

# Natural nitrogen filter fails in polluted raised bogs

LEON P. M. LAMERS,\* ROLAND BOBBINK† and JAN G. M. ROELOFS\*

\*Department of Aquatic Ecology and Environmental Biology, University of Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, the Netherlands, †Landscape Ecology, Department of Geobiology, Utrecht University, PO Box 800.84, 3508 TB Utrecht, the Netherlands

## Abstract

**Raised bogs are among the ecosystems most susceptible to atmospheric nitrogen pollution. Based on global data ranging from pristine to heavily polluted areas, a conceptual model is presented to explain the logistic response of these terrestrial carbon reservoirs to increased airborne nitrogen fluxes.**

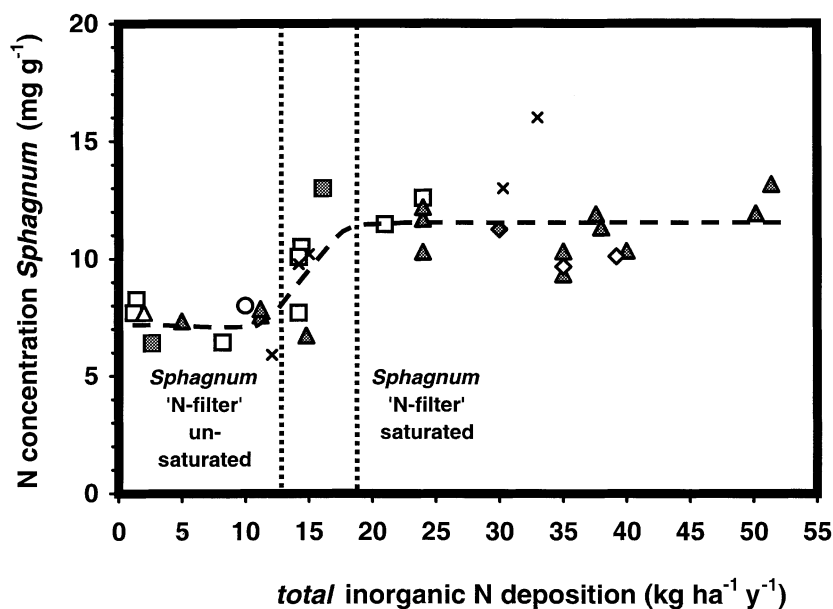
*Keywords:* carbon, eutrophication, nitrogen, peatlands, pollution, *Sphagnum*

*Received 7 October 1999; resubmitted and accepted 6 January 2000*

Peatlands, including raised bogs, receive much attention because they serve as an important terrestrial sink or source of carbon (C) and thereby influence global C cycling (Gorham 1991; Siegel *et al.* 1995). Raised bogs differ significantly from most other vegetation types in that they are strongly dominated by mosses, notably *Sphagnum* species (peat mosses). Dead *Sphagnum* decomposes very slowly, forming thick and solid peat layers and leading to a significant storage of C. Living *Sphagnum* mosses create an acidic, cold, wet or moist environment upon this, and exude allelopathic substances (Clymo & Hayward 1982; Malmer *et al.* 1994; Van Breemen 1995). They efficiently filter out airborne compounds that form the principal nutrient input into these ombrotrophic systems (Aerts *et al.* 1992; Malmer *et al.* 1994). Only a few vascular plants, present at low densities, are able to cope with this environment. Among these are members of the Cyperaceae and Ericaceae, and of insectivorous genera like *Drosera* and *Sarracenia*. In pristine bogs, the input of inorganic nitrogen (N) is low (<5 kg ha<sup>-1</sup> y<sup>-1</sup>) and largely provided by natural atmospheric N deposition and N fixation via cyanobacteria associated with *Sphagnum* and other plants. Carnivorous species acquire additional N from insects. Bog species are highly economic with their N, reallocating a large part of the nutrient before litter is produced. Given the low N input, and the high efficiency of N uptake and reallocation, we would expect a sensitive response to increased levels of airborne N from raised bogs.

