

Fine-scale vegetation distribution in a cool temperate peatland

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Abstract: Carbon (C) modeling and carbon dioxide (CO₂) flux measurements in peatlands are dependent on the distribution and productivity of vegetation in a system with a high degree of spatial variability, often linked to the position of the water table. We tested the hypothesis that at a fine-scale (tens of metres) water table position exerts a strong control on species abundance, plant biomass, particularly photosynthetically active tissues, leaf area index (LAI), and areal foliar N and chlorophyll at Mer Bleue, a cool temperate peatland in eastern Canada. Total aboveground biomass ranged from 147 to 1011 g·m⁻², with shrubs contributing between 42% and 72% of the total in the transects. We found significant ($P < 0.05$) positive relationships between foliar and total vascular plant biomass and mean water table position, and significant decreases in the shrub foliar:woody biomass ratio and moss biomass with a lower water table. However, there was no significant relationship between water table position and photosynthetically active tissues (vascular plant leaves and moss capitulum), ranging from 114 to 672 g·m⁻²) and the areal mass of N in these tissues, ranging from 1.5 to 6.7 g·m⁻². Multivariate analyses of vegetation and environmental data showed that species distribution could be explained by both water table and chemistry gradients and that unimodal rather than linear responses best described the species and water table relationships. LAI ranged from 0.1 to over 3 and was correlated with both water table position and with vascular foliar biomass. Percent cover of shrubs was correlated with foliar biomass and LAI. Our results suggest that the less labour-intensive estimates of percent cover can be used to predict the vascular plant foliar biomass and LAI measurements. The lack of relationship between photosynthetically active tissues, tissue N concentrations, and water table may also explain the surprising lack of spatial variability in peak growing season eddy flux net ecosystem CO₂ exchange in three different areas of the peatland.

Key words: biomass, bog, environmental gradients, multivariate analyses, vegetation distribution, water table.

Résumé : Dans un système avec un fort degré de variabilité spatiale, souvent lié à la position de la nappe phréatique, la modélisation du carbone (C) et les mesures du flux de bioxyde de carbone (CO₂) dans les tourbières, dépendent de la distribution et de la productivité de la végétation. Les auteurs ont vérifié l'hypothèse à savoir qu'à une échelle fine (dizaines de mètres), la position de la nappe phréatique exerce un contrôle sur l'abondance des espèces, la biomasse végétale, particulièrement les tissus photosynthétiquement actifs, l'index de surface foliaire (LAI), ainsi que la chlorophylle et le N aréaux, à Mer Bleue, une tourbière de région fraîche tempérée de l'est du Canada. La masse totale épigée est de 147 à 1011 g·m⁻², les arbustes constituant entre 42 % et 72 % du total dans les transects. On observe des relations positives significatives ($P < 0,05$) entre la biomasse foliaire et totale des plantes vasculaires, et la position moyenne de la nappe phréatique, ainsi que des diminutions significatives entre le rapport des biomasses foliaires:ligneuses des arbustes et la biomasse des mousses, avec une nappe phréatique plus basse. Cependant, il n'y a pas de relation entre la position de la nappe phréatique et les tissus photosynthétiquement actifs (feuilles des plantes vasculaires et capitulum), allant de 114 à 672 g·m⁻², et la masse aérale du N dans ces tissus, allant de 1,5 à 6,7 g·m⁻². Les analyses multivariées de la végétation et des données environnementales montrent que la distribution des espèces peut s'expliquer à la fois par les gradients de la nappe phréatique et de la chimie, et que ce sont des réactions unimodales plutôt que linéaires qui décrivent le mieux les relations entre les espèces et la nappe phréatique. Le LAI varie de 0,1 à plus de 3 et est fortement corrélé à la fois avec la position de la nappe phréatique et avec la biomasse foliaire vasculaire. Le pourcentage de couverture par les arbustes est corrélé avec la biomasse foliaire le LAI. Les résultats suggèrent que les estimés du pourcentage de couverture, qui exigent moins de travail, peuvent être utilisés pour prédire les mesures de biomasse foliaire vasculaire et le LAI. L'absence de relation entre les tissus photosynthétiquement actifs, la teneur en N des tissus, et la nappe phréatique explique également la surprenante absence de variabilité spatiale dans le flux net d'échange de CO₂ net dans l'écosystème, au pic de la saison de croissance, dans trois parties distinctes de la tourbière.

Mots clés : biomasse, tourbière, gradients environnementaux, analyse multivariée, distribution de la végétation, nappe phréatique.

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Introduction

Several studies have identified the overall controls of climate, hydrology, and nutrient status on the broad distribution of vegetation among and within northern peatlands (e.g., Vitt and Chee 1990; Glaser 1992; Gignac et al. 2004). An important feature of many temperate and boreal peatlands is a microtopography of hummocks and hollows created by differences in rates of organic matter production and decomposition (Økland 1990; Johnson and Damman 1993; Belyea and Clymo 2001). These distinctive features, which may vary in elevation by tens of centimetres, create fine-scale variability in microclimatology and particularly water table position that, in turn, influences the distribution and productivity of vegetation, creating niches for species (e.g., Vitt and Slack 1975; Malmer 1986; Økland 1990; Gignac et al. 1991; Glaser 1992). In Norway, Nordbakken (1996a, 1996b) has examined the fine-scale variation in coverage of species in relation to water table position within sections of individual peatlands. Although much of the variation in species distribution can be explained by the hummock–hollow or water table gradient, water chemistry, competition for limited resources, disturbance, and successional patterns are also important. A certain amount of unexplained spatial variation was also apparent in the Norwegian study, perhaps owing to the stochastic nature of bog vegetation in response to a combination of several environmental factors (Nordbakken 1996a).

