The Impact of Nitrogen Deposition in Forest Ecosystems: A Review

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1. Introduction

In recent decades, a trend towards increasing tree growth has been identified in many European forests (Spiecker et al. 1996). One possible factor contributing to this trend in some regions is the deposition of reactive nitrogen (N). Deposition of pollutant N may also contribute to the acidification and eutrophication of soil and waters (e.g. Nihlgård 1985, Hauhs and Wright 1986, Hauhs et al. 1989). To investigate the effects of N deposition on both tree growth and water quality a series of manipulation experiments have been conducted in Europe and the North America. Combined with survey data across N deposition gradients or repeated surveys at the same location over several decades, these provide a valuable resource with which to assess the impact of N deposition in forest ecosystems.

2. Experimental evidence for N-induced changes in tree growth

Many European N fertilisation experiments in forest stands have resulted in either a positive or neutral response of tree growth to N additions (e.g. Farrell 1985, Malkonen 1990, Tamm 1991). However, in a few areas with acid soils and already high N deposition, N fertilisation may result in a decrease in tree growth possibly due to soil acidification and a decline in availability of base cations. For example, Nys (1989) reported a significant decline in wood accumulation rates from 13 to 11.5 m³/ha/yr in a heavily polluted spruce forest in the French Ardennes, following an addition of 100 kgN/ha/yr as ammonium nitrate in 1981 and 1983 (Figure 1). The authors attributed the decline to a decrease in the availability of calcium, due to the acidification of the soil.

In the United States, Magill et al. (1997) applied N at 150kgN/ha/yr as ammonium nitrate to hardwood and pine stands in Harvard Forest. A decline in tree growth rate was observed in the pine stand, but an increase in the hardwood stand. The authors suggested that the different response to N additions in the two stands was related to land use history and the effect of this on soil N retention capacity, and thus the potential for nitrate and associated base cation leaching.
A decline in tree growth rate has also been observed in the Skogaby experiment in Sweden in response to N additions (Nilsson et al. 1998). Initial increases in tree growth in response to N inputs of 100 kgN/ha/yr as ammonium sulphate were observed despite a reduction in BC/Al ratios in soil solution (Binkley and Högberg 1997). However, recent data indicate that production rates decreased after the first six years of N additions and were 15% below production values of the control trees after ten years (Bertills and Nasholm, 2000).

All these studies indicate that on some sensitive soils, large N inputs alone can result in a decline in BC/Al ratios and a decrease in tree growth. However, the studies involved high doses of N which are unrepresentative of the inputs observed in many parts of Europe and the United States and therefore they may not accurately reflect responses to N deposition. Examination of tree growth response to experimentally changed N inputs of a more moderate nature that simulate increased N deposition (< 60 kgN/ha./yr), reveals that in temperate regions, few studies report any significant response of tree growth within the experimental period (Table 1). However, there are two notable exceptions.

One is a study in the spruce-fir stands of New England in which McNulty et al. (1996) reported both a trend towards increased mortality and, interestingly, a change in recruitment of different species following additions of a little as 22 kgN/ha/yr (Figure 3). Furthermore, there was a switch in net tree growth from an initial neutral or positive response to a decline after several years of N applications. Another example is a 50% increase in tree growth observed at Ysselsteyn in the Netherlands following a reduction of N and sulphur (S) inputs using an exclusion roof (Boxman et al. 1998) (Figure 4). The authors associated the improvement in tree growth with an increase in the availability of potassium and magnesium, as reflected in foliar K:N and Mg:N ratios following the exclusion of the highly acidic and N-rich throughfall. Why these stands appear particularly sensitive to increased N (and S) availability is unknown but could be due to a variety of factors, including the site fertility, previous land use practices and the specific tree species involved. Declines in tree growth are
usually associated with nutrient limitations resulting from soil acidification as in these studies, however the importance of secondary stress factors is poorly and deserves further study as there may be important interactions with tree nutrition.

