost to zero, leaching of inorganic nitrogen falls to low levels within a couple of years. The amounts of nitrogen directly available to plants also decrease rapidly in the years immediately following the cessation of inputs. Systems exposed to high deposition of nitrogen over a long period accumulate large quantities of this element, in plants and above all in organic matter in the soil. This can result in nitrogen being leached when trees are felled. It takes a long time for the vegetation to return to its initial state. Experiments show that, ten years after nitrogen inputs are stopped, the flora is still dominated by species favoured by nitrogen.

HOW ARE SOILS AND PLANTS AFFECTED BY NITROGEN DEPOSITION?

– A SYNTHESIS

TORGNY NÄSHOLM AND TRYGGVE PERSSON

Atmospheric deposition of nitrogen changes forest ecosystems in many different ways. It affects the flora of the forest floor, and also the species composition of mycorrhizal fungi and the number of fruiting bodies they produce. High inputs of nitrogen can lead to soil acidification and leaching of nitrate. However, studies in this field have provided no evidence that current levels of nitrogen deposition in Sweden are making the country's forest ecosystems less stable. In other words, deposition of nitrogen has considerable potential to alter biotic communities and the functioning of ecosystems, but most studies suggest that real damage to forests only occurs at very high deposition levels. Most forest ecosystems in Scandinavia are nitrogen-limited, and it therefore seems likely that deposition of this nutrient will result in an increase in tree growth in this region. A higher rate of growth means more timber and, at the same time, increased sequestration of carbon dioxide. There thus appears to be a potential conflict of interests, deposition of nitrogen having both beneficial and detrimental effects.

Critical loads – an assessment of how much nature can withstand

Considerable effort has been devoted to establishing critical loads, i.e. the levels of particular pollutants to which the natural environment can be exposed without harmful consequences arising for different ecosystem components. In negotiations on emission reductions, critical loads have proved an effective means of quantifying and illustrating the scale of adverse effects on ecosystems. Having defined levels of nitrogen deposition below which harmful effects do not occur, it is then possible to determine the area in which these critical loads are currently being exceeded. Ultimately, though, any attempt to define critical loads of nitrogen is dependent on our understanding of how nitrogen deposition affects forest and other ecosystems. It can be argued that, in nitrogen-limited ecosystems like the forests of Scandinavia, any increase in the supply of nitrogen will have effects. The critical load will then be determined by the level of effects which we consider harmful. This in turn leaves considerable room for subjectivity. How, for example, do we decide what constitutes a critical percentage cover of grasses in a forest where the field layer is naturally dominated by dwarf shrubs such as bilberry and cowberry? And how do we determine what changes in the species composition of mycorrhizal fungi can and cannot be accepted? A further complication is that we have to take into account the rates at which particular changes to the ecosystem occur at different levels of nitrogen deposition. One undesirable effect of nitrogen deposition is an increased risk of leaching of nitrogen. As chapter 4 makes clear, however, relatively few forest stands in Sweden are in fact leaching nitrogen. Consequently, if present-day nitrogen leaching from forest soils is used as the criterion for establishing the critical load, deposition will be found to be below the critical level virtually throughout the country. We will then be in danger of overlooking other effects of nitrogen deposition, effects which are perhaps more difficult to classify as ‘detrimental’ or ‘beneficial’, but which nevertheless represent significant changes to the forest ecosystem.

