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Response of *Sphagnum fuscum* to Nitrogen Deposition: A Case Study of Ombrogenous Peatlands in Alberta, Canada

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Abstract. *Peatlands cover about 30% of northeastern Alberta and are ecosystems that are sensitive to nitrogen deposition. In polluted areas of the UK, high atmospheric N deposition (as a component of acid deposition) has been considered among the causes of* Sphagnum *decline in bogs (ombrogenous peatlands). In relatively unpolluted areas of western Canada and northern Sweden, short-term experimental studies have shown that* Sphagnum *responds quickly to nutrient loading, with uptake and retention of nitrogen and increased production. Here we examine the response of* Sphagnum fuscum *to enhanced nitrogen deposition generated during 34 years of oil sands mining through the determination of net primary production (NPP) and nitrogen concentrations in the upper peat column. We chose six continental bogs receiving differing atmospheric nitrogen loads (modeled using a CALPUFF 2D dispersion model).* Sphagnum fuscum *net primary production (NPP) at the high deposition site (Steepbank—mean of 600 g/m²; median of 486 g/m²) was over three times as high than at five other sites with lower N deposition. Additionally, production of* S. fuscum *may be influenced to some extent by distance of the moss surface from the water table. Across all sites, peat nitrogen concentrations are highest at the surface, decreasing in the top 3 cm with no significant change with increasing depth. We conclude that elevated N deposition at the Steepbank site has enhanced* Sphagnum *production. Increased N concentrations are evident only in the top 1-cm of the peat profile. Thus, 34 years after mine startup, increased N-deposition has increased net primary production of* Sphagnum fuscum *without causing elevated levels of nitrogen in the organic matter profile. A response to N-stress for* Sphagnum fuscum *is proposed at 14–34 kg ha^{-1} yr^{-1}. A review of N-deposition values reveals a critical N-deposition value of between 14.8 and 15.7 kg ha^{-1} yr^{-1} for NPP of* Sphagnum *species.*

Peatlands are moss-dominated systems that represent an important component of the boreal forest, comprising 31% of the Central Mixedwood Subregion of northeastern Alberta (Vitt et al. 1996). Peatlands are subdivided into two major types; bogs that are ombrogenous and receive surface moisture and mineral deposition solely from the atmosphere, and fens that are geogenous with deposition from both the atmosphere and ground and/or surface waters (reviewed in Vitt 1994). The groundcover of these systems is dominated by a continuous mat of mosses (National Wetlands Working Group 1988; Vitt 1990) that have narrow tolerances to a wide suite of chemical and physical parameters (Gignac et al. 1991; Vitt & Chee 1990). Changes in species response and dominance are evident over relatively small areas (10's of cm) (Vitt et al. 1975). Bogs and poor fens are *Sphagnum*-dominated and presently occur over much of northern North America (Halsey et al. 2000), whereas rich fens are brown moss-dominated. The relatively high and stable water tables found in peatlands and the resistance of moss material to decay promotes the accumulation of peat through reduced decomposition with a large percentage of the accumulated peat composed of the moss component (Kuhry & Vitt 1996). As peatlands accumulate organic matter they act as repositories of ecological function and change (Wieder et al. 2003).

Nitrogen deposition associated with western Ca-

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nadian oil sands activity may impact peatland vegetation and ecosystem function (Turchenek et al. 1998). In polluted areas of the UK, high atmospheric N deposition has been considered a major cause for *Sphagnum* decline in bogs (Press et al. 1986; Woodin et al. 1985). In unpolluted areas of western Canada and northern Sweden, short-term experimental studies have demonstrated that *Sphagnum* responds quickly to nutrient loading, with the uptake and retention of much of the deposited N leading to increased production (Aerts et al. 1992*b*; Bayley et al. 1987; Li & Vitt 1997). However, in a 4-year fertilization study in unpolluted northern Sweden, a stimulation of *Sphagnum* production was not observed (Aerts et al. 2001). While high atmospheric N deposition can stimulate productivity in areas where N is limiting, in ecosystems where nitrogen saturation is attained both a negative effect and no effect on production have been reported (Aerts et al. 1992, 2001; Austin & Wieder 1987; Gunnarsson & Rydin 2000). However, additional factors may also affect *Sphagnum* production and interact with nitrogen deposition. In particular, bryophytes are known to respond to water table position (Gignac et al. 1991) and height of the peatland surface above the water level also can influence production (Thormann & Bayley 1997*a,b*).

As attempts to understand the ecological effects of acid rain (that include N effects) in North America have largely concentrated on aquatic and upland ecosystems, uncertainty remains as to the impact it has on peatland ecosystems (Gorham et al. 1983). For example, oceanic peatlands in the United Kingdom are substantially different from their continental counterparts. Oceanic bogs are located in areas of high rainfall that impacts these peatlands year round. These bogs are treeless and contain a distinct ground flora. These systems contrast to continental bogs that are exposed to a much lower frequency of rainfall that impacts peatlands only during the growing season and where yearly precipitation values are substantially lower than those of oceanic regions. Continental bogs always have tree cover and have a different ground flora. Dry acid deposition coupled with interception by tree cover could significantly decrease the amount of acid deposition reaching the ground layer. Experimental studies that simulate wet acid deposition below the canopy cover (Li & Vitt 1997; Raeymaekers & Glime 1986; Rochefort et al. 1990; Rochefort & Vitt 1988) are rare in continental areas.