Figure 3 Change in basal area of different tree species in the first two years and subsequent three years of low N additions. (Redrawn from McNulty et al. 1996)

Figure 4 The positive response in tree growth at Ysselsteyn to the removal of pollutants in throughfall (Redrawn from Boxman et al. 1998)
Table 1  Tree growth responses to experimentally changed N inputs (excluding large fertiliser dose experiments)

<table>
<thead>
<tr>
<th>Site</th>
<th>Forest Type</th>
<th>Change in N inputs (kgN/ha/yr)</th>
<th>Effect of N on tree growth</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hubbard Brook</td>
<td>Mixed hardwood</td>
<td>7 to 47</td>
<td>0</td>
<td>Christ et al. (1995)</td>
</tr>
<tr>
<td>Bearbrook</td>
<td>Mixed hardwood/spruce</td>
<td>5 to 33</td>
<td>0</td>
<td>Magill et al. (1996)</td>
</tr>
<tr>
<td>Havard Forest</td>
<td>Hardwood</td>
<td>8 to 58&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0</td>
<td>Magill et al. (1997)</td>
</tr>
<tr>
<td></td>
<td>Red pine</td>
<td>8 to 58&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0</td>
<td>&quot;</td>
</tr>
<tr>
<td>Mt. Ascutney</td>
<td>Spruce-fir</td>
<td>4 to 35 (max)&lt;sup&gt;2&lt;/sup&gt;</td>
<td>-</td>
<td>McNulty et al. (1996)</td>
</tr>
<tr>
<td></td>
<td>Spruce or fir</td>
<td>+ and -&lt;sup&gt;3&lt;/sup&gt;</td>
<td>0</td>
<td>Emmett et al. (1998b)</td>
</tr>
<tr>
<td>6 European NITREX sites</td>
<td>Scots pine</td>
<td>54 to &lt; 5 includes reduction of S</td>
<td>-</td>
<td>Boxman et al. (1998)</td>
</tr>
</tbody>
</table>

<sup>1</sup> Low-N treatment only reported here. A High-N treatment of 150 kgN/ha/yr resulted in a positive response in the hardwood stand and negative in the red pine. No replication in this study.

<sup>2</sup> Range of N application rates from 15.7 to 31.4 kgN/ha/yr. Positive responses observed in early years in the lower application rate plots.

<sup>3</sup> Addition experiments involved application rates of ca. 35 kgN/ha/yr. Reduction experiments reduced inputs from > 30 kgN/ha/yr to < 5 kgN/ha/yr.

3. Mechanisms underlying impacts on tree growth

Direct effects of N on tree growth may be important where forests are exposed to pollutant mist with high concentrations of both N (and acidity) (Sheppard et al. 2001). These high concentrations may cause direct damage possibly through the leaching of base cations from the foliage. This may be particularly important for upland forests where occult deposition can be a significant component of total inputs. An experimental misting study at Deepsyke in Scotland is unique in targeting the potential importance of these direct effects. The latest results indicate that N-rich mist alone can benefit tree growth however this switches to a negative effect when combined with high acidity inputs (Sheppard et al., Pers. Comm.).

Indirect effects through enrichment of foliage due to enhanced uptake of N either in the canopy or from the soil may also lead to significant changes in abiotic and biotic stresses including herbivory (Kennedy and Freer-Smith 2000) (Figure 5). The ecological importance of these stresses in controlling tree growth is uncertain and has rarely been demonstrated (Bertills and Nasholm 2000). Increased sensitivity to fungal
pathogens have also been proposed as a contributory factor in the changes of tree growth (Roelofs et al. 1985) although in certain circumstance improved nutrition of trees may actually reduce the impact of pathogens (Matson and Waring 1984, Annila and Kurkela 1989). Despite the potential importance of N on abiotic and biotic stresses, most research effort have been directed towards the indirect effects of nitrogen through the soil and particularly on acidification and loss of essential base cations. However, linking these changes in BC/Al ratios to tree growth responses is often difficult due to lags in the response of tree growth and the impacts of other confounding factors.