Many of these studies have employed species coverage estimates, but modern studies of the carbon dioxide (e.g., Bubier et al. 2003a; Lafleur et al. 2003) and methane (e.g., Moore and Roulet 1993; Bubier et al. 1995) exchange of peatlands and the cycling of nutrients require a quantification of the mass of photosynthetically active tissues and other biomass (e.g., Frolking et al. 2002) and their relationship to water table position, which influences the rate of decomposition of organic matter (e.g., Moore and Dalva 1993). Since peatlands store approximately one-third of the global pool of soil carbon (Gorham 1991) and vegetation structure strongly influences the C sink capacity of peatlands (Belyea and Malmer 2004), it is important to quantify and understand the environmental controls on plant community and biomass distribution. Ecological data are also essential for interpreting net ecosystem CO₂ exchange data from chambers and towers (Moore et al. 2002). These gas flux measurements involve scaling from the size of the chamber base (usually <1 m²) to the footprint of eddy covariance towers (several hundred square metres). Advances in remote sensing, both through hyperspectral characterization as well as pixel resolutions decreasing from hundreds of metres (e.g., LANDSAT, MODIS) to 1 m (e.g., QUICKBIRD) allow a better determination of the distribution and spatial structure of vegetation with patterned peatlands.

We conducted this study at Mer Bleue, a cool temperate peatland in eastern Canada at which carbon dioxide and methane gas fluxes are being made by chambers and eddy covariance towers. At a fine-scale, we set out to determine the relationships between species coverage, aboveground biomass (including photosynthetically active and “woody” parts), leaf area index (LAI), water chemistry, and water table position, the latter a surrogate for microtopography. Three transects were established in the bog (two) and poor

fen sections of the mire, and vegetation, water chemistry, and water table position data were collected from 93 0.5 m × 0.5 m quadrats. Eddy covariance towers were installed at each of the three sites, and the three transects were chosen to provide ecological information on the footprint within each tower, aiding in the interpretation of the CO₂ flux results. We also examined the species–environment relationships to improve carbon modelling studies, which need these data to predict ecosystem feedbacks to a drier or wetter climate. We hypothesized that there would be a strong relationship between the coverage and biomass attributes of the vegetation and the water table position. We also compared the ability of traditional species coverage values to estimate vegetation properties, such as biomass or photosynthetically active tissues, which are of utility in studies of carbon fluxes.

Materials and methods

Site

The Mer Bleue peatland is primarily a large ombrotrophic bog located in the Ottawa River Valley, 10 km east of Ottawa, Ontario, Canada (45.40°N, 75.50°W). Mean annual temperature is 6.3 °C and ranges from –10.5 °C in January to 21.0 °C in July. Mean annual precipitation is 943 mm, 268 mm of which falls during the summer months (Environment Canada; climate normals). Peat began to form approximately 8500 years ago, but the bog phase began later, about 6400 years ago (Lafleur et al. 2003; P. Richard, personal communication, 2004). The peat depth now ranges from 2 m at the edge to >5 m in the middle. Beaver ponds are found at the lagg margin of the bog.

The bog is dominated by plant communities composed primarily of the ericaceous shrubs *Chamaedaphne calyculata* (L.) Moench, *Ledum groenlandicum* Oeder, and *Kalmia angustifolia* L. Clusters of the deciduous shrub *Vaccinium myrtilloides* Michx. and the tufted sedge *Eriophorum vaginatum* L. are fairly common across the bog. The most common tree species found in the bog are *Larix laricina* (DuRoi) K. Koch., *Betula populifolia* Marshall, and *Picea mariana* (Miller) BSP, which occurs less frequently. In the poor fen, located to the north of the bog proper, community composition is primarily composed of the ericaceous shrubs listed above, including higher densities of *K. angustifolia* and *Andromeda glaucophylla* Link. The primary sedge in this area is *Carex oligosperma* Michx. All sites are dominated by an under story of bryophytes, mainly *Sphagnum magellanicum* Brid., *Sphagnum capillifolium* (Ehrh.) Hedw., and *Polytrichum strictum* Brid. in the bog, with *Sphagnum papillosum* Lindb. and *Sphagnum fallax* (Klinggr.) Klinggr. common in the wetter portions of the poor fen.

Vegetation sampling

Three areas were chosen to represent three patterns on the LANDSAT image. In each area, transects were established to cover the major variations in vegetation: the Tower (TW, adjacent to a permanent eddy covariance tower (Lafleur et al. 2003)), the Blue Dome (BD, a slightly wetter area, 200 m east of the TW transect) and the Poor Fen (PF, 1200 m north of the TW transect with a distinctive graminoid cover). Mobile eddy covariance towers were placed in

Fig. 1. (a) Variation in water table position from 15 May to 2 October (day of year 135 to 275) from 1998 to 2004 was recorded at a hummock at the eddy covariance tower at Mer Bleue (courtesy P.M. Lafleur). Average water table position for this period in each year is indicated in the legend. Measurement dates for the transect quadrats in 2004 are indicated by bars; their average at the tower was -36 cm, similar to the seasonal average for 2004. (b) Frequency of water table position for the above period. (c) Average water table position, based on the five sampling dates indicated in Fig. 1a, at the 93 quadrats along the three transects (TW, tower; BD, Blue Dome; PF, Poor Fen). (d) Porewater pH at the 93 quadrats. (e) Porewater electrical conductivity (EC_{corr}) at the 93 quadrats.

