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How bird droppings can affect the vegetation composition of ombrotrophic bogs

Hilde B.M. Tomassen, Alfons J.P. Smolders, Leon P.M. Lamers, and Jan G.M. Roelofs

Abstract: Ombrotrophic bogs depend on nutrient input from the atmosphere, so bird droppings may be a significant nutrient source. We studied the influx of N, P, and K by bird droppings, and the effects of this nutrient influx on the vegetation composition and development of Irish ombrotrophic bogs. Bird droppings significantly increased the influx of N, K, and particularly P. Concentrations of N, P, and K in the peat and vegetation were much higher at sites with bird droppings than at reference sites without bird droppings. *Pinus sylvestris* L. trees were able to grow much better at the sites with bird droppings, and growth was severely limited by P and K at the reference sites. Sites with bird droppings allowed atypical species to grow on ombrotrophic bogs. This change in vegetation composition alters the structure of the ombrotrophic vegetation locally, thereby affecting the atmospheric nutrient input and interception of precipitation.

Key words: nitrogen, nutrient limitation, potassium, phosphorus, *Pinus sylvestris*, soil CO₂ evolution, *Sphagnum*.

Résumé : Les tourbières ombrotrophes dépendent d'apports nutritifs en provenance de l'atmosphère, et conséquemment les déjections d'oiseaux peuvent constituer une source significative de nutriments. Les auteurs ont étudié l'arrivée de N, P et K provenant des fientes, ainsi que leurs effets sur la composition de la végétation et le développement de tourbières ombrotrophes, en Irlande. Les fientes augmentent significativement les apports en N, K et particulièrement en P. Les teneurs en N, P et K, dans la végétation et la tourbe, sont beaucoup plus élevées sur les sites recevant des fientes que sur des sites de référence n'en recevant pas. Les *Pinus sylvestris* L. poussent bien mieux sur les sites avec fientes et leur croissance est limitée par le P et le K sur les sites de référence. Les sites recevant des fientes permettent la croissance d'espèces atypiques pour les tourbières ombrotrophes. Cette modification de la composition de la végétation perturbe la structure de la végétation ombrotrophe localement, et conséquemment affecte l'apport en nutriment atmosphérique et l'interception de la précipitation.

Mots clés : azote, nutriment limitant, potassium, phosphore, *Pinus sylvestris*, évolution du CO₂ du sol, *Sphagnum*.

[Traduit par la Rédaction]

Introduction

Ombrotrophic bogs are unique ecosystems characterized by vegetation adapted to low nutrient availability. Increased atmospheric nutrient inputs (especially N) can have important effects on the vegetation composition in various natural and seminatural ecosystems (e.g., Bobbink et al. 1998; Bobbink and Lamers 2002) including ombrotrophic bogs (Tomassen et al. 2003; Limpens et al. 2003). As a result of high atmospheric nutrient influx, ombrotrophic bogs have been invaded by more nutrient-demanding species such as *Molinia caerulea* (L.) Moench. and *Betula* sp., a

development that has been accompanied by a decline of ombrotrophic species (Barkman 1992; Aaby 1994; Hogg et al. 1995; Risager 1998).

At low N deposition rates, N concentrations in the peat water are low as a result of high N uptake rates by *Sphagnum* (e.g., Lee and Woodin 1988; Jauhiainen et al. 1998), so vascular plants depend on N mobilized by mineralization processes in the underlying peat (Malmer 1993; Malmer et al. 1994). At high N deposition rates, some N leaches through the *Sphagnum* layer to the roots of vascular plants (Lee and Woodin 1988; Aerts et al. 1992; Lamers et al. 2000). Increased availability of nutrients in the rhizosphere leads to an increased cover of vascular plants and a reduction in *Sphagnum* growth because of shading (Hayward and Clymo 1983; Heijmans et al. 2001; Berendse et al. 2001). In addition to this indirect negative effect of N on *Sphagnum*, N can have direct toxic effects on *Sphagnum* mosses (Limpens et al. 2003).

In contrast to Dutch bogs, large-scale invasion of more nutrient-demanding species has not been observed on bogs in the Irish midlands, where total N deposition rates are relatively low (0.6–0.8 g·m⁻²·year⁻¹; Tomassen et al. 2004). Stands of *Betula* are, however, common in many parts of Ireland on cut-over and dried-out bogs, or are sometimes associated with flushes or soaks (Cross 1987), which are areas of

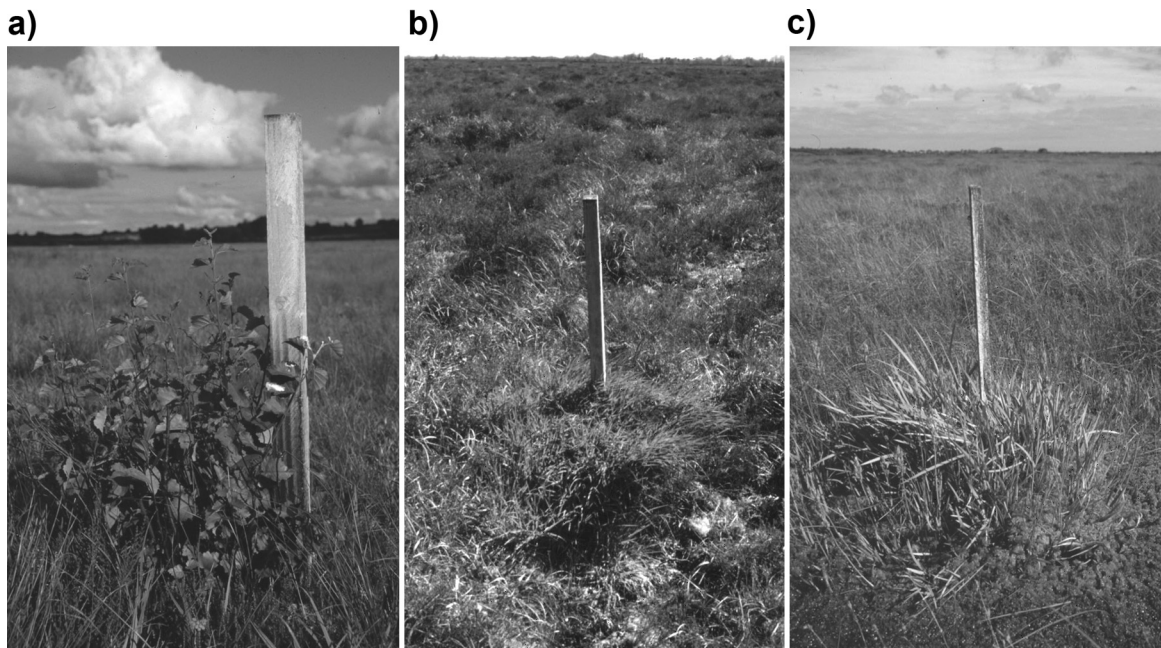
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Fig. 1. *Betula pubescens* (a), *Molinia caerulea* (b), and *Narthecium ossifragum* (c) growing in the vicinity of wooden survey posts on which birds perched and defecated over a period greater than 10 years.



