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Working Group on Effects
Convention on Transboundary Air Pollution

Model chains for assessing impacts of nitrogen on soils, waters and biodiversity: a review

by

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Executive summary

This review provides a synthesis of current progress in the development of linked biogeochemical and vegetation models with a particular focus on nitrogen to help inform participants of the workshop on nitrogen processes and dynamic modelling of Convention on Long-range Transboundary Air Pollution (LRTAP). The workshop was followed by the 6th meeting of the Joint Expert Group on Dynamic Modelling of the Working Group on Effects, held in Brighton, United Kingdom on 26-28th October 2005. An overview is provided of four model chains namely: FORSAFE-VEG; SMART2-SUMO-MOVE-NTM; MAGIC-GBMOVE and VSD-BERN. Three biogeochemical models with less focus on acidification have also been reviewed: MERLIN, PnET and CENTURY. Key processes represented in the biogeochemical and vegetation models are compared together with data requirements and driving variables. A comparison of the abiotic model outputs used to predict plant species occurrence highlights some similarities but also key differences in the importance placed on individual variables such as availability of other nutrients, salinity and management. This influences the suitability of the models for simulating particular habitats.

Remaining uncertainties and gaps to be discussed at the workshop include:

- What is a good measure of plant-available N and how good are our surrogate measures such as soil C/N in the models?
- Do models need to include direct effects of nitrogen above-ground not moderated by soil processes?
- Is there a need to separate nitrogen species (inorganic and organic) in both the biogeochemical and plant occurrence models?
- Do models focused on biodiversity require a higher level of complexity than those required for acidification and enrichment of soils and water?
- How do we include feedbacks between the vegetation and biogeochemical models and what limitations does this impose if they are not included?
- What limitations in future model applications arise from the fixed or incomplete carbon cycles in some of the models?
- What are the advantages (e.g. extending climate envelopes) and disadvantages (e.g. varying ecological niches) for sharing data and response functions between countries to develop species / community models?
- How do we acquire data for southern Europe?
- Do we need to ensure consistency of approach across Europe?
- Would it be valuable to compare models using one or several test sites, to help understand the implications of underlying differences and aid model development?
- Should we be linking to groups working on N effects in waters to develop integrated catchment/landscape scenarios?

Conclusions from the workshop will be synthesised together with recommendations in a summary report to help facilitate the future development and applications of dynamic models to meet both national and international requirements, in particular the LRTAP Convention and its Working Group on Effects.

Contents

1. Introduction.....	1
2. Effects of nitrogen deposition on soil and vegetation.....	4
2.1 Trends and effects of reactive N to the environment.....	4
2.2 Fundamental N processes	5
2.2.1 Overview of processes	5
2.2.2 Nitrogen fixation.....	6
2.2.3 Denitrification	6
2.2.4 Mineralisation	6
2.2.5 Nitrification.....	6
2.2.6 Immobilisation	6
2.2.7 Plant uptake.....	7
2.2.8 Nitrate leaching.....	7
2.2.9 N processes in aquatic ecosystems	7
2.2.10 Acid-base relationships of N processes	7
2.3 Asynchrony of effects on plants and soils	9
3. Models of nitrogen deposition effects on soil and vegetation	10
3.1 Soil biogeochemistry models.....	10
3.1.1 MAGIC7	10
3.1.2 SMART2.....	11
3.1.3 VSD.....	11
3.1.4 ForSAFE	12
3.1.5 MERLIN	12
3.1.6 PnET	13
3.1.7 CENTURY.....	14
3.2 Vegetation succession models	14
3.3 Summary and comparison of biogeochemical models	16
4. Effects of N availability on plant species occurrence.....	19
4.1 Direct effects of N.....	19
4.1.1 Dissolved organic, oxidised and reduced nitrogen	19
4.1.2 Deposition flux and soil solution N concentration	20
4.1.3 Shoot N exposure and uptake	22
4.1.4 Effects on different plant groups.....	22
4.1.5 Nitrogen location in relation to root uptake.....	22
4.2 Interactions of nitrogen deposition with other factors	23
4.2.1 Competition.....	23
4.2.2 Limitations of nutrients other than nitrogen	23
4.2.3 Water relations	24
4.2.4 Frost	24
4.2.5 Climate change.....	24
4.2.6 N fixing plants.....	24
4.2.7 Invertebrate herbivores	25
4.2.8 Grazing.....	25
4.2.9 Other biotic interactions.....	25
4.3 Effects of nitrogen on lichens, fungi, animals and other groups	26
4.4 Effects of nitrogen on semi-natural habitats	27

4.5 Approaches to predicting species occurrence	27
4.5.1 Environmental gradients, niches, and occurrence prediction	27
4.5.2 Events.....	29
4.5.3 Constructing species-environment relationships	30
4.5.4 Predicting community or species occurrence?.....	30
4.5.5 Interactions between factors	31
4.6 Measures of nitrogen exposure	33
4.6.1 Introduction.....	33
4.6.2 Soil total N	34
4.6.3 Carbon / Nitrogen ratio	34
4.6.4 Soil solution N	34
4.6.5 Extractable N	35
4.6.6 Mineralisable N.....	35
4.6.7 Gross mineralization and nitrification rates	35
4.6.8 Soil organic matter properties	36
4.6.9 Measures of N deposition	36
4.6.10 Plant tissue analyses.....	36
4.6.11 Indicators based on the plant species assemblage.....	37
5. Models of effects of N availability on plant species occurrence	38
5.1 Introduction to occurrence models.....	38
5.2 Calibrating relationships between occurrence and environmental factors	39
5.3 Abiotic model outputs used to predict occurrence.....	41
5.3.1 Summary of abiotic drivers of occurrence models	41
5.3.2 Interactions between variables.....	42
5.3.3 Predicting effects of grazing on probability of occurrence.....	42
5.3.4 Predicting effects of dispersal on probability of occurrence	42
5.3.5 Predicting species presence / absence from probability of occurrence.....	43
6. Potential for harmonising nitrogen effects modelling	44
Acknowledgements.....	46

1. Introduction

Critical loads, which define the tolerable pollutant load of an ecosystem, have been used by the United Nations Economic Commission for Europe (UNECE) Convention on Long-range Transboundary Air Pollution (LRTAP) to develop protocols for emission reductions. The underpinning scientific work has been largely conducted in the Working Group on Effects of the Convention and its effects-oriented activities. These activities include the Joint Expert Group on Dynamic Modelling, which organised a workshop on nitrogen processes and dynamic modelling, held in Brighton, United Kingdom on 26-28th October 2005.

Nitrogen (N) and sulphur (S) are the main air pollutants causing acidification, eutrophication and changes in biodiversity. Critical loads for N and S (Nilsson & Grennfelt, 1988) were developed for acidity, and for N as a nutrient, to link the air pollution to ecosystem damage via effect-based criteria. The critical load is 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. A cause (air pollution) was linked to an effect (ecosystem damage or risk of ecosystem damage) via criteria such as Al/BC ratio in soil water or critical nitrate concentration in soil water. Target loads are a further development of the critical loads concept that include the time dimension – when a change in the ecosystem will occur.

The difference between the target load for a given year and the critical load is essentially because of lag times in ecosystem responses to changing deposition. For sulphur, these lag times are mostly due to two soil processes – cation exchange in the soil and SO₄ adsorption. Both mechanisms will also delay recovery from acidification following a decrease in deposition. From both acidification and biodiversity points of view, the lag times and effects of S deposition are comparatively easily described and quantified with help of geochemical models. However, there are still some challenges in modelling nitrogen cycling and predicting NO₃ leaching and N availability. This is because the majority of nitrogen transformation processes are biologically mediated, there are several forms of N involved, and biogeochemistry of nitrogen is intimately coupled to that of several other elements, most importantly to carbon (C) and phosphorus (P).

There are two reasons for focusing on the fate and consequences of deposited nitrogen: predictions of nitrate (NO₃) leaching are needed for target load calculations, and predictions of N availability are needed as an input for biodiversity modelling. Predictions of long-term consequences of nitrogen deposition for soils and waters often depend heavily on assumptions made by modellers. Rather than a mechanistically based model calculation, expert judgements based on empirical evidence are often used to decide e.g. how much ammonium will be nitrified, what C/N ratio in forest floor will be linked to what percentage of NO₃ leaching, or the relationship between sequestration rates of C and N. The modelled ecosystem response to N deposition is then to an extent dependent on these assumptions. In the Steady State Mass Balance approach to calculating critical loads for soils and terrestrial habitats, any excess of deposited N over the removal fluxes (i.e. plant

uptake, immobilisation, denitrification, volatilisation, export in harvested products, and leaching losses all at the critical load) is assumed to cause N enrichment and acidification of the terrestrial or linked aquatic environments. In the First-order Acidity Balance (FAB) model for freshwaters, all excess nitrogen is assumed to be leached into the water body. However, such simplification is inadequate for dynamic models of acidification, eutrophication and biodiversity that are required to show the timing of responses to future deposition scenarios. Critical N loads may be strongly affected by management - for example, regular removal of N by grazing animals or in hay will result in a higher critical load.

Predicting biodiversity responses to nitrogen (N) pollution is a complex task, best broken down into two parts: predicting changes in N availability as a consequence of N deposition and soil and plant processes, see above; and predicting changes in species composition as a consequence of this level of N availability. Knowledge of plant responses to N availability is currently more advanced than knowledge of responses of other biota, and current models focus on predicting plant responses. These have been made by chaining a model of biogeochemical processes with a model predicting the occurrence of either plant species or assemblages. There are important feedbacks from species composition and vegetation type to biogeochemical processes, and some chains also include a model of vegetation succession (Figure 1).

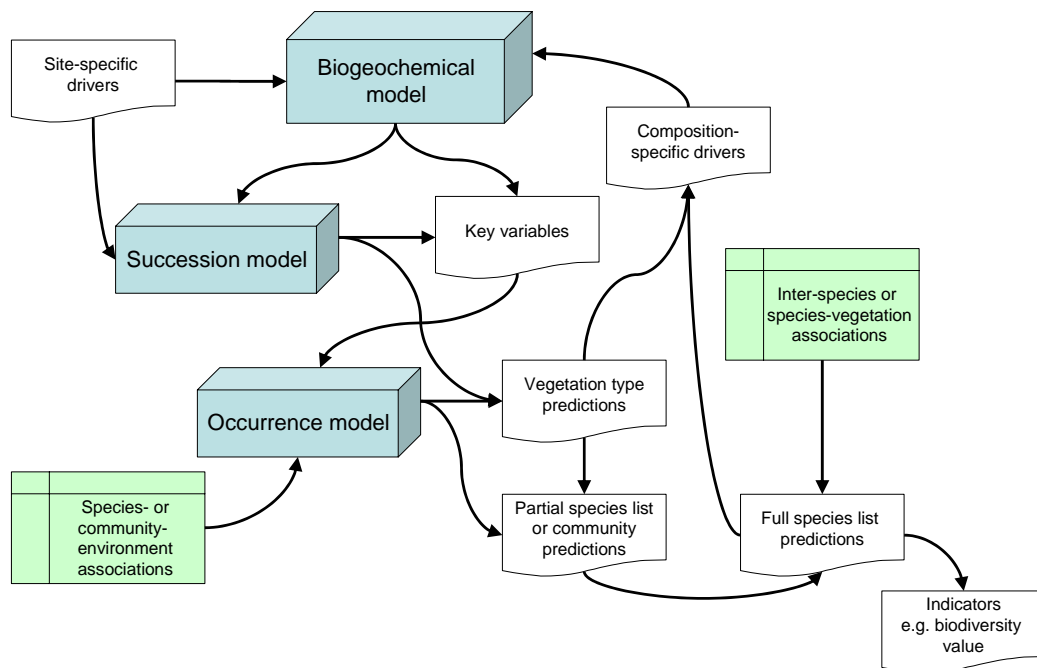


Figure 1 Generalised schema for modelling N impacts on plant diversity. Boxes represent models. Shaded tables represent datasets used for calibration. White pages represent site-specific information. Arrows represent information passes. Occurrence models include statistical approaches such as regression or classification and regression tree (CART), and dynamic modelling of abundance.

This review aims to summarise current methods for predicting soils, waters and plant responses to N pollution. Plant response models are based on current theory and evidence from experiments and surveys, and this is summarised in relation to biogeochemical models in section 2. In section 3, the soil and vegetation biogeochemistry models used in the reviewed chains are summarised. Models of floristic change are then considered, in relation to theory and evidence (section 4), and

current examples (section 5). Lastly, we suggest some approaches to harmonising the development and use of N impacts models and improving mutual learning (section 6).

Four model chains will be considered in this review (Figure 2):

- a) FORSAFE-VEG (Sverdrup *et al.*, 2005)
- b) SMART2-SUMO-MOVE-NTM (Kros, 2002; Wamelink *et al.*, In prep.)
- c) MAGIC-GBMOVE (Smart *et al.*, 2005)
- d) VSD-BERN (Schlutow & Huebener, 2004)

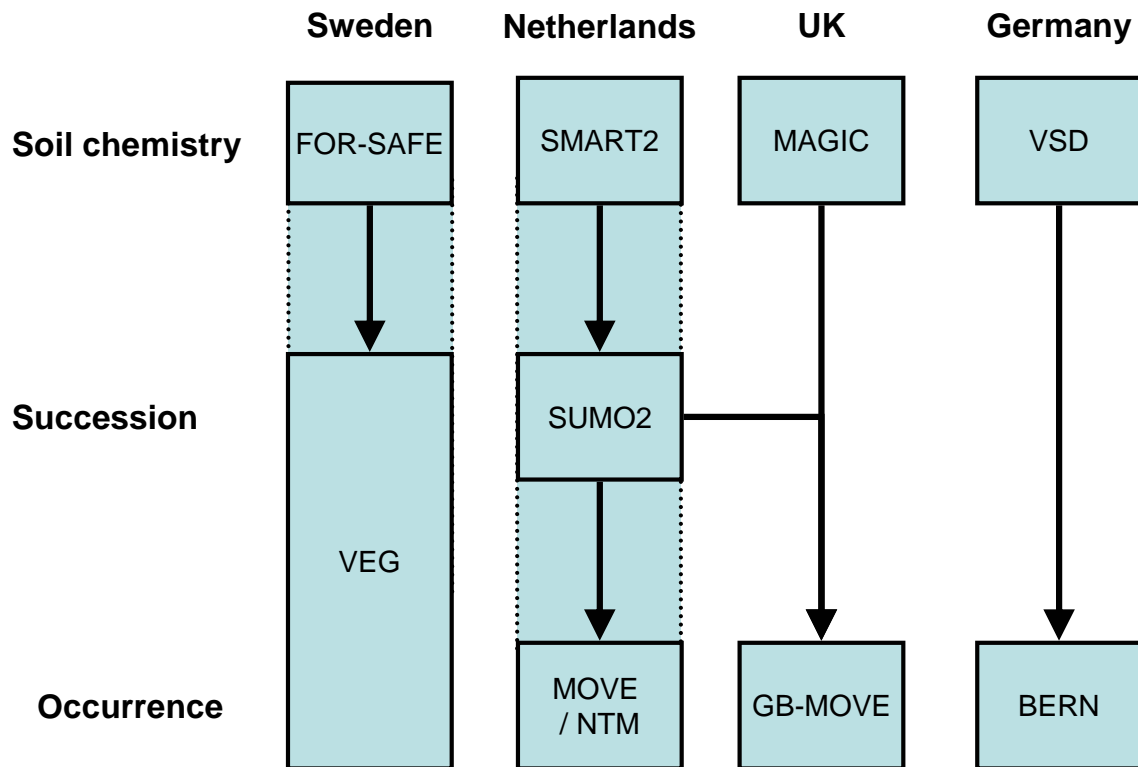


Figure 2 Model chains used by different European modelling groups. The Swedish and Dutch chains are largely implemented within the same modelling framework, as represented by the dashed lines.