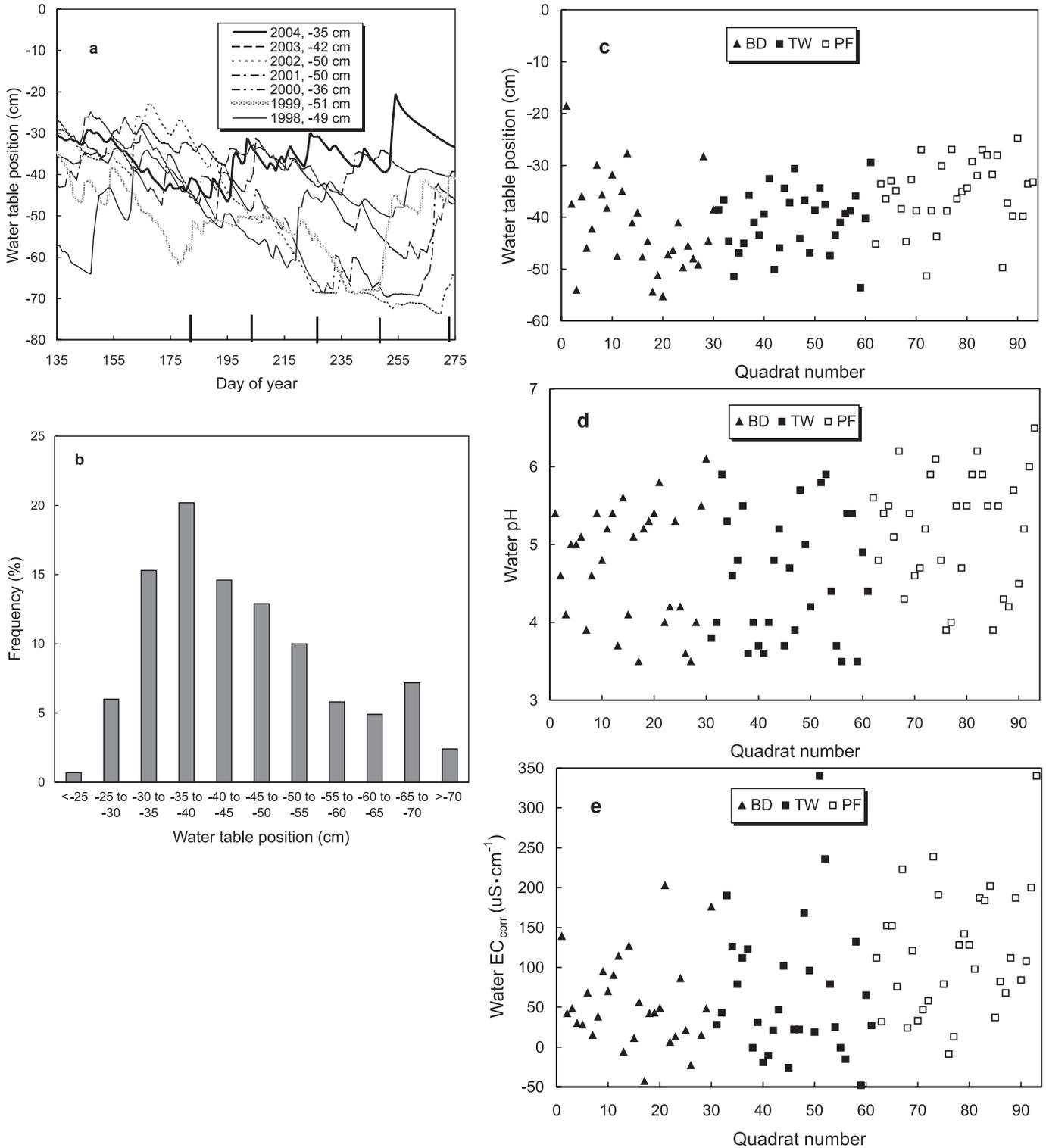


Table 1. Average aboveground biomass for the three transects (TW, BD, PF).

Vegetation type	Species	Aboveground biomass (g·m ⁻²)		
		Foliar	Combined	Woody
TW				
Shrub ^c	<i>C. calyculata</i>	46 (18)		67 (96)
	<i>K. angustifolia</i>	33 (24)		29 (21)
	<i>K. polifolia</i>	3 (3)		5 (4)
	<i>L. groenlandicum</i>	70 (44)		75 (47)
	<i>V. myrtilloides</i>	32 (30)		53 (56)
	<i>V. oxycoccus</i>		1 (1)	
Sedge and herb ^e	<i>S. trifolia</i>		2 (2)	
	<i>E. vaginatum</i>		18 (21)	
Moss ^h	<i>P. strictum</i>		26 (21)	
	<i>S. capillifolium</i>		67 (43)	
	<i>S. magellanicum</i>		65 (43)	
Total^a			591 (28)	
BD				
Shrub ^d	<i>C. calyculata</i>	39 (47)		54 (71)
	<i>K. angustifolia</i>	40 (21)		45 (35)
	<i>K. polifolia</i>	6 (6)		11 (9)
	<i>L. groenlandicum</i>	36 (26)		51 (35)
	<i>V. myrtilloides</i>	26 (27)		53 (67)
	<i>V. oxycoccus</i>		3 (6)	
Sedge and herb ^f	<i>S. trifolia</i>		2 (2)	
	<i>E. vaginatum</i>		8 (14)	
Moss ⁱ	<i>P. strictum</i>		27 (18)	
	<i>S. capillifolium</i>		50 (24)	
	<i>S. magellanicum</i>		32 (27)	
Total^b			488 (18)	
PF				
Shrub ^{cd}	<i>A. glaucophylla</i>	112 (58)		31 (18)
	<i>C. calyculata</i>	29 (28)		21 (20)
	<i>K. angustifolia</i>	82 (80)		59 (77)
	<i>K. polifolia</i>	8 (8)		11 (9)
	<i>L. groenlandicum</i>	36 (26)		51 (35)
	<i>V. myrtilloides</i>	6 (4)		6 (5)
	<i>V. oxycoccus</i>		2 (4)	
Sedge/herb ^g	<i>C. oligosperma</i>		36 (24)	
Moss ^j	<i>P. strictum</i>		60 (52)	
	<i>S. capillifolium</i>		83 (56)	
	<i>S. magellanicum</i>		107 (75)	
Total^a			654 (38)	

