



Plasticity in bog plant nitrogen concentration is related to recent weather conditions

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Abstract

Background and aims NO_x emissions from development of the oil sands resource in the Athabasca Oil Sands Region (AOSR) in Alberta, Canada have caused elevated N deposition, which has led to increased N concentrations in bog *Sphagnum* mosses and in leaves of some vascular plant species. Here, we address whether climate-related environmental variables affect N concentrations in bog species.

Methods Plant samples were collected from 5 bogs in the AOSR, cleaned, dried, ground, and analyzed

for N concentrations. Tissue N concentrations in 8 bog plant species were regressed against mean daily air temperature, precipitation, photosynthetically active radiation, atmospheric water potential, and atmospheric vapor pressure deficit over the 5, 10, 15, 20, 25, and 30 days prior to plant sampling using best subset regression.

Results Climate-related environmental variables explained 12–61 % of overall variability in plant tissue N concentration. Tissue N concentrations in more deeply rooted vascular species (*Maianthemum trifolium*, *Rubus chamaemorus*, *Rhododendron groenlandicum*, *Picea mariana*) respond to environmental variables over longer periods of time (the previous 25–20 days prior to sampling) than more shallow rooted vascular species (*Vaccinium oxycoccos*, *Vaccinium vitis-idaea*) or mosses (*Sphagnum capillifolium*, *Sphagnum fuscum*) (5–10 days prior to sampling).

Conclusion In the AOSR, N deposition and climate will continue to change. Understanding how bog plant N concentrations are affected by elevated N deposition from oil sands development and by climate will be key to the ability of monitoring programs to identify oil sands related effects on bog ecosystems across the AOSR.

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Abbreviations

AOSR	Athabasca Oil Sands Region
T_a	Air temperature (°C)
PAR	Photosynthetically active radiation
PPT	Precipitation (wet)
RH	Atmospheric relative humidity
VP_{sat}	Saturated atmospheric vapor pressure (kPa)
VP_{air}	Atmospheric vapor pressure (kPa)
VPD_a	Atmospheric vapor pressure deficit (kPa)
WP_a	Atmospheric water potential (MPa)

Introduction

The question of what controls foliar nutrient concentrations and stoichiometry has long intrigued plant physiologists and ecologists. Numerous studies have shown correlations between foliar N concentrations and broad environmental gradients regionally or globally, with parameters including air temperature, precipitation, soil moisture, evapotranspiration, light availability, and elevation (e.g., Yin 1993; Reich and Oleksyn 2004; Kranabetter et al. 2010; McNeil et al. 2012; Gong et al. 2020). Within individual species, tree foliar N concentrations/contents often increase upward through the canopy along with increasing light availability (see review by Hikosaka 2016). As foliar N content is a strong predictor of photosynthetic rates, changing foliar N contents within canopies may reflect an adaptive strategy for efficient N use. A synthesis of a global dataset of foliar N and P concentrations across 3700 species showed considerable between-species variability in foliar N (and P) concentrations, but also within-species variability that was linked to environmental variables, including N deposition, mean temperature of the coldest month, annual mean photosynthetic photon flux density, and mean daytime atmospheric vapor pressure deficit (Tian et al. 2024). Understanding how environmentally-driven genetic adaptation versus plasticity controls foliar nutrient chemistry is important when examining broad geographic patterns in foliar N concentrations under global change scenarios.

Here, we examine whether within-species variability in foliar N concentration can be linked to weather-related environmental variables at a regional scale in the oil sands region of northern Alberta, where the anthropogenic N deposition regime has varied over space and where N deposition has

increased since oil sands development began. Development of the Athabasca Oil Sands resource, beginning in the 1970s, has led to increasing emissions of NO_x (and SO_2) from upgrader stacks and mine fleet vehicles, which in turn has resulted in elevated wet and dry N (and S) deposition to regional ecosystems that decreases with distance from oil sands facilities (Fenn et al. 2015; Hsu et al. 2016; Wieder et al. 2016a, b; Wieder et al. 2021; Edgerton et al. 2020). Bogs, *Sphagnum*-dominated, ombrogenous, acidic, nutrient-poor wetlands with water table at or slightly below the surface and raised above the surrounding terrain, and an accumulation of moderately decomposed *Sphagnum* peat with the woody remains of shrubs (Warner and Rubec 1977), cover 6–10 % of the 140,329 km² Oil Sands Administrative Area (Wieder et al. 2016a). Because of their ombrogenous nature, bogs may be among the most sensitive ecosystems to increasing N deposition. Monitoring of bogs at different distances from oil sands facilities since 2009 has indicated that tissue N concentrations in *Sphagnum fuscum*, *Vaccinium oxycoccos*, *Vaccinium vitis-idaea*, and *Rubus chamaemorus*, but not in *Sphagnum capillifolium*, *Rhododendron groenlandicum*, *Maianthemum trifolium*, or *Picea mariana*, differed between bogs and decreased with distance from oil sands facilities. Negative exponential equations of N concentrations as a function of distance explained a small, but significant percentage of the total variation in plant tissue N concentrations (2–9 %) (Wieder et al. 2021). In light of these findings, here we ask to what extent can weather-related environmental variables – mean daily air temperature (T_a), precipitation (PPT), photosynthetically active radiation (PAR), atmospheric water potential (WP_a), and atmospheric vapor pressure deficit (VPD_a) – explain variation in bog plant tissue N concentrations across the oil sands region? Secondly, if environmentally-driven plasticity in bog plant N concentration exists, how quickly can N concentrations change? Are plant N concentrations most strongly related to environmental variables averaged over a consistent time lag, viz. the 5, 10, 15, 20, 25, or 30 days prior to sample collection? To better characterize the effects of oil sands-related N deposition on bog plant foliar N concentrations with changing N deposition and climate into the future, the effects of environmental weather-related variables on N deposition must be understood.

Methods

From 2009 through 2019, plant tissue samples were collected from five bog sites in the Athabasca Oil Sands Region, situated at different distances from the midpoint between the Syncrude and Suncor main upgrader stacks (Mildred, 56°55'49"N, 111°28'31"W, 11 km; JPH4, 57°6'45"N, 111°25'23"W, 12 km; McKay, 57°13'41"N, 111°42'11"W, 24 km; McMurray, 56°37'37"N, 111°11'44"W, 49 km; Anzac, 56°28'8"N, 111°2'34"W, 69 km) (see Wieder et al. (2021) for site descriptions). On each sampling date at each site, we collected five replicate samples of each plant species, one from each of five different areas within each bog separated by at least 20 m, on multiple dates during a growing season. In short, N concentrations were determined in capitula (the compact clusters of young branches at the apex of a *Sphagnum* moss plants) of *Sphagnum fuscum* (Schimp.) Klinggr., and *Sphagnum capillifolium* (Ehrh.) Hedw., the topmost 3–5 leaves of *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *Vaccinium vitis-idaea* L., all leaves of *Vaccinium oxycoccos* L. (presumably representing leaves that are 1–2 years old; Warming 1908; Jacquemart 1997), current year leaves of the deciduous forbs *Rubus chamaemorus* L. and *Maianthemum trifolium* (L.) Sloboda, and current year needles of *Picea mariana* (P. Mill.) B.S.P. The overall dataset used in this manuscript includes 6133 samples. The years over which samples were collected and the number of total samples collected and analyzed per species and site are given in Table S1; sampling dates are given in Table S2. Collected samples were cleaned of non-target plant material, dried, ground, and analyzed for N concentration on a LECO TruSpec C, N, S Analyzer. Details of plant collection, processing in the laboratory, and analysis for N concentrations are provided in Wieder et al. (2021).