In addition three more biogeochemical models are discussed in section 3, i.e. MERLIN, PnET and CENTURY. These are currently not used in chain with a biodiversity model, however they are advanced and widely used models of N cycling in soils and vegetation and are important as such. Hence they also have potential to become a part of model chains in the future.

2. Effects of nitrogen deposition on soil and vegetation

2.1 Trends and effects of reactive N to the environment

Levels of NO_x and NH_x emitted to the environment have increased rapidly during the past century, mainly due to an increase in the anthropogenic production of reactive N (Figure 1) and increased ammonia (NH_3) emissions due to the intensification of agriculture. Anthropogenic emissions of NH_x and NO_x are ca. 60 % and 70 % respectively of global total emissions (Asman, Sutton & Schjorring, 1998; Fowler et al., 1998). This has led to widespread increases in N deposition rates. It is likely that global anthropogenic N inputs will increase even further in the future due to increased global population and increased animal protein in human diets.

Figure 3 shows the emission trend of sulphur and nitrogen in Europe during 1880-2030 as estimated by Schöpp *et al.* (2003). These estimates clearly show that the emissions have decreased after an emission peak in the 80s. In Europe (including emissions from ships), the sulphur emissions had decreased by 56%, NO_x by 25%, NH_3 by 29% and VOCs by 40% between 1990 and 2003 (EMEP, 2005). Although some of the abated pollutants are expected to decrease substantially by 2010 and achieve the targets set in the Gothenburg Protocol, for nitrogen however, there is a very different scenario. In terms of NH_3 contributing to total nitrogen deposition, the prediction for the future is that emissions of ammonia are unlikely to change much between 2000 and 2010, and that areas with exceedance of critical nitrogen loads are unlikely to be reduced.

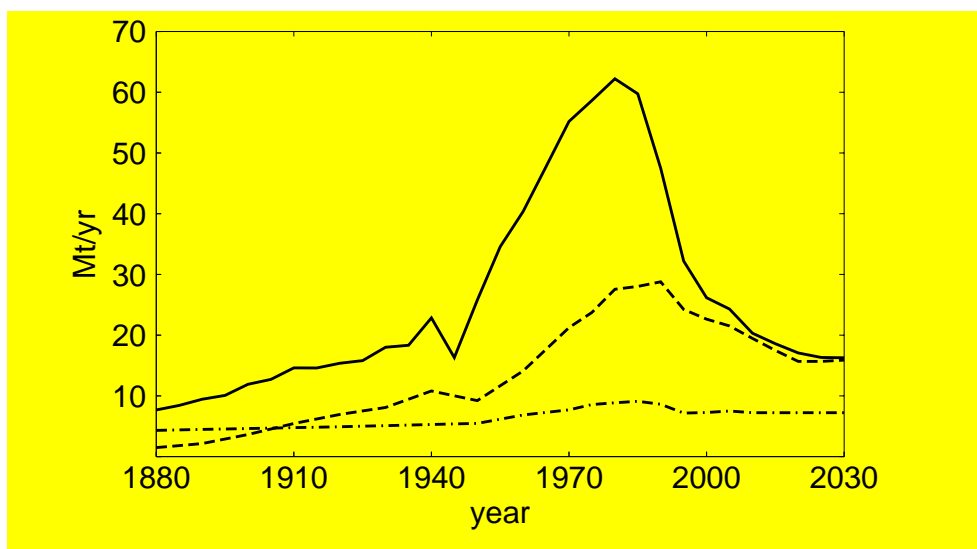


Figure 3 Emissions of sulfur and nitrogen in Europe over the period 1880-2030 as estimated by Schöpp *et al.* (2003). Units are Mt yr^{-1} of SO_2 (solid line), NO_2 (dashed line), and NH_3 (dot-dash line), respectively. (Source: Wright et al., 2005)

Although reasonably reliable estimates of reactive emission and deposition are available, the rate of nitrogen being accumulated in the environment is not as well

understood (Galloway & Cowling, 2002). This accumulation of N in the environment builds up large pools of reactive nitrogen in ecosystems, and studies suggest that many ecosystems today are either saturated or in the accumulation phase (Krupa, 2003; Curtis et al., 2005b). Even sensitive ecosystems in remote areas located far from sources can be affected by reactive nitrogen through long-range transport of ammonium and oxidised nitrogen (Asman, Sutton & Schjorring, 1998). When reactive N in any form is accumulating in pools in the environment, either in the atmosphere, the soil or in water, the 'natural' nutrient balance is disturbed and this can cause detrimental environmental effects, including eutrophication, acidification, species composition change and climate change. It may take a long time before the effects of increased levels of reactive N are noticeable in the environment, due to the buffering capacity of many soils.

2.2 Fundamental N processes

2.2.1 Overview of processes

To pinpoint which action needs to be taken to avoid detrimental impacts of nitrogen on the environment, good knowledge of the complex flows and processes of nitrogen within, into and out of the ecosystem is required. In this section, fundamental N processes and transformation paths of nitrogen in terrestrial ecosystems are explored, with a focus on soil processes. Furthermore, the way these processes are represented in current models of nitrogen biogeochemistry is reviewed.

The main source of N in terrestrial semi-natural ecosystems is deposition of N species from the atmosphere. Emissions of ammonia (NH₃) and nitrogen oxides (NO_x) and their reaction products (NH₄⁺, HNO₃ and NO₃⁻) are responsible for nitrogen deposition (Asman, Sutton & Schjorring, 1998). In the process of dry deposition, gases and particles are directly transferred to surfaces and deposit on soil and plant surfaces, while wet deposition is a result of the element species being dissolved in water droplets and deposited in rainfall, snow or hail (Brimblecombe, 1996).

The soil N cycle is connected to the global N cycle through several pathways, including biological N₂ fixation and denitrification (release of N₂ and N₂O to the atmosphere), but also NO₃⁻ leaching, NH₃ volatilisation and the deposition of N compounds (NH₃, NH₄⁺ and NO₃⁻) (Stevenson, 1986). Influxes of N to soil come from decomposition of plant residues, N fixation, atmospheric deposition, and applications of animal manures and fertilisers. Losses in soil N are mainly through crop removal, leaching and volatilisation, but N may also be lost from soils through soil erosion and surface runoff.

Many environmental factors influence the N transfer between soil and other ecosystem compartments, which makes it difficult to estimate N fluxes. Furthermore, the N-transformation processes occurring in the soil may be difficult to estimate, due to the interaction of many environmental variables. Nitrogen processes in the soil are mainly influenced by soil bacteria and plant uptake. Microbial activity and plant growth, and those environmental variables affecting bacteria and growth (soil moisture content, temperature and oxygen concentrations), are therefore the most important factors for N transformation in soil.

2.2.2 Nitrogen fixation

Elemental N (N_2) is highly stable through its triple bond ($N \equiv N$). However, plants and nitrogen fixing microorganisms can transform elemental N into organic forms, a process referred to as biological nitrogen fixation (Stevenson, 1986).

2.2.3 Denitrification

Denitrification refers to the transformation of NO_3^- into gaseous N (N_2) and nitrous oxide (N_2O) through biological denitrification by heterotrophic bacteria (Stevenson, 1986). These bacteria are able to use the oxygen of NO_3^- (and NO_2^-) as a substitute for O_2 in conventional metabolism. Denitrification is hence a reduction process that occurs in soils in the absence of oxygen, i.e. where the oxygen in the soil atmosphere is limited either broadly or locally within soil aggregates. Nitrogen losses in the soil through denitrification are dependent on NO_3^- levels, availability of organic matter and temperature and moisture status of the soil. Maximal denitrification rates are found when the temperature is high (25 °C and above), in soils with poor drainage, when the soil pH is near neutral, and when there is a good supply of readily decomposable organic matter (Stevenson, 1986). Both denitrification reaction products (N_2 and N_2O) are released to the atmosphere. N_2O is a gas that contributes to the greenhouse effect, and also causes damage to the ozone layer.

2.2.4 Mineralisation

The largest “pool” of N in the soil is in the form of organic N in microbial biomass and plant remains, but this organic N is not available to plants until it has been converted into inorganic forms or soluble and reactive organic forms such as amino acids. Mineralisation refers to the decomposition of organic matter into ammonium (NH_4^+) by soil micro organisms. Because it is an oxidative process (in contrast to denitrification), it is encouraged in well aerated soils (Kiely, 1997).

2.2.5 Nitrification

Nitrification is the biochemical oxidation of ammonium to nitrite and nitrite to nitrate by predominantly bacteria (called nitrifiers), although fungi can also contribute. Nitrification processes play a key role in the context of soil acidification as they may influence the acid-base relationships within the soil (Section 2.2.9). The resulting nitrate N remains in the soil solution and in free-draining soils can leach downwards through the soil to the ground water if it is not taken up by plants.

2.2.6 Immobilisation

Immobilisation (sometimes referred to as assimilation) is the reverse process of mineralisation, i.e. inorganic N (NO_3^-) is transformed into an organic form by microbes or plants. Plants incorporate inorganic N into plant tissue, and microorganisms in the soil incorporate inorganic N into microbial tissue.

2.2.7 Plant uptake

Plants take up N through mass flow (i.e. in water uptake), through active transport against an ionic gradient, and to a small extent through interception by growing roots (Marschner, 1995). Active transport is strongly regulated, particularly for nitrate which requires more energy to assimilate than ammonium. High rhizosphere ammonium concentrations and internal amino acid concentrations inhibit nitrate uptake (Gessler, Kopriva & Rennenberg, 2004) (see section 4.1.1). The rate of N uptake by plants thus depends on plant N demand and N availability. Demand is determined by growth rate, and is thus greatest during spring and summer. In forestry plantations, N demand depends on the age of the trees and peaks at around the time of canopy closure. Nitrogen availability depends on soluble N concentrations, and is also a function of the location of plant roots relative to this soluble N. Asynchrony of plant demand and soluble N availability is a major cause of leaching in many ecosystems (Myers et al., 1994).

2.2.8 Nitrate leaching

Nitrate leaching occurs when soil nitrate (NO_3^-) levels are high, and when the movement of water downwards is sufficient to move NO_3^- below the rooting depth (Stevenson, 1986). Nitrate in soils derives from the conversion of N species into nitrate by soil microbes (e.g. through mineralisation and nitrification). Soil microorganisms use carbon as an energy source, and the nitrate production in soils is therefore dependent on the C/N ratio available. A high C/N ratio encourages immobilisation and incorporation into microbial biomass, while a low C/N ratio may result in rapid conversion of nitrogen into nitrate, hence the potential for nitrate leaching is greater. Other factors important for nitrate leaching include plant uptake and soil characteristics, as soil texture and structure influence the aeration status of the soil and the rate and amount of water that moves through the soil (Kiely, 1997). High concentrations of ammonium in soil solution can inhibit microbial immobilisation of nitrate, and thus lead to an increase in nitrate leaching (Emmett, 2005).

2.2.9 N processes in aquatic ecosystems

Aquatic ecosystems are also affected by eutrophication, e.g. algal growth may increase, and the oxygen balance may be disturbed, with a resulting loss of fish and deterioration in water quality. The importance of N as a eutrophying factor in UK freshwater systems was recently reviewed by Maberly *et al.* (2004).

2.2.10 Acid-base relationships of N processes

Historically, sulphur deposition has been the main cause of acidification, but as sulphur oxides emissions in Europe have been reduced during the past couple of decades, the importance of reduced nitrogen for acidification has increased relative to other acidifying pollutants (Figure 3). Nitrate may be expected to be the main acidifying anion in many surface waters within a decade (Curtis *et al.*, 2005b).

Soil acidification is linked to acid-base relationships, hence the proportions of available acid and base species in soil (Reuss & Johnson, 1986). An acid is a proton

donor, and a base is a proton acceptor. The net production or consumption of H^+ ions (protons) in the soil therefore plays a key role in the context of soil acidification. The acidification effect in soils is dependent on the nitrogen deposition species as well as the transformation processes (mainly nitrification and uptake) occurring in the soil. Thus the nitrogen transformation processes could be either H^+ indifferent, H^+ consuming or H^+ producing.

Reuss and Johnson (1986) summarised the potential acidification effects of HNO_3 , $(NH_4)_2SO_4$ and NH_4NO_3 deposition (Figure 4). For instance, deposition of HNO_3 will not have an acidifying effect if NO_3^- is taken up by plants or micro-organisms, as the OH^- released in the uptake process will neutralise the H^+ ion to form water (Figure 4b). Consequently, if NO_3^- is not taken up, NO_3^- remains mobile, i.e. further acidification of the soil occurs.

The acidification effect of $(NH_4)_2SO_4$ and NH_4NO_3 is more complex, as it depends on the fate of the ammonium (NH_4^+), as well as the fate of the associated anion or cation. For NH_4NO_3 there will be no acidification effect if NO_3^- is taken up by plants (independently of whether nitrification has occurred or not). However, if NH_4^+ is not taken up, the acidification effect will be equal to that of 2 mol of HNO_3 following nitrification, and 1 mol of HNO_3 if no nitrification has occurred (Figure 4a).

The acidification potential following deposition of $(NH_4)_2SO_4$ will be 1 mol of H_2SO_4 if nitrification does not occur followed by uptake. However, if nitrification occurs, the acidification effect is either 1 or 2 mol of H_2SO_4 depending on whether or not nitrogen is taken up by plants and micro-organisms following nitrification (Figure 4c).

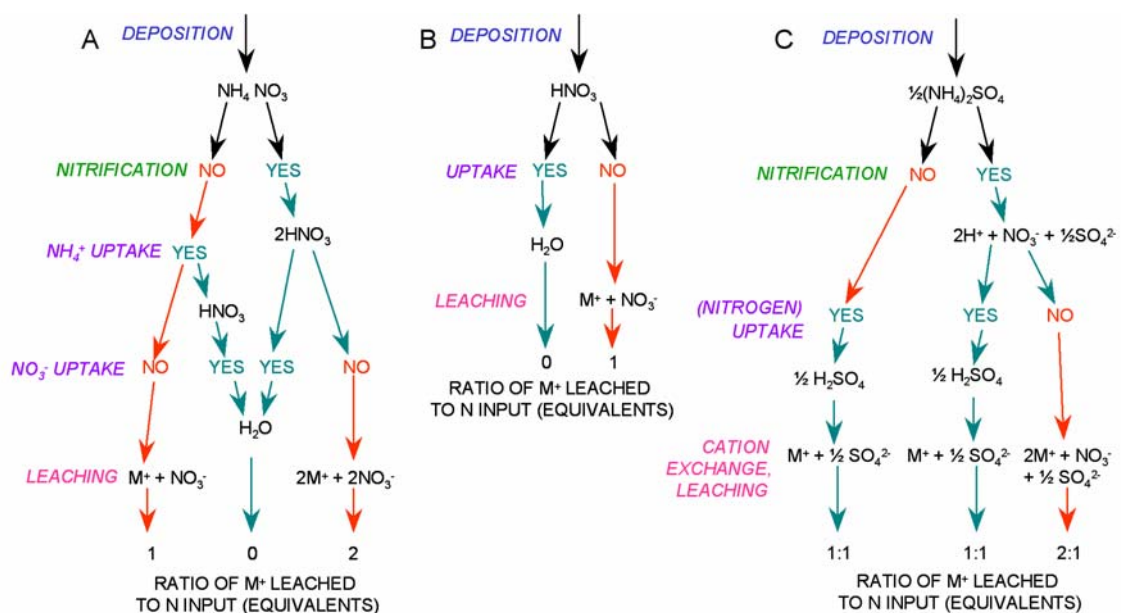


Figure 4 Acidification effects in soils associated with deposition of a) ammonium nitrate, NH_4NO_3 , b) nitric acid, HNO_3 , and c) ammonium sulphate, $(NH_4)_2SO_4$ (from NEGTA, 2001, after Reuss and Johnson, 1986)

2.3 Asynchrony of effects on plants and soils

The progressive response of soil-vegetation systems to increased annual N deposition was charted by (Aber *et al.*, 1989), and later revised in the light of results from the NITREX experiments (Aber *et al.*, 1998) and more recent work (Emmett, 2005). At first, uptake of N by plants and immobilisation into soil organic matter moderate the increase in soil solution N concentrations, and the main effect is an increase in growth of N-tolerant species. Competition-induced changes to the plant community can thus occur rapidly after an increase in N deposition. Increased plant growth results in greater litter inputs. Increased (carbon) production means that plant C / N may not decrease at first (Emmett, 2005), but a sustained decrease in N limitation results in a decrease in litter C / N. The effects on soil C / N of this litter input and of immobilisation of soluble N will be small at first, since soil organic matter C and N pools are large. Over decades, however, the soil C / N ratio will decrease (Figure 5a).

