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NITREX: responses of coniferous forest ecosystems to experimentally changed deposition of nitrogen

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Abstract

In large regions of Europe and eastern North America atmospheric deposition of inorganic nitrogen compounds has greatly increased the natural external supply to forest ecosystems. This leads to nitrogen saturation, in which availability of inorganic nitrogen is in excess of biological demand and the ecosystem is unable to retain all incoming nitrogen. 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 nitrogen input–output data from the NITREX sites are consistent with the general pattern of nitrogen fluxes from forest ecosystems in Europe. At annual inputs of less than about 10 kg ha^{-1} $year^{-1}$, nearly all the nitrogen is retained and outputs are very small. At inputs above about 25 kg ha^{-1} $year^{-1}$ outputs are substantial. In the range 10–25 kg ha^{-1} $year^{-1}$ these forest ecosystems undergo a transition to nitrogen saturation. The 10 kg ha^{-1} $year^{-1}$ apparently represents the minimum threshold for nitrogen saturation.

The NITREX experiments indicate that nitrogen outputs respond markedly across the 10–25 kg ha^{-1} $year^{-1}$ range of inputs. In contrast, the nutrient concentrations in foliage, a measure of tree response, is delayed by several years. Nitrogen saturation can apparently be induced or reversed within only a few years, at least with respect to the commonly used diagnostic of nitrogen saturation—nitrogen output in leachate or runoff.

Keywords: Nitrogen deposition; Forest ecosystem; NITREX project

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1. Introduction

Nitrogen limits growth in most north-temperate and boreal forests (Likens et al., 1976; Tamm, 1992). These ecosystems typically hold large stores of nitrogen (often 2–8 ton ha^{-1}), mainly bound as organic nitrogen in the soil (Gosz, 1981). Nitrogen is tightly cycled in these ecosystems, and outputs of inorganic nitrogen compounds in runoff from undisturbed forests is normally small (less than 1–2 kg N ha^{-1} $year^{-1}$) (Driscoll et al., 1989) and generally comes during periods of dormancy or associated with episodes of high water flux such as snowmelt (Stoddard, 1994).

In large regions of Europe and eastern North America atmospheric deposition of inorganic nitrogen compounds has greatly increased the natural external supply of nitrogen to forest ecosystems. This extra nitrogen acts as a 'fertiliser', and initially causes increased growth and productivity in nitrogen-limited systems. High levels of N deposition over prolonged time periods, however, leads to the condition termed 'nitrogen saturation' in which availability of inorganic nitrogen is in excess of biological demand and the ecosystem is unable to retain all incoming nitrogen (Aber et al., 1989). Nitrogen saturation is usually manifest by increased leaching of inorganic nitrogen from below the rooting zone and to runoff; losses then may also occur during the growing season and under all hydrologic conditions (Stoddard, 1994).

High N deposition causes major change and disruption in forest ecosystems. Nutrient imbalance in foliage, acidification of soils with subsequent mobilisation of inorganic aluminum and damage to fine roots, and changes in species composition of herbs and mycorrhizal fungi are among effects reported from heavily impacted ecosystems in areas such as the Netherlands (Van Breemen and Van Dijk, 1988). Nitrogen lost in runoff from forest ecosystems becomes inputs to aquatic ecosystems. Even small changes in nitrogen outputs from terrestrial ecosystems may have large impact on aquatic ecosystems downstream. Effects may include acidification of surface waters, and eutrophication of nitrogen-limited streams, lakes and coastal marine waters (Hinga et al., 1991).

Studies at European forest ecosystems clearly demonstrate that, on the one hand, undisturbed forests receiving low nitrogen deposition retain nearly all the incoming nitrogen, and on the other hand, forests receiving chronic high N deposition are nitrogen saturated (Abrahamsen, 1980; Grennfelt and Hultberg, 1986; Dise and Wright, 1995). However, the length of time required to move between these two states is uncertain. In particular there is little information regarding the nature and rate of response of ecosystems to increases in N deposition and the reversibility and recovery of impacted ecosystems following reductions in N deposition.