At each bog site, a WatchDog™ weather station recorded air temperature (T_a , °C), air relative humidity (RH, %), photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$), and rainfall (PPT, mm), hourly. Using the temperature and relative humidity data, hourly atmospheric water potential (WP_a) was calculated as:

$$WP_a(\text{MPa}) = \left(\frac{0.0831 \times (T + 273.014) \times \log_{10}\left(\frac{RH}{100}\right)}{18} \right) \times \frac{1000}{10}.$$

Hourly atmospheric vapor pressure deficit (VPD_a) was calculated as the difference between saturated vapor pressure of air (VP_{sat}) and the actual vapor pressure of air (VP_a):

$$VP_{sat}(\text{kPa}) = \frac{610 \times 10^{\frac{7.5 \times T_a}{237.3 + T_a}}}{1000},$$

$$VP_a(\text{kPa}) = \left(\frac{610 \times 10^{\frac{7.5 \times T_a}{237.3 + T_a}}}{1000} \right) \times \frac{RH}{100}, \text{ and}$$

$$VPD_a(\text{kPa}) = VP_{sat} - VP_a.$$

Mean daily T_a , PPT, PAR, WP_a , and VP_a were calculated over the 5, 10, 15, 20, 25 and 30 days prior to each plant tissue collection date for each site in each year. These calculated time lag variables served as independent variables upon which plant tissue N concentrations were regressed.

In light of well recognized biases and shortcomings of traditional stepwise multiple regression (cf. Whittingham et al. 2006), relationships between tissue N concentrations of each plant species and environmental variables were examined with best subset regression, using the minimum AiC value to determine which subset of environmental variables would be selected (PROC REG in SAS 9.4). For each species, separate best subset regression runs were conducted for tissue N concentrations as a function of environmental variables averaged over the 5, 10, 15, 20, 25, and 30 days prior to tissue collection. To determine regression coefficients and model overall and partial R^2 values, tissue N concentrations were regressed against the environmental variables identified from each best subset regression run (PROC REG, SAS 9.4).

As a check on the best subset regression approach to determining which environmental variables were selected as affecting plant N concentrations, model averaging with stepwise selection and AiC as the selection criterion was used. For each species and environmental variable time frame (5–30 days), 100 sample sets of 100 randomly selected observations were generated, with replacement. Subsequently, a second round of model averaging was carried out with 100 randomly

selected samples using only those variables that were selected at least 50 % of the time in the first round of model averaging. Model averaging was carried out using PROC GLMSELECT with $\alpha = 0.1$ in SAS 9.4.

Differences between sites in tissue N concentrations were evaluated using analysis of variance, with site and collection date as main effects. Differences between sites in environmental variables were evaluated using analysis of variance, with site and day as main effects. *A posteriori* mean comparisons were conducted using Tukey's HSD tests. The proportion of variation in tissue N concentrations accounted for by site and collection date or day, after excluding variance from day or collection date, respectively, was assessed using the partial η^2 -squared statistic (produced by the EFFECTSIZE statement in PROC GLM, SAS 9.4) (Lakens 2013).

Recognizing that N concentration responses to weather-related climate variables may be nonlinear, for each species, a 3-dimensional plot of *Sphagnum* capitulum or vascular plant leaf N concentrations was constructed using the two weather-related climate variables in the best subset regression for the number of days prior to sampling (denoted by the subscripts in x and y axis labels) with the highest partial R^2 values. Plots are based on the individual points with a loess smoothing value of 0.5 and a polynomial degree value of 1 (SigmaPlot 15.0).

Results

Site differences environmental variables and tissue N concentrations

For each of the five environmental variables, logged hourly or calculated at each site during the growing season, day-to-day differences explained a far greater proportion of partial variance (η^2) than site differences (Fig. 1). Nonetheless, all environmental variables except mean daily rainfall exhibited significant site differences ($p \leq 0.0001$). While mean daily PAR generally was higher at the two sites nearest to oil sands operations than at more distant sites, site differences for the other four environmental variables did not show this pattern.

For all plant species, temporal variation (sampling date across all years of sample collection) in tissue N concentrations explained a greater proportion

of partial variance (η^2) than site differences (Fig. 2). All plant species exhibited significant differences in tissue N concentrations between sites ($p < 0.0001$). For *S. capillifolium*, *S. fuscum*, *V. oxycoccos*, *V. vitis-idaea*, and *Rubus chamaemorus*, but not for *Maianthemum trifolium*, *Rhododendron groenlandicum*, or *Picea mariana*, tissue N concentrations decreased exponentially with distance from oil sands operations (Fig. S1). Not surprisingly, these patterns are similar to those reported in Wieder et al. (2021); here we use the same tissue N data set with additional sampling years of 2017, 2018, and 2019.

Temporal changes in best subset regression parameter estimates

In general, tissue N concentrations for all species and all environmental variables calculated for the different number of days prior to sampling, parameter estimates obtained using best subset regression were corroborated by model averaging (Table S3). For four of the species, *Maianthemum trifolium*, *Picea mariana*, *Rhododendron groenlandicum*, and *Rubus chamaemorus*, best subset regression model R^2 values generally increased with increasing number of days over which weather-related environmental variables were calculated prior to sampling (linear regression; $p \leq 0.016$), with highest values at 30, 25, 30, and 20 days, respectively (Fig. 3). For *Vaccinium oxycoccos* and *V. vitis-idaea*, model R^2 values generally decreased with increasing number of days over which environmental variables were calculated prior to sampling ($p \leq 0.0433$), with highest values at 5 days for both species (Fig. 3). *Sphagnum capillifolium* and *S. fuscum* exhibited no significant change in model R^2 values as a function of the number of days over which environmental variables were calculated prior to sampling ($p = 0.1904$ and 0.0872 , respectively), with highest values at 5 days prior to sampling for both species (Fig. 3).

Effect of weather-related environmental variables on tissue N concentrations

Both *Sphagnum* mosses, *S. capillifolium* and *S. fuscum*, behaved similarly, with environmental variables explaining 10.1 and 9.6 %, respectively, of the overall variation in N concentrations in capitula (Fig. 4). For the two *Sphagnum* species, capitulum N concentration was positively associated with T_a . Capitulum

