

Boreal bog *Sphagnum* refixes soil-produced and respired $^{14}\text{CO}_2$ ¹

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Abstract: Research on peatland C cycling has generally ignored refixation, *i.e.*, the photosynthetic fixation of soil-produced or respired CO_2 . We quantified refixation in a boreal bog by transplanting groups of living nonradioactive *Sphagnum fuscum* (5 cm length, 4 cm diameter) into N-, P-, and S-fertilized field plots that had been radioactively labeled by exposure to $^{14}\text{CO}_2$, and analyzing transplants retrieved at 2, 30, and 90 days post-labeling for ^{14}C activity. *Sphagnum* transplanted into plots that received both N and S had greater refixed ^{14}C activities (Bq g^{-1}) than control plot transplants. *Sphagnum capitulum* (top 1 cm), 1-2 cm, and 2-5 cm sections behaved similarly, with the capitula having the highest refixed ^{14}C activity and the 2-5 cm section having the lowest; differences between sections became more accentuated over time. Extrapolated to a m^2 basis, transplanted *Sphagnum* refixed 3.5-5.4% of the total ^{14}C initially incorporated into the living vegetation and top 10 cm of peat during labeling. Refixation may be an important pathway for C cycling within peatlands, potentially capturing significant proportions of peat-produced or respired CO_2 before it escapes to the atmosphere.

Keywords: *Sphagnum*, refixation, peatlands, carbon cycling, ^{14}C , carbon dioxide.

Résumé : La recherche sur le cycle du carbone dans les tourbières ignore généralement la refixation, c'est-à-dire, la fixation photosynthétique du CO_2 produit par le sol ou respiré. Nous avons quantifié la refixation dans une tourbière ombrotrophe en milieu boréal en transplantant des groupes de *Sphagnum fuscum* vivants et non-radioactifs (5 cm de long par 4 cm de diamètre) dans des parcelles fertilisées (N, P et S) marquées préalablement par une exposition au $^{14}\text{CO}_2$. Les transplants ont été récoltés 2, 30 et 90 jours après le marquage au ^{14}C . Les sphaignes transplantées dans les parcelles qui ont reçu à la fois de l'azote et du soufre ont montré une plus grande activité de refixation du ^{14}C (Bq g^{-1}) que les transplants situés dans les parcelles témoins. Les capitules de sphaigne (premier cm), les sections 1 à 2 cm et les sections 2 à 5 cm se sont comportés de la même façon, les capitules ayant les plus hauts taux d'activité de refixation du ^{14}C et les sections 2 à 5 cm les plus faibles. Les différences entre les sections se sont accentuées avec le temps. En extrapolant au m^2 , les sphaignes transplantées ont refixé de 3,5 à 5,4 % du ^{14}C total initialement incorporé dans la végétation, ainsi que dans les 10 premiers cm de tourbe. La refixation pourrait être une voie importante du cycle du carbone dans les tourbières, pouvant potentiellement capturer des proportions significatives du CO_2 produit par la tourbe accumulée ou respirée, avant qu'il ne s'échappe dans l'atmosphère.

Mots-clés : *Sphagnum*, refixation, tourbières, recyclage du carbone, ^{14}C , gaz carbonique.

Introduction

Through refixation, *i.e.*, photosynthetic fixation of soil-produced or respired CO_2 , terrestrial systems capture a fraction of total ecosystem respiration before that respired CO_2 escapes to the atmosphere. Refixation occurs in tropical (Medina & Minchin, 1980; Sternberg, Mulkey & Wright, 1989), temperate (Vogel, 1978; Schleser & Jayasekera, 1985), and boreal forests (Brooks *et al.*, 1997), but its importance to total photosynthetic CO_2 uptake is variable. This variability may be partially attributed to different methods for estimating refixation, including measurements of vertical gradients in $\delta^{13}\text{CO}_2$ and in leaf $\delta^{13}\text{C}$ ratios (Sternberg, Mulkey & Wright, 1989; Sternberg, 1997), and models based on fluxes of CO_2 and $^{13}\text{CO}_2$ between the soil surface and forest canopies (Lloyd *et al.*, 1996; 1997).

