NITREX: THE TIMING OF RESPONSE OF CONIFEROUS FOREST ECOSYSTEMS TO EXPERIMENTALLY-CHANGED NITROGEN DEPOSITION

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Abstract. In large regions of Europe and eastern North America atmospheric deposition of inorganic nitrogen (N) compounds has greatly increased the natural external supply to forest ecosystems. This leads to N saturation, in which availability of inorganic N is in excess of biological demand and the ecosystem is unable to retain all incoming N. The large-scale experiments of the NITREX project (NITRogen saturation EXperiments) are designed to provide information regarding the patterns and rates of responses of coniferous forest ecosystems to increases in N deposition and the reversibility and recovery of impacted ecosystems following reductions in N deposition.

The timing of ecosystem response generally followed a hypothesized "cascade of response". In all sites N outputs have responded markedly but to very different degrees within the first three years of treatment. Within this time significant effects on soil processes and on vegetation have only been detected at two sites. This delayed response is explained by the large capacity of the soil system to buffer the increased N supply by microbial immobilization and adsorption. We believe that this concept provides a framework for the evaluation and prediction of the ecosystem response to environmental change.

1. Introduction

NITREX is a consortium of European experiments in which nitrogen (N) deposition is drastically changed to whole catchments or large forest stands at 8 sites spanning a N deposition gradient (Dise and Wright, 1992; Wright and Van Breemen, 1995) (Figure 1; Table I). NITREX focuses on the impact of N deposition on forest ecosystems, in particular the factors and processes affecting N saturation. Nitrogen saturation is defined as the situation in which the supply of inorganic N exceeds the nutritional demand of biota and is operationally measured as increased leaching of N below the rooting zone (Aber *et al.*, 1989). At NITREX sites with low to moderate ambient N deposition (3-20 kg N ha^{-1} yr^{-1}) N is experimentally added to throughfall. At NITREX sites with high N deposition (>25 kg N ha^{-1} yr^{-1}) and significant leaching losses of N, N is removed from throughfall by means of roofs. Objectives of NITREX include measurement of the impact of changed N deposition on ecosystem functioning. Here we focus on the timing of the responses within three ecosystem components; water, soil and vegetation.

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TABLE I

Characteristics of the NITREX experiments

Site	Tree species	Ambient N flux in throughfall kg ha^{-1} yr^{-1}	Treatments	Experimental N flux in throughfall kg ha^{-1} yr^{-1}	Start Treatment	Key Reference
Sogndal	Alpine vegetation	3	add	8-24	1983	1
Gårdsjön	Norway spruce	12	add	49	1991	2, 3
Klosterhede	Norway spruce	27	add	61	1992-87	4
Alptal	Norway spruce	21	add	40	1994	
Aber	Sitka spruce	15	add	48-89	1990	5
Solling	Norway spruce	40	remove	0	1991	6
Speuld	Douglas fir	55	remove	0	1989	7, 8
Ysselsteyn	Scots pine	61	remove	0	1989	7, 8

1. Wright and Tietema (1995); 2. Moldan *et al.* (1995); 3. Stuanes *et al.* (1995); 4. Gundersen and Rasmussen (1995); 5. Emmett *et al.* (1995ab); 6. Bredemeier *et al.* (1995); 7. Boxman *et al.* (1995); 8. Koopmans *et al.* (1995).

2. Material and methods

As indicators of response we choose three key parameters; annual inorganic N input-output budget, net N mineralization rate in the organic layer, and the nutritional balance in newly-formed needles. Inorganic N inputs were measured as throughfall. The N output fluxes were calculated by multiplying concentrations in soil solution below the rooting zone or drainage water with simulated or measured water fluxes. Soil solution was sampled biweekly or monthly with lysimeters. Net N transformations were quantified with year-round *in situ* incubations of intact soil cores. As a measure of the nutritional balance of the needles, we used the K:N and Mg:N ratios in current year needles.