Nitrogen can cause acidification

Apart from the fertilizing (nutrient-enriching) effects discussed above, nitrogen deposition can also bring about changes in the pH of the soil (figure 9.1). With regard to pH, too, it is far more difficult to establish what effects nitrogen deposition will have on forest soils than it is in the case of sulphur deposition. This is because nitrogen can either cause or counteract acidification, depending on the form in which it is present. Nitrogen represents the biggest single component of the mineral nutrient uptake of trees (and other plants) from the soil. When ammonium ions are taken up by roots, the surrounding soil is acidified, while the opposite is true when nitrate ions are taken up. Uptake and metabolism of nitrate result in hydrogen ions being consumed, leading to lower acidity. However, whichever ionic form is involved, a higher uptake of nitrogen also means that cations (such as potassium and magnesium) have to be taken up to balance the nitrogen in the plant. This uptake results in a certain degree of acidification, and in a mature stand of Scots pine or Norway spruce the acidifying effect of cation uptake (excluding nitrogen) may be assumed to be 0.7 units of hydrogen ions per unit of nitrogen taken up (in terms of equivalents; figure 9.1). Thus, if the trees accumulate 14 kg of nitrogen per hectare per year (a reasonable figure for southern Sweden) and take this nitrogen up as ammonium, then 1 kg of hydrogen ions will be added to the soil as a result of the uptake of ammonium and 0.7 kg of hydrogen ions as a result of the uptake of other positively charged ions. However, this acidification is counteracted by mineralization in the soil itself. If, say, 5 kg of ammonium-nitrogen and 5 kg of nitrate-nitrogen per hectare per year are added to the soil and this nitrogen is taken up by vegetation, then these two forms of nitrogen will balance each other in terms of hydrogen ions. The uptake of 10 kg of nitrogen per hectare, however, will result in an additional uptake of base cations that causes acidification corresponding to 0.5 kg of hydrogen ions per hectare per year.

Another cause of acidification is the nitrification of ammonium to nitrate. Nitrification results in the production of hydrogen ions, but if the nitrate formed is taken up by vegetation this form of acidification is neutralized. However, no neutralization occurs if the nitrate is leached from the soil. The role of nitrogen in the acidification of forest soils thus depends on several factors, making it difficult to predict the net effect. Probably, however, nitrogen's nutrient-enriching effect is greater and more thoroughgoing than its contribution to acidification.

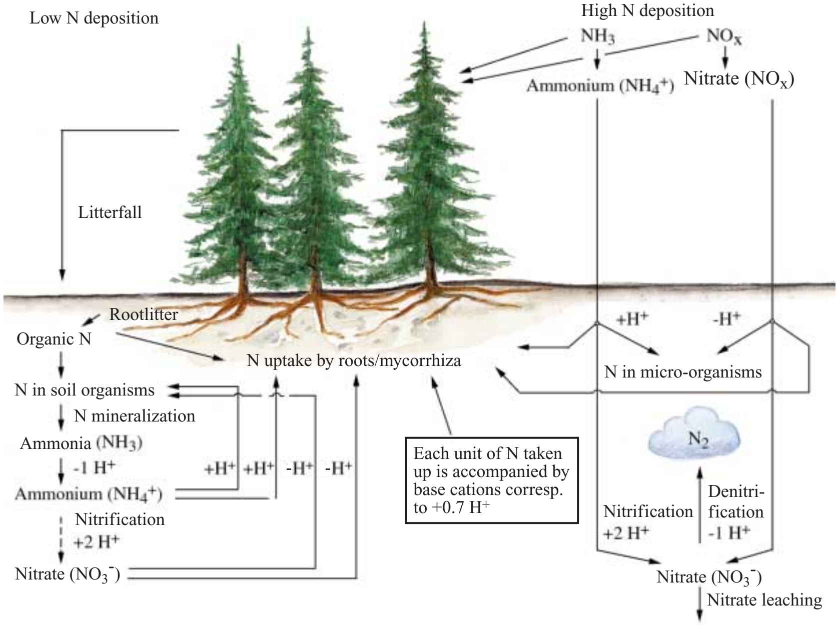


Figure 9.1. The effects of nitrogen cycling on soil acidification at low and high levels of nitrogen deposition. +1 H^+ means that one unit of hydrogen ions is released and –1 H^+ that one unit of hydrogen ions is consumed per unit of nitrogen turned over. Every unit of nitrogen that is taken up by plant roots and added to the biomass of the plant is accompanied by base cations. This uptake also contributes to soil acidification when deposited nitrogen enters the cycle. The figure +0.7 H^+ per unit of nitrogen is an average estimated uptake for Scots pine and Norway spruce stands. If all the processes are added together, we find that ammonium deposition, nitrification and removal of trees (particularly whole-tree harvesting) promote soil acidification, whereas nitrate deposition slightly counteracts acidification and denitrification (to gaseous nitrogen) has a clearly counteracting effect. Leaching of nitrate reduces the acidification-inhibiting effect and results in simultaneous leaching of aluminium and/or base cations.
Illustration: Gun Lövdahl.