Our interest in refixation focuses on the nearly continuous, photosynthetic moss layer of boreal peatlands, from a carbon cycling and global change perspective. Peatlands store about one-third of the world's soil carbon, yet this massive soil carbon pool may become increasingly vulnerable to

decomposition with global climate change (Gorham, 1991; 1994; 1995; Malmer, 1992). Predicting how peatland carbon cycling may respond to climate change requires an understanding of the balance between CO_2 fixation and gaseous carbon releases (Gorham, 1995). In a laboratory ^{14}C tracer study, Rydin & Clymo (1989) reported that approximately 8% of the ^{14}C initially incorporated into *Sphagnum* was transferred to neighboring, unlabeled *Sphagnum* plants in a four week period. Comparing records of atmospheric ^{14}C activity from 1955 to 1985 with peaks in ^{14}C concentrations measured in peat profiles resulting from nuclear weapons testing, Tolonen *et al.* (1993) estimated that approximately 20% of CO_2 emitted from deep peat was refixed into living *Sphagnum*. Refixation in peatlands, however, has not been tested directly in a field setting. Here, using field ^{14}C -labeling techniques, we directly demonstrate refixation in the *Sphagnum* moss layer in N-, P-, and S-fertilized plots of a boreal peatland.

Material and methods

Bleak Lake Bog (54° 41' N; 113° 28' W), an ombrotrophic forested bog located in central Alberta, is dominated by a *Sphagnum* moss canopy with a mixture of shrubs and trees,

¹Rec. 1999-01-04; acc. 1999-05-10.

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including *Ledum groenlandicum*, *Vaccinium oxycoccus*, *Smilacina trifolia*, *Rubus chamaemorus*, and *Picea mariana*. Bleak Lake Bog is situated within the boreal zone; total annual precipitation is 490 mm, whereas mean annual temperature and the frost-free period average 1.4°C and 118 days, respectively. Peat depth is about 5 m, with dry bulk density measurements of approximately 0.04 g cm⁻³ throughout the top 170 cm of peat. Surface water pH at Bleak Lake Bog is 3.9, base cation concentrations are low (Ca²⁺ · 91 µmol L⁻¹; Mg²⁺ · 87 µmol L⁻¹; Na⁺ · 138 µmol L⁻¹; K⁺ · 17 µmol L⁻¹). Interstitial water pH values increase with peat depth, suggesting that minerotrophic groundwater may affect water chemistry below 1 m in the peat profile (Vitt, Bayley & Jin, 1995).

Our study was conducted in the plots of a peatland nutrient amendment study (Jendro, 1998), in which 24 1-m² treeless plots were assigned to one of eight nutrient addition treatments: control (no added N, S, or P), medium N (dose equivalent to an atmospheric deposition of 44 mmol m⁻² yr⁻¹), medium S (40 mmol m⁻² yr⁻¹), medium N plus medium S, high N (88 mmol m⁻² yr⁻¹), high S (80 mmol m⁻² yr⁻¹), high N plus high S, and P (420 µmol m⁻² yr⁻¹). Nitrogen, S, and P were added as NH₄NO₃, Na₂SO₄, and NaH₂PO₄·H₂O, respectively, dissolved in 12 L of bog water. Field applications (12 L of the solutions per plot) were made at about three week intervals from May 15 through September 15, 1996. On June 30, 1996, after three nutrient applications, vegetation in each 1-m² plot was ¹⁴C-labeled by a single day's exposure to 3.7 MBq of ¹⁴CO₂ (Wieder & Yavitt, 1994). On the day following ¹⁴C-labeling, incorporation of ¹⁴C into vegetation and peat to a depth of 10 cm averaged 1.1 × MBq m⁻², based on the collection of one 10 cm diameter, intact peat core from each plot (Jendro, 1998). Of this total, 60% was in the living *Sphagnum* or below, with the remainder in aboveground vascular tissues (Jendro, 1998). On the day following ¹⁴C-labeling, small intact clumps of nonradioactive, Bleak Lake Bog *S. fuscum* (5 cm tall, ~ 4 cm diameter) were removed from locations at least 10 m away from the labeled plot area. Ten of these nonradioactive clumps were transplanted into each of the 24 ¹⁴C-labeled plots with the *Sphagnum* capitula (top 1 cm) at the same level as the native *Sphagnum* capitulum canopy.