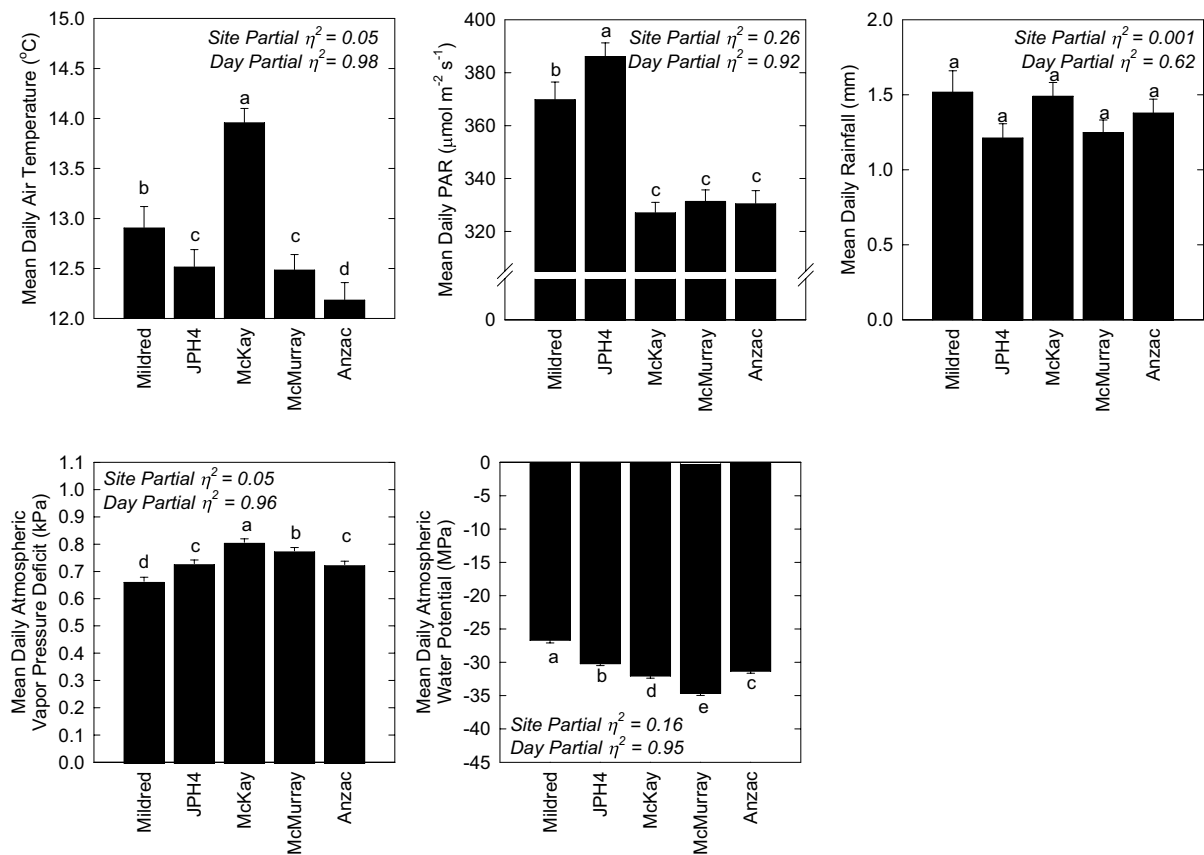


Fig. 1 Environmental variables across the five bog sites (means + one standard error). For each variable, means with the same letter do not differ significantly (ANOVA with site as a main effect and day as a blocked effect; *a posteriori* means

comparisons using Tukey's Honestly Significant Different test, $\alpha = 0.05$). Sites are arrayed from left to right in order of increasing distance from oil sands operations (midpoint between the Syncrude and Suncor main upgrader stacks)

N concentration was positively associated with WP_a for *S. fuscum*. The two *Vaccinium* species did not behave similarly. Foliar N concentration in *V. oxycoccus* was positively associated with T_a , WP_a , and VPD_a , and negatively associated with PPT ; these factors combined accounted for 20.1 % of the total variation in foliar N concentration. For *V. vitis-idaea*, foliar N was associated only with PPT , explaining 8.1 % of the overall variation. Environmental factors explained over 47 % of the total variation in foliar N concentration in the two deciduous forbs, *M. trifolium* and *R. chamaemorus*. For both species, foliar N concentrations were positively associated with PAR and negatively associated with WP_a and VPD_a , with these three variables explaining 31.3 and 58.4 % of total variation in foliar N concentration. Similarly to the two forb species, foliar N concentrations in *R.*

groenlandicum and *P. mariana* were positively associated with PAR and negatively associated with WP_a and VPD_a , with these three variables explaining 25.5 and 53.9 % of total variation in foliar N concentration, respectively.

Three-dimensional relationships

Both *Sphagnum* species and *V. oxycoccus* exhibited similar patterns in tissue N concentrations as a function of T_a and WP_a over the 5 days prior to sample collection (Fig. 5). Highest *Sphagnum* capitulum/leaf N concentrations occurred under conditions of relatively high WP_a (−11 to −18 MPa) in combination with relatively high T_a (22 $^{\circ}\text{C}$ for all of these three species). Lowest capitulum/leaf N concentrations occurred under conditions of relatively low WP_a

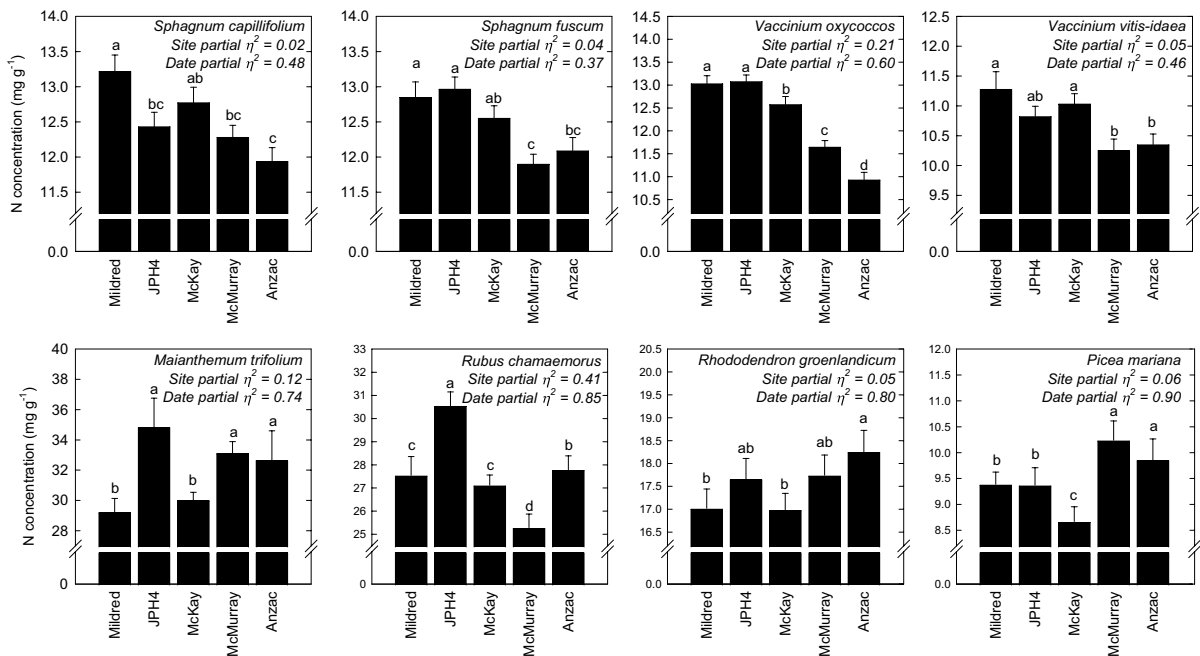
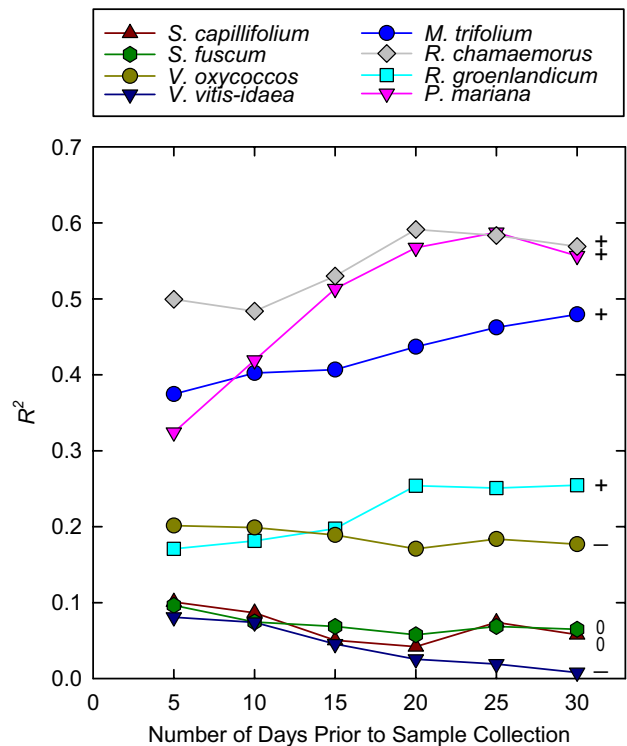


Fig. 2 Mean foliar N concentrations at the five bog sites (means + one standard error). For each variable, means with the same letter do not differ significantly (ANOVA with site as a main effect and collection date as a blocked effect; *a* *post*-

riori means comparisons using Tukey's Honestly Significant Different test; $\alpha = 0.05$). Sites are arrayed from left to right in order of increasing distance from oil sands operations (mid-point between the Syncrude and Suncor main upgrader stacks)

Fig. 3 R^2 values from best subset regressions of foliar N as a function of environment variables averaged over 5, 10, 15, 20, 25, and 30 days prior to sample collection. Symbols to the right of each plotted line indicate increasing (+), decreasing (-), or no significant change over time (0) (linear regressions, $\alpha = 0.05$)