nutrient enrichment. On several Irish bogs, growth of atypical species, such as *Molinia caerulea* and *Betula* trees, can be observed in the immediate vicinity of wooden survey posts that were placed there about 10 years ago (Figs. 1a, 1b). Birds regularly perch on these wooden posts (personal observations) and the increased influx of nutrients from their droppings may be responsible for the observed changes in vegetation composition in the immediate vicinity of the posts. Several studies have reported the effect of large densities of waterfowl on the availability of nutrients (N and P) in oligotrophic waters (Leentvaar 1967; Gould and Fletcher 1978; Paffen 1990). Information on the effects of bird droppings on terrestrial vegetation is limited, although there are several studies on the effects of marine bird and mammal faeces on terrestrial ecosystems (e.g., Lindeboom 1979; Cocks et al. 1998, 1999; Fariña et al. 2003). Marine-derived nutrients can be an important nutrient source affecting the development of flora and fauna (Lindeboom 1979). As far as we know there are no studies on the influence of nonmarine bird droppings on terrestrial vegetation.

We hypothesised that the input of nutrients originating from bird droppings might locally affect the vegetation composition and development of ombrotrophic bogs. To test this hypothesis, we measured the influx of major nutrients by bird droppings on Irish bogs. The effects of this influx on the vegetation were determined by comparing the growth of and nutrient concentrations in vegetation exposed to bird droppings with those on nearby unsupplemented reference sites, on three Irish bogs. The effects of bird droppings on the vegetation of ombrotrophic bogs are discussed and put in a larger context.

Materials and methods

Field sites

We studied the effects of bird droppings at three ombro-

trophic bogs in the midlands of Ireland: Clara bog, Raheenmore bog, and Sharavogue bog. The Irish midlands have a mean annual precipitation of 800–1000 mm (Jordan 1997). The mean annual temperature (1951–1980) is 9.3 °C and the July and January means are 14.8 and 4.4 °C, respectively. Clara bog (County Offaly; 53°19'N; 7°37'W) is situated in a depression adjacent to a complex of esker ridges, and its overall depth is in most cases around 10 m (Warren et al. 2002). Clara bog (665 ha) is 4.2 km long and 1.2 km wide and is divided by a road into a western and an eastern part. Raheenmore bog (County Offaly, 53°20'N; 7°21'W) developed in a depression between a number of low hills, and its peat reaches depths of up to 15 m (Warren et al. 2002). The actual bog covers approximately 160 ha. In 1990–1991, wooden posts were placed on both Clara bog and Raheenmore bog for hydrological research (Van der Schaaf 1999). The vegetation near these posts is dominated by atypical species such as *Molinia caerulea*, *Betula pubescens* Ehrh., *Pinus sylvestris* L., *Juncus effusus* L., and *Agrostis canina* L. (Figs. 1a, 1b). Among the bird species that use the survey posts are the Hooded crow (*Corvus corone cornix*), Common kestrel (*Falco Tinnunculus*), and the Stonechat (*Saxicola torquata*). Sharavogue bog (County Offaly, 53°02'N; 7°54'W) is characterized by several small *Pinus sylvestris* stands on the bog (223 ha). The understory vegetation of these stands includes species such as *Molinia caerulea* and *J. effusus*, which indicate more eutrophic conditions.

Vegetation

At Clara bog, five sites affected by bird droppings were selected in the vicinity of survey posts (area of 1 m²). The vegetation composition in the vicinity of all the posts showed distinct changes and five survey posts were selected randomly. Nearby these posts, five reference sites (area of 1 m²) were selected based on vegetation composition. At a

Table 1. Vegetation cover (%) at a reference site 2 m from the wooden survey posts and in the immediate vicinity of the posts at Clara bog ($n = 5$).

	Reference					Post				
	1	2	3	4	5	1	2	3	4	5
<i>Cladonia portentosa</i> (Dufour) Coem.	+		+		20					
<i>Dicranum scoparium</i> Hedw.			+		+					
<i>Drosera rotundifolia</i> L.	#		10	5	#					
<i>Menyanthes trifoliata</i> L.	+									
<i>Rhynchospora alba</i> (L.) Vahl	+	5	5		+					
<i>Vaccinium oxycoccos</i> L.		#								
<i>Andromeda polifolia</i> L.			+	+	+				5	+
<i>Calluna vulgaris</i> (L.) Hull	5	10	5	35	+		10		+	
<i>Carex echinata</i> Murray	5					#				
<i>Carex panacea</i> L.					0					10
<i>Erica tetralix</i> L.	5	20	5	5	5	+			5	
<i>Eriophorum angustifolium</i> Honck.	#	#	#	#	#	#		+		+
<i>Eriophorum vaginatum</i> L.	#	#	#	#	#			#	25	#
<i>Narthecium ossifragum</i> (L.) Huds.	10	30	#	#	5					30
<i>Potentilla reptans</i> L.	+					+	+			
<i>Sphagnum cuspidatum</i> Hoffm.	10	20				5				
<i>Sphagnum magellanicum</i> Brid.	25	15	30	10	+		#			
<i>Sphagnum papillosum</i> Lindb.	35	#	+		10	5				
<i>Sphagnum rubellum</i> Wils.	10		40	45	60					5
<i>Agrostis canina</i> L.						#				35
<i>Cerastium fontanum</i> Baumg. subsp. <i>vulgare</i> (Hartm.) Greuter & Burdet									10	+
<i>Comarum palustre</i> L.							+			
<i>Epilobium hirsutum</i> L.							+			
<i>Holcus lanatus</i> L.								85		
<i>Hydrocotyle vulgaris</i> L.							+			
<i>Molinia caerulea</i> (L.) Moench						90	80			
<i>Poa annua</i> L.									40	
<i>Polygonum persicaria</i> L.										20
<i>Polytrichum commune</i> Hedw.							10			
<i>Prunus</i> sp.						+				+
<i>Pteridium aquilinum</i> (L.) Kuhn							+			
<i>Rubus fruticosus</i> L.								10	5	
<i>Sambucus nigra</i> L.									+	
<i>Trifolium repens</i> L.									5	