In order to develop bioindicators for determining critical loads for the province of Alberta, we examined effects of 34 years of increased nitrogen deposition emanating from the oil sands mining development on *Sphagnum fuscum*. *Sphagnum fuscum* dominates continental ombrogenous peatlands (bogs). It is generally the most abundant ground layer species, has relatively high production values, high biomass, and contributes significantly to organic matter accumulation. *Sphagnum fuscum* is considered to be a keystone species of continental bogs. Here we use this species to evaluate responses to nitrogen deposition using two indicators: 1) net primary production, and 2) nitrogen concentration and accumulation in the top 25 cm of the *S. fuscum* peat profile.

METHODS

Nitrogen deposition and site selection.—To quantify the impacts of N-deposition on *Sphagnum fuscum* production and nitrogen concentration in the upper peat profile, six sites were chosen in northeastern Alberta (Fig. 1, Table 1). In 1996–1997, using a CALPUFF 2D dispersion model, NO_3^--N deposition ranged from between 1.13–2.26 kg ha^{-1} yr^{-1} at Steepbank Bog, 0.45–1.13 kg ha^{-1} yr^{-1} at Thickwood Bog, and 0.23–0.45 kg ha^{-1} yr^{-1} at the Anzac Bog sites (Conor Pacific 1998). In 2002, using a baseline of current and approved developments, a CALPUFF 3D dispersion model (Golder 2002) predicted Steepbank Bog to have a modeled NO_3^--N deposition rate of 4.04 kg ha^{-1} yr^{-1} and our other five sites (Anzac East Bog, Anzac West Bog, Bleak Lake Bog, Thickwood Hills Bog, and Wandering River Bog—Fig. 1) to have NO_3^--N deposition rates ranging from 0.07–0.47 kg ha^{-1} yr^{-1}. Since the baseline for this 2002 CALPUFF 3D model-run included existing as well as approved developments, it is an overestimate of nitrate deposition at the Steepbank locality. Modeled NOx emissions (expressed as NO_2) within the oil sands area have increased from 23.4 t/cd [tonnes per calender day] (1970–1979), to 43.0 t/cd (1980–1989) to 59.9 t/cd (1990–1999) to 124.0 t/cd in 2000–2002, and are predicted to increase to around 300 t/cd in the next decade (Golder 2002). Increases in N-emissions in the 1990's and early 2000's are largely due to a shift in mine operations from conveyor belt systems to truck and shovel that utilizes a diesel fleet.

All six sites are continental bogs and dominated by a tree layer of *Picea mariana*, a shrub layer of either *Ledum groenlandicum* or *Chamaedaphne calyculata*, and have extensive hummocks with a ground cover composed almost exclusively of *Sphagnum fuscum*. Other bryophytes include *Mylia anomala*, *Pohlia nutans*, *Polytrichum strictum*, and *Sphagnum magellanicum*, all occasionally present at low cover values ($<$5%). An effort to choose only *S. fuscum*-dominated sites was made in order to eliminate differences in response owing to species composition (Bayley et al. 1987). Canopy cover at each site was measured by densiometer with site means ranging from 17% canopy cover at Wandering River to 44% at Anzac West. Pairwise comparisons of canopy cover using a Dunnett C Test indicate significant differences only between Anzac West and Wandering River; Steepbank, is not significantly different from any of the remaining five sites. Steepbank had 43% canopy cover. Maximum tree heights ranged from 2.0 m at Wandering River to 6.0 at Anzac West and 6.2 m at Steepbank. pH ranged from 3.8 to 4.4 and varied little between sites, as would be expected for ombrogenous systems.

Depth to water table is known to have an impact on *Sphagnum* production (Thormann et al. 1998) and sites were also chosen to include a full range of variability of *S. fuscum* habitats. Water table depth from the peat surface

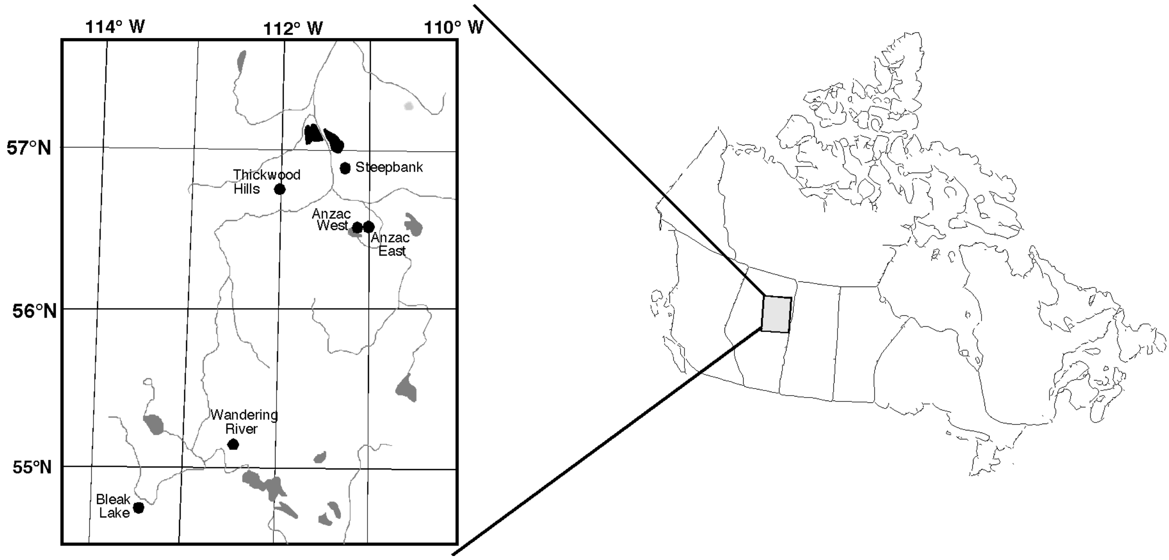

FIGURE 1. Location of six study sites in Canada. Blackened area of inset is the active area of oil sands mining in 2002.