The recovery of systems from N eutrophication following a reduction of N deposition flux has also studied, notably in the NITREX and EXMAN experiments (Wright & Rasmussen, 1998). Although soil solution N concentrations drop rapidly (Boxman, van der Ven & Roelofs, 1998), continued mineralisation of N from organic matter is likely to maintain soil solution N above pre-pollution concentrations for a considerable period (Figure 5b). Plant productivity will thus decline only slowly, and increases in plant litter C / N will be delayed. Increases in soil C / N have not been observed in experimental manipulations, which is logical since soil C / N will only increase after sustained inputs of high C / N plant material. Changes in plant productivity are likely to be associated with shifts in plant community composition, but N-sensitive species may not reappear until productivity approaches pre-pollution levels. Residual effects on the abundance of plant and fungi species have been observed 47 years after ceasing N fertiliser application (Strengbom *et al.*, 2001).

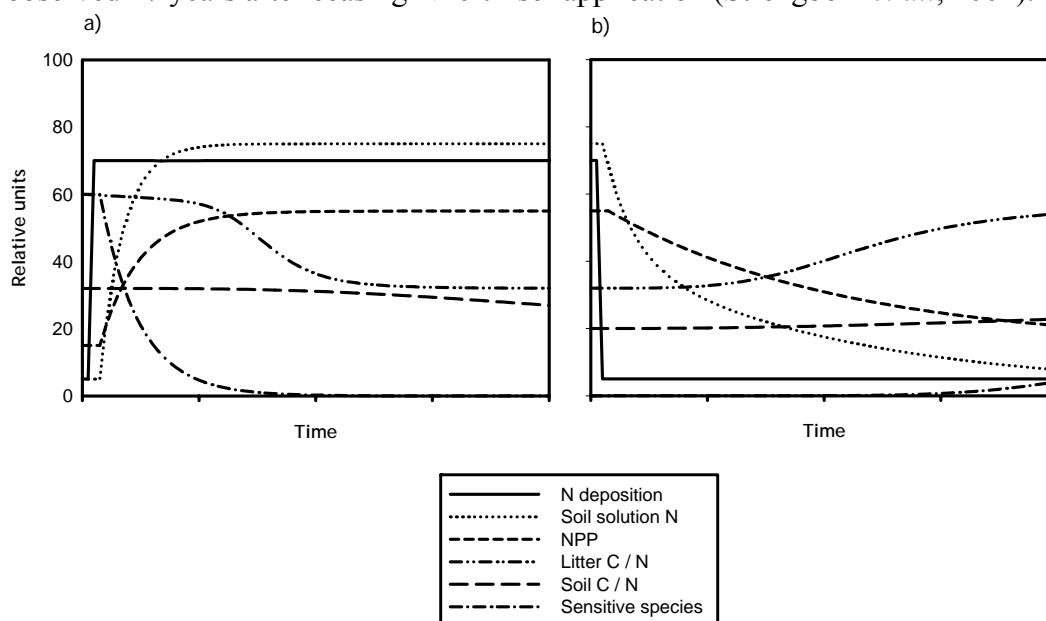


Figure 5 Hypothetical changes following a) an increase and b) a decrease in N deposition, to soil solution N concentration, net primary production (NPP), plant litter C / N, soil C / N, and abundance of N-sensitive plant species.

3. Models of nitrogen deposition effects on soil and vegetation

Models of nitrogen biogeochemistry can be applied to predict nitrogen cycling and the environmental impact of various pollution scenarios. These models comprise nutrient cycling of nitrogen within different compartments, such as the soil, vegetation and atmosphere, and these compartments are linked through various transportation paths, e.g. through deposition, plant uptake, litterfall and nitrate leaching. The first part of this section gives a brief overview of models for nitrogen cycling that are currently used to simulate the environmental impact of increased levels of reactive nitrogen to the environment. Section 2.3 focuses on models of vegetation succession. In section 3.3, these models are compared in more detail in summary tables.

3.1 Soil biogeochemistry models

3.1.1 MAGIC7

MAGIC7 (Model of Acidification of Groundwater in Catchments) (Cosby *et al.*, 2001) is a further development of the *MAGIC* model which was first published in 1985 (Cosby *et al.*, 1985b, 1985a). The *MAGIC* model consists of three major parts: a set of equations that quantitatively describe the equilibrium soil processes and the chemical processes that occur when the soil water enters the stream, catchment mass balance equations for input and output of major anions and cations, and a part which links the equilibrium and the mass balance parts. Since the original 1985 version, *MAGIC* has been refined several times with regards to aluminium solubility and organic acids buffering. A facility has also been added to simulate acid episodes, and several shells have been built around the model to simplify parameter-fitting and multiple-site applications.

The latest expansion of the model was an addition of process-based nitrogen dynamics in soils controlled by the N pool in the soil (*MAGIC 7*; (Cosby *et al.*, 2001). The N dynamics are conceptually based on the empirical model of Gundersen *et al.* (1998) which found relationships between soil organic matter C/N and NO₃ leaching. For that reason, a soil organic matter pool had to be added to the structure of the model. Atmospheric deposition of N, denitrification rates and a rate constant for mineralisation must be provided for the model. Plant uptake and litter production, and time series of inputs and outputs of organic carbon (and the C/N ratios of the organic matter), are also required inputs. Nitrogen mineralisation is derived from the carbon decomposition and the specified C/N ratio. Immobilisation of inorganic N is governed by the C/N of SOM. Two C/N thresholds need to be specified. At C/N values above the higher threshold the immobilisation of N is complete, and at C/N values below the lower threshold there is no inorganic N immobilisation into the SOM. Immobilisation at C/N ratios between the two thresholds increases linearly from 0 to 100 % immobilisation. For forest soils the typical values for the lower threshold are around 10 mol mol⁻¹ and for the upper threshold above 25 mol mol⁻¹. The mathematical formulation and process representation of N dynamics were derived from a simplification of the *MERLIN* model (Cosby *et al.*, 1997), described below.

3.1.2 SMART2

SMART2 (Simulation Model for Acidification's Regional Trends: Kros, 2002) is a soil acidification and nutrient cycling model and is an extension of the dynamic soil acidification model SMART (Kros *et al.*, 1995). The original model was a relatively simple simulation of the response of soil and soil water quality to atmospheric inputs. Improvements in SMART2 include processes of canopy interactions, litter fall, root decay, mineralization and root uptake of nutrients. SMART2 is integrated with the vegetation succession model SUMO (Wamelink *et al.*, in prep.), from which it can derive information about litterfall (including N and P content) and vegetation structure.

SMART2 predicts changes in pH, aluminium (Al^{3+}), base cations, nitrate, phosphorus and sulphate concentrations in the soil solution. The acidification status of the soil is assessed from the carbonate content, base saturation and readily available Al content. Soil solution chemistry is based solely on the net element input from the atmosphere and groundwater, canopy interactions, geochemical interactions in the soil and a complete nutrient cycle for N, P and basic cations. Transformation pathways and processes in the model include deposition, seepage, foliar uptake, foliar exudation, CO_2 equilibria, weathering of carbonates, silicates and/or Al-hydroxides, SO_4^{2-} sorption and cation exchange, litterfall, mineralisation, root uptake, immobilisation, nitrification and denitrification. Nitrogen fixation (by legumes) is incorporated as an option, but can also be obtained from SUMO. Processes not taken into account include NH_4^+ adsorption, and uptake, immobilisation and reduction of SO_4^{2-} . Influences of pH and moisture content on mineralisation, nitrification and denitrification are included.

Originally, SMART2 contained only one soil compartment, but the model has been extended to a two-compartment model with an organic layer and a mineral layer (Mol-Dijkstra, Kros & Salm, 1998). Similarly to the VSD model (see below), the soil water flux percolating from the soil is set equal to the annual precipitation minus evapotranspiration. Seasonal variations are not included in SMART2, as the time step in the model is one year.

3.1.3 VSD

VSD (Very Simple Dynamic soil acidification model) only includes a few key processes, such as cation exchange and N immobilisation, and a mass balance for cations and nitrogen (Posch, Hettelingh & Slootweg, 2003). Processes that have been omitted include canopy interactions, some nutrient cycling processes e.g. N fixation, NH_4 adsorption and plant N uptake, sulphate interactions (adsorption, uptake, immobilisation and reduction), formation and protonation of organic anions (RCOO) and complexation of Al with OH, SO_4 and RCOO . Nitrification is assumed to be complete (i.e. no NH_4^+ is leached), and denitrification occurs as a constant fraction of available nitrate. VSD does not consider seasonal variations as the time step in the model is one year.

The VSD model is based on mass balance equations that describe the soil input-output fluxes, and equations describing the rate-limited (e.g. uptake and silicate weathering) and equilibrium (e.g. cation exchange) soil processes. Soil solution chemistry is based

solely on the net element input from the atmosphere, i.e. deposition minus net uptake minus net immobilisation, and geochemical interactions in the soil, i.e. CO₂ equilibria, weathering of carbonates and silicates, and cation exchange. VSD simulates a single soil layer with a constant density and a fixed depth. The concentration of the soil water leaving the compartment is assumed to be equal to the annual precipitation excess.

3.1.4 ForSAFE

ForSAFE is a mechanistic model that simulates nitrogen and carbon cycling and soil chemistry. Climatic drivers within the model include temperature, precipitation, radiation and deposition. ForSAFE combines three established models (PnET-CN, Decomp and SAFE). PnET-CN (Aber, Ollinger & Driscoll, 1997) is used to predict forest growth within ForSAFE, through the simulation of carbon fixation, litterfall and carbon and nutrient allocation. Decomp (Walse, B.Berg & Sverdrups, 1998) is a dynamic, multi-layered process-oriented decomposition model that incorporates the influences of temperature, moisture, pH and aluminium. SAFE (Alveteg, 1998) is a dynamic, multi-layered, process-oriented soil chemistry model simulating soil chemistry (e.g. chemical weathering, cation exchange, leaching and solution equilibrium reactions).

Carbohydrate allocation in ForSAFE is dependent on the carbohydrate production in plants, which in turn is driven by photosynthesis. Hence, important parameters for determining carbohydrate allocation are maintenance respiration, tree growth and growth respiration, but also leaf % N and leaf area index (LAI), as photosynthesis is calculated as a function of LAI. Nutrient uptake in the model is calculated as the difference between the nutrient requirement for the forest, and the nutrient availability in the soil. The nutrient requirement for the forest is estimated based on the change in biomass following growth or litter removal, and the nutrient availability in the soil is calculated from the soil chemistry equilibrium. Litter decomposition and litter nutrients mineralisation in ForSAFE represents downward flows of matter from vegetation to soil. This is represented by three types of litterfall: foliage turnover, wood turnover and root turnover. The model defines four classes of decomposable organic matter: easily decomposable compounds, lignin, holocellulose and resistant compounds. The decomposition rate of this organic matter depends on temperature, moisture, soil pH and Aluminium.

The ForSAFE model has recently been extended to incorporate the influence of ground vegetation (ForSAFE-VEG; see also section 5). This model allows simulation of effects of climate change, soil acidification and eutrophication on ground vegetation and forest growth simultaneously. The integrated ForSAFE-VEG model includes the following ecosystem components: tree vegetation layer, ground vegetation layer, soil chemistry and geochemical processes, soil stocks and cycling of nutrients and carbon hydrology.

3.1.5 MERLIN

The MERLIN model (Model of Ecosystem Retention and Loss of Inorganic Nitrogen) models leaching losses of inorganic nitrogen (Cosby *et al.*, 1997). The model

simulates changes in nitrogen state variables (i.e. inorganic nitrogen species of NO₃ and NH₄, and organic nitrogen pools) in response to temporal changes in atmospheric deposition of inorganic nitrogen, and changing fluxes and/or pool sizes of organic carbon in the plant and soil compartments. MERLIN calculates outputs of NO₃ and NH₄ in soil solution runoff (drainage) as concentrations and fluxes; total nitrogen contents of the organic and inorganic compartments; C:N ratios of the aggregated plant and soil organic compartments; and rates of nitrogen uptake, immobilisation and mineralisation.

The MERLIN model comprises four compartments; two plant compartments (active and woody biomass) and two soil organic compartments (Labile Organic Matter (LOM) representing 'fresh' material, and Refractory Organic Matter (ROM) representing the rest of the soil organic carbon and nitrogen). Important processes in MERLIN include atmospheric deposition, hydrological discharge, plant uptake, litter and wood production, microbial immobilisation, mineralisation, nitrification and denitrification. Important parameters driving these processes include carbon productivity, C/N ratios of organic compartments and inorganic nitrogen in soil solution. Inputs for the model include soil characteristics (depth, porosity, bulk density, anion/cation exchange constants); temporal sequences of carbon fluxes and pools (litter and wood production, amount of organic matter in the bulk soil and its decomposition); time series of hydrological discharge through the soil; historical and current external sources of inorganic nitrogen; current nitrogen status in the plant and soil organic compartments; constants specifying the nitrogen uptake; and immobilisation characteristics of the plant and soil organic compartments.

3.1.6 PnET

PnET is a biogeochemical model for forest ecosystems that simulates the carbon, water and nitrogen dynamics within the ecosystem. PnET summarises physiological controls on water, C and N dynamics based on inputs that can be defined within a GIS. PnET is run for each 1 x 1 km² grid cell within the GIS data base, and calculates outputs of e.g. annual net ecosystem production, net primary production (NPP), wood production and water yields.

Three versions of the model have been developed: PnET-Day, PnET-II and PnET-CN. PnET-Day is a canopy flux model at daily resolution that predicts daily gross and net photosynthesis of whole forest canopies based on foliar mass, leaf weight, foliar N concentration, temperature and radiation flux (Aber, Reich & Goulden, 1996). PnET-II is a carbon and water model driven by nitrogen availability based on nutrient allocation, water balance and soil respiration at monthly resolution. PnET-II predicts NPP, transpiration and runoff based on carbon allocation and respiration terms and a full water balance (Aber *et al.*, 1995). PnET-CN is a further development of PnET-II that also includes compartments for woody biomass and soil organic matter, algorithms for biomass turnover and litter and soil decomposition, so that the carbon and nitrogen cycles are completed (Aber, Ollinger & Driscoll, 1997). Transformation paths for N and C within PnET-CN include e.g. gross photosynthesis, foliar respiration, allocation to plants, soil respiration, precipitation, water uptake, transpiration, drainage, mineralisation and N uptake. PnET-CN is also included in the ForSAFE model to predict forest growth.