Note: +, several individuals; #, large number of individuals but no significant cover.

distance of approximately 2 m from the survey posts, there were no visible changes in vegetation composition present. The vegetation was described in terms of the percentage cover of vascular plants, bryophytes, and lichens. In the case of species with an insignificant amount of cover (<5%), the number of individuals was estimated (+, several individuals; #, large number of individuals).

Input of nutrients by bird droppings

Input of nutrients by bird droppings was measured around three wooden survey posts on Clara bog east by collecting precipitation and bird droppings using a polyethylene container (10 L) connected to a circular funnel (22 cm diameter). Background input of nutrients ($n = 3$) was measured by collecting bulk precipitation using a black polyethylene bottle (2 L) connected to a funnel (9.75 cm diameter) according to Tomassen et al. (2004). The collectors were dug in the peat and contained 2 mL of a 200 mg·L⁻¹ HgCl₂ solution to

inhibit microbial activity. Between September 2000 and September 2001, rainwater including bird droppings and rainwater were collected eight times (November 2000, February, March, April, May, June, July, and September 2001) and the volume was measured in the field. Part of the bird dropping samples was filtered through a Whatman GF/C filter (pore size of 1.2 µm). This method allowed us to measure only the soluble part of the nutrients from the bird droppings and will underestimate the total nutrient input by bird droppings. Samples were stored at -20 °C until further analysis.

Effect of bird droppings on the nutrient concentrations in the vegetation

On Clara bog, nutrient concentrations in the top layer of the peat (0–10 cm) were measured in the immediate vicinity of the survey posts ($n = 5$) and at reference sites (2 m from the posts; $n = 5$). The peat was characterized as poorly

Table 2. Mean \pm SE ($n = 3$) influx from precipitation and precipitation including bird droppings (September 2000 – September 2001) of N (NH_4^+ and NO_3^-), P, and K at Clara bog.

	$\text{NH}_4^+\text{-N}$ ($\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$)	$\text{NO}_3^-\text{-N}$ ($\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$)	P ($\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$)	K ($\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$)
Influx from precipitation	0.3 \pm 0.1	0.14 \pm 0.00	0.02 \pm 0.00	0.2 \pm 0.1
Influx from bird droppings	18.4 \pm 2.3***	0.04 \pm 0.00***	3.52 \pm 0.76***	6.0 \pm 1.6***

Note: ***, statistical significance at $P \leq 0.001$ (t test).

Table 3. N, P, and K concentrations on a dry mass basis, C:N and C:P ratios, and CO_2 production rate (mean \pm 1 SE) of superficial peat (0–10 cm) at a reference site 2 m from the wooden survey posts and in the immediate vicinity of posts at Clara bog ($n = 5$).

	N ($\mu\text{mol}\cdot\text{g}^{-1}$)	P ($\mu\text{mol}\cdot\text{g}^{-1}$)	K ($\mu\text{mol}\cdot\text{g}^{-1}$)	C:N ratio ($\text{g}\cdot\text{g}^{-1}$)	C:P ratio ($\text{g}\cdot\text{g}^{-1}$)	CO_2 production rate ($\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$)
Reference	879 \pm 78	13 \pm 2	8.3 \pm 0.8	40 \pm 4	1246 \pm 119	11.7 \pm 5.9
Post	1832 \pm 274**	57 \pm 16***	28.6 \pm 2.8***	21 \pm 3**	350 \pm 66***	25.3 \pm 12.7*

Note: *, statistical significance at $P \leq 0.05$; **, statistical significance at $P \leq 0.01$; ***, statistical significance at $P \leq 0.001$ (t test).

Table 4. Capitulum N, P, and K concentrations on a dry mass basis, and N:P, N:K, and P:K ratios (mean \pm 1 SE) in *Sphagnum* from reference sites ($n = 6$) and sites affected by bird droppings ($n = 11$) at three Irish bogs (Clara bog, Sharavogue bog, and Raheenmore bog).

	N ($\mu\text{mol}\cdot\text{g}^{-1}$)	P ($\mu\text{mol}\cdot\text{g}^{-1}$)	K ($\mu\text{mol}\cdot\text{g}^{-1}$)	N:P ratio ($\text{g}\cdot\text{g}^{-1}$)	N:K ratio ($\text{g}\cdot\text{g}^{-1}$)	P:K ratio ($\text{g}\cdot\text{g}^{-1}$)
Reference	412 \pm 28	9 \pm 1	78 \pm 4	22 \pm 2	1.9 \pm 0.1	0.09 \pm 0.01
Post	1086 \pm 58***	49 \pm 4***	128 \pm 7***	11 \pm 1***	3.2 \pm 0.3ns	0.31 \pm 0.03***

Note: ns, not significant ($P > 0.05$); ***, statistical significance at $P \leq 0.001$ (t test).

Table 5. Length of longest leaf, N, P, and K concentrations on a dry mass basis, and N:P, N:K and P:K ratios (mean \pm 1 SE) in *Narthecium ossifragum* from a reference site 2 m from the posts ($n = 2$) and the immediate vicinity of posts ($n = 3$) at Clara bog.