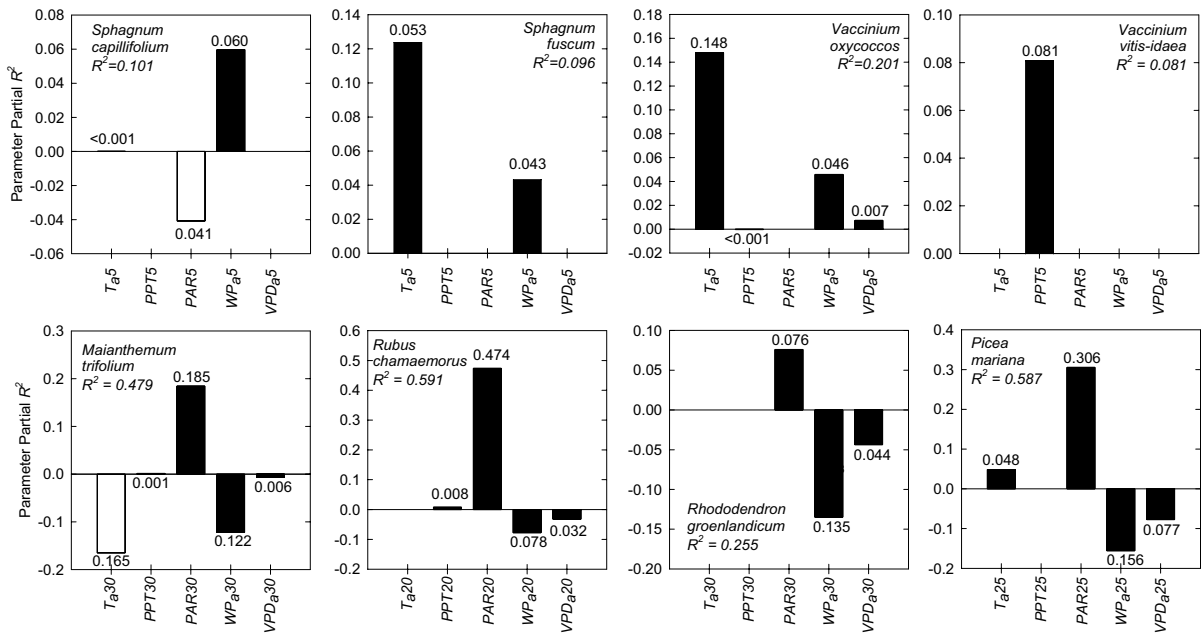


Fig. 4 Partial R^2 values for the environmental variables identified in the best subset regressions of tissue N concentrations as a function of environment variables. Variables on the x axes are mean daily air temperature (T_a), precipitation (PPT), photosynthetically active radiation (PAR), atmospheric water potential (WP_a), and atmospheric vapor pressure deficit (VPD_a) followed by a number indicating the number of days prior to sample collection that yielded the lowest AIC value for a par-

ticular species. Parameter estimates that are significant ($p < 0.10$) are filled in black; nonsignificant ($p > 0.10$) parameter estimates are filled in white. When an environment parameter was negatively associated with tissue N concentration, the parameter's R^2 value is plotted in the negative direction; this does not indicate a negative R^2 . Partial R^2 values are shown above or below each bar

(−38 to −45 MPa) in combination with relatively low T_a5 (−6 °C for all of these three species). Leaf N concentrations in *V. vitis-idaea* also were highest at high T_a (22 °C), but in combination with high PPT (54 mm), over the 5 days prior to sample collection (22 °C). For the two *Sphagnum* species and *V. oxycoccos*, the capitulum/leaf N concentration response to changing WP_a was much stronger at warmer temperatures than at cooler temperatures.

Leaf N concentrations in the four more deeply rooted vascular species (*M. trifolium*, *R. chamaemorus*, *R. groenlandicum*, *P. mariana*) exhibited somewhat similar responses, with highest N concentrations under low mean daily WP_a (−62 to −69 MPa) and moderate to high mean daily PAR (182 to 611 $\mu\text{mol m}^{-2} \text{s}^{-1}$) over the 20, 25, or 30 days prior to sample collection (Fig. 5). Three of these species (*M. trifolium*, *R. groenlandicum*, and *P. mariana*) had low leaf N concentrations when mean daily WP_a was higher than −40 mPa. For *R. chamaemorus*, leaf N concentrations were low at mean daily PAR values

lower than 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$. For all eight species, R^2 values for the 3-dimensional surfaces were higher than the sum of the partial R^2 values for the two independent variables obtained by best subset regression analysis (Fig. 4).

Discussion

Sphagnum capitulum N concentrations

Sphagnum mosses lack roots and rhizoids and do not form mycorrhizal symbioses (Read et al. 2000), which in most vascular bog plants are key to N acquisition. Growing *Sphagna* can acquire N by uptake of wet and dry deposited N and by uptake of N mineralized in organic matter decomposition that could reach growing *Sphagna* by diffusion and/or mass flow. Several studies have shown that N concentrations in *Sphagnum* increase with increasing N deposition along regional gradients (e.g. Lamers et al.

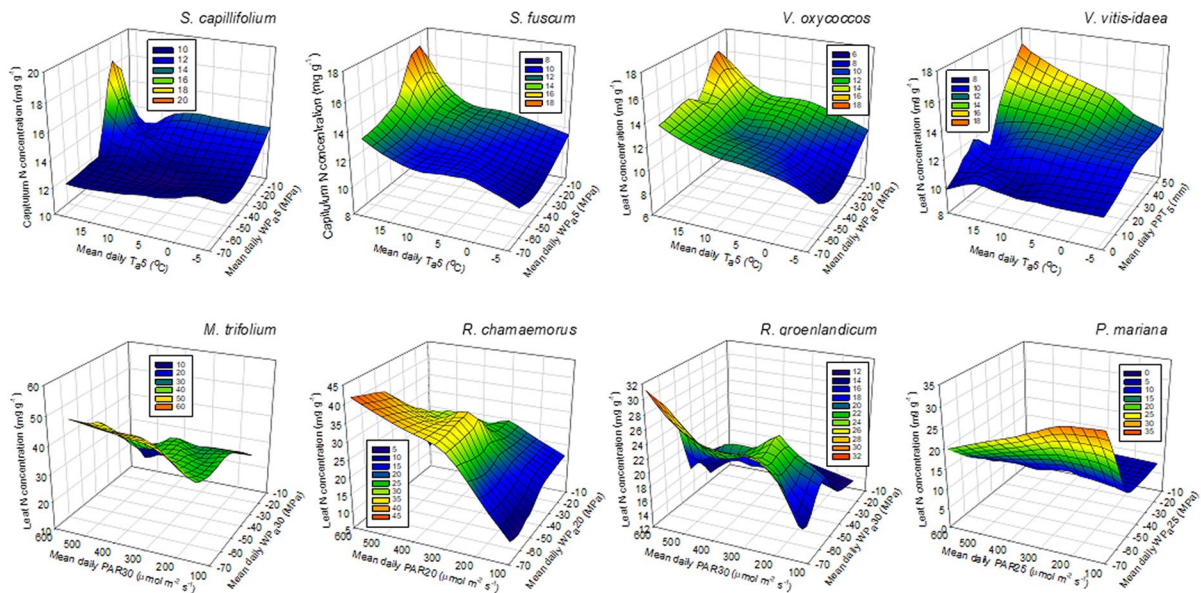


Fig. 5 Tissue N concentrations as a function of the two significant ($p < 0.10$) environmental variables with the highest partial R^2 in the best subset regression for the number of days prior to sampling (denoted by the numbers after the variable

names in the x and y axis labels) with the highest model R^2 . Plots are based on the individual points with loess smoothing, a sampling proportion value of 0.5, and a polynomial degree value of 1 (SigmaPlot 15.0)