The large-scale experiments of the NITREX project (nitrogen saturation experiments) are designed to provide such information at the ecosystem scale (Wright and Van Breemen, 1995). NITREX is a consortium of European experiments in which nitrogen deposition is drastically changed to whole catchments or large forest

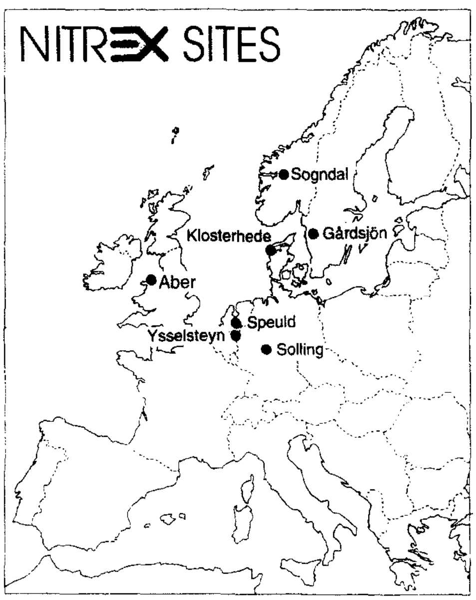

Fig. 1. Location of the NITREX sites.

stands at seven sites spanning the present day gradient of nitrogen deposition across Europe (Fig. 1) (Dise and Wright, 1992; Wright et al., 1992). At NITREX sites with low-to-moderate nitrogen deposition, nitrogen is experimentally added to precipitation; here nitrogen saturation may be experimentally induced. At NITREX sites with high nitrogen deposition and significant loss of nitrogen in leachate, nitrogen is removed from precipitation by means of roofs and ion-exchange systems; here the aim is to experimentally reverse nitrogen saturation. Together these experiments focus on the patterns and rates of responses of forest ecosystems to drastically changed inputs of inorganic nitrogen.

2. Results

Whole-ecosystem response to changed nitrogen deposition is often manifest by a change in the flux of nitrogen across the ecosystem boundaries. Input of inorganic nitrogen species to forest ecosystems is commonly measured as throughfall; output is measured as runoff at catchments, or soil leachate by lysimeters at forest plots. Gaseous inputs by processes such as nitrogen fixation, and outputs by denitrification are generally not measured, and often assumed to be of secondary importance. Organic nitrogen losses in runoff and leachate are also often overlooked. Input–output budgets for dissolved inorganic nitrogen species, however, provide a useful measure of ecosystem response to altered nitrogen supply and cycling in forest ecosystems (Tamm, 1992).

Prior to treatment the NITREX sites fit well into the general input–output relationships for nitrogen at European forest ecosystems (Dise and Wright, 1995; Tietema and Beier, 1995). Outputs are very low at the site with low nitrogen deposition (Sogndal), very low or moderate at the sites with intermediate N deposition (Gårdsjön, Klosterhede, and Aber), and high at the sites with high N deposition (Speuld, Ysselsteyn, and Solling) (Table 1, Fig. 2).

At the NITREX experiments the inputs of inorganic nitrogen are drastically altered. The experimentally changed nitrogen deposition caused rapid change in the output flux of inorganic nitrogen mostly as nitrate in leachate and runoff (Table 1, Fig. 3). At the low deposition site Sogndal (3 kg N ha^{-1} $year^{-1}$), the addition of 7 kg N ha^{-1} $year^{-1}$ resulted in increased output of nitrate from 0.3 to 0.7 kg N ha^{-1} $year^{-1}$ in the first year of treatment. The increased outputs come mainly in association with the nitrogen additions and during snowmelt. The situation has not changed significantly during 9 years of experimental addition. The ecosystem still retains about 90% of the incoming nitrogen and has not reached nitrogen saturation (Wright and Tietema, 1995).