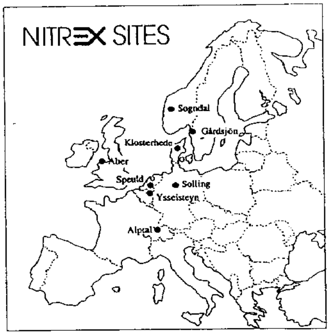

Fig. 1. Location of the NITREX sites.

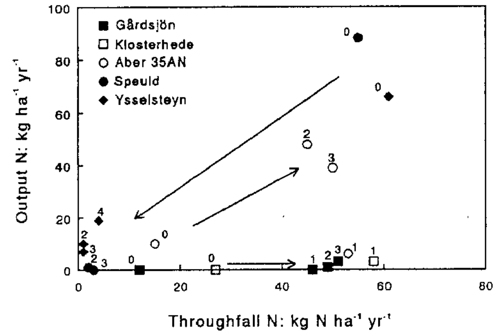

Fig. 2. Input-output budgets of inorganic N in the NITREX sites. The numbers indicate the treatment years; 0 refers to pre-treatment or control data.

Because for some of the sites time series of these parameters were not yet available, we have primarily used data from five of the seven forested NITREX sites, namely Gårdsjön, Klosterhede, Aber, Speuld and Ysselsteyn.

3. Results

The N input-output data from the NITREX sites are consistent with the general pattern of N fluxes from forest ecosystems in Europe (Wright *et al.*, 1995) (Figure 1). At annual inputs of less than about 10 kg ha^{-1} yr^{-1} nearly all the N is retained and outputs are very small. At inputs above about 25 kg ha^{-1} yr^{-1} outputs are substantial. In most sites changes in inorganic nitrogen output occurred during the first years after the start of the treatment (Figure 2). Changes were relatively low and slow at Gårdsjön and Klosterhede, sites previously not saturated; after two years N output has increased from zero to a maximum of 3 kg N ha^{-1} yr^{-1}. A fast and large response was found at Speuld and Ysselsteyn. Within the first two years of reduced input, N output decreased from about 80 to 10 kg N ha^{-1} yr^{-1}. The Welsh site Aber showed an intermediate response with no change in N output during the first year and a large increase (from 10 to 40 kg ha^{-1} yr^{-1}) during the second treatment year.

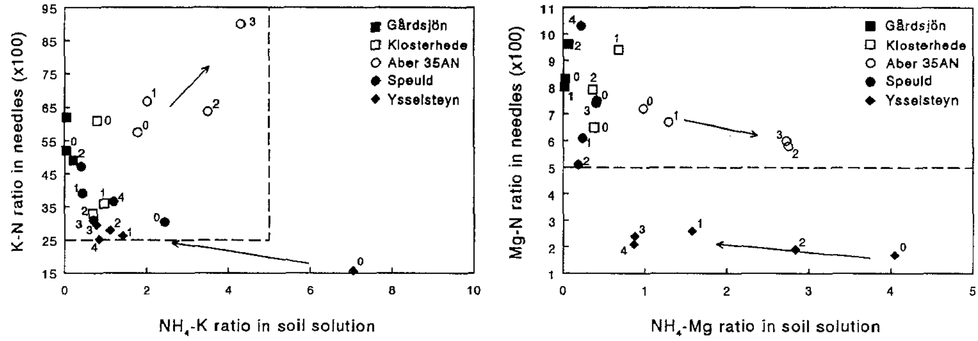

Fig. 3. Ratios between the total concentrations of K (left) or Mg (right) and N in current year needles as a function of the ratio of the concentrations (mol mol^{-1}) of NH_4 and K or Mg in soil solution (0-10 cm depth) in the NITREX sites. The dashed lines signify the levels of the ratios at which the supply of K and Mg becomes deficient (Boxman *et al.*, 1995). The numbers indicate the treatment years; 0 refers to pre-treatment (Gårdsjön and Klosterhede) or control data (Aber, Speuld and Ysselsteyn).