Large local variations in nitrogen deposition mean that effects vary widely

Atmospheric deposition of nitrogen is highest in the south and south-west of Sweden and decreases towards the north and north-east. In addition, local emissions of ammonia and nitrogen oxides, as well as the structure of the landscape, give rise to considerable local variations in deposition. For example, deposition is much higher on the edges than in the middle of a forest stand (see chapter 6; Grennfelt & Hultberg 1986). These wide local variations in deposition mean that we can expect substantial variations in effects, even over relatively limited areas.

Nitrogen deposition occurs in both wet and dry forms. Dry deposition consists of particles and gases, chiefly ammonia (NH_3) and nitrogen oxides (NO_x). Wet deposition is relatively easy to estimate, being the product of the amount of precipitation and the concentration of nitrogen in the precipitation. Dry deposition is far more difficult to estimate, since account has to be taken of atmospheric concentrations, deposition velocities to surfaces and uptake through stomata, as well as data on the total needle and/or leaf area of a stand. Owing to all these different factors, we have a clearer picture of the distribution and scale of the wet than of the dry component of nitrogen deposition. Nitrogen compounds can be both taken up from and released into water passing through the crown of a tree, and both the needles or leaves of the tree and the lichens, bryophytes and green algae growing on its surfaces are involved in these processes. For this reason, throughfall does not provide an accurate measure of total nitrogen deposition. In situations where dry deposition of nitrogen is high, e.g. in the vicinity of local ammonia sources, the true level of deposition may be appreciably higher than is indicated by measurements of deposition in throughfall. Modelling studies have indicated that, in southern and south-west Sweden, dry deposition makes a significant contribution to the total atmospheric input of nitrogen.

Soil – an effective nitrogen sink

Pollution of surface and ground waters is one of the most serious problems that follows in the wake of nitrogen deposition, and it is widespread in central Europe, especially the Netherlands. The need for treatment to remove nitrogen pollutants, primarily nitrate, greatly increases the cost of producing drinking water. In Sweden, attention has been drawn to leaching of nutrients from farmland into coastal sea areas, as a cause of eutrophication and losses of benthic fauna. Fears have been expressed about a possible increase in leaching of nutrients, particularly nitrogen, from forest soils, prompting research in this area. However, virtually all the studies undertaken have shown that forest soils still provide an effective sink for the nitrogen supplied by deposition (Binkley & Högberg 1997).

Retention of incoming nitrogen has been found to be very strong, and only small quantities appear to leach into surface and ground waters (see chapter 4). The mechanisms behind this retention are still largely unknown. What is clear, however, is that large amounts of nitrogen bind to soil organic matter and that certain fractions of this matter, especially the fraction occurring at greater depth in the soil, are broken down and turned over very slowly. In experiments in which nitrogen was applied to forest stands for many years, the availability of nitrogen in the soil was found to fall rapidly when applications were subsequently discontinued (see chapter 8; Quist *et al.* 1999).

Where nitrogen is leached from forest soils, it is chiefly in the form of nitrate, which may originate partly from deposition, and partly from production within the system. As was noted earlier, nitrate is produced by nitrification, and there is much to suggest that this is a key process with regard to nitrogen leaching. Whether or not it occurs in a soil depends on many different factors. Provided that nitrifying organisms are present, nitrification will chiefly be regulated by the concentration of ammonium (NH_4^+) ions, pH, oxygen levels, temperature and soil moisture. In nitrogen-limited systems – in this case, forest stands in which biomass production is limited by the availability of nitrogen – the competition for any nitrogen mobilized in the soil is fierce. Nitrifying organisms are usually regarded as weak competitors for nitrogen in such circumstances. When nitrogen is added to the system by deposition, concentrations of this element in the soil solution will rise. At the same time, as a number of studies have shown (see chapter 5), the instantaneous nitrogen uptake rate of tree roots will fall. More nitrogen will thus be left behind in the soil and the competition for it will consequently decrease. It seems likely that it is in this situation that nitrifiers are able to compete for ammonium in the soil. Thus, if more ammonium is liberated in the soil than plants (including their mycorrhizas) are able to assimilate, the conditions are right for nitrifiers and hence for the production of nitrate. If this nitrate is not taken up by vegetation, there is a risk of it being leached from the forest soil.