The transfer of soil organic matter (SOM) within PnET includes woody litter production, litterfall and fine root litter. Decomposition processes include C and N mineralisation and immobilisation, litter decay, humus formation and carbon release from SOM. The net N mineralisation is calculated as gross N mineralisation minus gross N immobilisation. N mineralisation in the model increases with decreasing C/N ratios, using the assumption that all mineralised N is re-immobilised when SOM is 1.5 % N, decreasing to zero re-immobilisation when SOM is 4.3 % N. This assumption is based on empirical data on N concentrations in litter when net N mineralisation begins, and on maximum observed N concentrations in soil organic matter, i.e. when re-immobilisation approaches zero.

A nitrification index is calculated in PnET, varying between 0 and 1. This is determined by the competition between nitrifiers and plants for NH_4^+ . Nitrification processes in the model are dependent on plant uptake, as nitrification increases as plant N increases. Plant uptake is calculated based on plant N demand and N availability. The degree of N limitation on plant growth is also incorporated into the model and is dependent on the interactions between carbon and nitrogen cycles. Leaching losses of nitrate from the soil system are estimated as the fraction of soil water that drains multiplied by the total nitrate available in the soil solution. This is based on the assumption that all available nitrate is in the soil solution.

PnET-BGC is an additional version of the PnET-CN model that uses additional cation elements and a full soil chemistry model to calculate cycling rates and predict stream and soil chemistry (Gbondo-Tugbawa *et al.*, 2001). PnET-BGC was developed from the soil equilibration processes model CHESS.

3.1.7 CENTURY

CENTURY is a model of C, N, P and S dynamics in soil and vegetation (Parton *et al.*, 1987). It includes a plant production submodel which can be parameterised for grassland, forest, cropland and savanna ecosystems and has been applied to a large number of sites globally, making it perhaps the most widely used and validated soil organic matter model. The CENTURY team run an informative website (NREL 2005).

The organic matter submodel in CENTURY includes three soil pools (active, slow and passive) with different potential decomposition rates, above and belowground litter pools, and a surface microbial pool associated with decomposing surface litter. Flows between these pools are mediated by C / N ratios, temperature and moisture content, and the total mineralised N is calculated. Different soil layers can be modelled. Plant production is controlled by moisture, temperature and availability of N, P and S using a von Liebig approach. The production model also includes the influence of events such as harvest, grazing, fire and cultivation.

3.2 Vegetation succession models

Models of vegetation succession are intermediate between models of ecosystem biogeochemistry and models of species composition, since they simulate changes in

element budgets but also changes of vegetation type. A model of this type is included in FORSAFE, and SUMO in the Dutch chain is a specific model for vegetation succession (Table 1). Both these models simulate the development of vegetation biomass and stocks of nutrient elements in relation to events such as fire, grazing, mowing or turf stripping. Budgets for nutrient elements include pollutant and fertiliser inputs, and losses via removal and leaching, denitrification, etc.. The development of particular types of plants is predicted from the differential effects of these events and processes on different plant groups. For example, grazing increases light availability and thus favours the growth of short-growing plants.

Table 1 Models used to simulate changes among vegetation types.

	SUMO	FORSAFE
Nutrient elements simulated	N, P	N, P, Base cations
Number of plant functional / vegetation types	5	8
Process timestep	Yearly	Monthly

SUMO simulates the biomass growth of five functional types of plants (climax trees, pioneer trees, shrubs, dwarf shrubs and herbs). Growth of each group is simulated using a maximum growth rate, which is reduced if there are limitations according to several reduction functions. It is closely integrated with the SMART2 model. A series of reduction factors restrict the maximum growth rate according to light, water, N and P availability. Competition between the vegetation types is governed by their root and leaf biomasses and canopy heights.

In FORSAFE, plants are first split into two groups: trees and ground vegetation. Tree growth is simulated according to light interception in a 50-layer canopy model. Tree leaf area index is incremented according to the C fixed in the previous growing season, in a routine derived from the PnET model (Aber & Federer, 1992). Tree leaf area index is then used to calculate the light flux reaching the ground vegetation, and this is used in the calculation of relative and total biomass of the ground vegetation components (species). Individual ground vegetation species are then categorised into seven groups (lichens, mosses, ericoids, other shrubs, graminoids, forbs and ferns).

Driving variables for models of vegetation type are summarised in Table 4. These consist mainly of descriptions of events, in particular the timing and intensity of grazing and other management events. Soil type and hydrology are also important determinants of vegetation type. SUMO drivers include water, N and P availability, which are currently derived from the SMART2 soil model. The fixation of N by legumes is modelled by SUMO.

Grazing has a large effect on transitions between broad vegetation types. Effects of grazing depend on the plant species in question, the grazing animal, and other environmental factors. Some generalisations can be made about how susceptible different plant functional types are to grazing. However, transitions between grassland and subshrub vegetation (e.g. heathland, maquis, garrigue, matorral) are not easy to predict without knowledge of the relative palatabilities of the graminoid and subshrub to local herbivores.

3.3 Summary and comparison of biogeochemical models

Table 2. Overview of biogeochemistry models.

ForSAFE	<ul style="list-style-type: none"> • Primarily an acidification model • Combines three established models: PnET-CN (to predict forest growth), Decomp (to simulate decomposition), and SAFE (to simulate soil chemistry) • Driving variables are deposition and climatic factors (temperature, precipitation and radiation) • Can use an unlimited number of soil horizons • Includes a full nutrient cycle • Does not include a representation of N saturation • Weathering rates calculated from mineralogy • Calibrates to present day base saturation
MERLIN	<ul style="list-style-type: none"> • Does not include an acidification module • Models nitrogen processes and fluxes of NO₃ and NH₄ in soil solution and runoff • Has two plant compartments (active and woody biomass), and two soil organic matter compartments (LOM – labile organic matter, and ROM – refractory organic matter) • Data on current C and N pools needed for calibration, designed for site-specific applications • Aggregated carbon dynamics are forcing functions for biotic transformations of nitrogen • Emphasis on the coupling and interaction of hydrological and abiotic processes affecting nitrogen with the biotic cycling of nitrogen within the ecosystem • Calibrates to present day N leaching and C and N pools
PnET	<ul style="list-style-type: none"> • Does not include an acidification module • Application to forested systems • GIS based (1-km grid resolution) • Combines three models: PnET-Day (predicts daily gross and net photosynthesis), PnET-II (a carbon and water model driven by nitrogen availability), PnET-CN (completes the carbon and nitrogen cycles) • Simulates water yields, nitrate loss and leaching • Models forest growth and nutrient cycling as a function of climate and N availability (rather than based on assumed growth sequences)
SMART2	<ul style="list-style-type: none"> • Primarily an nitrogen / nutrient cycling and acidification model • Designed for regional applications, largely relies on regional databases and default values for input data • Soil solution chemistry depends solely on atmospheric deposition, cation exchange in soil is simplified • Calculates soil base saturation and concentrations of major anions and cations in soil water and runoff water • Does not include an optimisation procedure • Calibrates to present day vegetation growth, and measured soil and stream water quality data
MAGIC7	<ul style="list-style-type: none"> • Primarily an acidification model • Soils are lumped but possible to apply up to three separate soil horizons • A relatively simple treatment of vegetation (net uptake) • Uses site-specific data; could be used regionally with help of automated optimisation routine • Represents N saturation based on changing N content of humus and thresholds of soil C/N ratios • A sophisticated optimisation procedure for weathering rates and initial base saturation • Calibrates to present day soil and soil- stream or lake water chemistry
VSD	<ul style="list-style-type: none"> • Primarily an acidification model • Useful for regional model assessments • Relies largely on regional-scale databases and defaults • A simplified representation of key processes (SO₄ adsorption not included, simplified organic acids, no complexation of Al) • Does not incorporate N processes except for an immobilisation term, uses C/N ratio (as model input) which determines NO₃ leaching
CENTURY	<ul style="list-style-type: none"> • Does not include an acidification module • Designed to simulate short-term and long-term changes in organic matter content and soil fertility • Detailed treatment of N cycling in soil and vegetation • Includes three compartments for soil (Active, Slow and Passive) and two for plant litter (Metabolic and Structural) with different turnover rates.

Table 3 Key processes represented in biogeochemical and vegetation models used in model chains for assessing impacts of nitrogen on biodiversity. ● = modelled dynamically; ○ = modelled indirectly or in a simplified way; k = included as constant or fitted term; - = not modelled.

Process	ForSAFE-VEG	SMART2	SMART2/SUMO	MAGIC	VSD	MERLIN	PnET-CN	CENTURY
Photosynthesis / tree growth	●	k	●	-	-	-	●	●
Competition / succession	●	-	●	-	-	-	-	-
Plant N uptake	●	●	●	○	-	○	●	●
Symbiotic nitrogen fixation	k	k	●	-	-	○	k	●
Litterfall	●	●	●	○	-	○	●	●
Decomposition	●	●	●	○	-	○	●	●
N mineralisation	●	●	●	○	○	○	●	●
Nitrification	●	●	●	○	k	○	●	●
Denitrification	○	●	●	○	○	○	●	●
Inorganic N leaching	●	●	●	●	●	●	●	●
Organic N leaching	○	-	-	○	-	-	-	-
N immobilization	●	●	●	●	●	○	●	●
Soil carbon dynamics	●	●	●	○	-	●	●	●
SOM pools with different reactivity	●	●	●	-	-	●	-	●
Major ion chemistry/acidity	●	●	●	●	●	●	-	-
Base cation weathering	○	○	●	k	k	-	-	-
Grazing	●	-	●	○	-	○	-	●
Fire	●	-	●	○	-	○	○	●
Sod cutting	-	-	●	○	-	○	-	-
Tree felling	●	-	●	○	-	○	●	●

Table 4 Data requirements for biogeochemical and vegetation models used in model chains for assessing impacts of nitrogen on biodiversity. ● = time series or seasonal variation data used; k = constant, average or initial value used; * = data not required, e.g. because modelled dynamically; - = not used.

Group	Variable	ForSAFE-VEG	SMART2	SUMO	MAGIC	VSD	MERLIN	PnET-CN	CENTURY
N and C	NO _x and NH _y deposition fluxes	●	●	●	●	●	●	●	●
	Soil or litter total N (or C / N)	k	●	●	k	k	k	k	k
	Soil N in different organic pools	*	●	●	-	-	k	k	k
	C / N leaching thresholds	-	-	-	k	k	k	k	-
Acidity	Cation and anion deposition fluxes	●	●	●	●	●	●	-	-
	Base saturation	k	●	●	k	k	k	*	-
	pH	k	●	●	k	*	k	*	k
	Soil mineralogy	k	k	k	-	-	-	-	-
Soil water	Drainage flux	-	k	k	k	●	k	-	-
	Water holding limits	k	-	-	-	k	-	-	k
Climate	Temperature	●	●	●	k	-	-	●	●
	Precipitation	●	●	●	●	●	●	●	●
	Light flux	●	-	●	-	-	-	●	-
	Wind velocity	●	-	-	-	-	-	-	-
	Atmospheric CO ₂ concentration	●	-	-	-	-	-	●	●
Plant growth	Tree growth parameters	k	k	●	-	-	-	k	k
	Plant N uptake	*	k	*	●	●	●	●	*
Management	N offtake in harvests	●	k	●	●	●	●	●	*
	Grazing intensity	●	-	●	-	-	k	-	●
	Type of grazer	k	-	●	-	-	-	-	-
	Fire events	●	-	●	●	-	●	k	●
	Sod cutting events	-	-	●	●	-	●	-	-
	Tree felling events	●	-	●	●	-	●	●	●

4. Effects of N availability on plant species occurrence

4.1 Direct effects of N

Exposure to increased N concentrations has direct effects on plant nutrition, growth and form. Plants supplied with adequate amounts of N grow more rapidly than N-limited plants. Other physiological changes also occur. Tissue N concentrations are higher, and C/N ratios lower, than in N-limited plants. Shoot / root biomass ratio increases relative to N-limited plants. These effects depend on the amount of uptake of N by the plant, which can be affected by the forms of N to which the plant is exposed and the route of exposure (via shoots or roots). Plant species also vary inherently in their ability to use high levels of N. Such variation is typically correlated with plant traits such as specific leaf area, relative growth rate and tissue N content. Hence, the extent to which increased N uptake results in increased productivity can depend upon the species composition and trait profile of the impacted assemblage.

Before the invention of the Häber-Bosch process for producing N fertiliser from N₂ gas, most habitats were nitrogen-limited (Vitousek & Howarth, 1991). Plant growth is reduced at low N availability because there is a lower limit of concentration in plant tissue, so for a given amount of nitrogen only a certain amount of biomass can be made. Species vary considerably in their lower limits for nitrogen concentration, and those that can continue to grow with minimal N uptake, or have other adaptations, are at a competitive advantage under low-nitrogen conditions. Species also vary in their maximal rate of growth, and those that can respond rapidly to favourable conditions are likely to outcompete more slow-growing species when nitrogen is not limited. Increased N deposition thus causes a loss of diversity in most habitats through competitive exclusion (Almufti *et al.*, 1977; Huston, 1979). In some extremely N-limited habitats species number may initially increase with N deposition, but distinctive species are likely to be lost (Bobbink, Hornung & Roelofs, 1998). This picture of N as a limiting resource is complicated by interactions with soil organic matter; by increasing evidence that species respond differently to different forms of N; by the acidifying effect of N deposition; by uncertainty over the effects of temporal changes in soil solution N concentration; by the uptake of gaseous and dissolved N through plant shoots; by differential effects on N fixing plants and other plant groups; and by other biotic interactions.

4.1.1 Dissolved organic, oxidised and reduced nitrogen

Plant-available nitrogen is by definition soluble and is in one of three forms: reduced (NH_y), oxidised (NO_x), or within simple organic molecules such as amino acids (dissolved organic N, DON). Different plant species are adapted to use different forms of available nitrogen, and may grow less vigorously unless provided with N in the preferred form. The ratio of reduced to oxidised N in soil depends on the rates of several processes that affect these forms differentially (see section 2.2), and also on the ratio of N forms in pollutant and agricultural inputs. Large DON concentrations are associated with more organic soils such as peats and peaty mineral soils, i.e. the same conditions as large dissolved organic carbon concentrations. These soils are often acidic, and are formed in waterlogged environments. This also results in low

rates of oxidation and therefore high $\text{NH}_y : \text{NO}_x$ ratios in the soil solution of more organic soils.

Ammonium ions are taken up by plants at less energetic cost than nitrate ions, but can easily reach toxic concentrations (Britto & Kronzucker, 2002), so plants taking up ammonium need to expend energy on detoxification (Fangmeier *et al.*, 1994). Growth and survival rates of plants adapted to calcareous or mesotrophic soils are generally reduced when these species are transferred to environments in which ammonium is the predominant form of N (Paulissen *et al.*, 2004). Conversely, growth of species from acid environments is either not affected or is increased when ammonium is the predominant form (Gigon & Rorison, 1972; de Graaf *et al.*, 1998). These effects may be stronger at greater N solution concentrations (Gerendas & Sattelmacher, 1990). *Carex* species were shown to be indifferent to the form of N at low concentrations, but at higher concentrations there were interspecific differences in the metabolism of NO_x and NH_y , which were related to the acidity of the typical environments of the species (Choo, Lee & Albert, 2002). Trees may not take up nitrate under field conditions if sufficient ammonium-N is available for their growth; *Picea abies* (L.) was found not to do so, and *Fagus sylvatica* (L.) only took up nitrate in one late-summer month (Gessler *et al.*, 1998). Under laboratory conditions, low temperatures greatly decreased nitrate uptake in these tree species, in contrast to ammonium uptake which was not much reduced by low temperature (Gessler *et al.*, 1998). Tree nitrate uptake is closely regulated by the current N status of the tree (Gessler, Kopriva & Rennenberg, 2004), and N-deficient trees are likely to take up nitrate.