To get an indication of the effects of increased atmospheric deposition of N, we plotted the N concentrations of ombrotrophic *Sphagnum* species against the total inorganic-N deposition values for different raised bog locations (Fig. 1). At low levels of N input, N is

rapidly taken up by *Sphagnum* because this nutrient limits growth (Aerts *et al.* 1992). The N concentration is therefore determined by productivity and not by N deposition level (Malmer 1988), and increased C uptake leads to a constant N concentration. At increasing N input (12–18 kg ha<sup>-1</sup> y<sup>-1</sup>), due to anthropogenic N emissions (Bobbink *et al.* 1998), the nutrient is no longer growth-limiting and it accumulates in the tissue, stored as free N and N-rich free amino acids. Some *Sphagnum* species (like *Sphagnum recurvum*) and shallow-rooting vascular species gain a competitive advantage at these input levels and become able to outcompete other species (Lütke-Twenhöven 1992). At higher levels, phosphate becomes growth-limiting for *Sphagnum* (Malmer 1988; Aerts *et al.* 1992). Above 18 kg ha<sup>-1</sup> y<sup>-1</sup>, however, the *Sphagnum* N concentration no longer increases, indicating that the airborne input is no longer bound in the moss layer. The maximum net C accumulation rate of 300–400 kg ha<sup>-1</sup> y<sup>-1</sup> estimated for *Sphagnum* peatlands (Kratz & DeWitt 1986; Belyea & Warner 1996; Kuhry & Vitt 1996) is at this level, giving a *Sphagnum* C/N ratio of 40–50, insufficient to sequester all N deposited. In other words, the natural N filter fails. As a consequence, one would expect the N availability in the soil moisture of the top layer to increase strongly, thereby making the bog vulnerable to invasions by competitive vascular plants that require a high N supply, e.g. Purple Moorgrass (*Molinia caerulea*) (Roelofs 1986). The growth of these species is still N-limited because of the *Sphagnum* filter above their roots. For wet heathlands, N-induced stimulation of graminoid growth is well known (Berendse & Aerts 1984; Roelofs 1986). A comparison between high-input Dutch and low-input Irish raised bogs shows the expected difference in N availability (Table 1). This corresponds to invasions by Moorgrass



**Fig. 1** The N concentration of ombrotrophic *Sphagnum* species (apical parts) shows a logistic response curve [ $y = 1 / [0.086 + (0.054 \times 0.9972)^{6.45E-07 \times x^{7.523}}]$ ]; best logistic goodness-of-fit for the atmospheric inorganic N input (estimated as two-times bulk deposition (Bobbink *et al.* 1992)). Data taken from literature (◆, Ferguson *et al.* 1984; □, Malmer 1988; ■, Aerts *et al.* 1992; ◇, Lütke Twenhöven 1992; ○, Van der Molen 1992; ×, Pitcairn *et al.* 1995; △, Johnson & Maly 1998) and ▲ collected by the authors (1998; Europe, USA).

	Ireland ( $n = 6$ )	The Netherlands ( $n = 10$ )
Total inorganic N deposition ( $\text{kg ha}^{-1} \text{y}^{-1}$ )†	8–12	35–50
$\text{NH}_4^+$ in soil moisture ( $\mu\text{mol L}^{-1}$ )‡	$3.2 \pm 0.4$	$105.0 \pm 25.5$

†Estimated as two-times bulk deposition (Bobbink *et al.* 1992).

‡Collected at 10 cm below soil surface by ceramic cup vacuum suction.

**Table 1** N availability in raised bogs ( $\pm$ SEM)

and Birch (*Betula* species) in Dutch but not in Irish raised bogs. Because only non-desiccated locations were selected, the observed differences cannot be attributed to drainage. In recent decades, Moorgrass and Birch have also invaded many other polluted raised bogs in north-western Europe, where previously they would have occurred only at very low densities. The invasions have led to a number of unfavourable indirect effects, as shown in Fig. 2. The increased growth of graminoids and trees stimulates N deposition by canopy interception (Heil *et al.* 1988; Bobbink *et al.* 1992) and depresses *Sphagnum* growth by shading. Decomposition and N mineralization are promoted by the production of N-enriched litter from *Sphagnum* and from an increasing amount of easily degradable vascular plant litter (both above- and below-ground). The exudation of organic substances and oxygen by roots of vascular plants further stimulates decomposition and mineralization. This increased mobilization and cycling of C will inevitably slow down peat accumulation.