at Steepbank Bog site ranged from 31 to 61 cm and from 22 to 97 cm at sites removed from oil sands activity. Current water table depths at one site (Wandering River Bog) are low (55 to 97 cm from the surface) due to recent drainage of a nearby portion for peat harvesting. Sites at Thickwood Hills Bog were located within internal lawns (areas regenerating after local permafrost melting) and had water table depths of 30 to 36 cm from the surface.

Turetsky et al. (2000) have shown that internal lawns have greater net organic matter accumulation than either bogs or permafrost mounds.

Nitrogen deposition.—Nitrogen emissions and deposition from oil sands mining activities were modeled by CALPUFF, a multi-layer, multi-species, non-steady-state puff dispersion model that can simulate the effects of time- and space-varying meteorological conditions on substance transport, transportation, and removal (Scire et al. 2000). Nitrate deposition for 1996–1997 was obtained from a CALPUFF 2D dispersion model run by Conor Pacific (1998), while emission data for 1970–2002 and onward and deposition data for 2002 were obtained from a CALPUFF 3D dispersion model run by Golder (2002).

TABLE 1. Geographic localities and modeled N-deposition rates (Golder 2002) for the six bog sites from current and proposed oil sands mining development in northeastern Alberta, Canada. Background deposition (ca 1.0 kg ha^{-1} yr^{-1}) is not included in this table.

Site	Modeled N-deposition kg N ha^{-1} yr^{-1}	Latitude	Longitude
Steepbank	4.04	56°53′ N	111°16′ W
Anzac West	0.43	56°27′ N	111°03′ W
Anzac East	0.43	56°27′ N	111°02′ W
Thickwood Hills	0.47	56°47′ N	112°01′ W
Wandering River	0.07	55°17′ N	112°28′ W
Bleak Lake	—	54°41′ N	113°28′ W

Background 1996 annual wet deposition was derived from contour maps using maps provided by the National Atmospheric Chemistry Database (Ro & Vet 2002). Northeastern Alberta deposition of NH_4^+-N is about 0.5 kg ha^{-1} yr^{-1} and NO_3^--N is also about 0.5 kg ha^{-1} yr^{-1}; hence the background for total nitrogen deposition in the study area is approximately 1.0 kg ha^{-1} yr^{-1}. In this paper all N deposition data are expressed as kg N ha^{-1} yr^{-1}, having been converted from a variety of units in the cited references.

Net Primary Production.—Production of *Sphagnum fuscum* was determined beginning in early June 2000 using the cranked wire method (Clymo 1970; Rochefort et al. 1990). The ''cranked'' wires used in this study were 33 cm long with a 90 degree 1-cm long horizontal crank placed 7-cm from the exposed end. Cranks were placed about 1-cm below the spring *Sphagnum* surface and served only to anchor the wire in place. At each of the six sites, five plots (approximately 1-m^2) were established, each located within a different randomly selected hummock composed of >95% cover of *Sphagnum fuscum*. Within each plot, 50 cranked wires were placed in a transect spanning the hummock surface, for a total of 250 wires per site. Growth in length was determined by measuring the length of the wire exposed above the *Sphagnum* surface on 6–8 June, 2000 and comparing it to the length of the wire exposed on 17–19 October, 2000 for all wires at all sites. For plots where disturbance by wildlife occurred, noted as tilted wires or as areas with visibly compressed peat, final measurements were not recorded. Since *Sphagnum* species are known to begin growth early in the season, our data are underestimates of total annual NPP.

Linear growth measurements (cm) were converted to mass per surface area (g m^{-2}) by extracting one 18 cm diameter core from each of the 30 plots in mid-October. After removal of the capitula of actively growing young branches, 10 1-cm^2 samples were randomly extracted from the frozen uppermost 1-cm thick layer. These 1-cm^3 samples were air-dried and weighed. Production for each plot was obtained by multiplying the total dry weight of the ten subsamples (in total − 10 cm^3) × 1,000 to yield the bulk density of the top-most cm, and then by the mean length increment change of the 50 wires over the study period. This approach assumes that the capitula of the plants do not change in weight over the study period with growth occurring by the addition of new plant biomass immediately below the capitula (Rochefort et al. 1990). It also assumes that the uppermost 1-cm increment is representative of the total annual length increment.

As moss production of peatland species is influenced by water table height (water availability) (Dise et al. 1993; Szumigalski & Bayley 1997; Thormann et al. 1998; Zoltai & Vitt 1990), the depth to the water table was determined for each of the wires within all plots in mid-October. For each plot, an adjacent hollow was cleared to the water table and the distance between the moss surface at each wire and the water table in the hollow was determined to the nearest 1-mm increment with use of string and level. Capillary rise of water under the hummocks may occur, and the water table levels presented here are larger than those within the actual hummocks.

Nitrogen concentration.—Five cores were collected from each of the six sites using a modified box corer that minimizes peat compaction during core collection (Beilman 2000). Cores were collected from each of the production plots to a depth that exceeded 35 cm, transported back to the lab in PVC pipe, and frozen until analyzed.