Nitrate-adapted species might be expected to have higher rhizosphere ammonium concentrations and nitrification rates than ammonium-adapted species. Olsson (2000) showed that the ratio of rhizosphere nitrification / bulk soil nitrification was greater in nitrate-adapted species, and proposed this ratio as a measure of nitrogen form preference.

The ability to use dissolved organic N (DON) was initially thought to be associated with mycorrhizal species (Abuzinadah & Read, 1986); in particular ericaceous plants (Bajwa & Read, 1985). However, non-mycorrhizal species can use DON directly (Chapin, Moilanen & Kielland, 1993). Miller (2003) demonstrated that plants from the same Alpine community varied in their preferred form of N, and that this preference was not related to the exchangeable N concentration found under the community. Grassland species also differ in their preference for N types, and greater preference for inorganic N is found in grassland species with greater biomass (Weigelt, Bol & Bardgett, 2005). Kielland (1994) suggested that partitioning of the nitrogen resource maintains plant diversity, and such partitioning (in terms of chemical form, location and timing) was demonstrated by McKane (2002) in arctic tundra; the more dominant species tended to prefer the dominant form of N.

4.1.2 Deposition flux and soil solution N concentration

Nitrogen deposition flux is strongly affected by the form of reactive N, and by the type of vegetation and its interception properties. Dense canopies with a large surface area, such as those of heathlands (Bobbink, Heil & Raessen, 1992) and woodlands, intercept more N from mist and by dry deposition than short, relatively open vegetation such as grassland. Ground vegetation under a woodland canopy is also

susceptible to increased N deposition since much of the N intercepted in the canopy will be washed directly through.

Dry deposition is an important route for plant uptake of reduced N, particularly in regions with higher NH_y emissions (Fangmeier *et al.*, 1994). European dry NH_y deposition was calculated by Asman (1992) to be greater than the wet deposition flux (Figure 6).

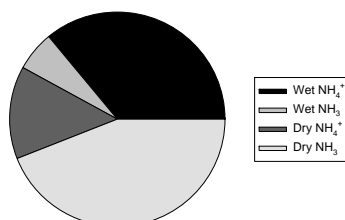


Figure 6 Relative contributions of wet and dry NH_3 and NH_4^+ to total deposition of European NH_y emissions. Adapted from Asman (1992).

Dry deposition fluxes are highly variable, being dependent on time of day, temperature, humidity, the roughness and pH of the receptor surface (Fangmeier *et al.*, 1994), and internal plant N concentrations. Canopies affect transport as well as deposition fluxes; direct uptake within the canopy can result in throughfall being less concentrated than rainfall. More commonly, particularly in polluted areas, throughfall is more concentrated than rainfall due to increased wet and dry NH_y interception in the canopy (Fangmeier *et al.*, 1994).

Plant exposure to soil N has most often been related to N concentration in soil solution, (although canopy uptake is also an important flux - see section 4.1.3). Soil solution concentration determines the rate of N uptake and the strength of any toxic effects. However, concentration is variable in time, and the mean annual concentration is conveniently calculated by dividing the annual leaching flux by the precipitation surplus. This approach has been taken in calculating critical nutrient N loads, which are based on the maximum concentration acceptable if changes in vegetation type are to be avoided (Spranger, Lorenz & Gregor, 2004). The approach makes two critical assumptions; that plants respond to chronic rather than to acute exposure, and that the concentration of N in the (sub-)soil solution indicates plant exposure.

The importance of occasional high concentrations relative to slightly but chronically raised concentration is not well-understood. Effects on plants have been observed after both prolonged exposure at rather low N concentrations and brief exposure at high N concentrations. It is currently unknown whether the effect of integrated exposure (concentration x time) is greater when concentrations are more variable. The buffering effect of microbial processes on soil solution N concentrations perhaps implies that acute effects are more likely above-ground.

The concentration of N in soil solution is affected by fluxes other than downward leaching such as immobilisation, decomposition, plant uptake, and lateral leaching. Whether plants are exposed to these N fluxes depends on whether they are synchronised in time and space with plant N uptake. Low soil solution N

concentrations can be the result of rapid plant uptake, and so do not necessarily indicate low rates of eutrophication.

4.1.3 Shoot N exposure and uptake

The N concentration in soil leachate is a useful indicator of plant exposure, but the direct exposure of plant shoots to atmospheric inputs can also be significant.

Toxic effects of ammonia are not usually a major driver of plant responses and vegetation change, but can occur in sensitive species close to point sources such as poultry or pig units. Visible leaf injuries occur in mosses at concentrations of 120 – 240 $\mu\text{g NH}_3 \text{ m}^{-3}$, or even as low as 30 $\mu\text{g NH}_3 \text{ m}^{-3}$ in sensitive species such as *Racomitrium lanuginosum* (van der Eerden *et al.*, 1991). Unpolluted background concentrations are typically 1 – 10 $\mu\text{g NH}_3 \text{ m}^{-3}$ (Fangmeier *et al.*, 1994). The susceptibility of plants to toxic effects of ammonia is related to their assimilation capacity, and chronic exposure causes damage at lower concentrations than acute exposure (Fangmeier *et al.*, 1994).

Uptake of N through plant shoots can have large effects on ecosystem N dynamics even at sub-toxic levels. Shoot uptake reduces N flux to the soil, although it still represents an ecosystem input. Uptake by bryophyte shoots can be substantial, and since recent N inputs are taken up by shoots, and these recent inputs are particularly susceptible to leaching (Tietema, 1998 #316), bryophytes may be important regulators of N leaching from moorlands (Curtis *et al.*, 2005a).

4.1.4 Effects on different plant groups

Applications of N have been observed to decrease bryophyte cover relative to that of grasses (Carroll *et al.*, 2000), but responses cannot be generalised for plant groups of this size. In fen vegetation, ammonium deposition had adverse effects on the growth of brown mosses, but not on fast-growing *Sphagnum* and *Polytrichum* moss species (Paulissen *et al.*, 2005). The range of fertility scores for bryophytes given by Siebel (1993) also indicates the diversity of their responses to N. Insensitive bryophyte species may also decline with increased N deposition, as result of increased competition from other species. Conversely, bryophytes that are not sensitive to N, but are tolerant of shading, may increase in abundance.

4.1.5 Nitrogen location in relation to root uptake

Nitrogen availability in soils can vary considerably with depth. Most N inputs are at the surface, and processes in the litter and upper soil layers can strongly affect the amount of N leaching into deeper soil layers. The vertical distribution of plant roots gives some indication of the depth from which they take up nitrogen (Rowe *et al.*, 1998-9). Spatial separation of plant root systems may allow resource partitioning and the coexistence of species. However, there are few data on typical vertical root and root activity distributions, which may hinder the development of models of plant N exposure. A useful generalisation is that the rhizoids of ectohydric bryophytes (i.e. those lacking water-conductive tissue) do not extend far into the mineral soil, although they are less exclusively dependent on precipitation N than had been thought (Bates, 1994). Annuals are more shallow rooting than perennials, at least in the early

stages of growth. Woody plants can be shallow or deep-rooting. More studies might reveal useful relationships between plant traits and rooting depth.

4.2 Interactions of nitrogen deposition with other factors

4.2.1 Competition

As has already been noted, competition between plants has large effects on their occurrence, and is the main mechanism through which N deposition changes vegetation. Increased shoot growth increases above-ground competition for light. Increased root growth also increases the ability of root systems to capture resources rapidly, and so increases below-ground competition. As N availability increases, there is a shift from root (soil nutrients & water) to shoot (light) competition, and so coexistence is increasingly a function of the asymmetry of above-ground competition for light. Hence, tall or highly clonal and fast growing species (grasses and tall forbs), are likely to dominate. Perennial species that can store N and remobilise it the following year, or which are able to recycle N from senesced material efficiently, will also be at a competitive advantage (e.g. *Brachypodium pinnatum* in calcareous grasslands; Bobbink, 1991).

Many competitive interactions can affect an individual species, and the effect of N on a particular interaction is difficult to predict. It may be possible to characterise plant species in terms of their competitive features (e.g. maximum height) and use this information within occurrence models. However, the outcome of a competitive interaction depends not only on features of the mature plant, but on the success of reproduction and establishment, the other species present, and other biotic interactions.

Models of community occurrence implicitly include competitive interactions between the species that make up the defined communities. However, changes in community composition, in particular the introgression of alien species, will change competitive interactions. These effects are difficult to separate from the effects of a changing environment.

4.2.2 Limitations of nutrients other than nitrogen

When plant growth is limited by nutrient supply, the most limiting nutrient has a dominant effect, although whether this effect overrides or interacts with other limitations is the subject of debate (see section 4.5.5). After N, phosphorus (P) is the most common limitation to plant growth in seminatural habitats. If P availability limits plant growth, nitrophilous species cannot respond to increased N availability (Pigott & Taylor, 1964; Chapman, Rose & Basanta, 1989) and so N deposition will have little effect on species composition. This may be particularly true for wetlands; in a survey of largely wetland Eurasian sites, limited P availability seemed to allow the persistence of more endangered species than limited N availability (Wassen *et al.*, 2005).

There is currently little evidence for plant growth limitation in seminatural habitats by deficiencies of nutrient elements other than N and P, although potassium is thought to

frequently limit growth in bogs (Morecroft *et al.*, 2005). Other limitations may become significant when N and P are maintained at high levels of availability but there is continued export of other plant nutrients.

4.2.3 Water relations

Acute exposure to high NH₃ concentrations has been shown to increase transpiration rates and drought susceptibility in *Calluna vulgaris* (van der Eerden *et al.*, 1991) and in *Pinus sylvestris* (Van der Eerden & Perez-Soba, 1992). Two mechanisms were proposed by Fangmeier *et al.* (1994): an increase in leaf C demand (for assimilating NH_y) causing increased stomatal opening; and an increased shoot / root biomass ratio.

4.2.4 Frost

Higher N concentrations in plant tissue may increase susceptibility to frost damage, although evidence for this effect is inconclusive (Sheppard, Rosengren & Emmett, 2003) and it may only be important during critical periods such as just before the start of spring growth (van der Eerden *et al.*, 1991). Low levels of N application to UK lowland heath accelerated spring budburst and therefore slightly increased frost sensitivity in April, although not in winter (Power *et al.*, 1998).

4.2.5 Climate change

Increasing CO₂ concentrations and temperatures may increase plant growth and N demand, which will tend to reduce N concentrations in soil solution. Since many of the adverse effects of N on habitats come from increasing canopy height and hence an increase in competition, this buffering is of limited value.

Since decomposition rates are temperature-dependent, increased temperature is also likely to increase mineralisation rates of soil organic matter. Nitrate flux in seepage water was shown to increase following night time warming on a heathland site in the Netherlands, although this effect was not seen clearly at another two European heathland sites (Schmidt *et al.*, 2004). Increased nitrate flux presumably indicates increased plant-available N. Freeze-thaw and wetting-drying cycles also tend to increase mineralisation rates and can cause pulses of nitrate leaching (e.g. Reynolds *et al.*, 1992).

Changing patterns of precipitation will also affect N fluxes. An increase in rainfall will generally increase rates of N transfer through soil and vegetation. It may also increase N deposition, since wet leaves take up more ammonia. However, increasing intensity of precipitation is likely to increase the amount of bypass flow (i.e. surface runoff and water movement through soil macropores, rather than through the soil matrix). This will decrease soil exposure to deposited N, although downstream effects will increase.

4.2.6 N fixing plants

Many plant species are N fixers, having formed symbioses with microorganisms which have the ability to fix N₂ from the air into usable forms. The majority of these plants are legumes, i.e. are in the Fabaceae. Nitrogen fixation has an energetic cost –

although this is similar to the energetic cost of assimilating nitrate (Giller, 2001) – and thus may reduce the competitiveness of species (Vitousek & Howarth, 1991). Where N is not the most limiting factor N fixing plants are likely to be outcompeted. Nitrogen fixing plants are thus not major components of most tall vegetation types in temperate and boreal regions, although there are exceptions such as *Alnus glutinosa* woodland and *Ulex* scrub. High concentrations of nitrate have been shown to inhibit nodulation (Carroll & Mathews, 1990) and N fixation (Streeter, 1988). Thus increasing N loads may be associated with a reduction in the abundance of N fixers.

4.2.7 Invertebrate herbivores

The nitrogen content of plant material has large effects on the growth rate, fecundity and survival of herbivores (Crawley, 1983). Increased substrate N content generally leads to a decrease in the substrate intake rates of invertebrate herbivores (although some species increase feeding rates), since less material is required for the same amount of N. This implies a reduction in herbivore damage with increasing N deposition, but this effect is likely to be counteracted by an increase in herbivore population. Low levels of N application to UK lowland heath increased growth rates of heather beetle *Lochmaea suturalis*, which is implicated in early gap formation in heather *Calluna vulgaris* canopies (Power *et al.*, 1998). Similar effects of N on heather beetle have been observed in the Netherlands (Brunsting & Heil, 1985) and Norway (Tybirk, Bak & Henriksen, 1995).

4.2.8 Grazing

Grazing has a large effect on vegetation and species occurrence, thus altering the sensitivity of a community to nitrogen deposition. For example, grazing may reduce the competitive advantage of a species able to exploit elevated nitrogen availability thus helping to maintain overall biodiversity (Wilson *et al.*, 1995). Alternatively, grazing may exacerbate the effects of nitrogen (van der Wal *et al.*, 2003).

Where animals cause a net increase in N losses (via offtake in meat and milk, and/or loss of ammonia from animals or excreta), this N export can moderate the effects of N deposition. However, grazing can cause a net addition of N, for instance when livestock are fed concentrates, or are stored on unproductive pasture during winter. (Emmett *et al.*, 2004b). Grazing-induced changes in soil structure may affect hydrological pathways and thus the retention and fate of deposited N (Emmett and Ferrier, 2005). Ruminants and non-ruminants respond differently to increased N content of herbage – intake rates by ruminants increase more or less linearly with digestibility, which is correlated with N content, whereas intake rates by non-ruminants decline (Crawley, 1983).

4.2.9 Other biotic interactions

Mycorrhizal associations may be inhibited by large rates of N deposition (Yesmin, Gammack & Cresser, 1996), although the effect appears to be less significant than the reduction in mycorrhizal function caused by acidification and aluminium toxicity (Bobbink, Hornung & Roelofs, 1998).

Parasitic and hemiparasitic plants reduce the vigour of their hosts and can change the competitive balance within plant assemblages. Many European hemiparasites derive nourishment from grasses. The hemiparasite *Rhinanthus minor* has received particular attention for its ability to reduce the dominance of graminoids and thus increase the species diversity of grassland (Bullock & Pywell, 2005). This is likely to affect overall productivity and hence plant N uptake. Effects of increased N deposition on the prevalence of (hemi-)parasitic plants are not well-understood, but it is clear that they can be keystone species with strong effects on community composition (Press & Phoenix, 2005) and on nitrogen cycling, for instance because of high litter N contents (Quested *et al.*, 2005).

Algae and lichens growing on leaf surfaces reduce light availability to their host plants, and may be favoured by increased N deposition.