![Graph showing the relationship between the number of insect damaged Scots pine trees and N deposition](image)

Figure 5 Relationship between the no. of insect damaged Scots pine trees and N deposition (Redrawn from Kennedy and Freer-Smith 2000).

Direct evidence for N-induced changes in BC/Al ratios in soil solution or on soil exchange sites have been observed in several studies (e.g. Emmett et al. 1998b, Stanturf et al. 1994). This occurs as a result of the acidifying effect of either ammonium uptake or nitrification of the applied ammonium. The effect of N inputs on soil solution will also depend on the pH, with elevated base cation leaching being observed in non-acidified soils and aluminium leaching in acidified soils (Berg et al. 1997). In the long-term, a decline in the BC/Al may still occur even in the less acid soils, due to the depletion of base cations on the exchange sites. Evidence for these changes in BC/Al ratios affecting tree growth is less well documented. Some evidence exists for both the Skogaby site and the Mount Ascutney site in the United States. In the latter study site, Ca/Al molar ratios in spruce foliage declined with net spruce growth as the N addition increased from zero to 31.4 kgN/ha/yr (Figure 6). Why this relationship occurred is not clear but dark respiration was greater in trees with low Ca/Al ratio foliage, possibly related to reduced membrane integrity (Schaberg et al. 1997). The importance of base cation availability was also clearly demonstrated at the Ysselsteyn site where the exclusion roof was built below the canopy thus protecting the soil from the high N and S inputs. Highly significant changes in tree growth were observed due to improved potassium and magnesium availability despite the canopy still being exposed to heavily polluted air (Boxman et al.1998).
Changes in soil chemistry other than BC/Al ratios have been proposed as a contributory factors affecting tree growth following N additions. In one study in Glencorse, Scotland, applications of N in combination with sulphuric acid caused a significant reduction in stem growth (Carriera et al. 1997). The authors suggested this response may have been due to a N-induced P deficiency in the N treated plots. A role for climate has also been proposed with a positive feedback between changes in tree growth and the acceleration of soil N transformations in response to heat and water flux as the canopy opens up. This in turn would result in further acidification and loss of base cations (Berg et al. 1997).

Much of the critical load approach for forests rely on the relationships derived between soil solution Ca/Al ratio and tree growth (Sverdrup and Warvinge 1993) despite criticisms of the approach (Hogberg and Jensen 1994, Cronan and Grigal 1995). Longer term studies which track changes in soil chemistry and tree growth are required together with a greater understanding of underlying mechanisms and their potential importance in determining long term trends in tree growth.

4. The importance of soil N transformations

As various authors have noted, nitrification is the key process that, once stimulated, can result in acidification, declining BC/Al ratios in sensitive soils and the onset of N leaching (Aber et al. 1989, Gundersen et al. 1998, Berg et al. 1997, Emmett et al. 1998a). A major controlling factor of nitrification is N availability, and thus nitrification would be expected to increase in response to N deposition. Evidence for a direct effect of increased N availability on soil N processes, including nitrification, has been reported in several studies, as summarised in Gundersen et al. (1998) and Aber et al. (1998). No significant changes in nitrification rates were observed in a series of European studies (Gundersen et al. 1998), though some evidence of increases in nitrification was found in studies in the United States (Aber et al. 1998).

One factor delaying the response of N transformation rates to chronic N additions may be the slow change in the quality of soil organic matter and the associated biotic community. Strong relationships between N deposition fluxes and nitrification rates across a deposition transect in the United States (McNulty et al. 1991) suggest a link between N inputs and accelerated nitrification rates if forests have experienced
elevated N inputs over a prolonged period. This appears to be linked to an N-enrichment of the soil organic matter. Several studies in a variety of different forest ecosystems all observed a stimulation of nitrification rates when the N content of forest floor material increased above 1.4%N (Wilson and Emmett, 1999) (Figure 7). This onset of net nitrification has been suggested to result from either reduced nitrate immobilisation by soil microbes (Stark and Hart 1997) or increased gross production (Tietema 1998). Most recently, direct suppression of nitrate uptake by soil microbes due to increased availability of ammonium has been reported possibly linked to suppression of the nitrate assimilation gene (Bradley 2001). Suppression of nitrate uptake by plants exposed to high inputs of N (Rennenberg and Gessler 1999) will further increase nitrate leaching from forests which have received N deposition over a prolonged period.