Note: Numbers in parentheses represent the standard deviation among the quadrats ($n = 30$ to 32 for each transect). Transect biomass values are statistically different (ANOVA, $p < 0.05$) where indicated by different superscripts letters for total (^{a,b}), shrub foliar (^{c,d}), sedge and herb (^{e,f,g}), and moss (^{h,i,j}) components.

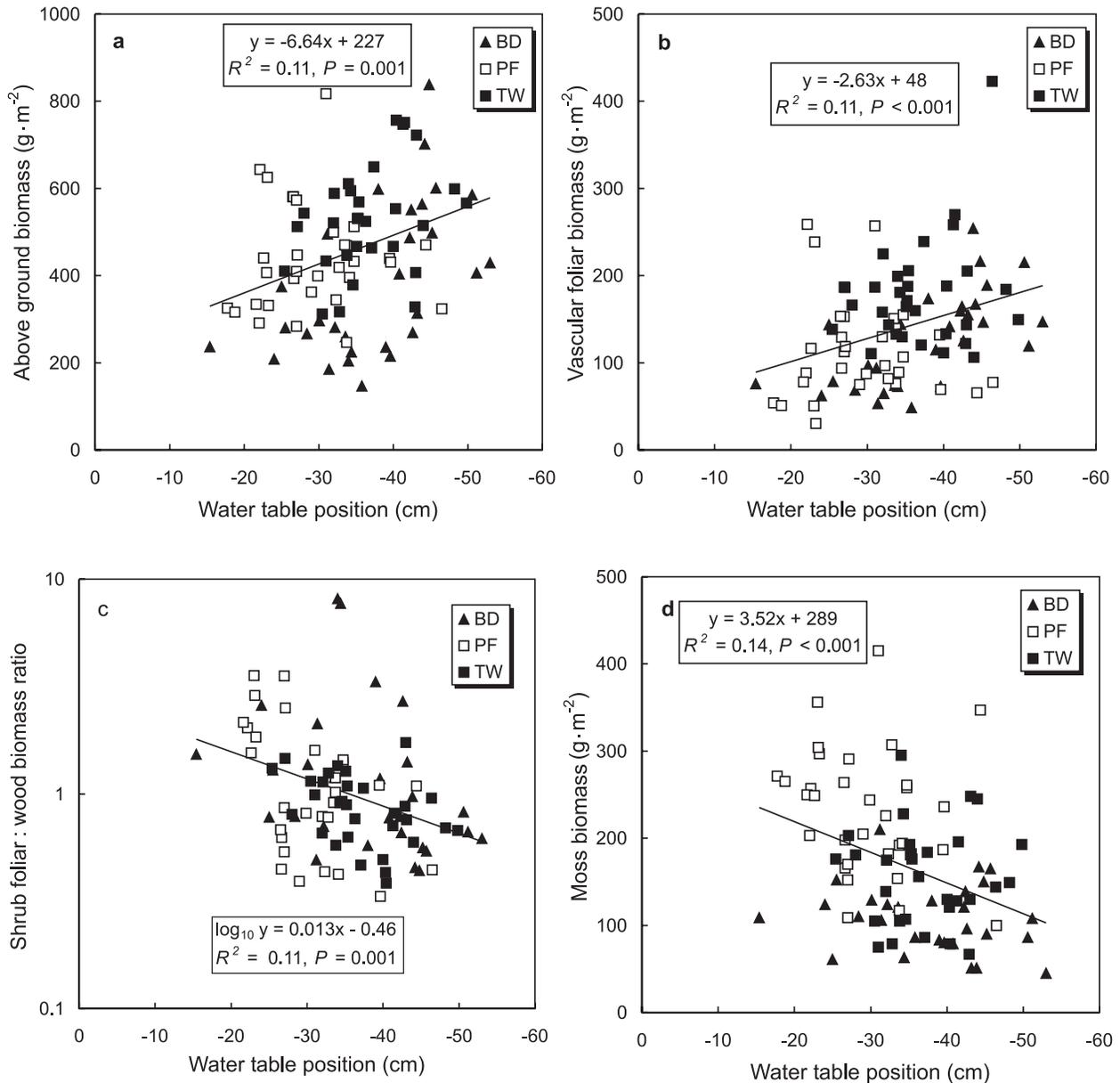
the latter two areas in 2004. The transects were 120, 110, and 120 m long, for TW, BD, and PF, respectively, in which 31, 30, and 32 quadrats were established, respectively. The quadrats, 0.5 m × 0.5 m, were established along the transects at 10 m intervals except for two 10 m sections within each transect where the spacing was 1 m.

For each quadrat, percent cover was estimated for each species; all species that did not represent 1% or more of the vegetation cover were recorded as 0.01%. On 28 August 2003, LAI measurements were made for each plot using a LI-COR LAI-2000. In early September 2003, each quadrat was harvested for aboveground vascular plant biomass, and

bryophytes were sampled from one 10 cm × 10 cm section of the quadrat: *Sphagnum capitula* and the part of *P. strictum* above the *Sphagnum* surface were harvested. The biomass was sorted by species; the vascular plants were divided into foliar or woody tissues (except sedges, *Vaccinium oxycoccus* L., and *Smilacina trifolia* (L.) Desf.), oven dried at 80 °C, and weighed.