2000; Bragazza and Limpens 2004; Bragazza et al. 2005; Wieder et al. 2016a, 2021), and experimental additions of N to *Sphagnum* in the field or in a greenhouse also have led to increased *Sphagnum* N concentrations (e.g. Granath et al. 2012; Juutinen et al. 2015). Experimental addition of N to a bog in northern Alberta, Canada led to increased N concentrations in *Sphagnum fuscum* stems, but not capitula (Wieder et al. 2019). Nonetheless, it is now evident that biological N_2 -fixation in surface *Sphagnum* may be a major, if not the dominant, source of new N in boreal and temperate bogs (Hemond 1983; Larmola et al. 2014; Vile et al. 2014; Yin et al. 2022). Further, the competitive success of boreal *Sphagnum* species may derive at least in part from biological N_2 -fixation being a major source of N (Lindo et al. 2013). Berg et al. (2013) showed that more than 35 % of cyanobacterially-fixed N was transferred to new growth of its water-loving *Sphagnum riparium* host; some of the fixed N may have been taken up by older *Sphagnum* shoots. Across 10 arctic mosses, including *Sphagnum compactum* and *S. fuscum*, N_2 -fixation (nitrogenase activity) and tissue N concentration were positively correlated (Rzepczynska et al. 2022). Given the importance of N_2 fixation to *Sphagnum*, in

the AOSR, we expected that environmental factors that favor N_2 -fixation also would be associated with high N concentrations in *Sphagnum* capitula.

N_2 -fixation in upland boreal mosses is affected by both temperature and moisture (cf. Rousk et al. 2017; Salemaa et al. 2019; Živković et al. 2022). The optimum temperature for nitrogenase activity has been reported to be about 25 °C (Houlton et al. 2008), although in cold arctic environments, diazotrophs may be adapted to much lower temperatures (Rousk et al. 2018). Our findings that N concentrations in *S. capillifolium* and *S. fuscum* were positively associated with T_a over the 5 days prior to sample collection (Fig. 4), with maximum capitulum N concentrations at 22 °C (Fig. 5) is consistent with higher rates of N_2 -fixation with warmer temperatures, and the transfer of some of that fixed N to *Sphagnum*.

Several studies have shown that decreasing moisture and/or increased evaporation diminish rates of N_2 -fixation in upland boreal mosses (e.g., Jackson et al. 2011; Gundale et al. 2009, 2012; Rousk et al. 2014, 2017; Živković et al. 2022). Our finding that N concentrations were positively associated with WP_a in *S. capillifolium* and in *S. fuscum* over the 5 days prior to sample collection (Figs. 4, 5) is consistent

with decreasing *Sphagnum*-associated N_2 -fixation with increasingly dryer air, reducing the supply of N to *Sphagnum* hosts. It appears that capitulum N concentrations, biological N_2 fixation, peat moisture, T_a , and WP_a are closely linked in boreal bog *Sphagnum* in the AOSR.

Vascular plant N concentrations

Unlike *Sphagnum*, vascular plants have leaves with cuticles that minimize water loss across the leaf/atmosphere interface and stomata that control opening and closing to limit transpirational water loss. The soil–plant–atmosphere continuum (Philip 1966) conceptualizes the movement of water into, through, within, and out of a plant, following gradients of progressively decreasing water potential. Transpiration lowers leaf water potential, which ultimately lowers root water potential such that soil water, containing dissolved N compounds and other nutrients, moves toward roots by mass flow (cf. Barber 1962, 1995). Root nutrient uptake lowers nutrient concentrations at the root/soil interface drawing nutrients to the root via diffusion (Barber 1995). When plant roots are mycorrhizal, these principles apply to the soil/hyphal interface in the fungus–soil–plant–atmosphere continuum (Allen 2009).

In some soils, rainfall dilutes nutrient concentrations in porewater, making the osmotic component of soil water potential less negative. Further, because rainfall increases peat moisture content, precipitation events should cause peat matric potential above the bog water table to become less negative (cf. Allen 2009). Given these factors, environmental parameters, including T_a , PPT , PAR , WP_a , and VPD_a , individually and in combination, have the potential to affect the water potential of peat porewater above the bog water table, and therefore affect leaf N concentration in vascular plants.

If leaf N concentration in *V. oxycoccos* and *V. vitis-idaea* are affected by environmental parameters, the responses of the two species were expected to be similar, but this was not the case (Figs. 4, 5). Indeed, the *V. oxycoccos* response was similar to both *Sphagnum* species (leaf N concentrations positively associated with warmer, moister air), and the *V. vitis-idaea* response, involving T_a and PPT , was unique among the eight vascular plant species (Figs. 4, 5). In *V. oxycoccos*, fine adventitious roots arise from axillary

buds on prostrate stems that become buried by growing *Sphagnum* (Jacquemart 1997), thus the roots are very close to the peat surface. That the *V. oxycoccos* leaf N concentration response to environmental parameters was similar to the response of the *Sphagnum* species is consistent with Malmer's et al. (1994) assertion *V. oxycoccos* has very shallow, short, ericoid mycorrhizal root systems that penetrate only a few cm into the peat and thus *V. oxycoccos* may rely on the same sources as *Sphagnum* for nutrients and water. High temperatures and high WP_a facilitate N_2 -fixation in near-surface peat, leading to higher N concentrations in both *Sphagnum* and *V. oxycoccos* leaves.

The only significant environmental parameter that affected leaf N concentrations in *V. vitis-idaea* was PPT (Fig. 4); the 2-parameter best subset regression describing leaf N concentrations included T_a5 and $PPT5$. Hair-like roots of *V. vitis-idaea* arise from axils of leaf scars of rhizomes that occur at 10–20 cm below the soil surface (Ritchie 1955; Smith 1962), so *V. vitis-idaea* roots are generally deeper in the peat profile than *V. oxycoccos* roots. Both *Vaccinium* species harbor ericoid mycorrhizae, which in general have saprotrophic capabilities that are greater than those of ectomycorrhizae or arbuscular mycorrhizae (cf. Ward et al. 2022). Across the 5 bog sites in the oil sands region, *V. oxycoccos* leaves had a slightly more negative $\delta^{15}N$ value (-7.91 ± 0.05 ‰) than *V. vitis-idaea* leaves (-5.71 ± 0.06 ‰) (Wieder et al. 2022). Given that the $\delta^{15}N$ of bog peat generally increases with depth (Kohzu et al. 2003; Blodau et al. 2006; Hobbie et al. 2017; Drollinger et al. 2019), the *V. vitis-idaea* N sources may be deeper in the peat than the *V. oxycoccos* N sources. Recent precipitation could facilitate N movement to ericoid roots of *V. vitis-idaea* by increasing mass flow and diffusion of peat porewater N toward *V. vitis-idaea* roots, which may be a more important mechanism of N acquisition than for *V. oxycoccos*.

The two deciduous, non-mycorrhizal species, *M. trifolium* and *R. chamaemorus*, have roots that are generally constrained to the acrotelm, although aerenchymal roots can extend below the water table (Taylor 1971, 1989; Rydin and Jeglum 2006; Murphy et al. 2009; Moore et al. 2011), so growth and N uptake may not be limited by access to water. *R. chamaemorus* transfers nutrients from leaves to roots and rhizomes in the fall and back to the new leaves as they appear in late spring/early summer

(Rydin and Jeglum 2006). As a result, leaf N concentrations are highest when the leaves first appear in June and progressively decrease through the growing season, in part from dilution by photosynthetically fixed carbon as leaves grow, a pattern also seen in *M. trifolia* (Wieder et al. 2021). In both *M. trifolium* and *R. chamaemorus*, leaf N concentrations were positively correlated with *PAR*, with partial R^2 values of 0.202 and 0.511, respectively (Fig. 4). This response is likely related to increased stomatal opening with increasing *PAR*. Indeed, *R. chamaemorus* leaves have been shown to exhibit a rapid photosynthetic response to increasing light intensity (Marks and Taylor 1978). Greater stomatal opening could facilitate transpiration and hence the mass flow of porewater, with dissolved nutrients, toward *R. chamaemorus* roots even below the bog water table, resulting in increased N concentrations in leaves.