Figure 7 The relationship between N concentration of the forest floor and net nitrate production in three studies based in Wales, NW Europe and North America (Redrawn from Wilson and Emmett 1999)

5. N-enrichment of soils

Large-scale $^{15}$N studies at the plot or catchment scale have been carried out to determine the relative importance of soil and trees as a sink for deposited N. These studies encompassed a range of N loadings in the United States and Europe (Tietema et al. 1998, Nadelhoffer et al., 1999). N was applied at moderate rates to a variety of different forest stands for several years prior to enrichment of the N additions with $^{15}$N for one to three years. The amount of $^{15}$N in trees, soils and, in some cases, drainage waters, was determined at the end of the enrichment period. In general, < 20% of N inputs, as indicated by $^{15}$N retention, were recovered from the trees, similar to the 15% calculated by Kauppi et al. (1995) for Finnish forests. The soil was the major sink for N but in some sites with large N inputs, leaching losses of $^{15}$N also represented a significant proportion of the total. The controls on long-term N accumulation rates in forest soils are not well understood but will ultimately determine the amount of N leached as nitrate and therefore net acidification of the soil (though ammonium may also be leached from more organic soils (Yesmin et al.1996)).
One of the controls on N accumulation is the fate of internally cycled N in litter. Increases in N concentration of litter have been observed across N deposition gradients (Tietema and Beier 1995). Evidence for this trend also being present in the forest floor can be inferred from a positive relationship between N concentrations in forest floor material and N inputs in wet deposition (Tietema and Beier 1995, McNulty et al. 1991). It is possible that the capacity of the soil to immobilise nitrogen is increased due to a reduction in decomposition rates of litterfall Whilst increased N concentration in litter are known to accelerate initial stages of decomposition they are also known to slow later stages. This would result in an increase build up of soil organic matter. These effects have been reviewed by Fog (1988), Berg (1996) and most recently Berg and Matzner (1997). Generally, the initial increase in microbial activity in response to increased N supply is greatest in litter from low fertility sites or substrates with high C/N ratios (e.g. Bååth et al. 1981). Berg and Matzner (1997) suggest that the slowing of the later stages of litter decomposition is due to a suppression of lignolytic enzymes in white rot fungi. The net effect of these changes in the dynamics of litter decomposition will be an increase of N accumulation rates in soils exposed to high N deposition thus accelerating the rate of both N and carbon (C) storage.

However, Aber et al. (1998) have suggested that the main mechanism for increasing N storage in soils with increasing deposition is through mycorrhizal assimilation. Reduced decomposition rates could delay the release of internally cycled N but would not account for the large accumulation of externally deposited N in the soil (Nadelhoffer et al. 1999). They argue that rates of abiotic fixation are insufficient to account for the magnitude of retention reported (although this remains an area of uncertainty), and C limitation of assimilation by soil microbes would prevent microbial immobilisation. Aber et al. (1998) suggest that only mycorrhizal fungi have a sufficient C supply to account for the large N accumulation in the soil. This N would be cycled within the soil pool through assimilation and exudation. Continued deposition of N could result in a decline in mycorrhizae, thus reducing competition and increasing availability of N for other soil microbes such as nitrifiers. The question surrounding the relative importance of abiotic fixation is due to recent work which identified rapid abiotic fixation of nitrate with dissolved organic matter producing dissolved organic N in acid forest soils (Dail et al. 2001). A continuing requirement for dissolved organic matter to supply this process would again link the fate of N with C supply and availability in soils. This is a highly active area of research at present and is likely to lead to a significant increase in our knowledge of key processes within the soil ‘black box’.