Samples of foliar tissues and mosses were collected from an area near the TW transect at 3 week intervals during the growing season and analyzed for N concentration with a Carlo Erba CN-2500 elemental analyzer and for chlorophyll *a* concentration using the methanol extraction and spectro-

Fig. 2. Relationships between water table position and total aboveground biomass (a), vascular foliar biomass (b), ratio of shrub foliar and woody biomass (c), and moss biomass (d).



photometric determination method of Porra et al. (1989). Average seasonal concentrations were then combined with biomass measurements to estimate the areal mass of N and chlorophyll *a* in each quadrat.

Water measurements

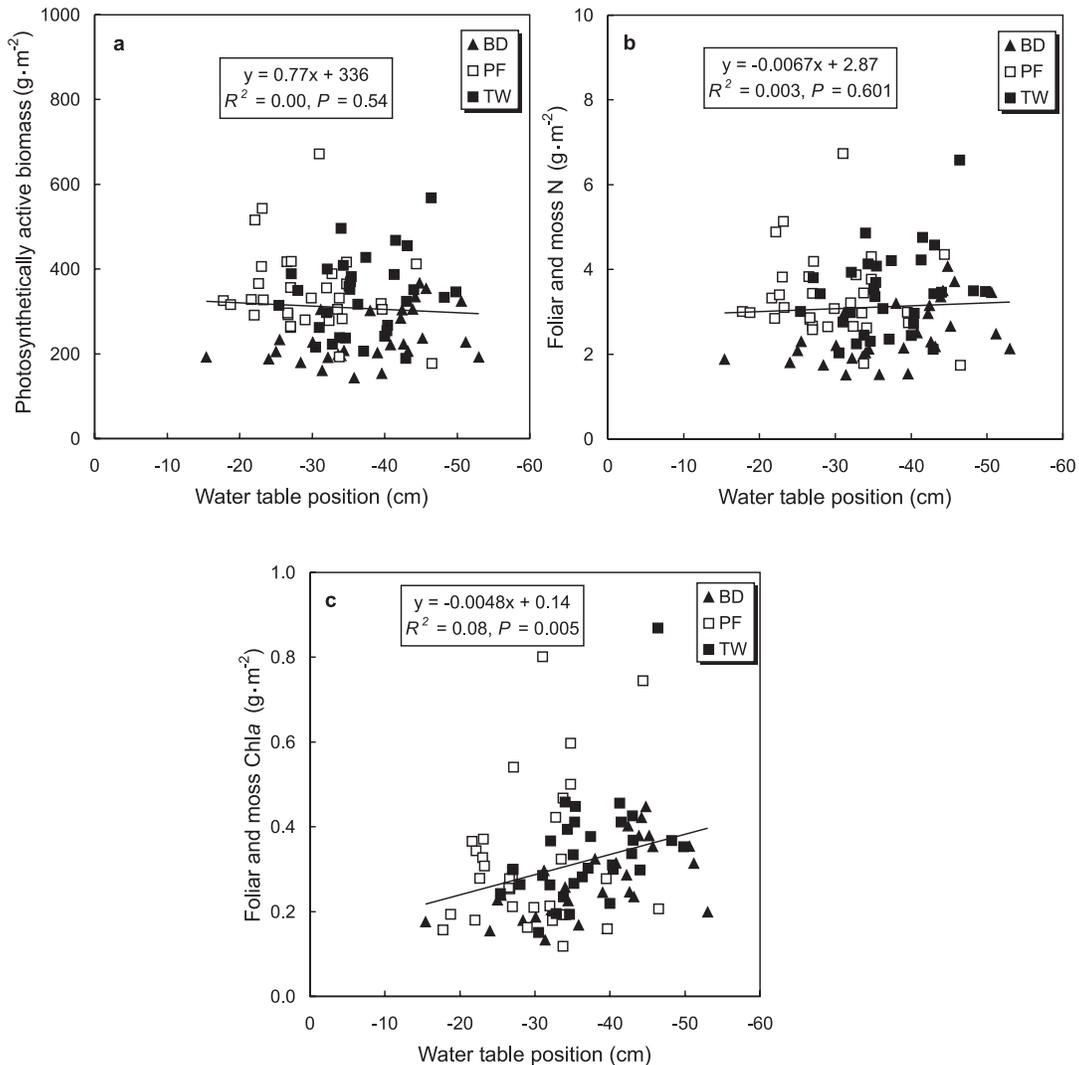
Water table tubes were inserted adjacent to each quadrat and water table position was measured five times from June to October 2004. These spot measurements were compared with a continuous record of water table depth taken at an eddy covariance tower located 150 m south of the TW transect. To establish the ombrotrophic nature of the sites, water from the water table tubes was sampled in mid-July and analyzed for pH, electrical conductivity corrected for pH and temperature to 20 °C (EC_{corr} , Sjörs 1950), and the concen-

trations of calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na).

Statistical analyses

We examined the relationships among biomass, LAI, species abundance, water table position, and water chemistry using linear regression as well as multivariate techniques. We examined the groupings among species using indirect gradient analysis and detrended correspondence analysis (DCA; Hill and Gauch 1980) and related the species associations with environmental gradients using canonical correspondence analysis (CCA) with the program CANOCO version 4.5 (Jongman et al. 1987; ter Braak and Smilauer 2002). Segment detrending and downweighting of rare species were used in addition to other standard options. The

Fig. 3. Relationship between water table position and photosynthetically active biomass (vascular leaves, *Sphagnum capitula*, and *Polytrichum*) (a), foliar and moss N (b), and foliar and moss chlorophyll *a* (c).



significance of the axes was tested with Monte Carlo permutations (McCune and Grace 2002). Multivariate analyses were performed only on vascular plant data because bryophyte sampling was limited to the three dominant species. Vascular plant species abundance data were transformed to an 8-point scale (0.1, 1, 2, 5, 25, 50, 75, and 100) based on cover values.