	Length of longest leaf (mm)	N ($\mu\text{mol}\cdot\text{g}^{-1}$)	P ($\mu\text{mol}\cdot\text{g}^{-1}$)	K ($\mu\text{mol}\cdot\text{g}^{-1}$)	N:P ratio ($\text{g}\cdot\text{g}^{-1}$)	N:K ratio ($\text{g}\cdot\text{g}^{-1}$)	P:K ratio ($\text{g}\cdot\text{g}^{-1}$)
Reference	86 \pm 5	1089 \pm 43	12 \pm 1	326 \pm 25	41 \pm 4	1.2 \pm 0.0	0.03 \pm 0.00
Post	206 \pm 7***	1291 \pm 57ns	24 \pm 1**	194 \pm 18*	24 \pm 1**	2.4 \pm 0.3*	0.10 \pm 0.01*

Note: ns, not significant; *, statistical significance at $P \leq 0.05$; **, statistical significance at $P \leq 0.01$; ***, statistical significance at $P \leq 0.001$ (t test).

humified *Sphagnum* peat. The peat was stored in airtight plastic bags at 4 °C until chemical analysis. Uptake of bird-derived nutrients by *Sphagnum* mosses was determined by comparing nutrient concentrations in the capitula (0–2 cm) of *Sphagnum magellanicum* Brid. or *Sphagnum papillosum* Lindb. at sites with bird droppings ($n = 11$) and at reference sites without bird droppings ($n = 6$). In addition to *Sphagnum* from Clara bog (posts), we also analysed *Sphagnum* plants from Raheenmore bog (around posts) and Sharavogue bog (underneath *Pinus sylvestris* trees). For *Narthecium ossifragum* L. the length of the longest leaf and foliar nutrient concentrations (15 plants per location) were measured in the immediate vicinity of wooden posts ($n = 3$) and at reference sites (2 m from the posts; $n = 2$) at Clara bog.

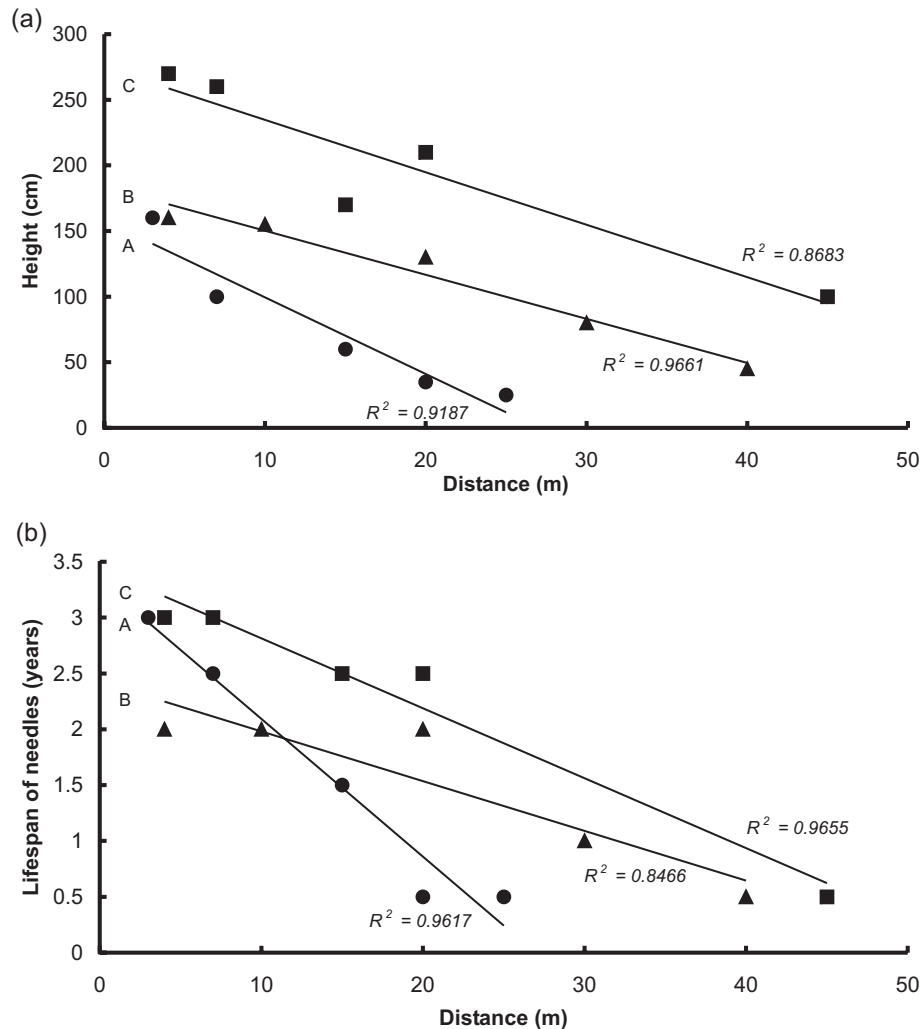
Sharavogue bog is characterized by several small groups of *Pinus sylvestris* trees with an understorey dominated by *Calluna vulgaris* (L.) Hull, *Molinia caerulea*, *B. pubescens*, *Vaccinium myrtillus* L., and *J. effusus*. The larger trees supported nests of the Hooded crow and bird droppings were obvious. All the small *Pinus* trees were established in 1989, which was an extremely dry year (Mills 2000). During this drought there was a fire that probably destroyed all *Pinus* seedlings. The young *Pinus* trees at a larger distance from

the “mother” tree were much smaller, though they all became established directly after the fire (1989). To determine the effects of bird droppings on the growth of these trees, tree height and lifespan of the needles (number of year classes present) were determined in three transects going out from a randomly chosen “mother” tree. On Clara bog east, the effects of bird droppings on *Pinus sylvestris* were examined experimentally by planting small *Pinus* trees near wooden posts ($n = 4$) as well as at a distance of 5 m from these posts ($n = 4$). Trees were planted in September 2000. The *Pinus* trees (height of 52 \pm 5 cm) were collected in a nearby cut-away. In July 2002, the growth of the trees was determined by measuring the increase in height, the length of the current year’s shoot and needles, and the lifespan of the needles. Needle samples were taken for analysis of major nutrient concentrations.