We propose that the living *Sphagnum* filter produces a logistic response curve to an increase in atmospheric N input, allowing graminoid and tree invasion only above a

certain threshold value. Thus, we predict that the N availability in the rhizosphere is increasing strongly at input levels above  $20 \text{ kg inorganic-N ha}^{-1} \text{y}^{-1}$ . The competitive advantage for relatively fast growing, nonrooting or shallowly rooting plant species is, however, already promoted at levels above  $10 \text{ kg ha}^{-1} \text{y}^{-1}$ , a value well in accordance with the proposed critical load for the atmospheric N input into bogs (Bobbink & Roelofs 1995). Because our input estimates for raised bogs (two-times bulk deposition) are rather crude, the critical load is expected to be even lower. The strong increase in airborne N input may not only threaten ecosystem functioning through vascular plant invasions, but it may also reduce, if not nullify, the capacity of these systems to act as a sink for atmospheric C, by the stimulation of decomposition.

### Acknowledgements

The authors wish to thank Paul van der Ven for conducting the chemical analyses of *Sphagnum* samples, and Jan van Groenendael, Hilde Tomassen and Fons Smolders for their helpful comments on an earlier version of the manuscript.

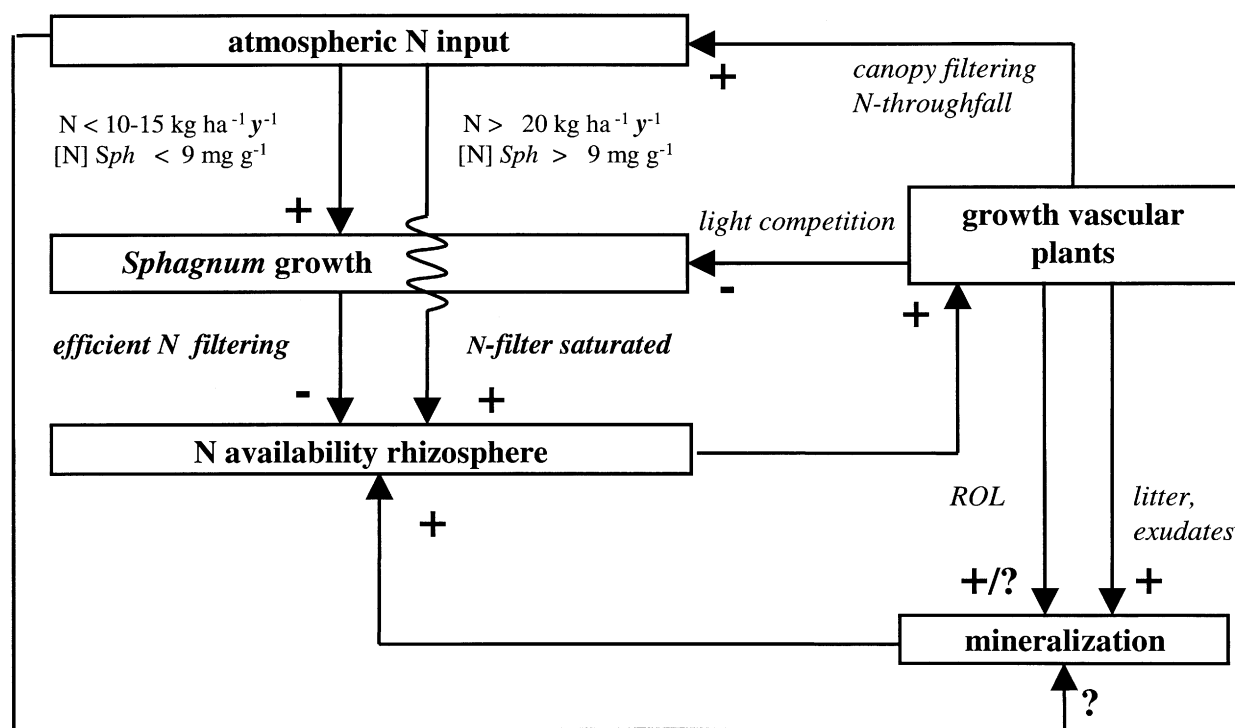


Fig. 2 The increased N availability in the rhizosphere produces a number of feedbacks, intensifying the unfavourable changes in raised bog functioning.  $[N] \text{ Sph}$ , N concentration *Sphagnum*; ROL, radial oxygen loss (by roots).

## References

- Aerts R, Wallén B, Malmer N (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *Journal of Ecology*, **80**, 131–140.
- Belyea LR, Warner BG (1996) Temporal scale and the accumulation of peat in a *Sphagnum* bog. *Canadian Journal of Botany*, **74**, 366–377.
- Berendse F, Aerts R (1984) Competition between *Erica tetralix* L. & *Molinia caerulea* (L.) Moench as affected by the availability of nutrients. *Acta Oecologia/Oecologia Plantarum*, **5**, 3–14.
- Bobbink R, Heil GW, Raessen MBAG (1992) Atmospheric deposition and canopy exchange processes in heathland ecosystems. *Environmental Pollution*, **75**, 29–37.
- Bobbink R, Hornung M, Roelofs JGM (1998) The effects of airborne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology*, **86**, 717–738.