For analyses of nitrogen, individual frozen cores were sampled in consecutive 1-cm increments with a 1-cm^2 cork borer to a depth of 25 cm^3 with the top sample taken directly below the capitula of the plants. These samples were air-dried for 48 hr and weighed to determine bulk density. Samples were then dried for 24 hr at 60 C and ground using mortar and pestle to ensure sample homogeneity. Percent nitrogen of each homogenized sample was determined by igniting 1–2 mg of sample at 975 C in a Controlled Equipment Corporation model 440 elemental analyzer.

RESULTS

Net Primary Production (NPP).—Production values for *Sphagnum fuscum* were not normally distributed for any of the five sites (Shapiro-Wilk test, $p < 0.0001$), with data for all sites exhibiting positive skewness, and for all sites except Anzac East exhibiting leptokurtosis. As a result, production was compared between sites using a nonparametric nested analysis of variance (taking into account that there were 50 cranked wires nested within each plot at each site) with *a posteriori* median comparisons made using the Bonferroni test (SAS Institute Inc. 1999). Median production differed significantly between sites ($F_{5,22} = 5.43$; $p = 0.021$). Median production at Steepbank of 486 g m^{-2} was greater than at Anzac West, Anzac East, Wandering River, or Bleak Lake (medians of 132, 154, 140, and 138 g m^{-2}, respectively), but not different from median production at Thickwood Hills (median of 216 g m^{-2}) (Fig. 2A).

Mean production of 600 g m^{-2} at the high deposition site (Steepbank) is 3.3 times the pooled means of 182 g m^{-2} at the background sites (Table 2). These latter values are similar to the 1991–1994 mean at Bleak Lake of 152 g m^{-2} and somewhat higher than the four year mean at ELA (western Ontario) of 99 g m^{-2}. Whether expressed as a mean or median value, net primary production at the Steepbank site is among the highest recorded for bogs in continental areas (Table 2).

Depth to water table data were not normally distributed at any of the six sites (Shapiro-Wilk test, $p < 0.0001$), so sites were compared using a nonparametric nested analysis of variance. Depth to water table differed significantly between sites ($F_{5,22} = 9.00$; $p < 0.0001$). Depth to water table was greatest at Wandering River and smallest at Thickwood Hills, with intermediate values for the other sites (Fig. 2B). A weak or nonsignificant relationship exists between NPP and water table depth for each of the six sites (Table 3). The wettest site (Thickwood Hills) has a significant positive relationship between NPP and water table level, while the driest site (Wandering River) has a significant negative relationship between NPP and water level, suggesting that a decreasing water table may enhance growth in wet sites, but will further inhibit growth in dry sites. Overall, these data of two negative slopes, two positive slopes (all with low R^2 values), and no significant relationship for two sites indicate no clear relationship is present between water level and NPP. However, the negative slope for the Steepbank data suggests that water level may be limiting NPP at drier microsites under high nitrogen deposition (Fig. 3).

Nitrogen concentration.—Nitrogen concentration data were examined for normality for each of the 130 site*depth combinations ($n = 5$ for each). In 12 of the 130 instances the data were not normally distributed (Shapiro-Wilk test, $p < 0.05$), so site and depth effects on nitrogen concentration were examined using a two-way nonparametric analysis of variance. For the total core depth of 25 cm, there were significant site ($F_{5,600} = 27.99$; $p < 0.0001$) and depth ($F_{24,600} = 5.44$; $p = 0.021$) effects, but no significant interaction between site and depth ($F_{120,600} = 0.64$; $p = 0.9987$). Peat nitrogen concentrations are greatest at the Steepbank, Anzac East, and Wandering River sites, and are lowest at the Anzac West site (Fig. 4). Peat nitrogen concentrations are highest at the surface, decreasing in the top 3 cm with no significant change with increasing depth (Fig. 5).

We were specifically interested in whether elevated N deposition resulted in enhanced nitrogen concentrations in near-surface peat only. Therefore, we compared N concentrations across the six sites for the upper two peat sections (0–1 cm and 1–2 cm) only using a two-way analysis of variance (data for each of the site*depth combinations were normally distributed, Shapiro-Wilk test, $p < 0.05$). This analysis yielded a significant site*depth interaction ($F_{5,48} = 2.51$; $p = 0.0428$). Surface (top 1-cm) N concentrations were elevated at Steepbank,