Net mineralization rates changed significantly only at Ysselsteyn; in the low N deposition plot at Ysselsteyn the net mineralization rate decreased to about 4% of that in the high deposition plot (Koopmans *et al.*, 1995). Unpublished results indicated that at Gårdsjön a four-fold increase in net mineralization rate occurred during the third year of N addition; there was no response during the first two years (Kjønaas, unpublished data). At Klosterhede, Aber and Speuld net N mineralization did not change significantly due to N addition or removal (Gundersen and Rasmussen, 1995; Emmett *et al.*, 1995b; Koopmans *et al.*, 1995).

In all sites except Ysselsteyn, nutrient concentrations in the foliage after 2-3 years of treatment indicated no significant changes (Boxman *et al.*, 1995; Emmett *et al.*, 1995a; Gundersen and Rasmussen, 1995). This is illustrated by the relation between the $K:NH_4$ and $Mg:NH_4$ ratios in soil solution and in current year needles (Figure 3). At Ysselsteyn a significant change in the foliage ratios coincided with a large change in soil solution ratios. At Aber the $NH_4:K$ and $NH_4:Mg$ ratios in soil solution increased due to a increase in NH_4 concentration. The nutritional balance in the needles showed no significant change during the first three treatment years. At all other sites, both ratios in soil solution as well as in the foliage showed no significant changes during the treatment years.

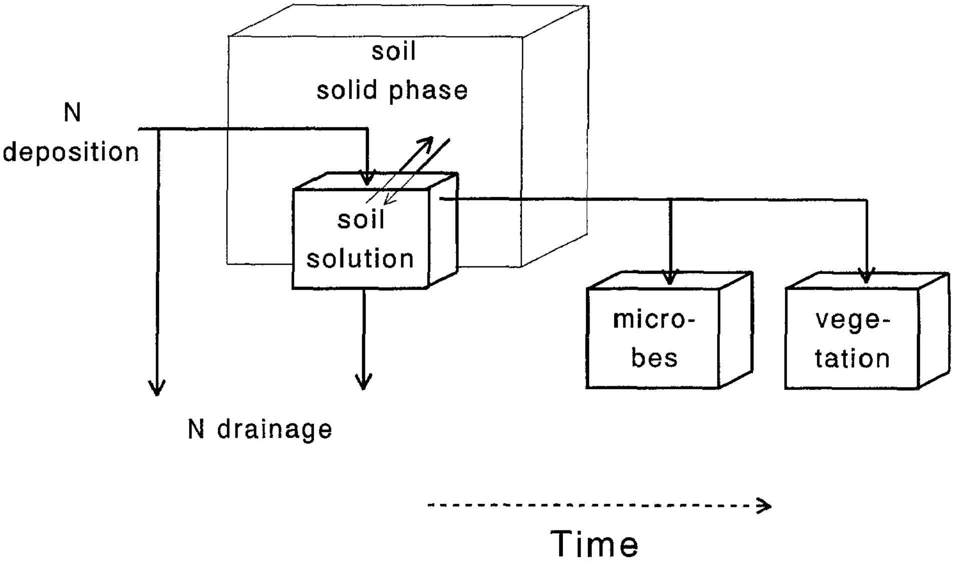

Fig. 4. Conceptual diagram of the hypothesized *cascade of response*. The diagram symbolizes the time sequence of ecosystem response in the ecosystem fluxes and compartments drainage, soil solution, microbes and vegetation, as a result of a change in N deposition.