After 2, 30, and 90 days, three replicate transplanted clumps were collected from each plot. The intact *Sphagnum* plants of each clump were sectioned into the capitulum, the 1 cm immediately beneath, and the remaining approximate 3 cm of the plants. Plant material from each depth section in each clump was dried, weighed and homogenized by manual grinding. Subsamples of 50-100 mg were combusted in a pure O₂ atmosphere in 500 mL Schöniger combustion flasks containing 50 mL of 0.5 M NaOH. After a two hour exposure period to allow for passive uptake of the ¹⁴CO₂ by the NaOH solution, ¹⁴C activity was quantified in three replicate 1 mL aliquots of the NaOH solution (in 10 mL of Scint-BD scintillation cocktail) on a Packard Tricarb 2000 liquid scintillation counter.

The effects of nutrient amendment (N, P, S additions), *Sphagnum* depth section (0-1 cm, 1-2 cm, 2-5 cm), and incubation period (2, 30, 90 days) on ¹⁴C refixation (¹⁴C activity in the plant material expressed as Bq g⁻¹) in transplanted *Sphagnum* were analyzed by a factorial 8 (nutrient

amendments) × 3 (*Sphagnum* depth sections) × 3 (incubation periods) analysis of covariance, with initial kBq/plot as the covariate to adjust for between-plot differences in initial total ¹⁴C inventories (on the day following ¹⁴C-labeling) in aboveground vegetation plus peat to a depth of 10 cm in each plot (SAS, 1990).

For each transplanted *Sphagnum* clump, capitulum ¹⁴C activity was multiplied by the mean capitulum dry bulk density (0.0388 ± 0.0023 g cm⁻³), whereas the ¹⁴C activities for the 1-2 cm and the 2-5 cm sections of each transplanted *Sphagnum* clump were multiplied by their mean bulk density (0.025 ± 0.0016 g cm⁻³) to extrapolate ¹⁴C refixation to a plot (m²) basis. *Sphagnum* bulk densities had been measured by Jendro (1998) in intact peat cores collected in each ¹⁴C-labeled plot using 10 cm diameter, 40-cm long PVC pipes. Refixation on a m² basis was divided by the initial (day after labeling) ¹⁴C inventory in aboveground vegetation plus peat to a depth of 10 cm in each plot. Resulting ¹⁴C data (expressed as a percentage of the total ¹⁴C initially present in each plot on the day after labeling) were arcsin-square root transformed and then analyzed by a factorial 8 (nutrient amendments) × 3 (incubation periods) analysis of variance (SAS, 1990).

Results

Nutrient amendment (N, S, P addition) had a significant effect on refixed ¹⁴C activity (expressed as Bq g⁻¹) in transplanted *Sphagnum*; none of the nutrient treatment interaction terms was significant (Table Ia). Only plants treated with both N and S, at either the high or medium dose, had a greater refixed ¹⁴C activity than plants in control plots (Figure 1a). Refixed ¹⁴C activity in transplanted *Sphagnum* plants also differed according to a depth section (0-1 cm,

TABLE I. a) Analysis of covariance assessing the effects of nutrient amendment (N, P, S additions), incubation period (2, 30, 90 days), and *Sphagnum* depth section (0-1 cm, 1-2 cm, 2-5 cm) on refixed ¹⁴C activity (expressed as kBq g⁻¹) in transplanted *Sphagnum*. The covariate is the total ¹⁴C initially present in each plot (kBq m⁻²) on the day after labeling. b) Analysis of variance assessing the effects of nutrient amendment and incubation period on refixation (expressed as a percentage of the total ¹⁴C initially present in each plot on the day following labeling); the analysis was performed on arcsin-square-root-transformed percentages

Source	df	Sum of squares	F	P
a) ANALYSIS OF COVARIANCE				
Model	72	1928.4	2.37	0.0001
Nutrient amendment	7	3033.2	3.73	0.0006
Incubation period	2	1741.5	2.14	0.1183
<i>Sphagnum</i> depth section	2	28840.1	35.48	0.0001
Nutrient × Incubation	14	948.5	1.17	0.2969
Nutrient × Depth section	14	856.2	1.05	0.3981
Incubation × Depth section	4	2936.8	3.61	0.0064
Nutrient × Depth section × Incubation	28	459.3	0.57	0.9664
Initial kBq per plot (covariate)	1	2863.6	3.52	0.0610
Error	573	812.9		
b) ANALYSIS OF VARIANCE				
Model	23	0.0077	1.24	0.2188
Nutrient amendment	7	0.0943	2.17	0.0384
Incubation period	2	0.0255	2.06	0.1307
Nutrient × Incubation	14	0.0565	0.65	0.8196
Error	189	0.0062		