Maximum likelihood calibration (C2 version 1.4, Juggins 2005; ter Braak and van Dam 1989; Birks et al. 1990) was used to estimate individual vascular plant species optima and tolerances relative to mean water table position. This method assumes that each species has a unimodal response to a given environmental variable; that is, each species reaches maximum abundance at its preferred or optimum position in relation to the environmental variable, and is less abundant at both higher and lower values of the particular variable (Juggins 2005). Analyses were run using vascular plant species percent cover, and foliar and total

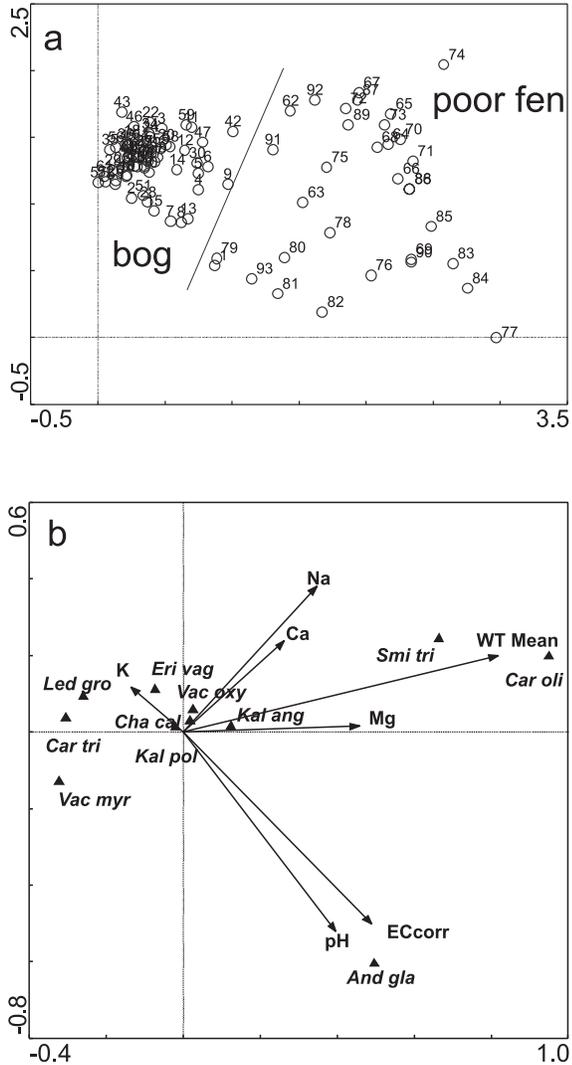
biomass. Bootstrapping was performed to assess model performance.

Results

Water table and chemistry

Water table position was measured five times in 2004, from late June to late September and we have used the mean of these measurements to define the water table variable in our analysis. To place this value in context, Fig. 1a shows the water table position determined at a hummock located near the eddy covariance tower, from mid-May to early October 1998 to 2004. These results show that there can be considerable variations in water table position both within the season, ranging from -19 to -74 cm, and among years, with the seasonal average ranging from -35 to -51 cm. The water table was between -30 and -45 cm for 50% of the time over this period (Fig. 1b). The highest average water ta-

Fig. 4. (a) Detrended correspondence analysis (DCA) of vascular plant species associations with indirect gradient analysis showing axes 1 (horizontal) and 2 (vertical). See Table 2a for Eigenvalues. Sample numbers refer to the 93 quadrats. (b) Canonical correspondence analysis (CCA) of vascular plant species associations and relationships with environmental variables showing axes 1 (horizontal) and 2 (vertical). See Table 2b for Eigenvalues.



ble (-35 cm) and a small seasonal range (26 cm) occurred in 2004, compared with other years. The average water table position at the tower derived from the five transect sampling dates in 2004 was very similar to the average water table position at the tower for the period mid-May to early October (-35.4 and -35.5 cm, respectively). Thus, given concordance between water table fluctuations at the tower and the three sampling transects, the water table we used is typical of the average growing-season water table, although probably somewhat higher than the long-term record for Mer Bleue.

Mean water table position of the quadrats ranged from -19 to -55 cm, with a similar range within each of the transects (Fig. 1c), although the poor fen transect was slightly wetter on average. From mid-May to early-October at the tower site in 2004, the water table ranged from a maximum of -20 cm to a minimum of -47 cm. A similar seasonal range

probably occurred at the quadrats, though our sampling of the water table from late June to late September revealed an average seasonal range of 11 cm. Water collected from the water table tubes in mid-July showed a pH range of 3.6 to 6.6 (mean 4.9 ± 0.8) and EC_{corr} ranged from slightly negative, associated with uncertainty in the correction terms (Sjörs 1950), to $>300 \mu S \cdot cm^{-1}$ (mean $80.2 \pm 79.7 \mu S \cdot cm^{-1}$; Figs. 1d and 1e). Concentrations of the cations ranged from 0.6 to 10.3 $mg \cdot L^{-1}$ for Ca (mean $3.3 \pm 2.7 mg \cdot L^{-1}$), from 0.1 to 2.8 $mg \cdot L^{-1}$ for Mg, from 0.3 to 10.4 $mg \cdot L^{-1}$ for K, and from 1.4 to 21.8 $mg \cdot L^{-1}$ for Na (data not shown).