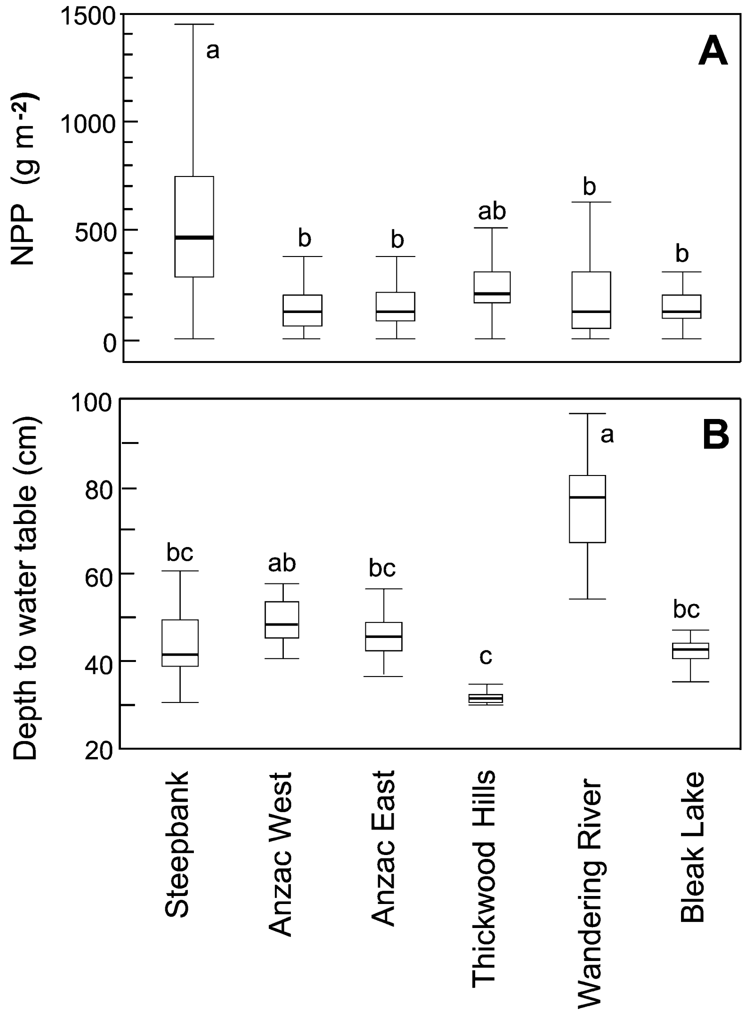

FIGURE 2. Growth of *Sphagnum* (A) and depth to water table (B) at the six sites, shown as standard box and whisker plots. For each site, the bold horizontal line represents the median growth (A) or depth (B), and the boxes represent the 25th and 75th percent quartiles. The whiskers extend to the closest data point within ±1.5 times the interquartile distance (vertical distance represented by the boxes). Sites with the same lower case letter do not differ significantly (*a posteriori* Bonferroni comparisons, $p = 0.05$, following a nonparametric nested analysis of variance). $n = 5$ plots with 50 length and 10 weight measurements per plot for each site.

and to a lesser extent at Wandering River; Steepbank was the only site at which N concentration in the top 1-cm of peat was significantly elevated compared to the peat section immediately below (1–2 cm; Table 4). Nitrogen concentrations did not differ across sites for the 1–2 cm depth sections (Table 4), as well as for deeper sections in the peat profiles.

DISCUSSION AND SUMMARY

The Steepbank Bog Site, which is located within the 1996–1997 1.13–2.26 kg N ha^{-1} yr^{-1} modeled nitrate deposition zone, has production values for *Sphagnum fuscum* that are significantly different from four of the five other continental bog sites located in areas of Alberta where NO_3^--N deposition was predicted, in 1996–1997, to be less than 0.45 kg N ha^{-1} yr^{-1} (Note: These values are in addition to 1.0 kg ha^{-1} yr^{-1} background N). Pooled net primary medians or means of *S. fuscum* from the Steepbank Bog site are three times higher than NPP rates at the five N-deposition sites with lower depositional values. Thus high nitrogen deposition appears to have a dramatic effect on the performance of this species.

A detailed experimental study conducted on oceanic bogs as part of the BERI program (Gunnarsson & Rydin 2000) suggested that the production of *S. fuscum* is enhanced at low levels of N addition, but is inhibited when loading rates of nitrogen are in-

TABLE 2. Mean and standard deviation of net primary production for *Sphagnum fuscum* at sites examined here and mean and standard deviation (if available) for NPP from other sites without treatments. Baseline N deposition is given as reported by individual authors. Nitrogen deposition values for this study are modeled 1996–97 values (Conor Pacific 1998) plus 1.0 kg ha^{-1} yr^{-1} background (see text). +Oceanic systems.

Site	Mean Production (g m^2)	N-deposition kg N ha^{-1} yr^{-1}	Reference
Steepbank, Alberta	600 ± 462	2.13–3.26	This study
Anzac West, Alberta	151 ± 114	1.23–1.45	This study
Anzac East, Alberta	154 ± 101	1.23–1.45	This study
Thickwood Hills, Alberta	245 ± 147	1.45–2.13	This study
Wandering River, Alberta	200 ± 103	1.23–1.45	This study
Bleak Lake 2000, Alberta	159 ± 103	1.23–1.45	This study
Bleak Lake Bog 1991, Alberta	64 ± 79	2.4	Szumigalski 1995
Bleak Lake Bog 1992, Alberta	119 ± 93	2.4	Szumigalski 1995
Bleak Lake Bog 1993, Alberta	156	2.4	Thormann & Bayley 1997a
Bleak Lake Bog 1994, Alberta	268	2.4	Thormann & Bayley 1997a
Seba Beach Bog 1994, Alberta	127 ± 22	2.8	Li & Vitt 1997
ELA Bog 239 1984, Ontario	69 ± 13	3.8	Rochefort et al. 1990
ELA Bog 239 1985, Ontario	91 ± 19	3.8	Rochefort et al. 1990
ELA Bog 239 1986, Ontario	116 ± 8	3.8	Rochefort et al. 1990
ELA Bog 239 1987, Ontario	119 ± 13	3.8	Rochefort et al. 1990
Akhultmyren Bog+, Sweden	168	7.2	Gunnarsson & Rydin 2000
Luttumyren Bog+, Sweden	165	4.2	Gunnarsson & Rydin 2000

creased above approximately 14 kg ha^{-1} yr^{-1} (Table 6). When we plotted all of the production data in Table 5 along with the production data from our six sites as a function of N deposition, it appears that production is highly variable at N deposition values up to about 3 kg ha^{-1} yr^{-1}, but then subsequently decreases in a seemingly exponential manner (Fig. 6A). Our data alone show a strong increase in production with increasing N deposition, while data from the controls in the experimental N augmentation studies show a slight, but significant decrease in N production with increasing N deposition for controls in the N augmentation studies (albeit a weak relationship with an R^2 value of 0.01; Fig. 6B).

