G.J. Heij and J.W. Erisman (Editors). Acid Rain Research: Do we have enough answers?

Evaluation; integration

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Introduction

Since the early 1980s the ecological effects of atmospheric deposition have become the subject of intense research activities. In this research the main focus of interest was forest, with emphasis on soil chemistry and tree physiology. The choice for this subject was primarily inspired by the work of Ulrich and co-workers (Ulrich et al. 1979, Ulrich 1983). Their publications resulted in a broad public concern over forest decline, in analogy with the fish decline in lakes and streams, which was a known result of acid deposition. Van Breemen et al. (1982) observed a nearly complete nitrification of atmospheric ammonia in acid forest soil, resulting in an internal generation of acidity. This publication strongly stimulated research in the field of forest soil chemistry. The past decade of research has unequivocally shown a strong relationship between atmospheric deposition and a large number of biological and chemical changes in forest ecosystems. These deposition-related changes are described in detail in the preceding papers. Some of the highlights are summarized below for the two main topics: the soil and the trees.

Effects of atmospheric deposition on forest soil

The most important results can be summarized in three points:

In spite of the high deposition, nitrogen is still largely retained in most forest soils; for sulphur, however, leaching equals deposition (De Vries 1994). In Dutch forests, soil solution is dominated by SO_4, NO_3 and Al. Absolute concentrations of these ions strongly depend upon the tree species, and decrease in the order spruce forest (Norway spruce, Douglas fir) > pine forest (Scots pine, black pine) > deciduous forest (oak, beech). Leaching of NH_4

hardly occurs; if nitrogen is leached this is in the form of NO_3, which may be partly derived from atmospheric ammonia through nitrification. If net nitrification occurs (i.e., if the leaching of NO_3 exceeds the deposition of NO_x), acidity is generated internally.

The deposited or generated acidity is largely buffered by the release of Al from secondary Al-compounds (Van Breemen et al. 1982; De Vries 1994). This buffer mechanism has two important implications. Firstly, a strong drop in pH may be expected if the store of secondary Al-compounds becomes exhausted. For some Dutch forest soils this may be the case within a few decades (see De Vries et al. 1995 for further discussion). Secondly, phytotoxic effects of Al may be expected. Critical levels of Al in soil solution for the occurrence of such effects have often been stated as Al/Ca = 1 (relative) or Al = 0.2 $mmol_c.m^{-3}$ (absolute) (De Vries & Heij 1991).

Atmospheric deposition of nitrogen compounds leads to a strong increase in the amount of plant-available N. A good quantification is lacking, but changes in both the physiology of trees (Steingröver & Jans 1995), and in the species composition of understorey vegetation (De Vries et al. 1995) indirectly show the importance of this effect.

There are a few general comments to be made.
(1) deposition of ammonia is often stated as an important source of acidity in forest soil. It should however be stressed that in the present situation in The Netherlands, the contribution of SO_2 to soil acidification exceeds the contribution of NH_3, due to the large retention of N in the soil/vegetation system (De Vries 1994). The relative importance of atmospheric compounds may however change in the future, depending upon the success of various abatement measures.
(2) These is still a large uncertainty about the phytotoxic effect of Al. The critical levels for Al in soil solution (and, consequently, the critical loads for acid) are based on model calculations and laboratory observations (De Vries & Kros 1991; Sverdrup & Warfvinge 1993). However, in a recent field survey no direct relation was found between Al concentration and tree vitality (Hendriks et al. 1994), and the kinetic model approach has also been criticized (Högberg & Jensén 1994). In laboratory experiments with herbaceous species the critical

levels for Al (both absolute and relative) far exceeded the above-stated values of Al/Ca = 1 or Al = 0.2 $mmol_c.m^{-3}$ (Pegtel 1987, Kroeze et al. 1989, Van Dobben 1991).

Effects of atmospheric deposition on tree physiology

Good knowledge exists concerning deposition-related changes in leaf and needle nutrient concentration in Dutch forests (Van den Burg & Kiewit 1989). However, there is considerable uncertainty about other effects of deposition on tree physiology. The most important known effects are summarized below.

Leaf and needle N concentrations are generally high (often exceeding the concentrations considered optimal for biomass increment), *and base cation and P concentrations are low* (often approaching or exceeding deficiency levels) (Hendriks et al. 1994). The low base cation levels are often ascribed to interference of Al or NH_4 with uptake (Roelofs 1991). Again, the relation with tree vitality is unclear. In the field survey mentioned earlier (Hendriks et al. 1994) vitality appeared to be only weakly correlated with leaf and needle N and P concentration.