4. Discussion

We hypothesize that the ecosystem response to the changed N input follows a temporal pattern which can be described as a *cascade of response* (Figure 4). Because the external change in the NITREX manipulation experiments affects the aqueous phase (precipitation and throughfall) and water is the principle transport medium, the response is expected first in the run-off or drainage. Depending on the physical properties of the soil compartment, soils may not fully interact with the incoming water. This will lead to a small fraction of the N signal passed through by runoff (or leachate) immediately. The next response will be in the soil; the signal is transmitted by way of the soil solution. Here major processes are microbial immobilization of N and adsorption. These processes generally proceed very rapidly and the soil represents a large pool for both processes; the soil will act as a buffer for the signal. As a result effects on soil solution and soil processes such as nitrogen mineralization will not appear until these pools have been altered significantly; i.e. the response will be delayed. Next to be affected will be the vegetation. Here the signal is passed through the soil solution, which in turn is influenced by the interaction with the soil.

At the NITREX sites the measured ecosystem response to experimentally-changed N deposition generally follows this cascade pattern. The behavior of each site can be explained within this theoretical pattern based on specific site characteristics such as tree species, soil type and degree of N saturation.

The non-forested NITREX catchment at Sogndal, Norway, is a good example of a site where the increased N input was followed by an immediate increase in inorganic N output in runoff (Wright and Tietema, 1995). High concentrations of NO_3^- in runoff were limited to periods during or immediately following N additions, and as the soil is thin and patchy in this site, this response was apparently solely hydrological. There were no measurable changes in soil or vegetation after the nine years of treatment (Wright and Tietema, 1995). At Gårdsjön inorganic N concentrations and fluxes in runoff have slightly but steadily increased during the 3 years of N addition (Moldan *et al.*, 1995). Here, the response of runoff is not simply hydrological; both frequency and magnitude of nitrate peaks in runoff increased during the first years of the experiment (Moldan *et al.*, 1995). In addition, the first results of the field incubation study showing the increased nitrogen mineralization rate three years after the start of the N addition (Kjønaas, unpublished data), indicates that the soil has responded without any response in vegetation. The non-saturated spruce forest at Klosterhede shows a response largely comparable to Gårdsjön; a steady but small increase of inorganic N leaching and no changes in nutritional balance of the needles (Gundersen and Rasmussen, 1995). However, in contrast with Gårdsjön, the observed increase in net mineralization rate was not significant. At Aber, increased N/NO_3 input resulted in increased N/NO_3 output of the same magnitude, whereas the increase in N/NH_4 input was retained in the system (Emmett *et al.*, 1995a). This indicates a limited N retention capacity at this site. No change in net mineralization rates nor in the nutritional balance of the vegetation was observed at Aber (Figure 3). The highly N saturated NITREX sites Solling in Germany and Speuld and Ysselsteyn in the Netherlands showed a very fast response of decreased inorganic N outputs due to decreased input; within a few months after the start of the treatment concentration in soil solution started to decrease (Bredemeier *et al.*, 1995; Boxman *et al.*, 1995). The other compartments in Speuld and Ysselsteyn showed a different response. At Speuld, no significant changes in net mineralization rates nor in nutritional balance of the needles was found, whereas at Ysselsteyn significant changes in net mineralization rates and nutritional balance in needles were found. These differences in response between Speuld and Ysselsteyn can be explained by a difference in the degree of nitrogen saturation. Despite excessive nitrate leaching in Speuld indicating nitrogen saturation, the Douglas fir trees grow reasonably well and the needles have normal N concentrations and N:Mg and N:K ratios above levels that are considered deficient (Boxman *et al.*, 1995). At Ysselsteyn, N concentrations in the needles are much higher than in Speuld and the nutritional balance of Mg and K relative to N has values below the deficiency level (Figure 3). From the fast response of the vegetation and soil processes in saturated Ysselsteyn compared to the delayed response in non-saturated Gårdsjön it appears that the soil pools are "one-way" in the response to changed N concentrations in soil solution. In non-saturated systems they are capable of rapidly removing large amounts of N from soil solution, but in saturated systems they do not release large quantities of N to soil solution.

The concept of cascade of response satisfactorily explains the observed ecosystem response to changed N deposition. The concept should be further verified by means of long-term field-scale manipulation experiments. We believe that it provides a framework for the evaluation and prediction of the ecosystem response to environmental change.

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