At the three sites with intermediate N deposition (11–20 kg N ha^{-1} $year^{-1}$), the response to experimental N addition of 35–75 kg ha^{-1} $year^{-1}$ varied. At Gårdsjön output in runoff increased during the first year of treatment from 0 to 0.4 kg ha^{-1} $year^{-1}$ and then further to 0.7 kg ha^{-1} $year^{-1}$ in the second year of treatment. The seasonal pattern has changed with runoff containing elevated concentrations of nitrate during the growing season. The catchment is still retaining over 95% of the incoming nitrogen (Moldan et al., 1995). At Klosterhede only 1 year of treatment data are available, and these indicate that the output flux increased from 0.3 to 2.3 kg ha^{-1} $year^{-1}$ (Gundersen and Rasmussen, 1995). The response at Aber forest was the most pronounced and the response was dependent on the form of nitrogen applied. At Aber, the ecosystem exhibited symptoms of nitrogen saturation prior to treatment. Over the 2 year period of nitrogen additions, the output of nitrate was approximately equal to the total input of inorganic nitrogen when applied as sodium nitrate at 35 kg N ha^{-1} $year^{-1}$ $NaNO_3$ and 75 kg N ha^{-1} $year^{-1}$ $NaNO_3$, but when applied as ammonium nitrate at 35 kg N ha^{-1} $year^{-1}$ all the ammonium was apparently retained and only the nitrate was lost (Emmett et al., 1995). The large increase in leaching losses in the second year relative to the first year in all treatments at Aber are due to a delay in the movement of nitrate through the soil profile rather than any increase in soil nitrate

Table 1
Input–output budgets for inorganic nitrogen at the NITREX sites. Inputs refer to throughfall plus experimental additions. Outputs are in soil leachate at over 50 cm or runoff. Treatments comprise experimental addition at Sogndal, Gårdsjön, Aber and Klosterhede and exclusion of ambient inputs by roofs at Klosterhede, Solling, Speuld and Ysselsteyn. Year indicates year of treatment; 0 is mean for 1 or more years of pre-treatment or untreated control during the experimental period. Year 1 data for Speuld and Ysselsteyn are incomplete and not included (units kg N ha^{-1} $year^{-1}$)

	Year	NO_3-N		NH_4-N		Total inorganic N		Data source
		In	Out	In	Out	In	Out	
Sogndal	0	1	0	1	0	3	0	Weight and Tietema, 1995
	1	6	1	1	0	7	1	
	2	8	0	1	0	9	0	
	3	8	1	1	0	9	1	
	4	8	0	1	0	9	0	
	5	8	1	1	0	9	1	
	6	8	2	1	0	9	2	
	7	8	3	1	0	9	3	
	8	8	1	2	0	10	1	
	9	8	1	1	0	9	1	
Gårdsjön	0	7	0	4	0	11	0	Moldan et al., 1995
	1	24	0	22	0	46	0	
	2	26	1	24	0	50	1	
Aber 35AN	0	9	9	8	1	17	10	Emmett et al., 1995
	1	29	5	26	1	55	6	
	2	27	42	23	5	50	47	
Aber 35SN	0	9	9	8	1	17	10	Emmett et al., 1995
	1	46	17	7	1	53	18	
	2	42	67	6	4	48	71	
Aber 75SN	0	9	9	8	1	17	10	Emmett et al., 1995
	1	87	32	7	0	94	32	
	2	78	140	6	4	84	144	
Klosterhede add	0	9	0	11	0	20	0	Gundersen and Rasmussen, 1995
	1	30	3	28	0	58	3	
Klosterhede roof	0	9	0	11	0	20	0	Beier and Rasmussen, 1994
	1	2	0	1	0	3	0	
	2	2	0	1	0	3	0	
	3	3	0	1	0	4	0	
	4	1	0	1	0	2	0	
	5	2	0	1	0	3	0	
Solling	0	20	36	18	1	38	37	Dise and Wright, 1992
Speuld	0	13	87	36	1	49	88	Boxman et al., 1995
	2	1	0	1	0	2	1	
	3	1	0	2	0	3	0	
Ysselsteyn	0	11	64	46	1	57	66	Boxman et al., 1995
	2	0	9	1	0	1	10	
	3	0	7	1	0	1	7	
	4	1	18	3	1	4	19	

production in the second year (Emmett et al., 1995).