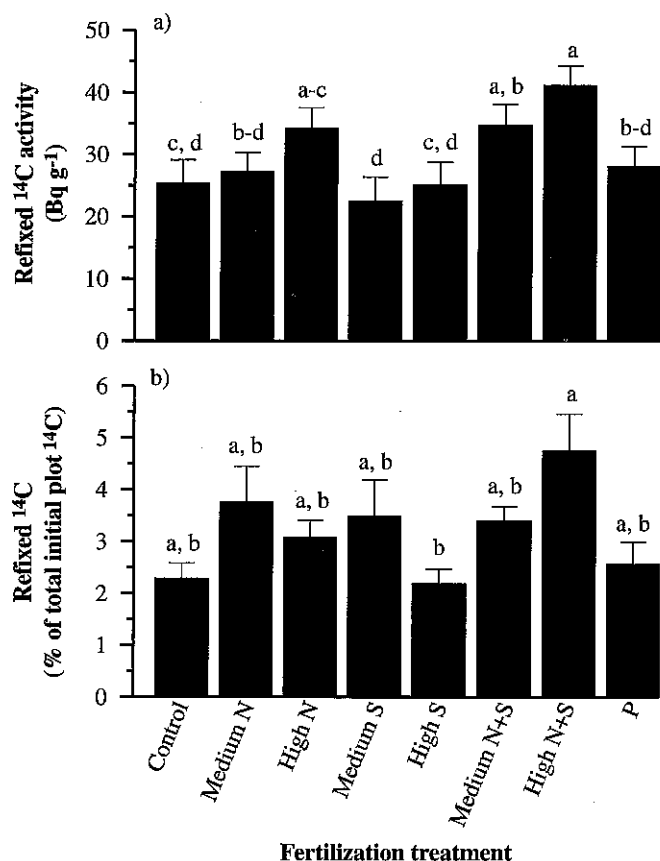


FIGURE 1. Refixed ¹⁴C under the eight nutrient amendments. a) Plotted values (expressed as Bq g⁻¹) are least squares means (corrected for the covariate, ± standard error, n = 81) averaged over all *Sphagnum* depth sections and all incubation periods. Means with the same letter superscript do not differ significantly (analysis of covariance, Table 1a, *a posteriori* *t*-tests). b) Plotted values (expressed as percentage of the total ¹⁴C initially present in each plot on the day after labeling) are means (± standard error, n = 27), averaged over all incubation periods and *Sphagnum* depth sections. Means with the same letter superscript do not differ significantly (analysis of variance, Table 1b, *a posteriori* Bonferroni tests).

1-2 cm, 2-5 cm) × incubation period (2, 30, 90 days) interaction, which was consistent across all treatments (nonsignificant depth section × incubation date × nutrient amendment term in the analysis of covariance; Table 1a). Qualitatively the capitula (0-1 cm), 1-2 cm, and 2-5 cm sections behaved similarly over time, with the capitula having the highest refixed ¹⁴C activity and the 2-5 cm section having the lowest (Figure 2). However, differences in the refixed ¹⁴C activities between sections on each incubation period became more accentuated over time (Figure 2). When expressed as a percentage of the total ¹⁴C initially present in each plot on the day after labeling, refixation was not affected by incubation period (Table 1b). Refixation was affected by nutrient amendment, although none of the treatment means differed significantly from the control mean (Table 1b, Figure 1b).

Discussion

When unlabeled *S. fuscum* plants were transplanted into ¹⁴C-labeled field plots they became radioactive (Figure 1), unambiguously demonstrating that refixation occurs within

the dense, nearly continuous *S. fuscum* cover typical of boreal bogs. Our data reveal that the major site for photosynthesis in *Sphagnum* is the capitulum (0-1 cm). Similarly, Rydin & Clymo (1989), in their laboratory ¹⁴C-labeling study, reported that the highest amounts of ¹⁴C were transferred from labeled *Sphagnum* to the capitula of neighboring, unlabeled *Sphagnum* plants. Increasing capitulum ¹⁴C activity over time (Figure 2) may reflect continuing refixation in these compact structures. As a consequence, decreasing ¹⁴C activity in the 2-5 cm sections of the transplanted *Sphagnum* may reflect an increasingly tenuous carbon balance of these shaded plant tissues, potentially accentuated by the small amount of vertical growth of the living *Sphagnum* that may have occurred during the 90-day study period. Lateral transfer of soluble ¹⁴C-labeled organic compounds to our transplanted plants remains possible; however, we feel this is extremely unlikely to occur at the bog surface, well above the water table.