Summarising these complex hypotheses it would appear that long term exposure to elevated N deposition produces two opposing effects; an increase in the amount of N accumulated in the soil but a decrease in the retention efficiency of deposited N. The controlling mechanisms underlying these two effects remain uncertain but the net effect is an increase in N enrichment of the soil and an increase in N leaching leading to a decline in drainage water quality in areas dominated by acid sensitive soils.
6. Impact on water quality

The impact of nitrogen deposition on the aquatic ecosystem will depend on the amount of N leaching and the accompanying cations leached in drainage water. The amount of N leached depends on the retention capacity of the soils and trees and their proximity to the water course.

Across the NITREX sites, leaching losses representing between < 5% and 80% of deposited N were reported depending on the initial nitrogen status of the site and the form of N deposited. Stands appeared to fall into two categories: (I) Low-N status (e.g. Gårdsjön and Klosterhede) where both ammonium and nitrate were retained with high efficiency; (ii) High-N status (e.g. Aber, Speuld, Solling, Ysselsteyn) where there is lower N retention due to excess availability relative to requirements and the magnitude of leaching losses is determined by the availability of the mobile nitrate-anion (Emmet et al. 1998a). Nitrate can originate from deposition or be internally generated from the microbial transformation of ammonium to nitrate in the soil. In sites with low rates of nitrification, leaching losses are therefore greater if nitrogen is deposited as nitrate rather than ammonium. This is experimentally demonstrated at the Aber site where nitrate leaching losses are double when nitrogen is applied as 100% nitrate relative to application as 50% ammonium and 50% as nitrate. In more N-rich stands, (e.g. Ysselsteyn), nitrification rates are greater and leaching losses are in excess of nitrate inputs alone.

7. Determining stand internal N status and predicting N retention

The internal N status which is so important in determining retention capacity of a stand is a consequence of historical N deposition and management. This accounts for the often poor relationship between N retention and current rates of N deposition. For example, soil disturbance through ploughing or a clay-rich soil may significantly enhance the N status of a stand above that predicted from deposition loadings alone (Emmet et al. 1998a). The internal N status can, however, be easily described by various individual components or by a discriminate variable combining individual factors of the ecosystem, e.g. N concentration of the forest floor, foliage or leaf litter (Tietema and Beier 1995, Gundersen et al. 1998).

The C/N ratio of the forest floor in particular is closely related to the onset of NO₃⁻ leaching (Figure 8). The strong relationship between forest floor C/N ratio and nitrate leaching losses is surprising. A more important role for the large bulk of mineral soil would have been expected but no relationship is observed between pool sizes or C/N ratio in the mineral soil and the N status of the NITREX sites (Gundersen et al. 1998). In addition, no reduction in retention efficiency of nitrate by the mineral soil was observed following a change in deposition loadings across the NITREX sites. A recent analysis of the IFEF database (Indicators of Forest Ecosystem Functioning) by Macdonald et al. (In Press) has enabled the % retention to be directly linked to both the C/N ratio and deposition loading. In Low-N status stands with a C/N ratio > 25, ca. 25% of inputs are leached. In High-N status stands with C/N ratios < 25 this increases to ca. 60% of inputs. This provides a simple rule-base which simplifies many of the general patterns observed.
Figure 9  The relationship between the C/N ratio of the forest floor and the nitrate leached from below the rooting zone in three studies based in Wales (Emmett et al. 1995), Germany (Matzner and Grosholtz 1997) and across Europe (Gundersen et al. 1995). Redrawn from Wilson and Emmett (1999).