During the past few decades, forest growth has strongly increased over large parts of Europe. A high production was noted at the Speuld monitoring site (Steingröver & Jans 1995). Survey studies based on tree-ring analyses indicate a 20-50% increase of forest production since c. 1950 (Kenk & Fisher 1988, Becker et al. 1994). This increase is usually ascribed to a higher availability of N through atmospheric deposition, although some authors state increased atmospheric CO_2 as a possible cause. At the Speuld site the increase in growth was accompanied by a strong increase in needle to fine root ratio (Steingröver & Jans 1995). This is probably a general phenomenon, which might increase the drought sensitivity of trees. A strong increase in productivity and concomitant increase in shoot/root ratio as a result of NH_3 deposition was also shown for some herbaceous species (Van Dobben 1991).

Very high levels of NH_3 deposition or concentration ($>$ c. 50 kg N $ha^{-1}.y^{-1}$ or $>$ c. 10 $\mu g.m^{-3}$ NH_3) probably result in a reduction of tree growth, at least for *Pinus sylvestris*. This was shown in both laboratory (fumigation) experiments

(Steingröver et al. 1995) and in field (fertilization) experiments (Tamm & Popovic 1995). Negative effects of NH_3 on tree growth may be enhanced in the presence of O_3 (Steingröver et al. 1995).

For most tree species there is no significant trend in vitality in The Netherlands since 1984 (Hilgen 1994). As stated above, the hypothesized relations between loss of vitality (defined as defoliation or discolouration) and soil chemistry (acidification or high Al or NH_4 concentrations) could not be confirmed in the field.

Critical levels and critical loads

The relation of some of the above-described phenomena with atmospheric deposition (of acidity, nitrogen, or both) is now well understood and in some cases quantitatively well described. The known quantitative relations have in turn led to the formulation of critical loads and critical levels, which have become important tools for policy makers (De Vries & Kros 1991). However, critical values are based on chemical or physiological criteria, and not on observed visible effects in the field. In general, it seems that up to now researchers have failed to confirm the hypothesized relationship between atmospheric deposition and forest decline (or, in particular, tree vitality) in the field. Therefore critical levels and critical loads must be considered as best guesses according to the present state of knowledge, of concentration or deposition values where the risk of ecological effects is reduced to an acceptable level. For a discussion of the differences in philosophy underlying critical levels and critical loads the reader is referred to Van der Eerden (1995).

The apparent absence of a simple and direct link between abiotic parameters and vitality has gradually caused a shift in research focus towards combinations of atmospheric deposition and other abiotic or biotic factors (see Van der Eerden 1995). However, the study of such combination stresses is a difficult one, be it only because the number of possible combinations tends to multiply explosively.

Table 1: Overview of changes in non-forest ecosystems in The Netherlands (including non-tree components of forests) that are partly or completely ascribed to atmospheric deposition.

ecosystem	effect	cause	source
soft water	extinction of many diatom spp., dominance of a few spp.	acidification	Van Dam et al. (1981), Van Dobben et al. (1992)
	decline of isoetid spp., increase of submerged mosses	acidification, eutrophication	Roelofs (1983), Arts (1990)
	decline of amphibians, hampered reproduction	acidification	Leuven et al. (1986), Van Dam & Buskens (1993)
heathland	replacement of Calluna and Erica by grasses	eutrophication	Aerts et al. (1990) Berdowski (1987),
	decline of rare spp.	acidification (eutrophication)	Van Dobben (1991), Houdijk et al. (1993)
chalk grassland	decrease in species richness, dominance of Brachypodium	eutrophication	Bobbink & Willems (1987), Bobbink (1989)
pine forest	extinction of terrestrial lichens, increase of grasses	eutrophication	De Vries (1982), Van Dobben et al. (1994)
	decline of mycorrhiza-forming fungi	eutrophication, (acidification?)	Jansen & Van Dobben (1987), Arnolds & Jansen (1992)
	hampered reproduction of great tit	acidification	Graveland et al. (1994)
epiphytic lichens	extinction of many spp.	SO_2 toxicity	De Wit (1976), Van Dobben (1993)
	change in dominance of spp.	acidification	
wet oligotrophic grassland	strong decline	eutrophication, (acidification?), desiccation, reclamation	Horsthuis & Schaminee (1993), Bink et al. (1994)
alder swamp	strong decline of characteristic spp. in undergrowth	eutrophication, desiccation	Bink et al. (1994)
dune grassland	decline of lichens, increase of grasses	eutrophication	Veer et al. (1993)
floating rich-fen	change in dominance of moss spp.	acidification	Kooyman (1993a,b), Van Wirdum (1993)
various pioneer communities	strong decline	eutrophication	Bink et al. (1994)