More abundant nitrogen reduces root biomass and nitrogen uptake

As has just been mentioned, the instantaneous nitrogen uptake rate of roots decreases when the supply of this element increases. At the same time, an enhanced supply of nitrogen causes a reallocation of tree biomass, in the form of a decrease in root biomass in proportion to the biomass of shoots (Majdi & Kangas 1997). This effect can render trees more sensitive to drought and storms, for example. However, there is no evidence at present that the ability of forest trees to withstand such stresses is adversely affected by the levels of nitrogen deposition currently occurring in Sweden.

Nitrogen changes the species composition of mycorrhizal fungi

Mycorrhizas are significantly affected by an increased supply of nitrogen (see chapter 5). The studies cited in this report show that, in stands exposed to nitrogen inputs over many years, virtually all the fine roots are still colonized by mycorrhizas. The studies also reveal, though, that certain types of mycorrhizal fungi disappear following fertilization with nitrogen, while others become more abundant. For example, *Cortinarius* species decline, while *Lactarius rufus* (rufous milk-cap) becomes more widespread. Such changes in species composition may represent a problem on several counts. First, and above all, there is a risk of nitrogen deposition leading to a depletion of biodiversity, given the normally very high species diversity of mycorrhizal fungi. Second, it is likely that shifts in balance from one species to another will also entail functional changes of some kind. In coniferous forest ecosystems, many mycorrhizal fungi perform key functions as decomposers of moderately complex substances, thanks to their ability to secrete various hydrolytic enzymes. These fungi might be put at a disadvantage by elevated soil concentrations of inorganic nitrogen, and this could reduce the turnover of soil organic matter. In addition, the biodiversity of higher plants has been found to be linked to that of mycorrhizal fungi, and several studies have shown biodiversity to be positively correlated to both ecosystem stability and biomass production. There is thus good reason to regard the effects of nitrogen on mycorrhizal fungi with considerable concern.

Nitrogen deposition not a threat to trees in the short term

While we have a relatively good understanding of how nitrogen fertilization affects forest trees, there is still some uncertainty as to how well it simulates the effects of atmospheric deposition. Normally, the amount of nitrogen taken up by needles or leaves is relatively small compared with the total uptake (Pearson & Stewart 1993, Wellburn 1991). The main exception is where levels of ammonia (NH_3) are high, as can be the case in the vicinity of local emission sources such as chicken, pig or fur farms; in such areas, a significant proportion of the nitrogen taken up by plants may pass through leaves or needles (Pearson & Stewart 1993). Uptake of nitrogen via foliage may have different effects to uptake by other routes, effects not linked primarily to the amount of nitrogen involved, but rather to the qualitative nature of the uptake. It has for example been found that nitric oxide (NO) acts as a chemical messenger in plants, a role that has received considerable attention in human medicine. Uptake of nitric oxide from the atmosphere could thus interfere with plants' chemical signal systems, causing physiological disturbances. It has also been claimed that uptake of ammonia might affect the internal regulation of pH in plants (Pearson & Stewart 1993). Nitrogen deposition therefore not only entails a quantitative increase in nitrogen availability in forest ecosystems, but also a qualitative change in terms of in what parts of plants and in what forms the nitrogen is taken up.