When data from only the experimental N augmentation studies are considered, removing as many inter-site confounding effects as possible, the effect of initial stimulation of production followed by inhibition of production is even more evident. Whether the dependent variable is the absolute difference in production between N-augmented and control production (Fig. 6C), or this difference is expressed as a percentage of control production (Fig. 6D), N augmentation increases *S. fuscum* production relative to controls at low deposition rates. Eventually, however, production is inhibited relative to control values as N deposition increases. When the data in Fig. 6C and 6D are described by a negative exponential equation (SAS 1999), the best fit curves intersect at y = 0 (no effect of N deposition on *S. fuscum* production) at N deposition values of 15.7 and 14.8 kg ha^{-1} yr^{-1} in Fig. 6C and 6D, respectively. Therefore, across the wide range of N deposition values encompassed by the studies cited in Table 5, negative impacts on *S. fuscum* production begin to occur, on average, as N deposition reaches 14.8–15.7 kg ha^{-1} yr^{-1}. We argue that this approach reveals a critical N deposition value (be-

TABLE 3. Results of linear regressions of net primary production as a function of depth to water table.

Site	Slope	p	R^2
Steepbank	−9.0 ± 3.4	0.0082	0.03
Anzac West	—	0.8489	—
Anzac East	+4.6 ± 1.3	0.0003	0.05
Thickwood Hills	+47.6 ± 9.6	<0.0001	0.20
Wandering River	−2.5 ± 1.2	0.0480	0.02
Bleak Lake	—	0.3625	—

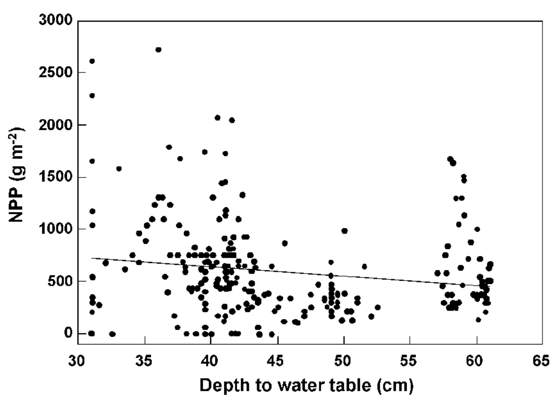

FIGURE 3. Relationship between growth (NPP) of *Sphagnum fuscum* and depth to water table at Steepbank (see Table 3 for regression statistics).

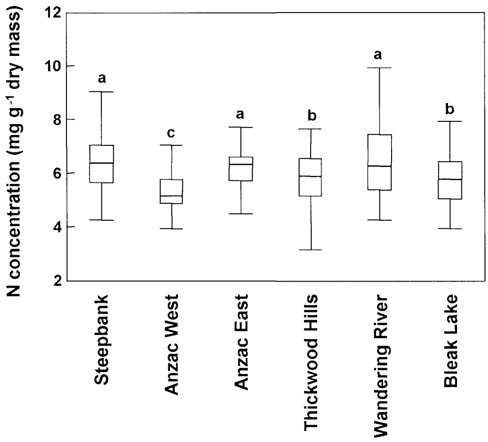

FIGURE 4. Peat nitrogen concentrations, averaged across all depths, at the six sites, shown as standard box and whisker plots ($n = 25$ depths at each of five plots). See Figure 2 for explanation of the box and whiskers plots. Sites with the same lower case letter do not differ significantly (*a posteriori* Bonferroni comparisons, $p = 0.05$, following a nonparametric analysis of variance).

TABLE 4. Nitrogen concentrations (means ± standard deviations, $n = 5$) in the top two 1-cm depth increments at the six sites. Values with the same letter superscript do not differ significantly (*a posteriori* Bonferroni comparisons, $p = 0.05$, following a two-way analysis of variance).

pSite	1 cm	2 cm
Steepbank	11.4 ± 2.1^{a}	8.4 ± 1.2^{bc}
Anzac West	7.0 ± 1.1^{bc}	6.0 ± 0.6^{c}
Anzac East	7.1 ± 0.8^{bc}	6.7 ± 1.0^{c}
Thickwood Hills	7.2 ± 0.4^{bc}	6.4 ± 0.2^{c}
Wandering River	9.5 ± 1.6^{ab}	7.2 ± 1.8^{bc}
Bleak Lake	6.8 ± 0.3^{c}	6.5 ± 0.3^{c}

tween 14.8 and 15.7 kg ha^{-1} yr^{-1}) for the production of these bryophyte species. We note, however, that lower 95% confidence intervals intersect at $y = 0$ at N deposition values of 8.3 (Fig. 6C) and 9.6 (Fig. 6D) kg ha^{-1} yr^{-1}, representing the most conservative critical values for the influence of N deposition on *S. fuscum* production.