- Bobbink R, Roelofs JGM (1995) Nitrogen critical loads for natural and semi-natural ecosystems: the empirical approach. *Water, Air and Soil Pollution*, **85**, 2413–2418.
- Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: *Bryophyte Ecology* (ed. Smith AJE), pp. 229–290. Chapman & Hall, London.
- Ferguson P, Robinson RN, Press MC, Lee JA (1984) Element concentrations in five *Sphagnum* species in relation to atmospheric pollution. *Journal of Bryology*, **13**, 107–114.
- Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, **1**, 182–195.
- Heil GW, Werger MJA, De Mol W, Van Dam D, Heijne B (1988) Capture of atmospheric ammonium by grassland canopies. *Science*, **239**, 764–765.
- Johnson KW, Maly CC (1998) Greenhouse studies of *Sphagnum papillosum* for commercial harvest and peatland restoration in Minnesota. *Proceedings of the 1998 International Peat Symposium*, 49–55.
- Kratz TK, DeWitt CB (1986) Internal factors controlling peatland-lake ecosystem development. *Ecology*, **67**, 100–107.
- Kuhry P, Vitt DH (1996) Fossil carbon/nitrogen ratios as a measure of peat decomposition. *Ecology*, **77**, 271–275.
- Lütke-Twenhöven F (1992) Competition between two *Sphagnum* species under different deposition levels. *Journal of Bryology*, **17**, 71–80.
- Malmer N (1988) Patterns in the growth and the accumulation of inorganic constituents in the *Sphagnum* cover on ombrotrophic bogs in Scandinavia. *Oikos*, **53**, 105–120.
- Malmer N, Svensson BM, Wallén B (1994) Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobotanica et Phytotaxonomica*, **29**, 483–496.
- Pitcairn CER, Fowler D, Grace J (1995) Deposition of fixed atmospheric nitrogen and foliar nitrogen content of bryophytes and *Calluna vulgaris* (L.) Hull. *Environmental Pollution*, **88**, 193–205.
- Roelofs JGM (1986) The effect of airborne sulphur and nitrogen

- deposition on aquatic and terrestrial heathland vegetation. *Experientia*, **42**, 372–377.
- Siegel DI, Reeve AS, Glaser PH, Romanowicz EA (1995) Climate-driven flushing of pore water in peatlands. *Nature*, **374**, 531–533.
- Van Breemen N (1995) How *Sphagnum* bogs down other plants. *Trends in Ecology & Evolution*, **10**, 270–275.
- Van der Molen PC (1992) *Hummock-hollow complexes on Irish raised bogs*. PhD Thesis, University of Amsterdam, The Netherlands.