Plants may also facilitate the growth of other plant species, through mechanisms such as:

- Hosting epiphytic, parasitic and hemiparasitic species
- Increasing shading and thus favouring shade-adapted ground layer species
- Accumulating litter and nutrients and thus favouring more mesotrophic species
- Accumulating acidic litter and thus favouring calcifuge species

Many facilitative interactions can be characterised in terms of an abiotic factor, such as increased shading or changing soil pH or C/N ratio.

4.3 Effects of nitrogen on lichens, fungi, animals and other groups

Plant diversity underpins diversity in other groups, for instance by providing animals with a variety of food and shelter (Silvertown, 2004). Other groups are however also important from a biodiversity conservation perspective and for the functioning of the ecosystem. How much diversity is necessary for ecosystem function is the subject of debate, and there is certainly much functional redundancy in groups such as decomposers.

Around 10 % of lichen associations or “species” have a cyanobacterial photobiont which is negatively affected by N (Bobbink, Hornung & Roelofs, 1998). The remainder have a green algal photobiont, and may respond positively or negatively to N. Many of the European cyanobacterial lichens have become rare, and their decline along a gradient from the Netherlands to Sweden was found to be significantly correlated with N deposition rates of over 5-10 kg N ha⁻¹ y⁻¹ (Goransson, 1990). In a survey of N uptake rates by 14 lichens, Dahlman (2004) found lower nitrate uptake rates by cyanobacterial lichens. All species were able to take up amino acid N at comparable rates to mineral N.

Fungi also differ in their responses to N deposition. Sporocarp production from mycorrhizal fungi was found to be reduced on formerly N-fertilised plots in Swedish boreal forest, even 47 years after fertiliser application ceased (Strengbom *et al.*, 2001). However, in the same experiment a leaf-parasitic fungus was found to be more abundant on formerly N-fertilised plots.

Investigations of animal responses to N deposition are comparatively poorly advanced. Abundance of larger animal species has not been much considered in relation to N pollution impacts, although vertebrate herbivores are included within SUMO and FORSAFE-VEG, and models have been developed of grazing within European semi-natural habitats (e.g. Armstrong, (1997). Characterising invertebrate species in relation to environmental gradients would require much new survey and experimental work. Invertebrate traits could be used as indicators of likely susceptibility to change (c.f. Hodgson, (1993). Foliar herbivores respond strongly to phloem N concentration (see section 4.2.7), and increasing N is thus likely to drive an increase in prey availability, at least of those species that are herbivores on plant species favoured by increased N. The complexity and importance of multitrophic interactions is however illustrated by the decline in the red-backed shrike in northern Europe, which has been related to N pollution-driven loss of open areas in sand dunes and consequent loss of shrike prey diversity (de Vries *et al.*, 2005).

4.4 Effects of nitrogen on semi-natural habitats

The effects of N pollution on species diversity of European habitats were well reviewed by Bobbink *et al.* (1998); in the NEG-TAP report (NEG-TAP 2001) and during the revision of the critical loads for nitrogen at the UN/ECE Expert Workshop held in Berne in 2002 (Bobbink *et al.*, 2003).

4.5 Approaches to predicting species occurrence

4.5.1 Environmental gradients, niches, and occurrence prediction

Species occur in a region, called an envelope or the species' niche, within a space defined by multiple environmental factors (Hutchinson, 1957). The envelope within which the species could occur in the absence of competition and other biotic interactions is known as its fundamental niche. The envelope within which the species actually occurs, the realised niche, is smaller than the fundamental niche, e.g. because disease, herbivores or competition from better-adapted species restrict occurrence at extremes of a species' range.

The distribution of probability of occurrence of species in relation to environmental gradients has been hypothesised as having a unimodal Gaussian normal function (Gauch, 1982), although other distribution types are possible (Figure 7).

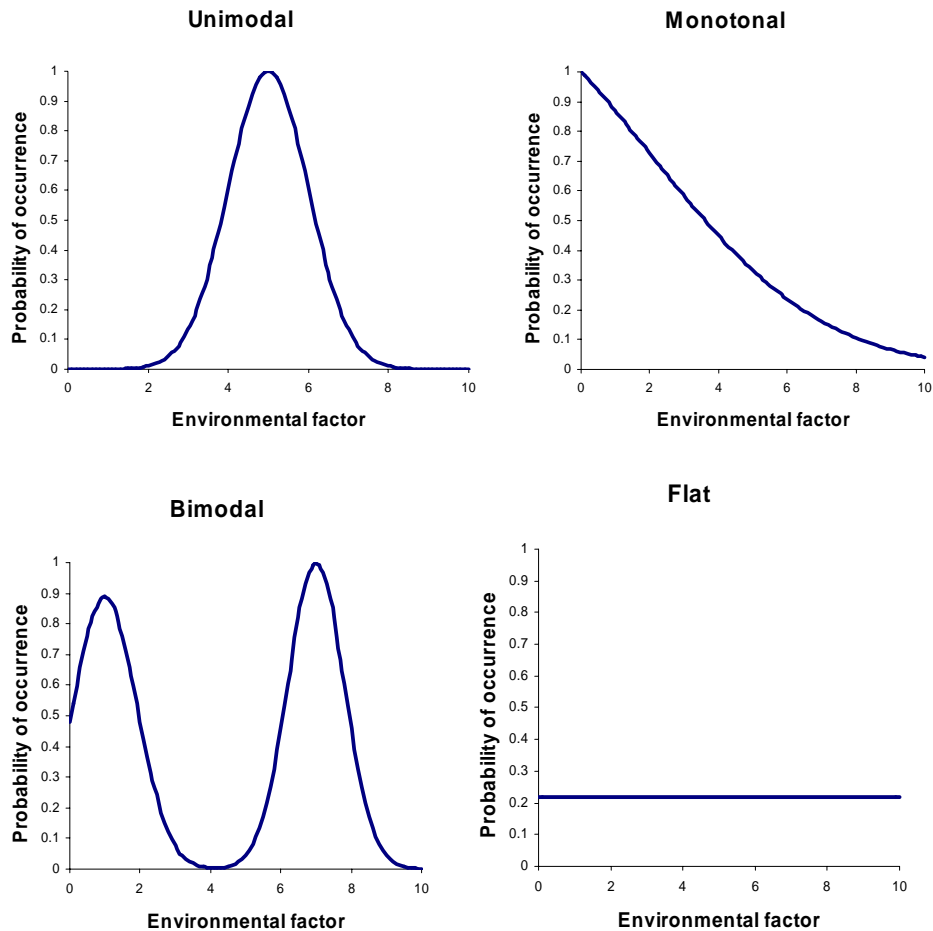


Figure 7 Unimodal (Gaussian), monotonal, bimodal and flat distributions of probability of occurrence for four hypothetical species in relation to an environmental gradient.

There are difficulties with this approach:

- The x-axis may be hard to define – integrated exposure of a species to an environmental factor is difficult to measure, and indicative or surrogate measures may not be good indicators of exposure.
- Probability of occurrence cannot be interpreted literally as the chance of the species occurring on a site of particular size.
- Many distributions are flat, i.e. a species may have a wide tolerance in relation to an environmental factor.
- Some species have a wide tolerance but are replaced by more competitive species in the centre of the environmental gradient, and hence have bimodal probability of occurrence distributions (Figure 7).
- Many environmental factors, particularly *events*, do not map onto continuous gradients.
- Species occurrence is governed by the interaction between several environmental factors.

According to the principle of competitive exclusion, if two species share the same resource, the more dominant of the two will eventually use all of that resource and exclude the less dominant species. The coexistence of plant species presents a challenge to this theory, if all plants are competing for the simple resources of light,

water and nutrients. Large numbers of plant species do coexist in many habitats. Potential explanations for species coexistence were recently described by Silvertown (2004), and can be summarised as follows:

- Regeneration niche. If species have different requirements for dispersal and establishment they can coexist.
- Storage effect. If resources vary from year to year, perennial species (or those with persistent seed banks) with different strategies for storing resources can coexist.
- Nitrogen form preference. If species have different ability to use the different forms of N they can coexist.
- Microbial mediation. If there are species-specific relationships with microorganisms which facilitate plant nutrient uptake, this further partitions the effectively available nutrient pools.
- Below-ground heterogeneity. If species access nutrients from different depths they can coexist.
- Resource ratio model. If two limiting nutrients vary in relative concentration within a habitat, this can allow the coexistence of more than two species.
- Competition-colonization tradeoff. If traits needed for efficient colonisation cannot be combined with traits associated with high competitive strength, species can coexist in a dynamic equilibrium.

These considerations illustrate the fact that a simple measure of N exposure may not be enough to predict whether any individual species will occur. Nevertheless, the amount of N exposure does have a strong influence on species' competitiveness. Measures that can be used to indicate nitrogen exposure will be considered further in section 1.3. Methods for predicting species occurrence in relation to environmental factors using static and dynamic distribution models and knowledge-based approaches were reviewed by Guisan (2000). Unimodal or skewed distributions do seem to be the most common type, at least in relation to the dominant environmental factor. This was true for Danish woody (Lawesson & Oksanen, 2002) and grassland species (Ejrnaes, 2000), and for Swedish woodland species (Diekmann & Falkengren-Grerup, 1998). However, species may show more complex bimodal or multi-modal relationships, as was demonstrated by Wamelink *et al.* (2005) by fitting spline curves to data relating species occurrence to measured pH.

4.5.2 Events

Events such as dispersal, fire, climatic extremes, ploughing, timber harvesting, etc., are not easily transformed into a variable onto which probability of species occurrence can be regressed. The probability of the event's occurrence could be used as the x-axis, although some management events are effectively unpredictable. Another approach is to first predict occurrence in relation to environmental gradients, and then filter the results according to actual or predicted events.

Although dispersal is a highly stochastic process, plant and / or site characteristics can be used to estimate the chance of introgression. Species growing nearby or having efficient dispersal and establishment mechanisms are more likely to invade a site than distant species or those that disperse poorly. Even if conditions are optimal for a species, it will not occur unless it is already present locally, or propagules are able to disperse to the site. Plants differ in their methods and rates of dispersal, and

introgression from even an adjacent site may take 10-20 years (Tilman, 1998). Grazing has strong effects on dispersal, via gap creation and the transfer of propagules.

4.5.3 Constructing species-environment relationships

The relationship between each gradient and probability of occurrence can be constructed using a set of relevés, i.e. site-specific data on plant species presence and abundance, that have associated environmental data. Distribution data reflect the realised rather than the fundamental niche, since they are derived from stands in which plants are competing. Species-environment relationships may vary across the geographical range of a species, and so the origin of the training dataset used for calibrating these relationships is important. The training sets used for the different models reviewed in this report are described in section 2.5.

The work of Ellenberg (1974) is important in this context. He defined scores on a scale from 1 to a maximum of 12 for many European vascular plant species in relation to six environmental axes: Fertility, pH, Wetness, Light, Temperature and Continentality. These can be seen as representing the maximum probability of occurrence of each species, or its environmental optimum. They do not however give any information about how probability changes along the axis. The scores were based on a synthesis of experimental and descriptive studies in Central Europe, and may become less accurate with distance from this region (Hill *et al.*, 2000). Axis definitions are somewhat ambiguous, and generally do not relate to easily measurable environmental factors. The fertility gradient, which is the most relevant for N effects, does not distinguish between nutrient elements, although (confusingly) it is referred to as the “N” gradient. The distribution of assigned scores is not consistent among the different axes. With these provisos, Ellenberg scores represent a useful summary of environmental optima (Diekmann, 2003).

Later works by the same authors (Dull, 1991; Ellenberg *et al.*, 1992) included indicator scores for bryophytes. Environmental indicator scores were also defined for Dutch bryophytes by Siebel (1993) and recently for British bryophytes by Hill *et al.* (2005).

The calibration of species-environment relationships is predicated on the assumption that these are at equilibrium, i.e. that changes in species occurrence track changes in the environment. In a changing environment, species presence will also be affected by the time taken for loss or invasion. If environmental change occurs more rapidly than species change, species-environment relationships are likely to be obscured.

4.5.4 Predicting community or species occurrence?

Plant species occur in distinctive associations, and typical European plant communities have been extensively described, notably by Braun-Blanquet (1965). Inasmuch as discrete plant communities can be identified, their occurrence can be described and predicted in relation to environmental factors in a similar way to species occurrence (e.g. Schlutow, 2004). The “organismic” concept of discrete plant communities has a long history (e.g. Cowles, 1899; Clements, 1916) but has been challenged from its early days by those making the “individualistic” argument that

each species is distributed in relation to environmental factors, including the occurrence of other species (Gleason, 1917). This implies that plant associations vary continuously, and so discrete communities can only be defined by placing artificial limits in space and time.

Plant associations have undoubtedly changed in response to climatic variation in the recent past (Prentice, 1986; Birks, 1993), and their composition varies geographically. In view of the multiple changes to climate, land use, pollutant load, rainfall pattern and biotic factors that are currently affecting vegetation, it is likely that typical plant associations will change again. Species occurrence models are therefore more generally appropriate for predicting changes to plant associations in a dynamic environment. Community occurrence models nevertheless have a role, since they include competitive and complementary interactions between species which are not well-described by occurrence models based purely on environmental data. Also, since there are too few data to define relationships between probability of occurrence and environmental factors for all species, the occurrence of less common species may be predicted from association with well-defined species even in individualistic models, which blurs the distinction between community and species models.

4.5.5 Interactions between factors

Interactions between environmental factors may also change the size of the realised niche. The effect of multiple stresses on plant performance has long been the subject of debate. The idea that plant yield is always limited by the most limiting resource (the “law of the minimum”) was introduced by Sprengel (1828) and promulgated by von Liebig (1840) (van der Ploeg, Bohm & Kirkham, 1999). This was refuted by Liebschner (1895), who stated that the limiting resource is used more efficiently if other factors are close to their optimum. The response of species’ probability of occurrence to a resource or limitation will differ mathematically from crop yield response curves. Nevertheless, similar principles apply to the formulation of probability of occurrence surfaces and hypersurfaces in response to two or more interacting environmental factors.

These concepts result in different conceptions of the realised niche (Figure 8). von Liebig’s concept is expressed by simply taking probability of occurrence to be the minimum of the probabilities of occurrence in relation to two or more factors (Figure 8. a, d). Liebschner’s concept can be formulated by calculating probability of occurrence in relation to two factors as the product of the probability of occurrence in relation to each factor singly (Figure 8. b, e). If there are large interactions between two factors, as for example when water availability affects the availability of nitrogen, the maximum PO on the axis for one of the factors will depend on the level of the other (Figure 8. c, f).