Vascular plant and moss biomass

Total aboveground biomass in the quadrats ranged from 147 to 1011 $g \cdot m^{-2}$, with average values for the TW, BD, and PF transects of 591, 488, and 654 $g \cdot m^{-2}$, respectively (Table 1). In each transect, shrub biomass dominated (average 173–372 $g \cdot m^{-2}$, or 42% (PF) to 72% (TW) of the total) with moss biomass also being important and significantly different among the transects (109–250 $g \cdot m^{-2}$). The TW transects had the highest shrub biomass, while the PF transect had significantly higher sedge and herb, and moss biomass than either bog transect. The *Sphagnum* mosses dominated over *Polytrichum* at all sites. The BD transect had the lowest total biomass, but greater microtopographic variation and correspondingly higher species diversity. In terms of individual species differences, *K. angustifolia* dominated the BD transect with 28% of the total biomass, while *L. groenlandicum* dominated the TW transect at 37%. *Chamaedaphne calyculata* was the second most important species at the bog transects, composing 24% to 27% of total biomass. At the PF transect, *K. angustifolia* and *A. glaucophylla* were codominant with 40% and 31% of total biomass, respectively.

When grouped together, there were significant relationships between the quadrat total aboveground biomass and vascular foliar biomass and water table position, with both biomass types increasing with a lower water table (Figs. 2a and 2b). The ratio between shrub foliar and woody biomass decreased as the water table fell (Fig. 2c). Moss biomass (*Sphagnum capitula* and *P. strictum*) also decreased as the water table fell (Fig. 2d). In all these cases, the R^2 value was modest (0.11–0.14), showing scatter within the relationships.

Combining moss and vascular plant biomass together, there was no relationship between photosynthetically active tissue and water table (Fig. 3a). Areal mass of N in the vascular leaves and mosses ranged from 1.5 to 6.7 $g \cdot m^{-2}$ and had no significant relationship with water table depth (Fig. 3b) (N concentration data are not presented). Areal mass of chlorophyll *a* ranged from 0.12 to 0.87 $g \cdot m^{-2}$ and there was a significant increase with a decline in water table, primarily because of the larger chlorophyll *a* concentrations in vascular leaves than in *Sphagnum capitula* (Fig. 3c) (chlorophyll *a* concentration data are not presented).

Multivariate analyses

Indirect gradient analyses of the vascular plant species data using detrended correspondence analysis (DCA) showed that species were associated primarily with the bog – poor fen gradient (Fig. 4a). However, since the poor fen was gen-

Table 2. Indirect (DCA) and direct (CCA) gradient analyses results.

	Axes				Total inertia
	1	2	3	4	
(a) Indirect gradient analysis*					
Eigenvalues	0.545	0.165	0.102	0.072	1.373
Lengths of gradient	2.969	3.072	2.048	1.885	
Cumulative percent variance of species data	39.7	51.7	59.2	64.4	
Sum of all eigenvalues					1.373
(b) Direct gradient analysis†					
Eigenvalues	0.193	0.069	0.024	0.019	1.372
Species–environment correlations	0.615	0.595	0.391	0.431	
Cumulative percent variance of species data	14.1	19.1	20.8	22.2	
Cumulative percent variance of species–environment data	62.1	84.1	91.8	98	
Sum of all eigenvalues					1.372
Sum of all canonical eigenvalues					0.311

*See Fig. 4a for ordination of vascular plant species.

†See Fig. 4b for ordination of vascular plant species and environmental variables.

erally wetter than either bog transect, it is difficult to distinguish the effects of water table and chemistry. Eigenvalues are 0.54 and 0.16 for axes 1 and 2, respectively, and the cumulative percentage variance of species data are 39.7% for axis 1 and 59.2% for axes 1, 2, and 3 combined (Table 2a).

Direct gradient analysis of vascular species with environmental variables using canonical correspondence analysis (CCA; CANOCO) showed that both mean water table position and water chemistry (pH, EC_{corr}) have the longest vectors and are associated with the first two axes of species variability (Fig. 4b). Wet hollow species such as *C. oligosperma* and *S. trifolia* are located in the upper right quadrant of the diagram, while drier hummock species *V. myrtilloides* and *C. trisperma* are located on the lower left. Species found primarily in bog environments such as *L. groenlandicum* and *E. vaginatum* are located in the upper left quadrant, while poor fen species *A. glaucophylla* is found in the lower right. Species–environment correlations are 0.62 for axis 1 and 0.60 for axis 2 (Table 2b).

In addition to species groupings and associations, we examined the relationships between attributes of individual plant species and water table position in several ways. First, we plotted the log-transformed individual quadrat results against average water table position using linear regression: *C. calyculata* and *V. myrtilloides* both showed a significant increase in foliar and total biomass with a fall in water table, whereas *K. angustifolia* showed the reverse pattern (Fig. 5). There was no significant relationship for *L. groenlandicum*, and only *S. magellanicum* of the mosses showed a significant relationship to water table position, increasing with a rise in the water table (data not shown).

We also analyzed the individual species cover, biomass, and water table relations using maximum likelihood calibration (C2 version 1.4, Juggins 2005). Instead of linear responses, this technique assumes a unimodal response of species to environmental variables (Fig. 6). This technique was more robust for predicting species – water table relations than simple linear regressions. The model has an r^2 of 0.61 with a root mean square error (RMSE) of 6.98; predicted versus observed water table levels is shown in Fig. 7.