Chemical analysis

To analyse nutrient concentrations in plant tissue and peat, dried samples (48 h at 70 °C) were ground in liquid nitrogen. Nitrogen and carbon concentrations were measured in dried samples with a CNS analyser (type NA1500; Carlo Erba Instruments, Milan, Italy). Potassium and phosphorus

Fig. 2. Height (a) and lifespan of needles (b) of *Pinus sylvestris* trees measured in three transects (A–C) starting from the “mother” tree (0 m) at Sharavogue bog, September 2000. All trees were 11 years old. Linear regression yields for height: $P_A = 0.01$, $P_B = 0.003$, and $P_C = 0.02$; linear regression yields for lifespan of needles: $P_A = 0.003$, $P_B = 0.03$, and $P_C = 0.003$.



concentrations were determined by digesting 200 mg of dried material in sealed Teflon vessels in a Milestone microwave oven (mls 1200 Mega, Sorisole, Italy) after addition of 4 mL HNO₃ (65%) and 1 mL H₂O₂ (30%). After dilution, the digests were kept at 4 °C until analysis.

Nitrate and ammonium concentrations of water samples and digests were measured colorimetrically with a Traacs 800+ auto-analyzer, using hydrazine sulphate (Technicon 1969) and salicylate (Grasshoff and Johannsen 1977), respectively. Potassium concentrations were measured by flame photometry (FLM3 Flame Photometer, Radiometer, Copenhagen, Denmark). Phosphorus was determined by inductively coupled plasma emission spectrophotometry (Spectroflame, Spectro Analytical Instruments, Kleve, Germany).

Potential CO₂ production rates of the collected peat were measured by incubating 50 g of fresh peat in air-filled 250-mL infusion flasks, sealed with airtight stoppers. Duplicate incubations were made. The flasks were kept in the dark at 20 °C, and over a period of 4 weeks CO₂ concentrations in the headspace were measured weekly. CO₂ concentrations were measured using an infrared carbon analyzer (model

PIR-2000, Horiba Instruments, Irvine, California). CO₂ production rates were calculated by linear regression of the measurements and expressed on a dry mass basis.

Statistical analysis

Prior to statistical analysis, data were log-transformed to make the variance less dependent on the means and so that the data were approximately Gaussian. All statistical analyses were carried out using SPSS[®] for Windows software package (version 10.0.7; SPSS Inc., Chicago, Illinois). Differences between sites with bird droppings and reference sites without bird droppings were tested with an independent samples *t* test. Correlations between height and lifespan of the needles of the small *Pinus sylvestris* trees and the distance from the “mother” tree were analysed with a Pearson correlation test and described by a linear regression analysis. For clarity of presentation, the means and standard errors (SE) presented in the tables are for the untransformed data.

Results

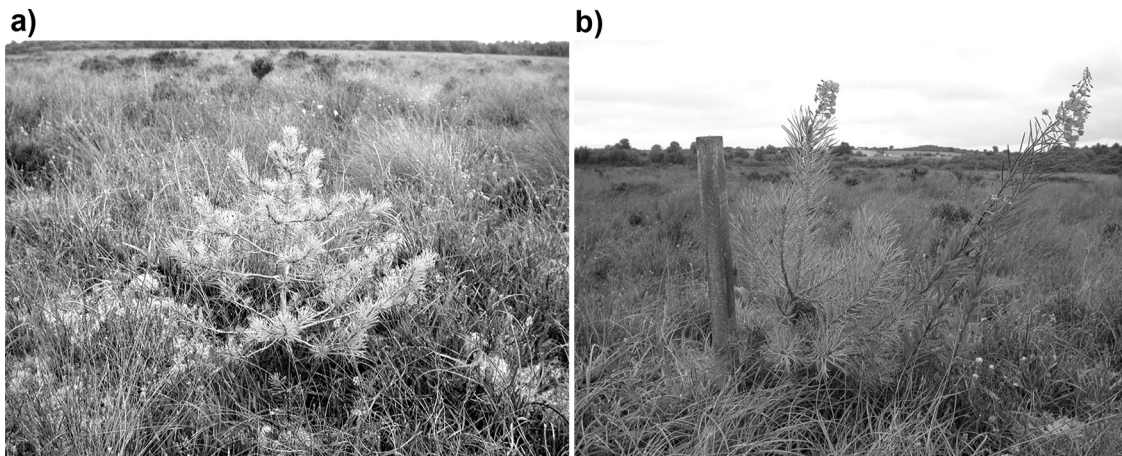
The vegetation around the wooden posts on Clara bog was

Table 6. Growth variables, nutrient concentrations on a dry mass basis, and ratios in current year's needles (mean \pm 1 SE) of *Pinus sylvestris* in July 2002, 2 years after transplantation (September 2000) to reference sites 2 m from the survey posts and to the immediate vicinity of survey posts, at Clara bog ($n = 4$).

Variable	Reference	Post
Length of current year's shoot (cm)	4.0 \pm 0.5	28.5 \pm 3.5***
Total height (cm)	59 \pm 10	86 \pm 3*
Length of needles (cm)	3.0 \pm 0.5	5.9 \pm 0.4**
Lifespan of needles (years)	1.6 \pm 0.1	2.8 \pm 0.1***
Increase in height between 2000 and 2002 (%)	13 \pm 3	80 \pm 21*
Change of length of current year's shoot between 2000 and 2002 (%)	-47 \pm 15	201 \pm 64*
N ($\mu\text{mol}\cdot\text{g}^{-1}$)	1104 \pm 172	811 \pm 59ns
P ($\mu\text{mol}\cdot\text{g}^{-1}$)	17 \pm 3	37 \pm 8*
K ($\mu\text{mol}\cdot\text{g}^{-1}$)	84 \pm 25	65 \pm 8ns
N:P ratio ($\text{g}\cdot\text{g}^{-1}$)	33 \pm 8	10 \pm 1*
N:K ratio ($\text{g}\cdot\text{g}^{-1}$)	5.8 \pm 1.5	4.7 \pm 0.8ns
P:K ratio ($\text{g}\cdot\text{g}^{-1}$)	0.2 \pm 0.1	0.5 \pm 0.2ns

Note: ns, not significant; *, statistical significance at $P \leq 0.05$; **, statistical significance at $P \leq 0.01$; ***, statistical significance at $P \leq 0.001$ (t test).

Fig. 3. *Pinus sylvestris* trees growing at a reference site 2 m from a wooden survey post (a) and in the vicinity of a wooden survey post (b) at Clara bog east, 2 years after transplantation.