Non-forest ecosystems

Research into the ecological effects of atmospheric deposition was not completely restricted to forests; other (semi-)natural ecosystems have also been the subject of study. Surprisingly, clear effects of atmospheric deposition on presence or vitality of organisms in non-forest ecosystems are claimed by a great number of authors, and for a highly diverse group of ecosystems, despite a significantly lower research effort. These ecosystems include freshwater (both plankton and macrophytes), cryptogamic epiphytes, heathland, coastal and inland dunes, but also forest undergrowth. Effects on animals have been reported as well, e.g. on amphibians and birds, besides the well-known fish decline. These effects are treated in detail by e.g. Cals et al. (1993), Bink et al. (1994) or Bobbink & Roelofs (1995), and are summarized in Table 1. In some of these cases, field observations are supported by experimental results, both from field (manipulation) and laboratory studies. In the terrestrial environment the latter is especially true for the heathland ecosystem (Aerts & Berendse 1989, Van Dobben 1991, Houdijk 1993).

Comparison of forest and non-forest ecosystems

We might wonder to what extent the insight gained in the study of non-forest ecosystems could also be applicable to forests. In general, two mechanisms seem to underlie the field effects of atmospheric deposition: (a) intolerance to acidification, and (b) differential growth response of species to nitrogen enrichment, resulting in competitive displacement. Now the most intensively studied forest trees generally belong to acid-resistent species (most conifers, oak, beech etc.); and inter-species competition is either absent (in monocultures) or only effective on a very long time-scale (possibly longer than one rotation period). Still, some of the processes shown in lower vegetation might also be effective in forests. This can be made clear with an example. Common heather, *Calluna vulgaris*, is a woody and long-living species (like forest trees), but by the simple fact of its lower stature, lends itself better for an experimental approach (Heil 1984, Berdowski 1987, Van Dobben 1991). The results of field and experimental work done with this species are summarized below.

An example: Calluna

Calluna appeared to be highly resistent to both high SO_2 concentrations and low soil pH. In monoculture, a high availability of nitrogen (either as dissolved NH_4 or as gaseous NH_3) initially leads to a strongly enhanced growth. However, under high levels of atmospheric deposition, several mechanisms cause trouble for this species in the long run:

(1) an increased shoot/root ratio decreases its drought tolerance;
(2) an increased amino acid content increases its palatability for plague insects;
(3) a decreased sugar content decreases its frost hardiness.

In general, the species becomes more susceptible to various stress factors, which will ultimately lead to its replacement by grasses which are more competitive in a nitrogen-rich environment.

It is tempting to transfer this mechanism directly to forest trees. Both the enhanced growth, the change in shoot/root ratio and the increase in amino acid content have also been shown there. There is little reason to suppose that the enhanced susceptibility for plagues or extreme weather conditions found for *Calluna* is absent in trees. Increased sensitivity to frost and fungal infections has in fact been shown in some cases (Aronsson 1980, Van Dijk et al. 1992). The analogy with lower vegetation may therefore be considered as a warning signal for the forest (De Visser 1994). If this analogy is true, strong effects have not occurred hitherto in forest trees because of (a) the absence of inter-species competition, and (b) a long response period.

Conclusion

The above warning signal was derived from the physiological response of the trees to atmospheric deposition. However, some of the effects on other forest components than the trees may be considered as warning signals indicating a tendency towards destabilization of the forest ecosystem as a whole. The most apparent of these signals are (a) the depletion of soil buffer substances, in particular Al, (b) the increase of ruderal species in undergrowth, and (c) the decline of mycorrhiza-forming fungi.

The relation between the above changes and tree vitality is still unclear. However, each has a possible link with tree vitality. Aluminium is phytotoxic, but also serves as a buffer that protects forest soils from a dramatic drop in pH. Forest undergrowth may be an important sink for nutrients (Mugasha & Pluth 1994, Melin et al. 1983) but it may also hamper rejuvenation of trees (Wagner 1994). Mycorrhiza fungi are important for water and nutrient uptake by trees. Changes in these factors show us that the forest is at risk, and at any given moment large changes might be triggered by some secondary factor. Such changes could be comparable to the changes observed in the ecosystems summed up in Table 1, and might therefore include a decline of the dominant species (i.e., forest dieback). It is clear that this risk will become larger as the magnitude and duration of critical load exceedence increases. On the other hand manipulation experiments (Boxman et al. 1995) have shown that at least some of the parameters that are now at 'danger' levels may rapidly return to 'safe' levels if deposition drops below the critical load.

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