Current N deposition in the oil sands region of Alberta of about 4 kg ha^{-1} yr^{-1}, is well below this critical range. We point out, however, that studies in which N deposition has been augmented experimentally are all short-term, none lasting more than four years. The situation in the oil sands region of Alberta represents 34 years of chronic and increasing N deposition, which may explain, at least in part, the exceptionally high production values that we obtained at the Steepbank site. At this point, we cannot say with certainty that the critical range of N deposition of about 15 kg ha^{-1} yr^{-1}, determined from short-term manipulative studies, necessarily applies to long-term, chronic, and increasing N deposition.

Nonetheless, if current and future N deposition in the oil sands region enhances *S. fuscum* produc-

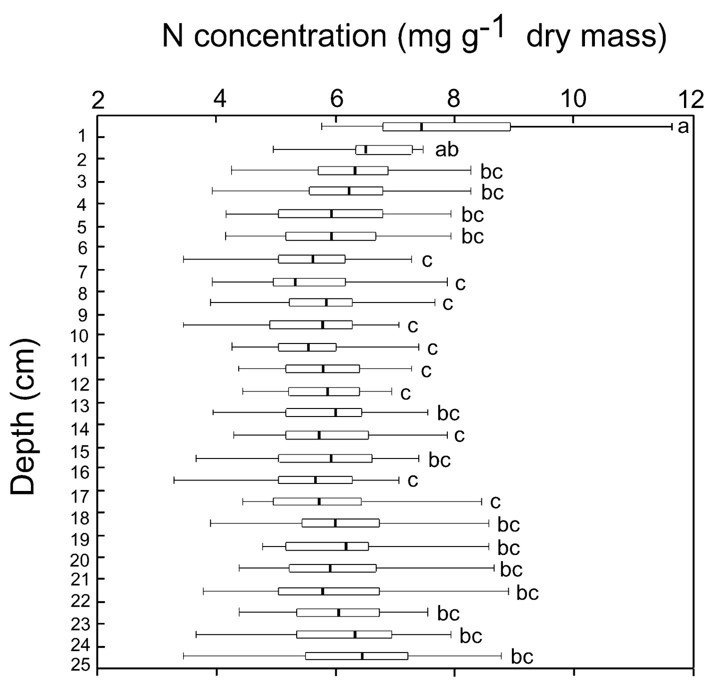

FIGURE 5. Nitrogen concentrations in peat as a function of depth, averaged across the six sites (means ± standard errors, $n = 30$). Sites with the same lower case letter do not differ significantly (*a posteriori* least significant comparisons, $p = 0.05$, following a two-way analysis of variance).

TABLE 5. Net primary production (NPP) of *Sphagnum fuscum* at sites where nitrogen (N) has been experimentally added. Total deposition has been calculated by including baseline N-deposition. Percent NPP change is calculated relative to control baseline N deposition level. In the %NPP change column, "C" designated the control (no additional N added) condition.

Bog Sites	Mean Production (g/m^2)	% NPP Change	Total N-deposition kg N ha^{-1} yr^{-1}	Reference
CONTINENTAL BOGS				
Mire 239	69	C	3.8	Rochefort et al. 1990
1984	219	+217%	8.4	
Mire 239	91	C	3.8	
1985	255	+180%	8.4	
Mire 239	116	C	3.8	
1986	217	+87%	8.4	
Mire 239	119	C	3.8	
1987	218	+83%	8.4	
Seba Beach	103	C	2.8	Li & Vitt 1997
1994	145	+41%	33.6	
Bleak Lake	268	C	2.4	Thormann & Bayley 1997b
1994	105	−61%	152.4	
OCEANIC BOGS				
Luttumyren	166	C	4.2	Gunnarsson & Rydin 2000
	184	+11%	14.2	
	161	−3%	34.2	
	138	−17%	54.2	
	122	−27%	104.2	
Akhultmyren	163	C	7.2	Gunnarsson & Rydin 2000
	122	−25%	17.2	
	155	−7%	37.2	
	87	−47%	57.2	
	83	−49%	107.2	

tion as dramatically as our data suggest, regional peatland carbon cycling certainly will be influenced. Without data on the effects of N deposition on peat decomposition, however, we cannot determine how enhanced N deposition and resulting enhanced *S. fuscum* production will influence the carbon source/sink relationships of peatlands in this region.

Differences in depth to water table may also play a role in explaining the variation between ground cover production of sites (Thormann & Bailey 1997*a,b*). Results from this study are inconclusive, but suggest that for *S. fuscum*, microsites on low hummocks (and wetter) and those on very high hummocks (and drier) both produce less than those with intermediate water tables. Production of *Sphagnum fuscum* in continental peatlands may partially be limited by water levels and not nutrients—further work is needed. Although for the year 2000, our data indicate that N is the overriding limiting factor, for another year with drier conditions, water availability may become more important. If this is true, then nitrogen saturation may be more critical during dry years. We suggest that future monitoring efforts should be conducted: 1) in sites with comparable water table depths and 2) over several years as variation in annual precipitation may be critical to understanding the direct effects of added nitrogen.

Other factors that could impact performance of *S. fuscum* such as shade, differing water chemistry, or associated vegetation (see methods) do not differ significantly among our sites (canopy cover) or in the cases of vegetation and pH are almost identical (data not shown).

Across all six of our study sites, nitrogen depth profiles reveal elevated concentrations only in the upper 1–2 cm, but the surface N enrichment was especially high at the Steepbank site. *Sphagnum* is known to recycle labile nitrogen from one season's cell material to the next. Li and Vitt (1997) demonstrated that 19–20% of year one labeled N (^{15}N) was found in year two biomass. However, over time as N is set in more permanent cell wall components and stabilizes at 0.50–0.60%. As decomposition proceeds, it releases carbon at a greater rate than nitrogen, often with an apparently slight increase in N concentration (0.50–0.70%).