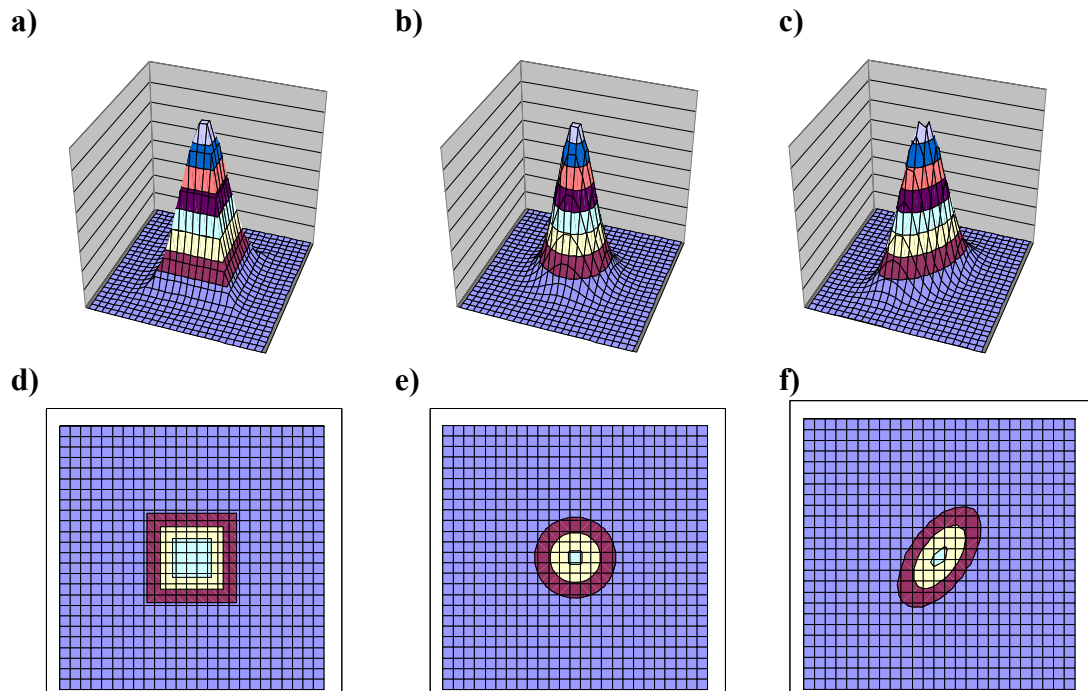


Figure 8 Hypothetical realisations of probability of occurrence in relation to two environmental gradients, assuming that these act in combination: (a, d) as the minimum probability of occurrence in relation to each factor; (b, e) as the product of the two probabilities of occurrence; and (c, f) assuming that the response to one factor varies with the level of the other. Probabilities of occurrence were rescaled to the same range for each of these three methods.

4.6 Measures of nitrogen exposure

4.6.1 Introduction

To connect theory on nitrogen dynamics in soil with models of plant species occurrence, a measure of nitrogen exposure, i.e. of plant-available N, is required. The N to which an individual plant is exposed is a function of:

- soluble N concentration in soil solution
- total flux of soluble N
- type of soluble N
- soluble N dynamics, including immobilisation, nitrification, denitrification and volatilisation
- rate of N transport to the root, which is strongly influenced by soil water content
- timing of availability in relation to plant demand
- root distribution in relation to spatial N heterogeneity
- leaf N uptake, which is affected by the type of deposition (wet vs. dry; NO_x vs. NH_y)

Monitoring these factors even for a single plant would be a major undertaking. Many different measures to integrate N exposure into a single indicator have been proposed. These can be grouped as follows:

- Soil total N
- Measures of soil solution N (NO_3 , NH_4 , DON)
- Measures of soil mineralisable N
- Compound indicators (e.g. nitrification/immobilisation ratio)
- Other indicators of soil N reactivity (C/N, light fraction N, spectroscopy)
- Measures of N deposition (total N, NH_y , NO_x)
- Measures of plant chemistry (tissue total N, N/P, specific compounds)
- Other biotic indicators

Many biotic indicators (such as occurrence of typical plant species, or the performance of an allochthonous test plant) are unsuitable for summarising outputs from a biogeochemical model. Indicators derived from plant assemblage composition also cannot be used to summarise biogeochemical model outputs, but they are commonly invoked as an intermediate step between biogeochemistry and species occurrence models.

To predict N availability it is necessary to understand how reactive the soil organic matter is. Most theoretical treatments of organic matter decomposition assume that it consists of discrete pools each with a first-order rate constant for decomposition, i.e. undergoing exponential decay. Models of N release (and C oxidation) from SOM are reviewed in section 3.1. Attempts have been made to relate such theoretical SOM pools to measurements e.g. (Sohi *et al.*, 2001). These rely on either a) artificially decomposing the more labile organic matter by incubation (this method is also used to measure mineralisable N; see section 4.6.6); or b) measuring how protected the nitrogen in organic matter is from decomposition. Protection is related to soil texture,

C / N ratio and content of humified / phenolic compounds. The release of N from fresh plant litter is governed by similar factors.

The following discussion of N exposure measures is based on a review by Morecroft (2005), which gives further information on sampling protocols and costs.

4.6.2 Soil total N

The total soil N pool is largely inactive, and so is not a good indicator of N availability (Tamm, 1991).

4.6.3 Carbon / Nitrogen ratio

The concept of N saturation (Aber *et al.*, 1989) has been used to explain the dynamic relationship between soil solution N and total soil C / N (or organic horizon C / N) seen particularly in forest systems. With a sustained increase in N deposition, immobilisation buffers soil solution N, and C / N decreases without large changes to solution N concentrations. According to this model, soluble N concentrations only start to increase after a threshold C / N value is reached (Dise, Matzner & Gundersen, 1998). This threshold C / N approach has been used in several models of N leaching such as SMART2 (Posch & De Vries, 1999), MAGIC (Cosby *et al.*, 2001) and VSD (Posch & Riends, 2005). However, it is becoming clear that C / N thresholds can be affected by vegetation type (Rothe & Mellert, 2004) possibly due to the carbon measurement not reflect the reactive C pool and /or differences in the microbial community and their carbon and nitrogen requirements (Wright *et al.* 1998). In addition, microbial uptake may also be altered by increased ammonium supply independent of changes in carbon supply (e.g. Bradley 2001). These feedbacks on controls on nitrogen uptake by microbes are critically important for nitrate leaching, as ¹⁵N tracer work indicates that much of the nitrate leached is recently deposited (Tietema *et al.*, 1998).

4.6.4 Soil solution N

The soluble nitrogen pool is in principle immediately available to plants (although species differ in their ability to use different forms of soluble N, i.e. NH₄⁺, NO₃⁻ and DON – see section 4.1.1). In addition to the total inorganic-N concentration, the ratio of ammonium to nitrate in solution may provide information relevant to species occurrence and also the potential for microbial uptake of nitrate (Hughes *et al.* Submitted, Emmett *et al.* Submitted). However soil solution only reflects the nitrogen in excess of uptake demands and leaching losses and thus may underestimate total N availability to plants. Concentrations are very dynamic both spatially and temporally and thus single measurements of soil solution N concentrations are thus of limited use. Trends, and measures integrated over time such as mean or maximum annual or growing season concentration, are more reliable indicators of N status. Sampler type and depth may affect concentrations with standardisation generally required (Wu, Baker & Allmaras, 1995) (Reynolds *et al.*, 2004). Solution extraction methods were reviewed by Titus (1996). Samples may not be available during dry periods unless a slurry method is used.

4.6.5 Extractable N

The amount of N extractable from fresh plant litter or soil horizons using salt solution (usually KCl) can provide information even in dry conditions. Again the data will reflect excess nitrogen remaining after plant uptake and recent leaching losses and therefore will underestimate availability. Sampling should ideally be standardised in relation to rainfall events – recent rainfall is likely to leach out mineral N, particularly nitrate. Results again very dynamic both spatially and temporally. As with soil solution nitrogen the ratio of ammonium to nitrate in extractant may provide information relevant to species occurrences and also microbial uptake.

4.6.6 Mineralisable N

Mineralisable N provides index of net production of inorganic-N. Methods developed to determine the amount of easily mineralisable N are based on measuring soluble N concentrations after incubation under standard conditions. These are designed to mimic either field conditions or optimum conditions for decomposition, and various standard temperatures and moisture contents have been proposed. (Stanford & Smith, 1972; Waring & Bremner, 1964; Diekmann & Falkengren-Grerup 1998). Methods are generally designed to mimic either field conditions or optimum conditions for decomposition, and various standard temperatures and moisture contents have been proposed. Disturbance has a large effect, and so disturbance level must also be standardised (e.g. intact cores, roots removed, sieved). Aerobic incubation may stimulate microbial immobilisation, especially in soils with high C / N ratios, and so anaerobic incubations have been recommended for waterlogged and high C systems (Keeney, 1980; Williams & Sparling, 1988). N mineralisation is highly variable in space and time, and measurements need to be standardised for soil horizon and season. Organic matter content also affects mineralisation, and clearer comparisons will be obtained by expressing results in terms of N mineralised per unit organic matter (Morecroft *et al.*, 2005).

Absolute rates may be reported, or converted to indices reflecting potential mineralisable N and the relative amount of mineralised N converted to nitrate. Diekmann & Falkengren-Grerup (1998) assessed ammonium and nitrate release after an incubation of 15 weeks at 18 °C and approximately 40-60 % of water-holding capacity, and defined a “Functional N Index for Species” as the linear combination of these two variables that gave the best correlation with species scores on the first axis of a floristic ordination. This index was less susceptible to changes in nitrification rate, etc., than mineralised ammonium, and thus better correlated with species occurrence.

4.6.7 Gross mineralization and nitrification rates

Measurement of gross rates of both mineralization and nitrification reflect the internal cycling of nitrogen and this potentially the maximum inorganic-N pool available to the plants albeit in competition with microbial uptake. A large ratio of gross nitrification / gross immobilisation has been suggested as indicating ecosystem nitrogen saturation, i.e. excess N over what can be retained by soil and vegetation (Goulding *et al.*, 1998). This is because nitrification tends to increase with cumulative N deposition and storage, whereas the immobilisation rate tends to decrease (Aber,

1992). Aber (1992) suggests that the ratio of gross / net mineralization and nitrification will decrease with increasing N saturation. More recently, a decline in gross rates of nitrate immobilisation associated with ammonium turnover and availability (Hughes et al. Submitted) has been proposed as an indicator of the onset of nitrate leaching and the start of nitrogen saturation (Emmett et al. Submitted). Measurements of gross fluxes require isotope dilution studies and so may not be practical for wide application.

4.6.8 Soil organic matter properties

Many attempts have been to relate N mineralisation rate to soil organic matter properties. Large amounts of phenolic compounds inhibit N mineralisation, whether these are insoluble compounds such as lignin or microbial cell wall components, or soluble compounds such as tannins. The rate of decomposition of litter, in particular, has been predicted using measures such as lignin / N or (lignin + soluble polyphenol) / N (Berendse *et al.*, 1987; Vanlauwe *et al.*, 1997), and protein binding capacity (Handayanto, Cadisch & Giller, 1994). The lignin (and cellulose) content of organic materials can be approximated by sequential extraction using acid detergent solutions. Organic nitrogen is also protected by association with small mineral particles. Thus many measures of soil reactivity are based on size-density fractionation, using combinations of sieving and flotation to separate large, light, labile organic matter from small, mineral-associated, dense, recalcitrant organic matter (Cambardella & Elliott, 1993). Near infra-red reflectance spectroscopy has also been used to characterise soil organic matter (Alabbas, Swain & Baumgard, 1972), for example to assess soil total N and mineralisable N (Russell, 2003), or crop N uptake (Borjesson *et al.*, 1999). The method may need to be calibrated separately for different soil types (Russell, 2003), and may not accurately reflect mineralisable N (Reeves, McCarty & Meisinger, 1999), but its speed and low cost are major advantages.

4.6.9 Measures of N deposition

The buffering and processing of nitrogen by soil microorganisms modifies plant exposure, so N deposition flux is not a complete measure of exposure for plants rooting in soil and may thus not adequately reflect direct above-ground effects. Deposition flux does however accurately reflect the exposure of species with limited root systems, particularly bryophytes and lichens. Depending on land use history, current local N deposition may be a good indicator of cumulative deposition. Where local N deposition data are available, they may be better used to drive a soil N balance model.

4.6.10 Plant tissue analyses

The use of tissue concentrations of N and other compounds as indicators of N deposition was recently reviewed by Sutton (2004). Increased plant N uptake is likely to lead to increased tissue N concentrations (McNulty, Aber & Boone, 1991), and tissue N concentrations in particular species have been shown to increase with atmospheric N input e.g. (Baddeley, Thompson & Lee, 1994; Pitcairn, Fowler & Grace, 1995). Ammonium concentrations in plant tissue are more closely related to plant uptake than is total N, and thus indicate recent exposure (Sutton, Pitcairn & Whitfield, 2004). Tissue concentrations of amino acids (van Breemen & van Dijk,

1988; Nasholm et al., 1994; Pitcairn et al., 2003) and N / P ratios (Gusewell, 2004) have also been related to N availability. Tissue concentrations vary considerably – among species, with plant part and tissue age / phenological stage, seasonally, interannually, and with nutrient supply, grazing, or other management (e.g. Emmett (2004). Nevertheless, if these factors can be controlled for (e.g. by sampling a standard part, from a single species or group, at a standard time of year) tissue concentrations of N and amino acids may be good indicators of N exposure (Pitcairn *et al.*, 2001) and in principle could be outputs from biogeochemical models.

4.6.11 Indicators based on the plant species assemblage

As has been discussed (see section 4.5.3), environmental indicators have been defined for European vascular plants and bryophytes (Ellenberg *et al.*, 1991; Siebel, 1993). Mean scores for these indicators can be used to describe a plant assemblage (Pitcairn *et al.*, 2004). Mean scores may also be suitable targets for prediction by biogeochemistry and vegetation type models. Mean Ellenberg fertility (EbN) scores have been shown to be good indicators of soil N availability (van Dobben, 1993), although the relationship usually shows large variation (Wamelink *et al.*, 2002) and appears to correlate best with annual above-ground biomass production rather than soil nutrient status (Hill & Carey 1997; Schaffers 2002). This variation may be reduced by forming relationships separately for different phytosociological groups (Wamelink, van Dobben & Berendse, 2003).

According to van Dobben (1993), the relationship between N availability and mean EbN score is better when mean EbN is simply based on presence / absence data rather than being abundance-weighted. This may be because species presence / absence is less subject to inter-seasonal variation than cover. Changes in species presence / absence are likely to be slower than changes in abundance, and so mean Ellenberg scores are better-correlated with environmental conditions in ancient woodlands than in recent woodlands (Dzwonko, 2001).

5. Models of effects of N availability on plant species occurrence

5.1 Introduction to occurrence models

Static species or community occurrence models are calibrated by regressing the frequency of occurrence within a set of relevés against environmental factors. The environmental factor can be a measurement (see section 4.6), or an indicator derived from the floristic data such as mean Ellenberg score. Indicators derived from floristic data have been more widely used, since most relevés do not have corresponding measurements of abiotic site factors. This method of estimating environmental conditions also reduces error due to temporal and spatial variability in actual measurements (Kros, 2002). However, to then predict species occurrence from environmental measurements or biogeochemical model outputs, the relationship between these measurements and mean Ellenberg scores must be established. This two-stage approach introduces extra uncertainty (Schouwenberg *et al.*, 2001), but it is the only one currently practical for many species-environment relationships. Surveys relating occurrence directly to field measurements are likely to reduce uncertainty. For example, Wamelink *et al.* (2005) found that an acidity score based on the mean soil pH on sites where a species is found was a more efficient predictor of the pH of a new site than the species' Ellenberg score.

In the case of the dynamic species occurrence model VEG, occupancy fraction is used rather than frequency of occurrence. A competitive strength index is calculated for each species, determined by the site's position on several environmental axes. An optimal position on each axis was defined for each species, although this was done by a group of experts rather than using a set of calibration relevés. The relative strengths of all the species are converted to equilibrium occupancy fractions. The rate of change in occupancy fraction is then calculated from the difference between current and equilibrium occupancy fractions, and a typical regeneration time.

All of these approaches are predicated on the assumption that species occurrence tracks environment change, i.e. that species-environment relationships are static. However, if environmental change occurs more rapidly than species responses, the accuracy of these relationships will be reduced.