Apart from the increased levels of various nitrogen compounds in air, atmospheric deposition entails a shift in the available forms of nitrogen in the soil. In boreal coniferous forests, soils have high concentrations of organic nitrogen compounds, such as free amino acids, amides and amines, and low levels of inorganic nitrogen, i.e. ammonium and nitrate (Näsholm *et al.* 1998). Nitrogen deposition results in a relative increase in inorganic forms of nitrogen, compared with organic forms. What such qualitative changes in plant-available nitrogen entail in terms of the conditions for competition between different plant species is not known, though. While we can, to some extent at least, describe the effects of nitrogen deposition on forest trees, we still know too little to establish how these changes will affect tree survival, growth and reproduction in the long term (see chapter 5). However, the many fears about the detrimental effects of nitrogen that were voiced in the mid-1980s have not been borne out by experimental studies. In the Skogaby experiment in Halland, south-west Sweden, for example, the trees have admittedly shown a gradual decline in growth during the last few years of treatment, but this effect did not manifest itself until very large doses of nitrogen and sulphur (100 kg of nitrogen and 114 kg of sulphur per hectare per year) had been applied over a good many years. While certain stands in southern areas of Sweden have, in total, been exposed to corresponding amounts of nitrogen over the last few decades, it is questionable whether adverse effects on growth occur at lower annual inputs. Thus, in the short term at least, nitrogen deposition does not appear to pose a direct threat to coniferous trees such as Scots pine and Norway spruce, and probably not to deciduous trees either. Nevertheless, we do not know enough to be able to determine whether or not it represents a risk to forest trees in the longer term.

Floristic changes an early and serious effect of nitrogen deposition

There is much to suggest that the flora is one of the ecosystem components to be affected first and most markedly by nitrogen deposition. Despite this, it is often difficult to establish what effect deposition has had on the flora of a given area, since vegetation is also affected by a host of other factors. In chapter 6 we presented a number of different types of study that can be used to determine the effects of nitrogen on flora. None of these studies alone provides a basis for assessing how nitrogen deposition has affected vegetation, but by comparing the results of retrospective, gradient and experimental studies we can obtain a picture of its effects. As has already been noted, deposition not only increases the supply of nitrogen in the soil, but also brings about a qualitative change in that supply. The FNIS index, developed to establish correlations between nitrogen and flora, is based on both the amounts and the kinds of nitrogen present, and in fact provides a better picture than earlier indices of the links between nitrogen availability and plant species distribution. Using a nitrogen index of this type, it is possible to study whether vegetation changes are moving in the direction of higher nitrogen scores and whether such shifts accord with the temporal and spatial distribution of nitrogen deposition. An analysis of this kind has indicated that an appreciable shift towards a more nitrogen-dependent flora has occurred in recent decades in southern and central parts of Sweden.

Since nitrogen acts as a fertilizer, its effects are likely to be more far-reaching in ecosystems where it is originally available in very limited amounts. In chapter 6, the changes observed in the vegetation of two mire ecosystems were described, for example. Especially in the case of the more southerly Åkhultmyren, there are indications that the floristic change that has occurred could be attributed to the increased level of nitrogen deposition. The change in the flora of Skattlösbergs Stormosse, located further north, may be due more to acidification. This illustrates the complexity of the relationship between different environmental perturbations such as deposition of sulphur and nitrogen. One experiment involving low doses of nitrogen showed a clear vegetational change only three years after the first treatment. An increased supply of nitrogen, and/or a change in the composition of the nitrogen available, alters the competitive balance between species, with the result that species capable of using more nitrogen and/or other forms of it, and efficiently converting this nitrogen into biomass production and reproduction, will outcompete other, slower-growing species. Initially nutrient-poor systems are often dominated by one or a few plant species, which means that it takes a very long period of deposition for a vegetation change to arise, even though the original species cannot compete with fast-growing species under the new conditions. In other words, nitrogen deposition changes the parameters of competition, but for a vegetation change to arise some kind of disturbance of the original plant community is necessary. One such disturbance is attack or infection by a natural enemy. In the case of *Calluna* heaths in the Netherlands exposed to increased levels of nitrogen deposition, it has been demonstrated that the original vegetation does not change until the heather is attacked by a particular species of beetle (*Lochmaea suturalis*). Similarly, the nitrogen fertilization experiments in northern Sweden show that modification of the original bilberry-dominated vegetation only occurs in the presence of a parasitic fungus that infects bilberry plants.