At the high deposition (38–56 kg N kg ha^{-1} $year^{-1}$) nitrogen-saturated sites, the output flux of nitrogen responded immediately to the experimentally reduced N deposition. At Speuld and Ysselsteyn in the Netherlands nitrogen outputs were reduced from about 70 to 1 kg and 10 kg ha^{-1} $year^{-1}$, respectively, in the first year of treatment, and have remained low for subse-

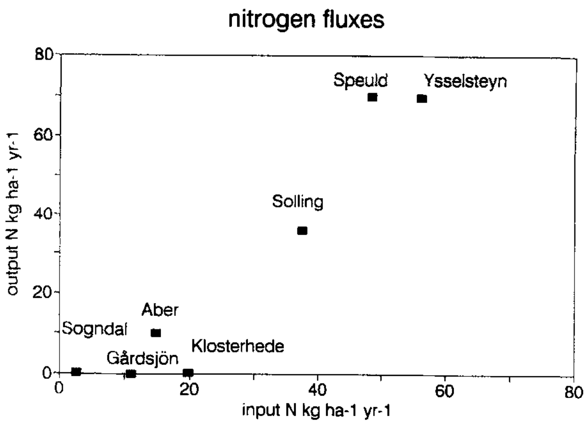

Fig. 2. Annual fluxes of inorganic nitrogen in throughfall (inputs) and in leachate or runoff (outputs) at the NITREX sites (untreated controls or pre-treatment periods) (from Dise and Wright, 1992).

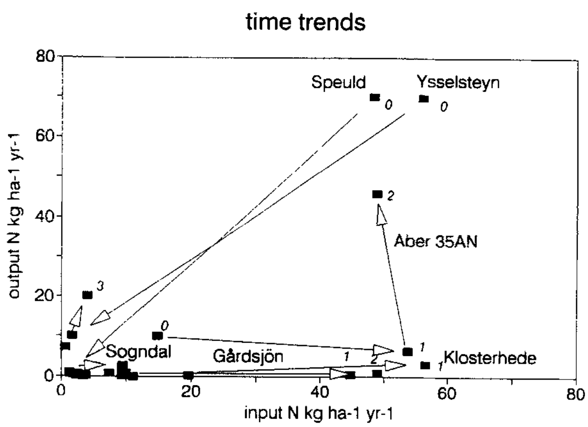

Fig. 3. Annual fluxes of inorganic nitrogen in throughfall (inputs) and in leachate or runoff (outputs) at the NITREX experiments. Numbers in italics indicate treatment year; 0 refers to pre-treatment or control data. The arrows indicate the changes following 1–9 years of treatment. Data from Moldan et al. (1995), Emmett et al. (1995), Boxman et al. (1995), Wright and Tietema (1995) and Gundersen and Rasmussen (1995). The Aber 35SN, Aber 75SN and Solling treatments are not shown (flux data for Solling from the first year of treatment are not yet available).

quent years of the experiment up to the present (Table 1, Fig. 3) (Boxman et al., 1995). The flux data for the first year of treatment at Solling are not yet available.

3. Discussion

The nitrogen input–output data from the NITREX sites are consistent with the general pattern of nitrogen fluxes from forest ecosystems in Europe (Dise and Wright, 1995). At annual inputs of less than about 10 kg ha^{-1} $year^{-1}$, nearly all the nitrogen is retained and outputs are very small. At inputs above about 25 kg ha^{-1} $year^{-1}$, outputs are substantial. In the range 10–25 kg ha^{-1} $year^{-1}$ forest ecosystems apparently undergo a transition to nitrogen saturation. The 10 kg ha^{-1} $year^{-1}$ represents the minimum threshold for nitrogen saturation. The NITREX control catchments and plots and pre-treatment data fit this general pattern (Fig. 2).