From an ecosystem perspective, it is more meaningful to consider refixation on an aerial basis. We estimated that, on average, 3.2% of the total ¹⁴C initially incorporated into the living vegetation and top 10 cm of peat during labeling would have been refixed into a uniform 1 m² carpet of

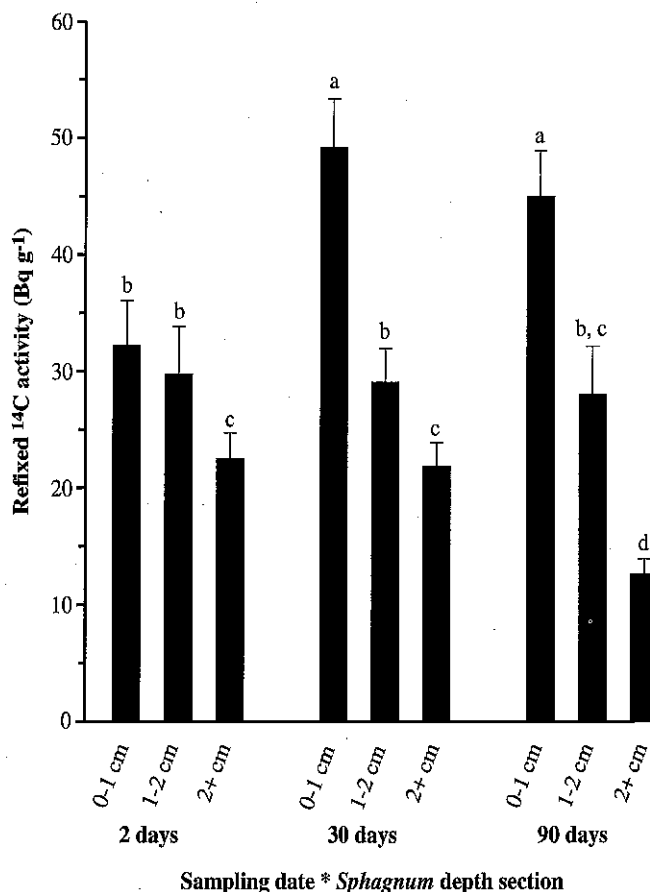


FIGURE 2. Interaction of incubation period and *Sphagnum* depth section on refixed ¹⁴C activity (expressed as Bq g⁻¹). Least squares means (corrected for the covariate; Table 1a) ± standard error, n=72, averaged over all eight fertilization treatments. Means with the same letter superscript do not differ significantly (analysis of covariance, see Figure 1a, *a posteriori* *t*-tests).

transplanted *Sphagnum* plants. When peatland vegetation has been ^{14}C -pulse-labeled, on the day following exposure, ^{14}C is recovered in both aboveground plant tissues and in belowground peat and roots (Wieder & Yavitt, 1994; Jendro, 1998). It seems unlikely, however, that $^{14}\text{CO}_2$ released from respiring aboveground vascular plant leaves and stems would be refixed by the underlying *Sphagnum* layer, at least over the 90-day period, as the diffusion gradient for respired $^{14}\text{CO}_2$ in the immediate vicinity of the *Sphagnum* capitula should be upward. Taking this into consideration, we estimate that 5.4% of the total ^{14}C initially incorporated into the plots from the top of the living *Sphagnum* downward 10 cm (*i.e.*, excluding ^{14}C incorporated into aboveground vascular plant tissues during labeling from each plot's initial total ^{14}C inventory) would have been refixed into a uniform 1 m^2 carpet of transplanted *Sphagnum* plants.

Below the capitulum canopy, CO_2 produced via living *Sphagnum* respiration, vascular plant root respiration, or soil microbial respiration all are potential sources of refixed ^{14}C . We are unable to differentiate between these three potential contributors. Nonetheless, our results demonstrate that refixation by *Sphagnum* occurs in the field and represents a previously unquantified pathway for carbon cycling within peatlands, potentially functioning to capture substantial proportions of soil-produced or respired CO_2 before it escapes to the atmosphere.