Why is there this threshold at C/N of 25? As discussed previously, this appears to be associated with the relationship between the forest floor C/N ratio and net nitrate release in the soil. Nitrification rates increase as C/N ratios decline or nitrogen concentration increases (Figure 7) thus decreasing the N retention efficiency of the forest floor as demonstrated in $^{15}$N studies (Tietema et al. 1998c). The mobilised NO$_3^-$ is not retained in the deeper mineral soil and is thus leached from the system. The importance of site nitrogen status in determining the potential of N loss has also been identified in clearcut sites (e.g. Vitousek et al. 1982) indicating similar controls on nitrogen retention may be relevant in both N-polluted and clearcut sites.

8. Effect of tree species and consequences for fauna and flora and forest expansion

Initial stand composition may affect both the amount of N captured from the atmosphere and its fate within the stand (Wilson and Emmett 1999). Some studies have compared the effect on tree growth, soil processes and water quality with some data suggesting a fundamental different in the plant-soil interactions in broadleaved stands compared to coniferous stands (Ollinger et al. 2002). Forest expansion into temperate grassland has been associated with comparatively low rates of N deposition (Köcky and Wilson 2001). This may be a result of increased water-use efficiency of woody invaders or an increase in the competitive advantage of tall or fast-growing trees as competition for light increases with N availability. There is convincing evidence that ground flora composition in forest stands may change with increased N inputs. Changes are most likely to be observed in woodland flora compared to low, open vegetation such as grassland due to the greater scavenging of N pollution from the atmosphere by trees increasing inputs by up to 100% (NEGTAP 2001). Evidence from species change comes from repeated sampling of permanent plots (e.g. Brunet et al. 1996), sampling across gradients (Pitcairn et al. 1998) and manipulation studies (Boxman et al. 1998). A trend towards more nitrogen loving species is generally
reported although this change may be slower on acidic soils (Falkengren-Grerup et al. 2000). These authors also suggest the ratio of oxidised to reduced nitrogen (i.e. nitrate to ammonium) may affect species composition although field evidence is sparse. Likely explanations for the change in composition in response to N deposition include differential growth response to N supply which affects the competitive balance between species, and increased fungal and insect attacks of some species again affects the competitive balance (e.g. Strengbom et al. 2002). As with the ground flora, different tree species may be differentially affected by N deposition. Changes in flora inevitably have consequences for the fauna with reported changes in invertebrate fauna affecting some birds species in some highly polluted stands (Graveland et al. 1994, van Tol et al. 1998, Ball et al. 2000).

9. Conclusions

There remain major areas of uncertainty however significant progress has been made in identifying the effects of N deposition in forest stands. Soil is clearly the largest sink for N deposition however this is not inexhaustible in the long term. Reduced litter decomposition due to inhibition of some microbial enzymes may increase the storage capacity of the soil, but continued deposition in excess of plant productivity requirements in the long term will result in gradual N-enrichment of the soil. In time, this results in a gradual saturation of the immobilisation capacity of the soil for incoming nitrogen, resulting in the onset of nitrate leaching. Increased nitrification rates enhances the pool of nitrate available for leaching as will the suppression of nitrate uptake by tree and soil microbes due to increase ammonium availability.

Ammonium uptake by vegetation and soil microbes and increased nitrification can lead to acidification of some sensitive soils and a reduction in the availability of other nutrients. In combination with the increased availability of N, this can have both positive and negative consequences for tree growth and forest expansion and can change ground vegetation composition and possibly associated fauna. Remaining areas of uncertainty include: (i) the relative importance of abiotic and biotic soil processes in controlling the capacity of the soil to retain N and the interaction with C supply, (ii) the controlling mechanism underlying changes in tree growth and vegetation composition and the relative importance of indirect biotic stresses such insect and fungal attack, (iii) the factors controlling the timing of responses and (iv) the influence of tree species in determining stand sensitivity. Finally, the influence of climate in controlling the inter-annual variability and regional trends of plant and soil responses and streamwater quality will become an area of increasing interest as dynamic modelling activities increase.
References

Graveland, J., van der Wal, R., van Balen, J.H., van Noordwijk; 1994, Nature 368, 446 - 448