R. groenlandicum is an ericaceous shrub with ericoid mycorrhizal roots. As peat vertically accumulates, *R. groenlandicum* adventitious roots develop from buried stems, such that roots occur throughout the peat above the bog water table (Calmes and Zasada 1982; Moola et al. 2024). As with *M. trifolium* and *R. chamaemorus*, leaf N concentrations in *R. groenlandicum* were positively associated with dryer, sunnier conditions over the 30 days prior to leaf sample collection, which collectively may foster stomatal opening and transpirational water losses, ultimately facilitating the movement of water and its dissolved nutrients toward *R. groenlandicum* mycorrhizal roots. Indeed *R. groenlandicum* has much higher stomatal conductance and leaf N than *P. mariana* (Hébert et al. 2010). All of these factors collectively may contribute to *R. groenlandicum* outcompeting *P. mariana* for N (Inderjit and Mallik 1996), even though both species have roots throughout upper layers of peat above the bog water table. In the AOSR bogs, *R. groenlandicum* does show a peak in N concentration in first-year leaves in mid to late June, most likely reflecting retranslocation of stored N from perennial plant tissues to support new growth (Wieder et al. 2021). Here we show maximum *R. groenlandicum* leaf N concentration being associated with low mean daily WP_a and high mean daily *PAR* over the past 30 days (Fig. 5), conditions that are more characteristic of mid-summer. Thus, temporal variability in leaf N concentration for *R. groenlandicum* may have both phenological and weather-related

environmental components with differential importance at different times of the year.

Picea mariana is the only ectomycorrhizal species in the five Alberta bog sites in the AOSR. Because roots of *P. mariana* lack aerenchyma, they are restricted to unsaturated peat above the water table, with most roots in the upper 20 cm of peat in wetter sites (Liefers and Rothwell 1987). In general, ectomycorrhizae have less saprotrophic ability than ericoid mycorrhizae (Ward et al. 2022). Nonetheless, *P. mariana* first year needles have lower $\delta^{15}\text{N}$ values than other species in the Alberta bog study sites (Wieder et al. 2022) suggesting that ectomycorrhizal transfer of isotopically light N to *P. mariana* roots is a major source of needle N (Michelsen et al. 1998; Emmerton et al. 2001; Craine et al. 2015). First-year needle N concentrations were negatively associated with both WP_a and VPD_a averaged over the 25 days prior to sampling; with these two environmental variables combined explaining 53.8 % of the overall variation in first-year needle N concentrations (Fig. 4). In the 3-D plots, WP_a and *PAR* explained 54 % of the overall variation in first-year needle N concentrations (Fig. 5). These patterns are consistent with a decreasing WP_a causing a greater water potential gradient between the atmosphere and peat porewater, stimulating transpiration and the movement of peat porewater, with its dissolved nutrients toward *P. mariana* ectomycorrhizal roots, enhancing N uptake and transport to needles. The negative association between needle N and VPD_a is consistent with VPD_a functioning as a major controller of stomatal aperture in *P. mariana* (cf. Dang et al. 1997; Pepin et al. 2002). Like *R. groenlandicum*, *P. mariana* first-year needles show a peak in N concentration in mid to late June (Wieder et al. 2021), with maximum needle N concentrations being associated mainly with very low WP_a , and to a lesser extent low mean daily *PAR* (Fig. 5), conditions that could prevail in early summer. Unlike *R. groenlandicum*, *P. mariana* needle N concentrations may be affected by phenological and weather-related environmental parameter components coming to bear at the same time during the growing season.

Summary and conclusions

Prior to development of the oil sands resource beginning in 1970, ecosystems of the AOSR received low inputs of N through wet and dry

deposition. As oil sands development has proceeded, N emissions from upgrader sacks and mine fleet vehicles have increased, resulting in increasing N deposition. This increasing N deposition may affect aspects of ecosystem function, especially in nutrient poor ecosystems, like bogs. Previously, we showed that across five bogs in the AOSR, N concentrations in *Sphagnum* capitula and leaves of vascular plants exhibited variability within a bog on a particular day, between sampling dates at a particular bog, and between bogs. Here, we confirm that N concentrations in capitula of *S. capillifolium* and *S. fuscum* and in leaves of *V. oxycoccus*, *V. vitis-idaea*, and *R. chamaemorus* decreased exponentially with distance from oil sands facilities, a pattern consistent with N emissions and subsequent deposition related to oil sand development affecting plant tissue N concentrations. Distance explained 4–16 % of the variability in plant tissue N concentrations. Here, we have shown that climate-related environmental variables, T_a , PPT , PAR , WP_a , and VPD_a can explain 12–61 % of the variability in N concentrations within species. Tissue N concentrations in more deeply rooted vascular species (*M. trifolium*, *R. chamaemorus*, *R. groenlandicum*, *P. mariana*) respond to environmental variables over longer period of time prior to sample collection (the previous 20–30 days) than more shallow rooted vascular species (*V. oxycoccus*, *V. vitis-idaea*) or mosses (*S. capillifolium*, *S. fuscum*), which respond to environmental variables over shorter periods of time (the previous 5–10 days). Looking forward, if oil sands development in the AOSR continues to expand, N emissions and thus N deposition is likely to continue to increase. Ongoing climate change may bring warmer and possibly wetter conditions to boreal Alberta (Eum et al. 2023). Because precipitation is the vehicle by which N is delivered to ecosystems in wet deposition, precipitation quantity as an environmental variable and wet N deposition as a biogeochemical variable are confounded. Nonetheless, precipitation quantity and wet nitrogen deposition may affect bog plant tissue N concentrations interactively. Disentangling how bog plant N concentrations are affected by N deposition versus environmental climate-related factors will be key to the ability of monitoring programs to be able to identify oil sands related effects on natural ecosystems across the AOSR.

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Data availability All tissue N concentration data are available on the Oil Sands Monitoring Program Data Catalog: <https://osmdatalog.alberta.ca/dataset/wetland-vegetation-tissue-content>

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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References

- Allen MF (2009) Bidirectional water flows through the soil-fungal-plant mycorrhizal continuum. *New Phytol* 182:209–213. <https://doi.org/10.1111/j.1469-8137.2009.02815.x>