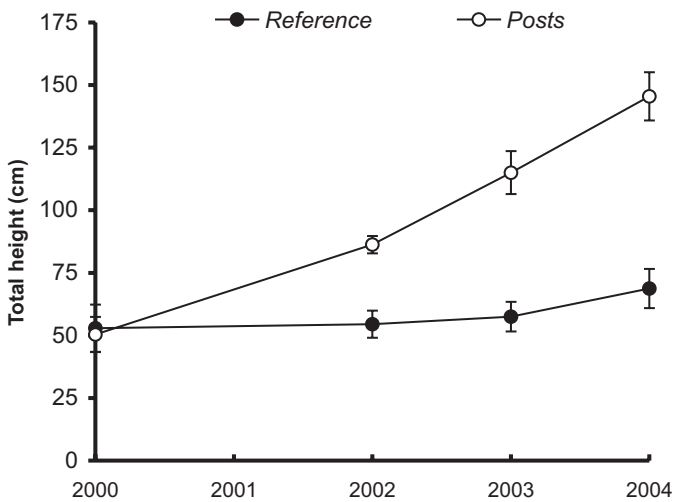
frequently dominated by atypical species, including *Molinia caerulea*, *Agrostis canina*, *Epilobium hirsutum* L., *Rubus fruticosus* L., *Holcus lanatus* L., *Poa annua* L., and *Trifolium repens* L. (Table 1), all of which were absent from the reference sites. Some typical bog species, such as *Sphagnum* mosses, had lower amounts of cover; others such as *Drosera rotundifolia* (L.) Vahl and *Rhynchospora alba* L. were absent from the areas around the posts (Table 1).

Table 2 shows that the influx of N, P, and K in bird droppings was tens or hundreds of times greater than that in precipitation. This difference was reflected in the peat (Table 3), although the concentration at the site with bird droppings was only a fewfold greater than at the reference site. At sites with bird droppings, peat C:N and C:P ratios were significantly lower, and the potential CO₂ production rate was increased (Table 3). Increased input of N, P, and K by bird droppings significantly affected nutrient concentrations in *Sphagnum* (Table 4). The N:P ratio in *Sphagnum* was significantly lower, and the P:K ratio significantly higher at the site with bird droppings than at the reference site. *Narthecium ossifragum* (L.) Huds. plants were significantly taller and P concentrations, and N:K and P:K ratios

were significantly greater at the site with bird droppings than at the reference sites (Table 5 and Fig. 1c). Foliar N concentrations were unaffected, but K concentrations and N:P ratios were significantly lower at the site with bird droppings.

At Sharavogue bog, the small *Pinus sylvestris* trees of similar age were significantly taller closer to the "mother" tree than at greater distances (Fig. 2a). The lifespan of the needles was significantly longer close to the "mother" tree (Fig. 2b). Overall, the trees were more vigorous closer to the "mother" tree. On Clara bog, transplantation of small *Pinus sylvestris* trees to the immediate vicinity of the wooden posts significantly stimulated the growth of these trees compared with trees transplanted to reference sites (Table 6). The trees growing around the posts were more vigorous (Fig. 3) and the length of the current year's shoots (of the 2002 growing season) was significantly greater, while the needles had a longer lifespan (Table 6). The total height increase of the trees between September 2000 and July 2002 was 13% at the reference sites, compared with 80% around the posts. The length of the current year's shoots in 2002 was 47% smaller than that for 2000 at the reference sites and

Fig. 4. Change in total height (mean \pm 1 SE; $n = 4$) of *Pinus sylvestris* trees between September 2000 and June 2004, 4 years after transplantation to reference sites 2 m from survey posts and to the immediate vicinity of the posts at Clara bog. Results for General Linear Model (GLM) for repeated measures are as follows: $P < 0.01$ for bird-droppings effect, $P < 0.001$ for time effect, and $P < 0.01$ for bird dropping \times time interaction.



201% larger than that for 2000 next to the wooden posts (Table 6). P concentrations measured in the current year's needles (2002) of the *Pinus* trees were significantly increased in the immediate vicinity of the posts, whereas N and K concentrations remained unaffected (Table 6). N:P ratios in the needles were significantly greater at the reference sites.

Discussion

Bird droppings and vegetation composition

Ombrotrophic bogs are oligotrophic ecosystems that are very sensitive to changes in nutrient availability (Aerts et al. 1992; Bobbink et al. 1998). The total N deposition rates in the Irish midlands are below the critical N load for ombrotrophic bogs (0.5–1.0 g·m⁻²·year⁻¹; Bobbink and Roelofs 1995; Risager 1998; Tomassen et al. 2003), and invasion of atypical species such as *Molinia caerulea* and *B. pubescens* has not been observed. By contrast, atypical species were able to grow in the immediate vicinity of wooden survey posts (Fig. 1), whereas characteristic species decreased in amount of cover or even disappeared. The colonizing species include eutrophic species such as *Molinia caerulea*, *Rubus fruticosus*, *Holcus lanatus*, and *Poa annua*. Although the survey posts will influence the air flow regime, thereby affecting the evapotranspiration of plants in the immediate vicinity of the posts, these effects will be trivial compared with the effect of the extremely high input of nutrients by bird droppings (Table 2). The input of nutrients leaching from the wooden posts will be negligible since this is very likely to be a slow process. The development of this fast-growing and dense vegetation limits light availability for *Sphagnum* and lichens (Hayward and Clymo 1983; Heijmans et al. 2001; Limpens et al. 2003). The disappearance of *Sphagnum* mosses and lichens from the bird-dropping sites will lead to higher nutrient concentrations in