Species occurrence is also affected by factors that do not map easily onto Ellenberg gradients, particularly grazing intensity and dispersal. Efforts have been made to define a quantitative indicator for grazing intensity preference; Briemle and Ellenberg estimated a grazing indicator value for grassland species, which was improved and extended to all (Dutch) species by Wamelink (unpublished). Data on species' response to grazing and chance of dispersal have however generally been used to modify probabilities of occurrence after initial prediction from abiotic measures / Ellenberg scores. Final lists of species' probability of occurrence may then be converted into actual predictions of presence / absence. This allows the use of standard techniques for assessing biodiversity value. However, actual occurrence may

be poorly predicted because of the stochastic nature of dispersal and establishment events. Changes in probability of occurrence may thus be better interpreted as changes in habitat suitability, and the risk to biodiversity evaluated according to the impact of changes in these indices on the species present (Smart *et al.*, 2005).

5.2 Calibrating relationships between occurrence and environmental factors

The different occurrence models have used different datasets for calibrating relationships between plant or community occurrence, and environmental factors (Table 5).

Table 5 Datasets used in different models to calibrate relationships between probability of occurrence and environmental factors estimated from floristic data.

Model	Calibration relevés			Number of species / communities with derived models			
	Number	Location	Habitats	Vascular plants	Bryophytes	Lichens	Communities
VEG	*	Sweden	Various	5			41
MOVE	ca. 100000	Netherlands	Various	900†	-	-	-
NTM3	160000	Netherlands	Various	-	-	-	††
GBMOVE	32483	UK	Various	1046	233	74	-
BERN	5218	N German lowlands and hilly area	Forest, extensive grassland, pasture, heath, bog	720*	-	-	674

* Based on an unspecified number of published studies and empirical observations

† Vascular plants and bryophytes not distinguished

†† Any number of communities, provided at least 50 relevés are available

Abiotic measurements are available for relatively few relevés, and in the MOVE, NTM and GBMOVE models the relationships were first derived for environmental factors obtained from floristic data such as mean Ellenberg scores. Relationships between measured abiotic variables and mean Ellenberg scores were then derived from smaller sets of relevés – for example, in MOVE mean Ellenberg scores were calibrated against abiotic measurements using 193 relevés for Ellenberg F, 2235 relevés for Ellenberg R and 3336 relevés for Ellenberg S. These relationships are not exact, and represent the largest source of uncertainty in vegetation model chains (Schouwenberg *et al.*, 2001). The accuracy of prediction can depend on the level of the abiotic factor, as illustrated by the relationship between Ellenberg fertility and C / N in GBMOVE calibration relevés. While C/N values above ca. 20 g g⁻¹ provide some indication of Ellenberg fertility, C/N values below ca. 20 g g⁻¹ are associated with a wide range of fertility scores (Figure 9).

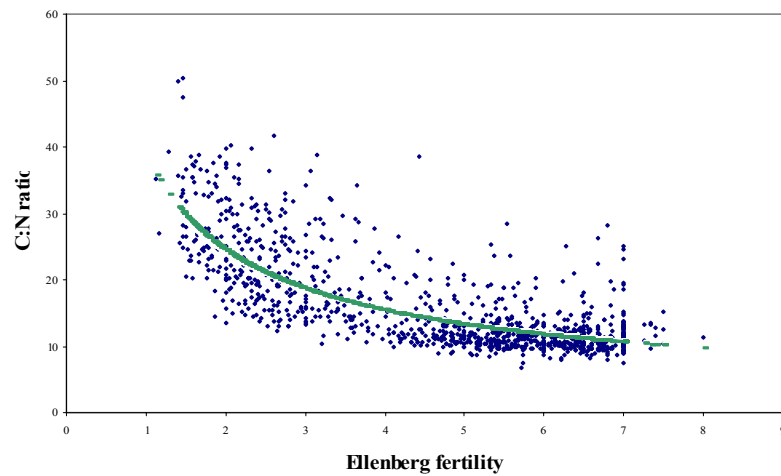


Figure 9 Relationship between mean Ellenberg fertility score (i.e. derived from floristic data) and C/N ratio as used in calibrating GBMOVE (Smart *et al.*, 2005).

Relationships between floristic-derived environmental scores and abiotic measures can be improved by calibrating separately for different vegetation types (Wamelink *et al.*, 2002). New abiotic measures, separately or in combination with measures such as C / N or vegetation category, might provide more accurate predictions of mean Ellenberg scores. However, this implies making these new measurements on enough relevés to calibrate new relationships.

5.3 Abiotic model outputs used to predict occurrence

5.3.1 Summary of abiotic drivers of occurrence models

Models of soil biogeochemistry and / or vegetation succession drive models of occurrence of plant species or communities via a set of key variables. The key variables used in the different model chains are listed in Table 6.

Table 6 Key variables derived from biogeochemical and vegetation models that drive plant species / community occurrence models in the different model chains. ● = direct or indirect explanatory variate; ○ = *post hoc* filter; * = implemented but not tested; - = not used.

Group	Variable	FORSAFE- VEG	MOVE	NTM	GBMOVE	BERN
Nutrients	Available (soil solution) N	●	●	●	-	-
	C / N ratio	-	-	-	●	●
	Soil solution P	*	-	-	-	-
	Soil solution base nutrient cations (K, Mg, Ca)	●	-	-	-	-
	Soil base nutrient cation (K, Mg, Ca) saturation	-	-	-	-	●
Hydrology	Soil moisture (e.g. % vol / vol)	●	-	-	●	●
	Precipitation	-	-	-	●	-
	Spring water table depth	-	●	●	-	●
Acidity	Soil pH	●	●	●	●	●
	Soil base saturation	-	-	-	-	●
	Soil solution base cations	●	-	-	-	-
	Soil solution Al	●	-	-	-	-
	Soil solution base cations / Al ratio	-	-	-	-	*
Salinity	Salinity	-	●	-	-	-
	Temperature (annual, or winter + summer means)	●	●	-	*	-
Climate	Windchill	*	-	-	-	-
	Wind tatter	*	-	-	-	-
	Precipitation	-	-	-	*	-
	Precipitation / temperature / continentality / vegetation duration category	-	-	-	-	●
Light	Vegetation height	●	-	●	●	-
	Light flux (at ground, or by layer)	●	-	-	-	*
Management	Grazing intensity e.g. Livestock Units ha ⁻¹	●	○	-	○	-
Topography	Slope category	-	-	-	-	●
	Aspect category	-	-	-	-	●
Dispersal	Local abundance	*	-	*	○	-
	Morphological attributes	-	-	-	○	○

Phosphorus has only been implemented as a key variable in one of the model chains (FORSAFE-VEG), and this routine is still untested. Two occurrence models (GBMOVE and BERN) have explicitly excluded phosphorus because of a lack of experimental evidence for an association with plant distributions. This may be because the effect of P is obscured by the larger and often confounded effect of nitrogen status, or may relate to the difficulty of assessing plant-available P. Phosphorus chemistry in soil is complicated and highly pH-dependent. Phosphorus is

rather immobile in soil and so roots can access soil P only over very short (mm) distances. Mycorrhizae are thus particularly important for P uptake since they greatly increase the effective root system length. While there are simple tests for different phosphorus pools (e.g. total P, resin-extractable P, carbonate-extractable P), there is little agreement on which of these best represents immediately or potentially plant-available P.

5.3.2 Interactions between variables

In BERN the probability of community occurrence is the minimum of the probabilities derived in relation to all of the environmental factors, thus assuming that there are no interactions between factors (Schlutow & Huebener, 2004). In VEG, competitive strength is derived as the product of the controlling factors, i.e. nutrients, water, acidity, grazing, temperature and windchill, wind tatter, ground light intensity, competition in relation to light and below-ground resources, and ambient CO₂. Nutrient limitation is currently obtained (using a von Liebig approach) as the minimum of the N and P factors, but this is likely to be changed soon to use the product of N and P factors (Belyazid, *pers. com.*). MOVE uses an elimination approach rather than calculating interactions; occurrence is said to be probable if the species is between the 10th and 90th percentile value in relation to the response curve in relation to every factor (Kros, 2002). In GBMOVE, calibrations between controlling factors and probability of occurrence are not carried out individually, but rather in a multiple logistic regression including those interactions and quadratic terms that are statistically significant.

5.3.3 Predicting effects of grazing on probability of occurrence

Grazing by livestock and by large and small wild herbivores is a key control on vegetation development and species composition in many semi-natural habitats. Responses to grazing are a function of the interaction of the plant and herbivore species, which can be highly specific. Responses can also depend on the season of grazing. Some measure of general resistance to grazing can however be obtained from plant traits such as thorniness, height, growth form and content of antinutritive compounds such as tannins (Smart *et al.*, 2005).

5.3.4 Predicting effects of dispersal on probability of occurrence

Several plant traits, obtainable from databases, are associated with longer-distance dispersal. Plants that typically propagate themselves vegetatively have shorter dispersal distances than those that typically propagate from seed. Seeds dispersed by animals generally have longer dispersal distances, although this is not true for invertebrate-dispersed species. Large numbers of seeds, and small seed weight, imply longer dispersal distances. Taller plants tend to disperse further. Long dispersal distances are also associated with annuals, although this is not clear-cut and some perennials disperse long distances. Species with seeds that persist in the soil seed bank tend to disperse further, since they are more likely to be present when a gap forms. A dispersal filters based on plant traits and local abundance is included in GBMOVE, and a similar filter is being developed to correct the predictions of MOVE and NTM.

5.3.5 Predicting species presence / absence from probability of occurrence

It may be useful to convert a predicted probability of occurrence for a species or community into a prediction of actual presence / absence. This can either be done for each species individually, or after first predicting the total number of species present.

Methods for deriving occurrence thresholds were recently compared by Liu (2005). An arbitrary value of PO can be used, above which presence is assumed, e.g. 0.5 (Manel, Williams & Ormerod, 2001; Stockwell & Peterson, 2002) or 0.05 (Cumming, 2000). However, occurrence distributions are typically skewed (Guisan & Theurillat, 2001), and the prevalence of uncommon species is likely to be underpredicted. Where data are available for calibration this threshold can also be set more objectively, for example at the midpoint between mean probability of occurrence for the present and absent groups (Fielding & Haworth, 1995). Calibration data also allow the determination of optimal thresholds that maximise model prediction success as measured using statistics such as Kohen's kappa or the odds ratio (Fielding & Bell, 1997).

An alternative approach is to estimate the number of species (species richness). This may be sufficient in itself for scenario analysis. Alternatively, species richness can be used to set the size of a list which is then populated either by choosing the species with the highest probability, or stochastically using occurrence probabilities to weight a random selection. In GBMOVE, species richness is predicted using a generalised linear mixed model from a combination of vegetation height, soil pH, soil C / N and soil moisture content. Interactions and quadratic terms are also included in the model used.

For less common species, it is difficult to obtain enough relevés to characterise their distributions along environmental gradients. The presence of such species is predicted from association with better-characterised species.

6. Potential for harmonising nitrogen effects modelling

Uncertainties and gaps in current data and models

Plant available N: uncertainty in species-environment relationships could be reduced by relating species occurrence data to direct measurements of abiotic factors, instead of to derived (e.g. Ellenberg) indicators (Wamelink *et al.*, 2005). However, the best abiotic factor for explaining species occurrence may vary with habitat. For example, the C / N ratio may be useful in defining N availability in more organic soils, but seems to be inadequate as a predictor of N availability for mesotrophic habitats with low C / N (Smart *et al.*, 2005). An analysis is required of the most appropriate abiotic factor indicating N availability in individual habitats and / or habitats in general.

Nitrogen species: separation of nitrogen species in both the biogeochemical and vegetation models varies at present. Modelling N species separately may need to be considered in view of the potential importance for impacts on acidification of soils and waters and effects on plant species.

Direct above-ground effects: Direct effects of nitrogen above-ground (i.e. not mediated through soil processes) are not included in current models. Does this limit applications, particularly for species with limited root systems?

Carbon dynamics: The incorporation of carbon dynamics into models is very variable at present. The limitations this may impose on the applications of some models need to be identified.

Salinity: Salinity has only been implemented as a driving variable in one of the model chains reviewed (SMART2-MOVE), although it is a major determinant of species occurrence in coastal habitats. To model change in coastal habitats, occurrence / salinity relationships need to be defined for these species, and salinity needs to be included as an output of biogeochemical models. This is trivial (within acidification models) where salinity is derived from deposition, but the influences of tidal inundation and of groundwater salinity are not easily calculated and require further work.

Southern Europe: The model chains for predicting N impacts on species occurrence have all been developed in northern European countries, and there is a corresponding bias towards cool temperate and boreal systems. Ellenberg scores are not available for many southern species, and much survey work would be necessary to define species-environment relationships for southern European habitats (e.g. steppe, Mediterranean and Alpine habitats). New aspects of biogeochemical models may also need to be developed and tested for these environments, in particular models of fire frequency, intensity and seasonality for pyrogenic vegetation.

Data sharing: What are the advantages (e.g. extending climate envelopes, greater power) and disadvantages (e.g. spatial variation in ecological niches) for sharing data and response functions between countries to develop species / community models?

Impacts in waters: Would models of N impacts on terrestrial ecosystems benefit from better links to groups developing approaches in aquatic ecosystems (both freshwater and marine)?

Key variables

The biogeochemical models currently used to predict deposition effects may oversimplify processes, and may not yet provide outputs adequate for models predicting plant responses. There is an inevitable tension between the desire for a complete model that does not miss out any important processes, and the desire for a simple model that can be understood and parameterised. The principle of parsimony or just-sufficient complexity is an important and old concept in science. Thus while the “key variables” currently passed to occurrence models may be simplistic, and perhaps should be extended to include variables such as ammonium / nitrate ratio, there is no point in generating variables for which relationships with occurrence are poorly defined. The explanatory variables used in models of species or community occurrence have necessarily been those soil properties measured during floristic surveys, or indicators derived from the floristic composition. If new indicators of N status are considered necessary, key questions will be:

- a) Can the biogeochemistry models be adapted to accurately predict the key variables used in the floristic models?
- b) Can sufficient calibration data be found to derive relationships between occurrence and new / combined indicators of N status?

Model comparison

It is useful to have several concurrent efforts to model plant diversity. The model chains used are complex, and it is thus difficult to assign certainty to model outputs. Comparative studies of the performance of the model chains in predicting change on a single site would be useful, as tests of the model chains and to aid model improvement. Comparisons could include:

- a) using the same drivers, do the biogeochemistry / succession models produce the same values for key variables?
- b) using the same calibration data, do the occurrence models produce the same relationships between occurrence probability / strength and environmental factors?
- c) using the same values for key variables, do the (identically calibrated) floristic models predict the same species composition, or at least the same direction and strength of changes in species abundance?

The calibration data used for each model chain could in principle be used to calibrate other model chains, either separately or lumped in with the original calibration data. Including more relevés allows better definition of relationships with environmental factors, but if the geographic spread of the sample is increased these relationships may be affected.

Feedbacks

Vegetation type, growth stage and species composition can have large effects on N fluxes via changes in interception, decomposition and plant uptake rates. These

feedbacks have not been widely implemented in the model chains. This is in part because of a lack of species-level or vegetation-type-level data on plant characteristics, such as litter quality, which are useful for biogeochemical models. Another barrier is the difficulty of integrating static and dynamic models, or models written in different languages or with different timesteps.

Methods for integrating ecological models and data have hitherto received inadequate attention (Classen & Langley, 2005). Methods are becoming available for automating data transfers within model / database chains e.g. (Villa, 2001; Rizzoli et al., 2005; SEEK, 2005). These are based on machine-readable metadata standards for descriptions of the data and models, which could include their origin, units, variability, reliability and analytical method, and also potentially their conceptual context and underlying assumptions (Comber, Fisher & Wadsworth, 2005). Standardised methods for integration and analysis would aid model chain development, comparison and testing, particularly if the number and complexity of drivers and feedbacks increases.

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