To sum up, changes in the flora can be described as an early and serious effect of nitrogen deposition. However, our understanding of the part played by deposition in bringing them about is limited.

Nitrogen – necessary nutrient and environmental problem

The majority of the measures undertaken in agriculture and forestry are designed to increase the supply of nitrogen and thereby boost productivity. Up to the middle of the 1980s, the Swedish forestry sector used large quantities of nitrogen to this end. However, following reports in the early 1980s about the adverse effects of nitrogen deposition, this practice declined dramatically. The prevailing view of nitrogen changed: what had previously been seen as beneficial was now regarded as a problem. In recent years, a more complex picture of nitrogen's effects has emerged, a picture encompassing both unfavourable and favourable elements. Some of the problems that were earlier seen as imminent threats – such as nitrogen leaching and nitrogen saturation – have been found to arise only at higher levels of deposition than those currently occurring in Sweden. The greenhouse effect has assumed greater prominence on the environmental agenda, and as long as nitrogen is the growth-limiting nutrient in forest ecosystems it can be argued with some justification that nitrogen deposition counteracts this effect – at least in the short term. Consequently, there is now a renewed interest in reintroducing large-scale nitrogen fertilization in the forestry sector. In a recently published study, however, it is claimed that deposition of nitrogen results in only limited accumulation of carbon in temperate forest ecosystems (Nadelhoffer *et al.* 1999).

This complex picture has created a need to weigh up the pros and cons of nitrogen, resulting in turn in the emergence of the concept of 'nitrogen management'. This approach involves weighing the desirable and undesirable effects of nitrogen against one another, in order to arrive at an overall assessment and evaluation of its effects in different ecosystems. In forest stands exposed to appreciable levels of nitrogen deposition, it might be possible, according to this view, to counteract any adverse effects by removing a larger quantity of biomass in conjunction with felling. The chief objection to such a procedure is that we currently have too limited an understanding of the biogeochemical cycle of nitrogen and the effects of nitrogen deposition to make assessments of this kind meaningful. Moreover, there is much to suggest that nitrogen deposition has both direct and indirect effects, and that not only the amount of nitrogen, but also the form in which it is supplied to a forest is of great importance. As this report has made clear, many questions concerning the long-term impacts of nitrogen on the structure and functioning of forest ecosystems have still to be answered. This is not, of course, an argument for postponing action to tackle the effects of nitrogen. But it is an argument for seeking in the first instance to reduce emissions, and for restraint as regards other forms of action.

In many respects, Sweden occupies a strategic position when it comes to the nitrogen issue. In the early debate on acidification, it was often argued that Scandinavia, with its slow-weathering bedrock, was particularly sensitive to deposition of acidifying pollutants. A similar argument holds for nitrogen. Many of our natural forest ecosystems are characterized by meagre supplies of nitrogen (see e.g. Tamm 1991). Although nitrogen deposition is on the whole considerably lower in Scandinavia than in the rest of Europe, it is probably the case that our ecosystems are more sensitive to it. Many European countries have had high levels of nitrogen deposition for several decades, and a good many nitrogen-induced changes have probably already taken place in the areas affected. We therefore have every reason to safeguard our northern ecosystems against increased atmospheric deposition of nitrogen.

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Effects of Nitrogen Deposition on Forest Ecosystems

INCREASED ATMOSPHERIC DEPOSITION OF NITROGEN has affected the forest ecosystems of Sweden and many other countries. Many of Sweden's forests are characterized by a limited natural supply of this nutrient. Although nitrogen deposition is on the whole much lower in Scandinavia than in the rest of Europe, the region's ecosystems are more sensitive to it. There is therefore every reason to seek to safeguard these ecosystems against elevated deposition of nitrogen.

This report summarizes the present state of knowledge concerning the effects of nitrogen on soil, trees and forest flora. It also describes current and expected future levels of nitrogen deposition, international and national environmental objectives, critical loads, and how forest ecosystems recover when nitrogen inputs are reduced.

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