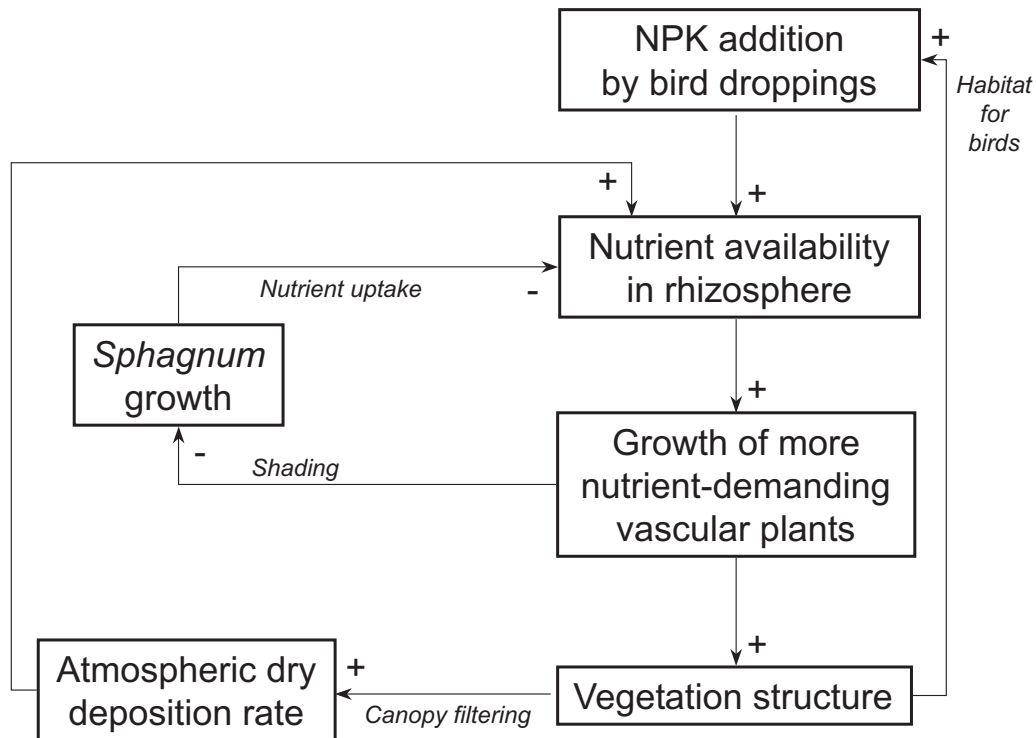
the rhizosphere and stimulate the colonization by atypical species (Lamers et al. 2000; Tomassen et al. 2003; Limpens et al. 2003). At low nutrient availability, *Sphagnum* immobilizes most of the nutrients, leading to relatively low nutrient availability in the rhizosphere of vascular plants (Lamers et al. 2000; Berendse et al. 2001). Increased nutrient input will ultimately lead to higher nutrient availability for (more nutrient-demanding) vascular plants as the *Sphagnum* filter becomes saturated (Lamers et al. 2000). In addition, high nutrient concentrations can be toxic for *Sphagnum* and lichens and retard the growth of these species (Limpens et al. 2003; Tomassen et al. 2004). Summarizing, the lack of *Sphagnum* cover in the vicinity of the posts because of poisoning by bird droppings and competition with vascular plants at elevated nutrient levels, is an important mechanism that has paved the way for atypical plant species. Van der Wal et al. (2004) found that faeces of reindeer (*Rangifer tarandus platyrhynchus*) had cascading effects on tundra ecosystems by promoting grasses while suppressing mosses.

Bird droppings and nutrient limitation in ombrotrophic vegetation

We measured the input of nutrients in the vicinity of the survey posts by collecting bird droppings. Only the input of soluble inorganic N was measured, but even then bird droppings increased the total inorganic N input rate to 18.5 g·m⁻²·year⁻¹. The actual input of N will be much higher since bird droppings contain large amounts of organic N compounds (e.g., urea) and some of the N could have been volatilized. The input rate of inorganic N far exceeds the critical N load for ombrotrophic bogs: 0.5–1.0 g N·m⁻²·year⁻¹ (Bobbink and Roelofs 1995). Above this critical N load, changes in the vegetation composition can be expected, as has been found in the Netherlands, where total N deposition rates are extremely high (approx. 4 g N·m⁻²·year⁻¹; e.g., Tomassen et al. 2003). The sites with bird droppings were characterized by increased availability of all major nutrients, and the top peat layer had significantly higher N, P, and K concentrations (Table 3). Cocks et al. (1999) also found that soils near Snow petrel nests contained high levels of N and P (K was not measured) and that the effects of the bird droppings were no longer noticeable at a distance of 2 m. We also found that the influence of the bird droppings was very local given the large differences in peat nutrient concentrations over a limited distance of only 2 m (Table 2).

Nutrient availability usually limits the activity of decomposing organisms and it seems likely that decomposition processes are stimulated when C:N, C:P, or C:K ratios are low and N, P, or K concentrations are high (e.g., Swift et al. 1979; Updegraff et al. 1995; Smolders et al. 2002). In our study, the potential CO₂ production rate of the peat was greater around the posts, where nutrient concentrations were significantly increased (Table 3). The effects of changes in peat quality on decomposition and nutrient cycling result in stimulated mobilization and availability of nutrients for the vegetation. The NPK fertilization by bird droppings had a remarkable effect on the vegetation near the posts, within a relatively short period (Table 1). Maksimova and Yudina (1999) showed that even much lower NPK fertilization rates (0.5, 1, and 0.75 g·m⁻²·year⁻¹, respectively), applied for 6 years in a Sedge-*Sphagnum* bog, led to rapid changes in the vege-

Fig. 5. Simplified scheme of the effects of bird droppings on ombrotrophic bog vegetation.



tation composition, even 15 years after their application ceased. We need to address that they supplied a relative higher amount of P when compared with the NPK composition of bird droppings (Table 2).

The increased input of nutrients around the posts was also reflected in much higher N, P, and K concentrations in the capitula of *Sphagnum* mosses (Table 4). A stable isotope study in Antarctica showed that bird droppings were a major source of N for the vegetation (Cocks et al. 1998). The tissue N:P ratio exceeded 16, indicating that growth of *Sphagnum* at the reference sites was limited by P and growth at the sites with bird droppings was limited by N (N:P ratio < 14; Koerselman and Meuleman 1996). Limpens et al. (2004) also found that growth of *Sphagnum* in Ireland (Clara bog) is limited by P. Although N deposition rates in Ireland are below the critical N load for ombrotrophic bogs, *Sphagnum* productivity is limited by P. If, however, K is also taken into account, *Sphagnum* growth at the reference sites was co-limited by P and K, while growth at the sites with bird droppings was limited by K alone (a tissue N:K ratio above 1.4 indicates K limitation; Hoosbeek et al. 2002). The P:K ratio was significantly higher at the bird dropping sites, indicating the relative limitation of K compared with P. According to Hoosbeek et al. (2002), *Sphagnum* growth in bogs of north-western Europe is often limited (or co-limited) by K.