- Barber SA (1962) A diffusion and mass-flow concept of soil nutrient availability. *Soil Sci* 93:39–49. <https://doi.org/10.1097/00010694-196201000-00007>
- Barber SA (1995) Soil nutrient bioavailability: A mechanistic approach, 2nd edn. Wiley, New York
- Berg A, Danielson Å, Svensson BH (2013) Transfer of fixed-N from N₂-fixing cyanobacteria associated with the moss *Sphagnum riparium* results in enhanced growth of the moss. *Plant Soil* 362:271–278. <https://doi.org/10.1007/s11104-012-1278-4>
- Blodau C, Basiliko N, Mayer B, Moore TR (2006) The fate of experimentally deposited nitrogen in mesocosms from two Canadian peatlands. *Sci Total Environ* 364:215–228. <https://doi.org/10.1016/j.scitotenv.2005.06.002>
- Bragazza L, Limpens J (2004) Dissolved organic nitrogen dominates in European bogs under increasing atmospheric N deposition. *Global Biogeochem Cy* 18:GB4018. <https://doi.org/10.1029/2004GB002267>
- Bragazza L, Limpens J, Gerdol R, Grosvernier P, Hájek M, Hajkova P, Jansen I, Iacumin P, Kutnar L, Rydin H, Tahvanainen T (2005) Nitrogen concentration and $\delta^{15}\text{N}$ signature of ombrotrophic *Sphagnum* mosses at different N deposition levels in Europe. *Glob Change Biol* 11:106–114. <https://doi.org/10.1111/j.1365-2486.2004.00886.x>
- Calmes MA, Zasada JC (1982) Some reproductive traits of four shrub species in the black spruce forest type of Alaska. *Can Field Nat* 96:35–40. <https://doi.org/10.5962/p.354760>
- Craine JM, Brookshire ENJ, Cramer MD, Hasselquist NJ, Koba K, Marin-Spiotta E, Wang L (2015) Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant Soil* 396:1–26. <https://doi.org/10.1007/s11104-015-2542-1>
- Dang Q-L, Margolis HA, Coyea MR, Sy M, Collatz GJ (1997) Regulation of branch-level gas exchange of boreal trees: roles of shoot water potential and vapor pressure difference. *Tree Physiol* 17:521–535. <https://doi.org/10.1093/treephys/17.8-9.521>
- Drollinger A, Kuzyakov Y, Glatzel S (2019) Effects of peat decomposition on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ depth profiles of alpine bogs. *CATENA* 178:1–10. <https://doi.org/10.1016/j.catena.2019.02.027>
- Edgerton ES, Hsu Y-M, Landis MS, White EM (2020) Ambient concentration and total deposition of sulfur, nitrogen and base cations in the AOSR. *Sci Total Environ* 706:134864. <https://doi.org/10.1016/j.scitotenv.2019.134864>
- Emmertson KS, Callaghan TV, Jones HE, Leake JR, Michelsen A, Read DJ (2001) Assimilation and isotopic fractionation of nitrogen by mycorrhizal fungi. *New Phytol* 151:503–511. <https://doi.org/10.1046/j.1469-8137.2001.00178.x>
- Eum H-I, Fajard B, Tang T, Gupta A (2023) Potential changes in climate indices in Alberta under projected global warming of 1.5–5 °C. *J Hydrol: Reg Stud* 47:101390. <https://doi.org/10.1016/j.ejrh.2023.101390>
- Fenn ME, Bytnerowicz A, Schilling SL, Ross CS (2015) Atmospheric deposition of nitrogen, sulfur and base cations in jack pine stands in the Athabasca Oil Sands Region, Alberta, Canada. *Environ Pollut* 196:497–510. <https://doi.org/10.1016/j.envpol.2014.08.023>
- Gong H, Li Y, Yu T, Zhang S, Gao J, Zhang S, Sun D (2020) Soil and climate effects on leaf nitrogen and phosphorus stoichiometry along elevational gradients. *Global Ecol Conserv* 23(2020):e01138. <https://doi.org/10.1016/j.gecco.2020.e01138>
- Granath G, Strenghom J, Rydin H (2012) Direct physiological effects of nitrogen on *Sphagnum*: a greenhouse experiment. *Funct Ecol* 26:353–364. <https://doi.org/10.1111/j.1365-2435.2011.01948.x>
- Gundale MJ, Gustafsson H, Nilsson M-C (2009) The sensitivity of nitrogen fixation by a feathermoss–cyanobacteria association to litter and moisture variability in young and old boreal forests. *Can J for Res* 39:2542–2549. <https://doi.org/10.1139/X09-16>
- Gundale MJ, Wardle DA, Nilsson M-C (2012) The effect of altered macroclimate on N-fixation by boreal feather mosses. *Biol Lett* 8:805–808. <https://doi.org/10.1098/rsbl.2012.0429>
- Hébert F, Thiffault N, Ruel JC, Munson AD (2010) Comparative physiological responses of *Rhododendron groenlandicum* and regenerating *Picea mariana* following partial canopy removal in northeastern Quebec, Canada. *Can J for Res* 40:1791–1802. <https://doi.org/10.1139/X10-124>
- Hemond H (1983) The nitrogen budget of Thoreau's Bog. *Ecology* 64:99–109. <https://doi.org/10.2307/1937333>
- Hikosaka K (2016) Optimality of nitrogen distribution among leaves in plant canopies. *J Plant Res* 129:299–311. <https://doi.org/10.1007/s10265-016-0824-1>
- Hobbie EA, Chen J, Hansen PJ, Iversen CM, McFarlane KJ, Thorp RN, Hofmockel KS (2017) Long-term carbon and nitrogen dynamics at SPRUCE revealed through stable isotopes in peat profiles. *Biogeosciences* 14:2481–2492. <https://doi.org/10.5194/bg-14-2481-2017>
- Houlton BZ, Wang Y-P, Vitousek PM, Field CB (2008) A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454:327–331. <https://doi.org/10.1038/nature07028>
- Hsu Y-M, Bytnerowicz A, Fenn ME, Percy KE (2016) Atmospheric dry deposition of sulfur and nitrogen in the Athabasca Oil Sands Region, Alberta, Canada. *Sci Total Environ* 568:285–295. <https://doi.org/10.1016/j.scitotenv.2016.05.205>
- Inderjit, Mallik MAU (1996) Growth and physiological responses of black spruce (*Picea mariana*) to sites dominated by *Legum groenlandicum*. *J Chem Ecol* 22:575–585. <https://doi.org/10.1007/BF02033656>
- Jackson BG, Martin P, Nilsson M-C, Wardle DA (2011) Response of feather moss associated N₂ fixation and litter decomposition to variations in simulated rainfall intensity and frequency. *Oikos* 120:570–581. <https://doi.org/10.1111/j.1600-0706.2010.18641.x>
- Jacquemart J-E (1997) *Vaccinium oxycoccus* L. (*Oxycoccus palustris* Pers.) and *Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh. (*Oxycoccus microcarpus* Turcz. ex Rupr.). *J Ecol* 85:381–396. <https://doi.org/10.2307/2960511>
- Juutinen S, Moore TR, Laine AM, Bubier JL, Tuitilla E-S, De Young A, Chong M (2015) Responses of the mosses *Sphagnum capillifolium* and *Polytrichum strictum* to nitrogen deposition in a bog: growth, ground cover, and CO₂ exchange. *Botany* 94:127–138. <https://doi.org/10.1139/cjb-2015-0183>