Nutrient amendments did not have dramatic effects on refixation. Only the medium N+S and the high N+S treatment *Sphagnum* transplants had significantly greater refixed ^{14}C activity (Bq g^{-1}) than control plants (Figure 1a). Increasing either N or S alone did not significantly affect refixation. The combined N and S fertilization may stimulate refixation in *Sphagnum*, if N deposition enhances photosynthesis and thereby $^{14}\text{CO}_2$ fixation (Rocheffort, Vitt & Bayley, 1990; Baxter, Ehmes & Lee, 1992; Li & Vitt, 1997) and if simultaneously, S deposition enhances carbon mineralization through sulfate reduction (Wieder, Yavitt & Lang, 1990; Nedwell & Watson, 1995), thereby increasing the quantity of $^{14}\text{CO}_2$ available for refixation. It is possible that without an accelerated photosynthetic ^{14}C fixation associated with N deposition, *Sphagnum* plants might not be able to refix much of the additionally available ^{14}C coming from enhanced sulfate reduction. Under such a scenario, an effect on refixation would result only when combining N and S deposition; neither treatment alone would be sufficient. We note, however, that when expressed as a percentage of the total ^{14}C initially present in each plot on the day after labeling, refixation in control *Sphagnum* transplants was not different from refixation in any of the fertilized treatment *Sphagnum* transplants (Figure 1b).

Refixation has implications for the application of ^{13}C techniques in peatlands. In the field, refixation of isotopically light (compared to bulk peat) soil-produced or respired CO_2 certainly could influence $\delta^{13}\text{C}$ ratios in photosynthesizing *Sphagnum* (Proctor, Raven & Rice, 1992; Rice & Giles, 1996). Slight decreases in $\delta^{13}\text{C}$ ratios of bulk peat approaching the peat surface from below (Wieder & Yavitt, 1994) could result both from isotopic fractionation during carbon mineralization and from refixation of upwardly diffusing, isotopically light $^{13}\text{CO}_2$.

Signals present in $\delta^{13}\text{C}$ ratios of sedges and mosses in peat have been proposed as tools for long-term reconstructions of atmospheric CO_2 concentrations (White *et al.*, 1994). This approach assumes that the $\delta^{13}\text{C}$ ratios of mosses depend on atmospheric CO_2 concentration and available water only. Failure to consider refixation of isotopically light CO_2 as a process that could influence moss $\delta^{13}\text{C}$ ratios may represent an important, unrecognized source of error in these long-term reconstructions, especially if refixation turns out to be substantial in the surface *Sphagnum* layer of peatlands across broad geographic and climatic regimes.

Acknowledgements

We thank S. Bridgman, J. Doubt, L. Halsey, P. Hughes, J. Jendro, and M. Vile for field assistance, the Meanook Biological Research Station staff for their support, and R. Bryant for access to Bleak Lake Bog. We also acknowledge R. Clymo, E. Gorham, J. Janssens, D. Vitt, J. Waddington, C. Williams, and other reviewers for their thoughtful comments on the research and on previous versions of this manuscript. This research was supported by a grant from the National Science Foundation (DEB-9408043) to R. K. Wieder and J. Yavitt (Villanova and Cornell Universities), the Howard Hughes Medical Institute, and the Department of Biology at Villanova University.

Literature cited

- Baxter, R., M. J. Ehmes & J. A. Lee, 1992. Effects of an experimentally applied increase in ammonium on growth and amino acid metabolism of *Sphagnum cuspidatum* Ehrh. ex. Hoffm. from differently polluted areas. *New Phytologist*, 120: 265-274.
- Brooks, J. R., L. B. Flanagan, G. T. Varney & J. R. Ehleringer, 1997. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO_2 within boreal forest canopies. *Tree Physiology*, 17: 1-12.
- Gorham, E., 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, 1: 182-195.
- Gorham, E., 1994. The future of research in Canadian peatlands: A brief survey with particular reference to global change. *Wetlands*, 14: 206-215.
- Gorham, E., 1995. The biogeochemistry of northern peatlands and its possible responses to global warming. Pages 169-187 in G. M. Woodwell & F. T. Mackenzie (ed.). *Biotic Feedbacks in the Global Climatic System: Will the Warming Feed the Warming?* Oxford University Press, New York.
- Jendro, J., 1998. Effects of anthropogenically deposited nitrogen and sulfur on short-term carbon balance in a boreal ombrotrophic bog. M.Sc. Thesis. Department of Biology, Villanova University, Villanova, Pennsylvania.
- Li, Y. & D. H. Vitt, 1997. Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. *Écoscience*, 4: 106-116.
- Lloyd, J., B. Kruijt, D. Y. Hollinger, J. Grace, R. J. Francey, S.-C. Wong, F. M. Keliher, A. C. Miranda, G. D. Farquhar, J. H. C. Gash, N. N. Vygodskaya, I. R. Wright, H. S. Miranda & E.-D. Schulze, 1996. Vegetation effects on the isotopic composition of atmospheric CO_2 at local and regional scales: Theoretical aspects and a comparison between rain forest in Amazonia and a boreal forest in Siberia. *Australian Journal of Plant Physiology*, 23: 371-399.