Across the intermediate range of N deposition, the NITREX data indicate that for the first 2 years most of the added N was lost to runoff at Aber where N losses were already large prior to treatment, whereas most of the added N is retained at Gårdsjön and Klosterhede where N losses were negligible prior to treatment. Thus at Aber the output was approximately equal to input of nitrate during the 2 year period of ammonium nitrate additions (approximately 50% of added nitrogen), whereas at Gårdsjön and Klosterhede over 90% of the added N was retained. The data from Aber further indicate that this rapid response is dependent on the form of nitrogen added; ammonium was effectively retained within the forest ecosystem whereas the added nitrate resulted in an equivalent increase in nitrate output (Emmett et al., 1995). The ammonium retention at Aber occurs in the mineral soil and is believed to be a result of cation exchange on clays (Emmett et al., 1995). The increased output of nitrogen at Klosterhede and Gårdsjön following nitrogen addition and the development from the first to the second year of treatment at Gårdsjön, suggest that nitrogen outputs will continue to increase with additional years of treatment at these sites. As is the case for Aber, the initial increase in nitrogen leaching is likely to be at least partly due to reduced retention of incoming nitrate although increased soil nitrate production may also contribute to increased nitrogen leaching losses at some sites (Kahl et al., 1993).

Nitrogen gasses represent a second type of ecosystem boundary flux. Changed nitrogen deposition could also affect the flux of one or more nitrogen gases between the atmosphere and the forest ecosystem. Such an effect is known for nitrous oxide (N_2O) (Bowden et al., 1991) which can be a product of nitrification as well as of denitrification. Compared with an estimated range of total gaseous nitrogen losses in undisturbed ecosystems of less than 1 to perhaps 10 or 20 kg N ha^{-1} $year^{-1}$ (Bowden, 1986), recent measurements of N_2O emissions in forest ecosystems with increased nitrogen availability indicate N_2O emission rates of 8 (Brumme and Beese, 1992) and 20 (Tietema et al., 1991) kg N ha^{-1} $year^{-1}$. In the latter study, a total gaseous nitrogen flux of 35 N ha^{-1} $year^{-1}$ was found in a periodically wet, nitrogen-saturated beech forest (Tietema and Verstraten, 1992). These results indicate that gaseous nitrogen losses at high nitrogen input rates might be of quantitative importance for the nitrogen budget. Systematic measurements of gases such as N_2O are now underway at several of the NITREX sites.

Response within the ecosystem to changes in nitrogen deposition might entail changes in individual components or processes. Investigations at the NITREX sites include a variety of ecosystem components and processes (Wright and Van Breemen, 1995). To date, the results for most are incomplete or of insufficient duration to provide the basis for cross-site comparisons.

Nutrient concentrations in needles measured at all NITREX sites except Sogndal indicate little or no changes during the first year of treatment. Such changes become apparent after more than 2 years of treatment at the two sites in the Netherlands, Speuld and Ysselsteyn. After 4 years of reduced N deposition at Ysselsteyn the concentration of potassium relative to nitrogen has increased for the first time to a level above that considered deficient (Boxman et al., 1995). Thus, in contrast with the rapid response of leachate and runoff to changed N deposition, the nutrient concentrations in foliage, a measure of tree response, is delayed by several years.

Fine-root studies at several of the NITREX sites indicate that negative effects caused by air pollution may be reversed by reducing the level of deposition. Thus, at the roof experiments at Gårdsjön and Ysselsteyn fine-root development and vitality improved following decrease in S and N deposition (Boxman et al., 1995; Clemensson-Lindell and Persson, 1995). The nitrogen addition experiments at Aber and Gårdsjön, however, do not give a clear picture. Apparently, the year-to-year variations in climatic conditions mask possible changes due to 1–2 years of increased nitrogen deposition (Clemensson-Lindell and Persson, 1995).

The NITREX results to date suggest that when N deposition is changed across the threshold range of 10–25 kg ha^{-1} $year^{-1}$, nitrogen outputs from forest ecosystems respond rapidly. A similar large-scale N addition experiment in Maine, USA (Watershed Manipulation Project) fits this pattern (Kahl et al., 1993). The data indicate that the critical load for nitrogen for these ecosystems lies at less than 10 kg ha^{-1} $year^{-1}$.

Additional data from NITREX sites and similar studies elsewhere are necessary before generalisations can be made with respect to the response of individual ecosystem components and processes to drastically altered N deposition. In particular, the ongoing ^{15}N studies within NITREX may provide such information (Kjønaas et al., 1993a,b). Together, the NITREX data give new information on the rate of response of forest ecosystems to changes in N deposition.

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