- Kohzu A, Matsui K, Yamada T, Sugimoto A, Fugita N (2003) Significance of rooting depth in mire plants: Evidence from natural ^{15}N abundance. *Ecol Res* 18:257–266. <https://doi.org/10.1046/j.1440-1703.2003.00552.x>
- Kranabetter JM, Simard SW, Gray RD, Coates KD (2010) Species patterns in foliar nitrogen concentration, nitrogen content and ^{13}C abundance for understory saplings across light gradients. *Plant Soil* 327:389–401. <https://doi.org/10.1007/s11104-009-0062-6>
- Lakens D (2013) Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for *t*-tests and ANOVAs. *Front Psychol* 4:863. <https://doi.org/10.3389/fpsyg.2013.00863>
- Lamers LPM, Bobbink R, Roelofs JGM (2000) Natural nitrogen filter fails in polluted raised bogs. *Global Change Biol* 6:583–586. <https://doi.org/10.1046/j.1365-2486.2000.00342.x>
- Larmola T, Leppänen SM, Tuittila E, Aarva M, Merilä P, Fritze H (2014) Methanotrophy induces nitrogen fixation during peatland development. *P Natl Acad Sci USA* 111:734–739. <https://doi.org/10.1073/pnas.1314284111>
- Lieffers VJ, Rothwell RL (1987) Rooting of peatland black spruce and tamarack in relation to depth of water table. *Can J Bot* 65:817–821. <https://doi.org/10.1139/b87-111>
- Lindo Z, Nilsson M-C, Gundale MJ (2013) Bryophyte-cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change. *Global Change Biol* 19:2022–2035. <https://doi.org/10.1111/gcb.12175>
- Malmer N, Svensson BM, Wallén B (1994) Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobot Phytotax* 29:483–496. <https://doi.org/10.1007/BF02883146>
- Marks TC, Taylor K (1978) The carbon economy of *Rubus chamaemorus* L. I. Photosynthesis. *Ann Bot* 42:165–179. <https://doi.org/10.1093/oxfordjournals.aob.a085437>
- McNeil BE, Read JM, Driscoll CT (2012) Foliar nitrogen responses to the environmental gradient matrix of the Adirondack Park, New York. *Ann Assoc Am Geog* 102:1–16. <https://doi.org/10.1080/00045608.2011.595654>
- Michelsen A, Quarmby C, Sleep D, Jonasson S (1998) Vascular plant ^{15}N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia* 115:406–418. <https://doi.org/10.1007/s004420050535>
- Moola F, Ni YZ, Mallik AU (2024) Clonal response of a recalcitrant understory shrub, Labrador tea (*Rhododendron groenlandicum* Oeder.) to forest gaps. *Can J for Res* 54:1296–1310. <https://doi.org/10.1139/cjfr-2024-0021>
- Moore TR, Young AD, Bubier JL, Humphreys ER, LaFleur PM, Roulet NT (2011) A multi-year record of methane flux at the Mer Bleue Bog, southern Canada. *Ecosystems* 14:646–657. <https://doi.org/10.1007/s10021-011-9435-9>
- Murphy MT, McKinley A, Moore TR (2009) Variations in above- and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland. *Botany* 87:845–853. <https://doi.org/10.1139/B09-052>
- Pepin A, Plamondon AP, Breitel A (2002) Water relations of black spruce trees on a peatland during wet and dry years. *Wetlands* 22:225–233. [https://doi.org/10.1672/0277-5212\(2002\)022\[0225:WROBST\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2002)022[0225:WROBST]2.0.CO;2)
- Philip JR (1966) Plant water relations: some physical aspects. *Ann Rev Plant Physiol* 17:245–268. <https://doi.org/10.1146/annurev.pp.17.060166.001333>
- Read DJ, Duckett JG, Francis R, Ligrone R, Russell A (2000) Symbiotic fungal associations in ‘lower’ land plants. *Phil T Roy Soc B* 355:815–831. <https://doi.org/10.1098/rstb.2000.0617>
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *P Natl Acad Sci USA* 101:11001–11006. <https://doi.org/10.1073/pnas.0403588101>
- Ritchie JC (1955) *Vaccinium vitis-idaea* L. *J Ecol* 43:701–708. <https://doi.org/10.2307/2257030>
- Rousk K, Jones DL, DeLuca TH (2014) The resilience of nitrogen fixation in feather moss (*Pleurozium schreberi*)-cyanobacteria associations after a drying and rewetting cycle. *Plant Soil* 374:513–521. <https://doi.org/10.1007/s11104-013-1984-6>
- Rousk K, Pedersen PA, Dyrnum K, Michelsen A (2017) The interactive effects of temperature and moisture on nitrogen fixation in two temperate-arctic mosses. *Theor Exp Plant Phys* 29:25–36. <https://doi.org/10.1007/s40626-016-0079-1>
- Rousk K, Sorensen PL, Michelsen A (2018) What drives biological nitrogen fixation in high arctic tundra: Moisture or temperature? *Ecosphere* 9:e02117. <https://doi.org/10.1002/ecs2.2117>
- Rydin H, Jeglum JK (2006) Adaptations to the peatland habitat. In Rydin H, Jeglum JK (eds) *The biology of Sphagnum*, 1st edn. Oxford Academic, Oxford, pp 45–47. <https://doi.org/10.1093/acprof:oso/9780198528722.003.0003>
- Rzeczynska AM, Michelsen A, Olsen MAN, Lett S (2022) Bryophyte species differ widely in their growth and N₂-fixation responses to temperature. *Arctic Sci* 8:1236–1251. <https://doi.org/10.1139/AS-2021-0053>
- Salemaa M, Lindroos A-J, Merilä P, Mäkipää R, Smolander A (2019) N₂ fixation associated with the bryophyte layer is suppressed by low levels of nitrogen deposition in boreal forests. *Sci Total Environ* 653(2019):995–1004. <https://doi.org/10.1016/j.scitotenv.2018.10.364>
- Smith DW (1962) Ecological studies of *Vaccinium* species in Alberta. *Can J Plant Sci* 42:82–90. <https://doi.org/10.4141/cjps62-01>
- Taylor K (1971) *Rubus chamaemorus* L. *J Ecol* 59:293–306. <https://doi.org/10.2307/2258468>
- Taylor K (1989) The absence of mycorrhiza in *Rubus chamaemorus*. *Ann Bot Fenn* 26:421–425. <https://www.jstor.org/stable/23725674>. Accessed 6 Jan 2025
- Tian D, Schmid B, Kattge J, Fang J (2024) Stocker BD (2024) Environmental versus phylogenetic controls on leaf nitrogen and phosphorous concentrations in vascular plants. *Nat Commun* 15:5346. <https://doi.org/10.1038/s41467-024-49665-4>
- Vile MA, Wieder RK, Živković T, Scott KD, Vitt DH, Hartsock JA, Iosue CL, Quinn JC, Petix M, Fillingim H, Popma JMA, Dynarski KA, Jackman TR, Albright CM, Wyckoff DD (2014) N₂-fixation by methanotrophs sustains carbon and nitrogen accumulation in pristine peatlands. *Biogeochemistry* 121:317–328. <https://doi.org/10.1007/s10533-014-0019-6>

- Ward EB, Duguid MC, Kuebbing SE, Lendemer SC (2022) Bradford MA (2022) The functional role of ericoid mycorrhizal plants and fungi on carbon and nitrogen dynamics in forests. *New Phytol* 235:1701–1718. <https://doi.org/10.1111/nph.18307>
- Warming E (1908) The structure and biology of arctic flowering plants. I. Ericineae. I. Morphology and Biology Meddelelser Om Groenland 36:1–71
- Warner BG, Rubec CDA (eds) (1997) The Canadian wetland classification system, 2nd edn. Wetlands Research Centre, University of Waterloo, Waterloo, Ontario, Canada, National Wetlands Working Group, p 68
- Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? *J Anim Ecol* 75:1182–1189. <https://doi.org/10.1111/j.1365-2656.2006.01141.x>
- Wieder RK, Vile MA, Scott KD, Albright CM, McMillen K, Vitt DH, Fenn M (2016a) Differential effects of high atmospheric N and S deposition on bog plant/lichen tissue and porewater chemistry across the Athabasca Oil Sands Region. *Environ Sci Technol* 50:12630–12640. <https://doi.org/10.1021/acs.est/6b03109>
- Wieder RK, Vile MA, Albright SM, Scott KD, Vitt DH, Quinn JC, Burke-Scoll M (2016b) Effects of altered atmospheric nutrient deposition from Alberta oil sands development on *Sphagnum fuscum* growth and C, N, and S accumulation in peat. *Biogeochemistry* 129:1–19. <https://doi.org/10.1007/s10533-016-0216-6>
- Wieder RK, Vitt DH, Vile MA, Graham JA, Hartsock JA, Fillingim H, House M, Quinn JC, Scott KD, Petix M, McMillen KJ (2019) Experimental nitrogen addition alters structure and function of a boreal bog: Critical load and thresholds revealed. *Ecol Monogr* 89:e01371. <https://doi.org/10.1002/ecm.1371>
- Wieder RK, Vile MA, Scott KD, Albright CM, Quinn JC, Vitt DH (2021) Bog plant/lichen tissue nitrogen and sulfur concentrations as indicators of emissions from oil sands development in Alberta. *Canada Environ Monit Assess* 193:208. <https://doi.org/10.1007/s10661-021-08929-y>
- Wieder RK, Vile MA, Vitt DH, Scott KD, Xu B, Quinn JC, Albright CM (2022) Can plant or lichen natural abundance ^{15}N ratios indicate the influence of oil sands N emissions on bogs? *J Hydrol Regional Stud* 40(2022):101030. <https://doi.org/10.1016/j.ejrh.2022.101030>
- Yin X (1993) Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. *Can J for Res* 23:1587–1602. <https://doi.org/10.1139/x93-199>
- Yin T, Feng M, Qiu C, Peng S (2022) Biological nitrogen fixation and nitrogen accumulation in peatlands. *Front Earth Sci* 10:670867. <https://doi.org/10.3389/feart.2022.670867>
- Živković T, Helbig M, Moore TR (2022) Seasonal and spatial variability of biological N_2 fixation in a cool temperate bog. *J Geophys Res-Biogeosciences* 127:e2021JG006481. <https://doi.org/10.1029/2021JG006481>

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