Although the vegetation around the posts was frequently dominated by atypical species, *N. ossifragum*, which is a characteristic plant for bogs, was also able to profit from the increased input of nutrients by increasing its length (Fig. 1c and Table 5). The growth rate of *N. ossifragum* on mires in the United Kingdom has been found to be determined by the supply and uptake of phosphate and calcium (Summerfield and Rieley 1975). Based on the N:P ratio we measured, growth of *N. ossifragum* was limited by P at both the refer-

ence and bird dropping sites (Koerselman and Meuleman 1996). A fertilization experiment in southern Sweden showed also that P is a growth-limiting nutrient for *N. ossifragum* (Malmer et al. 2003). At the sites with bird droppings, we measured significantly lower foliar K concentrations, and significantly higher N:K and P:K ratios, indicating that K could be co-limiting growth (Table 5). We must consider, however, that strongly increased growth paired with decreasing nutrient concentrations can indicate a considerable increase in nutrient uptake, although at a lower rate than the rate of biomass accumulation. Tissue nutrient concentrations are therefore not the best measure of the effect of bird droppings because the bird droppings had a strong effect on the biomass (measured as length of the longest leaves) of *N. ossifragum*.

Pine bogs with *Sphagnum* dominance in the bottom layer are widespread, although not in Ireland. Sharavogue bog, however, features small groups of *Pinus sylvestris* trees. The larger trees had several Hooded crow nests and the understorey indicated more eutrophic growth conditions. Tissue nutrient concentrations in the *Sphagnum* growing underneath the *Pinus* trees were higher than those at the reference sites (Table 4). All the smaller trees appeared to have become established in the same year, although their height differed significantly (Fig. 2). Abiotic conditions were obviously more suitable for tree growth closer to the "mother" tree. Although factors such as light and moisture could have affected growth along the transect, these factors were probably of less importance than the increased nutrient availability resulting from bird droppings. A 40-year study in south-central Sweden revealed that vascular plant species, including tree species, increased in frequency probably as a result of increased availability of N and drier conditions (Gunnarsson et al. 2002).

On Clara bog, the trees that had been planted in the immediate vicinity of the survey posts were also able to grow rapidly and appeared very vigorous (Fig. 3*b*). In contrast, the small *Pinus* trees that we planted at the reference sites had very poor growth and yellowish needles (Fig. 3*a* and Table 6). Recent measurements of the height of the *Pinus* trees, 4 years after transplantation, show that the difference in growth rates of *Pinus* at reference sites and in the vicinity of survey posts has become even more pronounced (Fig. 4). Comparing the tissue nutrient concentrations of the current year's needles with the threshold values of nutrient concentrations for nutrient deficiency in *Pinus sylvestris* as given by Houdijk and Roelofs (1993), the P and K concentrations were too low for optimal growth at the reference sites. Around the wooden posts only K seemed suboptimal for growth. Growth of *Pinus sylvestris* on Clara bog was limited by both P and K, whereas growth at the sites with bird droppings was only limited by K, owing to the huge input of P from bird droppings. Finér (1992) also found that the growth of trees on bogs is often limited by P and K, as PK and NPK fertilization increased, the growth of *Pinus sylvestris* growing on an ombrotrophic pine bog. Once established, an increased tree cover can have radical effects on the bog ecosystem (Frankl and Smeidl 2000; Ohlson et al. 2001). *Pinus sylvestris*, for instance, is capable of creating and maintaining a fundamentally different environment in bogs, and inevitably brings an end to *Sphagnum* dominance by altering local hydrological conditions and increasing the accumulation of litter (Frankl and Smeidl 2000; Ohlson et al. 2001).

Effect of bird droppings on ombrotrophic bogs

Based on our results, we conclude that non-characteristic herbs and trees are only able to grow on ombrotrophic bogs if nutrient availability, especially that of P and K, is sufficiently high. Sites on bogs characterized by increased nutrient availability include the so-called flushes or soak systems (Kelly 1993), but also sites eutrophicated by the presence of birds. Avian communities of typical open raised bogs are generally poor in species. Increased structural complexity of the vegetation, particularly in terms of the vertical component, increases the plant density, and thus, increases foraging and nesting opportunities for birds (Bölscher 1995). On Clara bog, the plants that most notably affected the increase in structural complexity were *Molinia caerulea*, *Myrica gale*, *J. effusus*, *R. fruticosus*, *B. pubescens*, and *Pinus sylvestris*, but the wooden survey posts were also proven to attract birds. The major increase in nutrient availability from bird droppings allowed these plant species in particular to grow on the bogs. This increase in vegetation structure provides birds with foraging and nesting opportunities, which leads to greater densities of birds and a further increase in nutrient availability (Fig. 5). We assume that this is a self-enhancing process that may even result in small patches of bog forest in the long term.

In addition, the increased structure of the vegetation results in more efficient filtering of dry atmospheric deposition, and thus increases the total nutrient deposition rate (e.g., Ivens 1990). Increased canopy density can also intercept larger amounts of rainfall and reduce the amount of water reaching the peat surface (Tomassen 2004). Since most

Irish bogs suffer from the effects of water table draw-down as a result of small-scale peat extraction and the presence of drainage ditches, reduced water input from precipitation may enhance the water shortage for ombrotrophic vegetation. In *Sphagnum* suffering from water stress, gas exchange is suppressed, resulting in reduced photosynthetic rates and growth (Hayward and Clymo 1983; Schipperges and Rydin 1998), reduced immobilization of nutrients by the *Sphagnum* layer (Aldous 2002), and increased availability of nutrients for vascular plants. All these processes will ultimately stimulate the growth of atypical grasses and trees and are disastrous for characteristic ombrotrophic species. Cascading effect of nutrient subsidies have also been found for tundra ecosystems, where faeces of reindeer promoted grasses while suppressing mosses (Van der Wal et al. 2004).

We conclude that once a tree has become established on a bog, it can have significant effects on the vegetation composition in its direct vicinity because of bird droppings. Bird droppings may have a large impact on the vegetation composition, organic matter decomposition, and structure of ombrotrophic bogs, which may even result in the development of small patches of bog forest. For treeless bogs, such as Clara bog, these small patches of bog forest will largely affect the typical open landscape.

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