- Lloyd, J., B. Kruijt, D. Y. Hollinger, J. Grace, R. J. Francey, S.-C. Wong, F. M. Keliher, A. C. Miranda, G. D. Farquhar, J. H. C. Gash, N. N. Vygodskaya, I. R. Wright, H. S. Miranda & E.-D. Schulze, 1997. An alternative interpretation of the appropriateness and correct means for the evaluation of CO₂ recycling indices. *Australian Journal of Plant Physiology*, 24: 399-405.
- Malmer, N., 1992. Peat accumulation and the global carbon cycle. *Catena Supplement*, 22: 97-110.
- Medina, A. & P. Minchin, 1980. Stratification of $\delta^{13}\text{C}$ values of leaves in Amazonian rain forests. *Oecologia*, 45: 377-378.
- Nedwell, D. B. & A. Watson, 1995. CH₄ production, oxidation and emission in a U.K. ombrotrophic peat bog: Influence of SO₄²⁻ from acid rain. *Soil Biology & Biochemistry*, 27: 893-903.
- Proctor, M. C.F., J. A. Raven & S. K. Rice, 1992. Stable carbon isotope discrimination measurements in *Sphagnum* and other bryophytes: Physiological and ecological implications. *Journal of Bryology*, 17: 193-202.
- Rice, S. K. & L. Giles, 1996. The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnum*. *Plant, Cell and Environment*, 19: 118-124.
- Rochefort, L., D. H. Vitt & S. E. Bayley, 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology*, 71: 1986-2000.
- Rydin, H. & R. S. Clymo, 1989. Transport of carbon and phosphorus compounds about *Sphagnum*. *Proceedings of the Royal Society of London*, 237: 63-84.
- SAS, 1990. SAS/STAT User's Guide, Version 6, Fourth Edition. SAS Institute, Inc., Cary, North Carolina.
- Schleser, G. H. & R. Jayasekera, 1985. $\delta^{13}\text{C}$ variations of leaves in forests as an indication of reassimilated CO₂ from the soil. *Oecologia*, 65: 516-542.
- Sternberg, L., 1997. Interpretation of recycling indexes. *Australian Journal of Plant Physiology*, 24: 395-398.
- Sternberg, L., S. S. Mulkey & S. J. Wright, 1989. Ecological interpretation of leaf carbon isotope ratios: Influence of respired carbon dioxide. *Ecology*, 70: 1317-1324.
- Tolonen, K., G. Possnert, H. Jungner, E. Sonninen & J. Alm. 1993. High resolution ¹⁴C dating of surface peat using the AMS technique. *SUO*, 43: 271-275.
- Vitt, D. H., S. E. Bayley & T.-L. Jin, 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 587-606.
- Vogel, G. C., 1978. Recycling of carbon in a forest environment. *Oecologia Plantarum*, 13: 89-94.
- White, J. W. C., P. Clais, R. A. Figge, R. Kenny & V. Markgraf, 1994. A high-resolution record of atmospheric CO₂ content from carbon isotopes in peat. *Nature*, 367: 153-156.
- Wieder, R. K. & J. B. Yavitt, 1994. Peatlands and global climate change: Insights from comparative studies of sites situated along a latitudinal gradient. *Wetlands*, 14: 229-238.
- Wieder, R. K., J. B. Yavitt & G. E. Lang, 1990. Methane production and sulfate reduction in two Appalachian peatlands. *Biogeochemistry*, 10: 81-104.