This case study demonstrates that after 34 years of nitrogen deposition since oil sands mine start-up, high N-deposition compared to other regions of Alberta has increased net primary production of *Sphagnum fuscum*, and has led to elevated levels of nitrogen of the uppermost 1-cm of the soil profile.

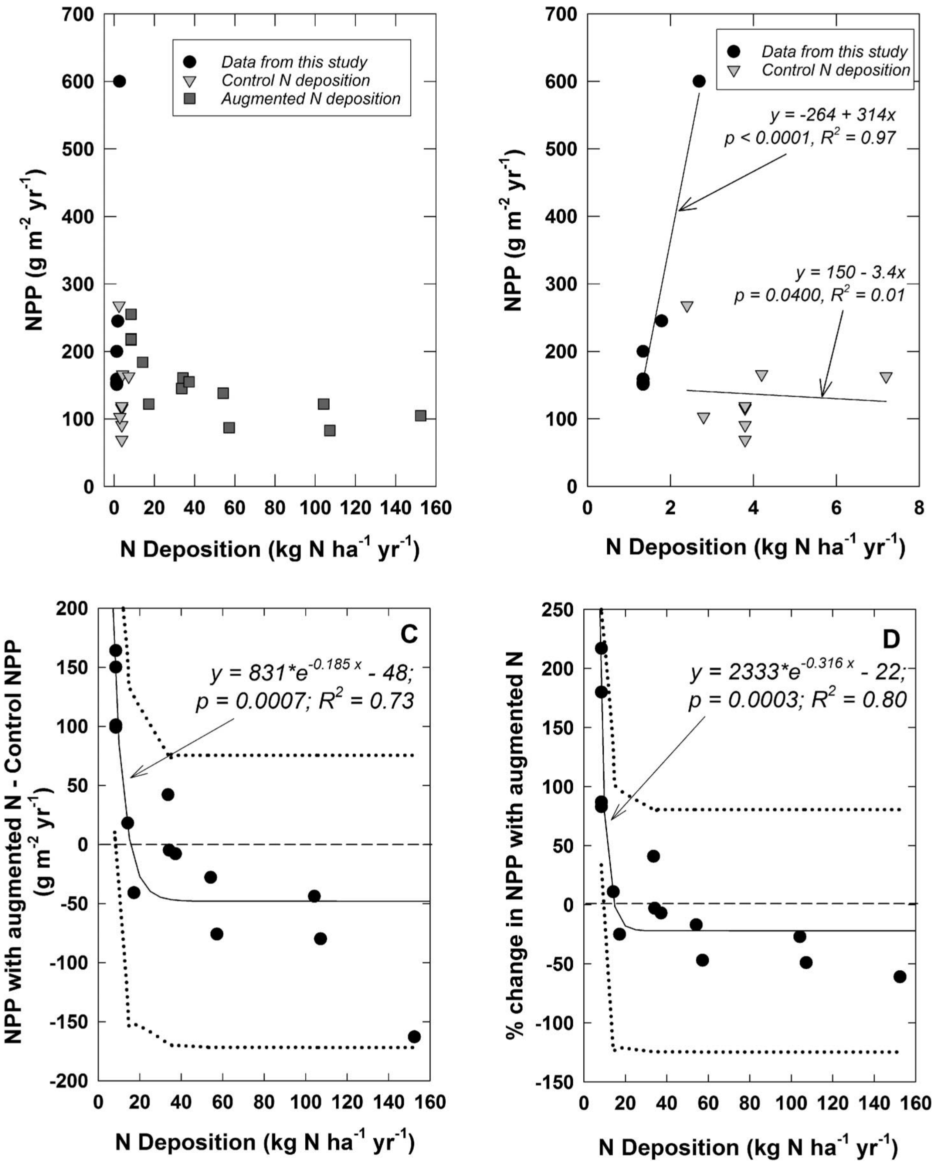

FIGURE 6. Influence of N deposition on *S. fuscum* NPP based on all of the data in Table 5 (controls and augmented N deposition values), as well as data from this study (A), based on data from this study (Table 2) and controls only from N augmentation studies (Table 5) (B), based on only studies in which N deposition has been experimentally augmented, with NPP expressed as the absolute difference in production between N-augmented and control production (C), or as the percentage change in production with augmented N (D). Dashed horizontal lines in C and D represent no effect of N deposition on production. Negative exponential fits to the data in C and D also are shown, along with the best fit equation. Using PROC NLIN in SAS (1999), simple exponential decay equations were modified by including a constant to allow for negative values of the dependent variable. Equations of the form $y = A * e^{-B \times N\ deposition} - C$ were fit to the data, where *A*, *B* and *C* are estimated parameters and *y* is the dependent variable in Figure 5C and 5D. Best fit equations (smooth solid curve) and 95% confidence intervals (dotted curves) are shown.

This case study is one of the first to utilize ongoing patterns of pollution on the boreal landscape and we feel that these data are useful for comparison to experimental results from nitrogen fertilization. Bryophyte growth and nitrogen retention are ecosystem processes critical to soil carbon storage and peatland development, and we argue that they should be carefully monitored with continued N-deposition. Furthermore, the effects of increased N-deposition on peatland ecosystems in the future need to be carefully evaluated through the maintenance of a NPP-monitoring system.

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