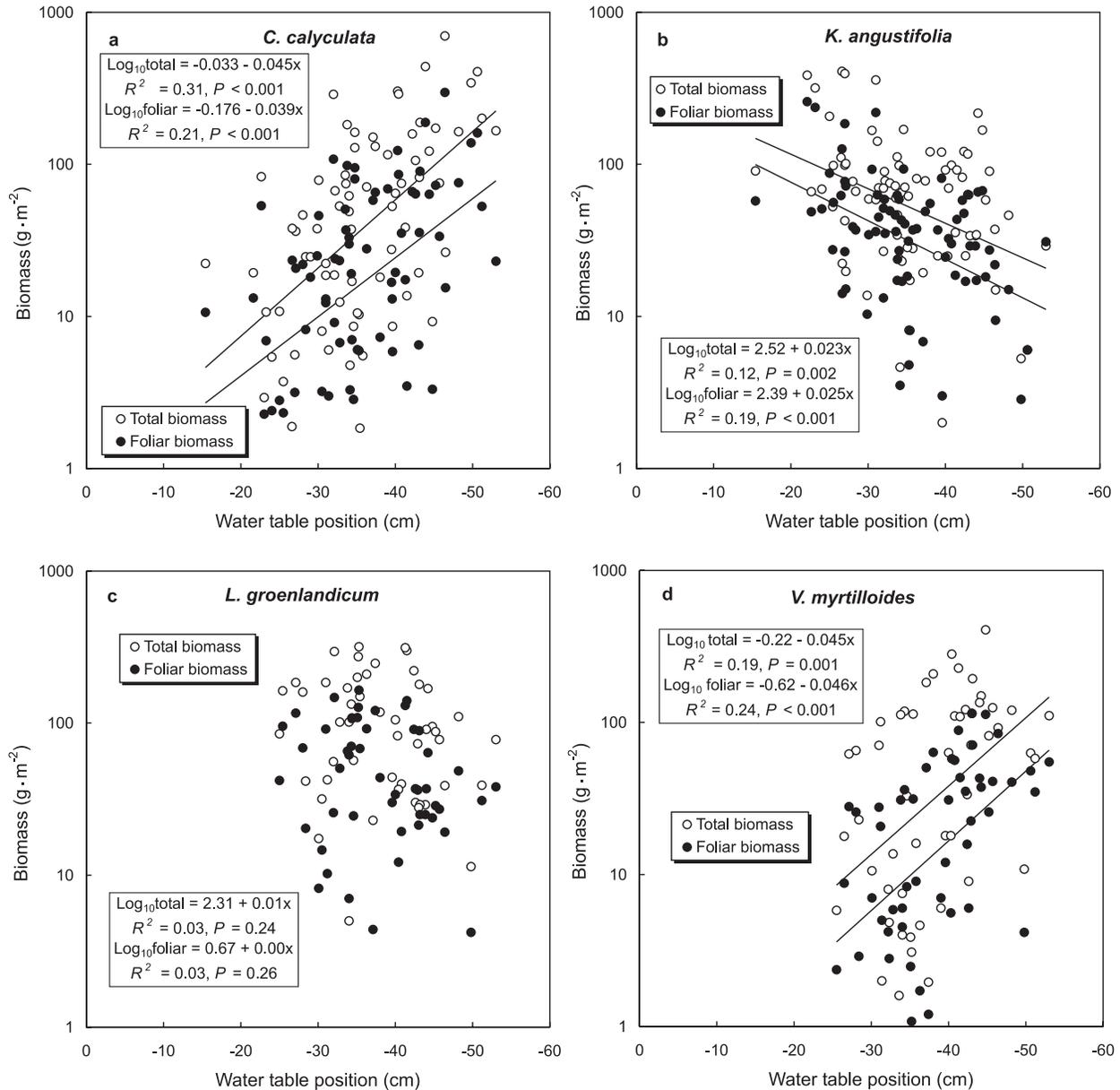
Table 3 shows the optima and tolerances for each species with *V. myrtilloides* and *C. calyculata* occupying the driest microtopographic positions (-48 to -50 ± 8 – 17 cm), while *C. oligosperma* and *K. angustifolia* are found in the wettest microhabitats (-8 to -21 ± 11 – 19 cm). Similar analyses were performed on the vascular plant foliar and total biomass data. These models were not as strong as the percent cover model; however, the vascular total biomass model performed nearly as well with an r^2 of 0.53 and RMSE of 5.58. The total biomass model yielded similar species coefficients for water table optima and tolerances as the percent cover model (data not shown).

Finally, we examined the more general relationships among biomass, percent cover, and LAI. LAI ranged from 0.1 to over 3 and was correlated with both water table position and with vascular foliar biomass (Fig. 8). Percent cover of shrubs was correlated with foliar biomass and LAI (Fig. 9).

Discussion

The importance of both water table position and water chemistry as controls on vegetation distribution has been emphasized in numerous peatland studies (e.g., Malmer 1986; Økland 1990; Glaser et al. 1990, 2004). In our study, water table, pH, and EC_{corr} were found to be almost equally important in explaining species associations and distribution (Fig. 4). The cumulative percent variance of species data are relatively low, probably because of the small range in both water table position and chemistry among our transect points compared with the much larger range in these gradients seen in other studies of rich fens to bogs (Glaser et al. 1990; Bubier 1995; Gignac et al. 2004). The poor fen pH (5.2 ± 0.7) and Ca (3.9 ± 2.3) values in our study are similar to those reported by Vitt et al. (1995) for poor fens of western Canada, and the species associations are comparable to those reported for poor fens throughout North America (Vitt and Chee 1990; Glaser et al. 1990, 2004).

The biomass accumulated over varying periods of time, and so it is not a measure of productivity. The biomass : water table relationships were strongest when considering

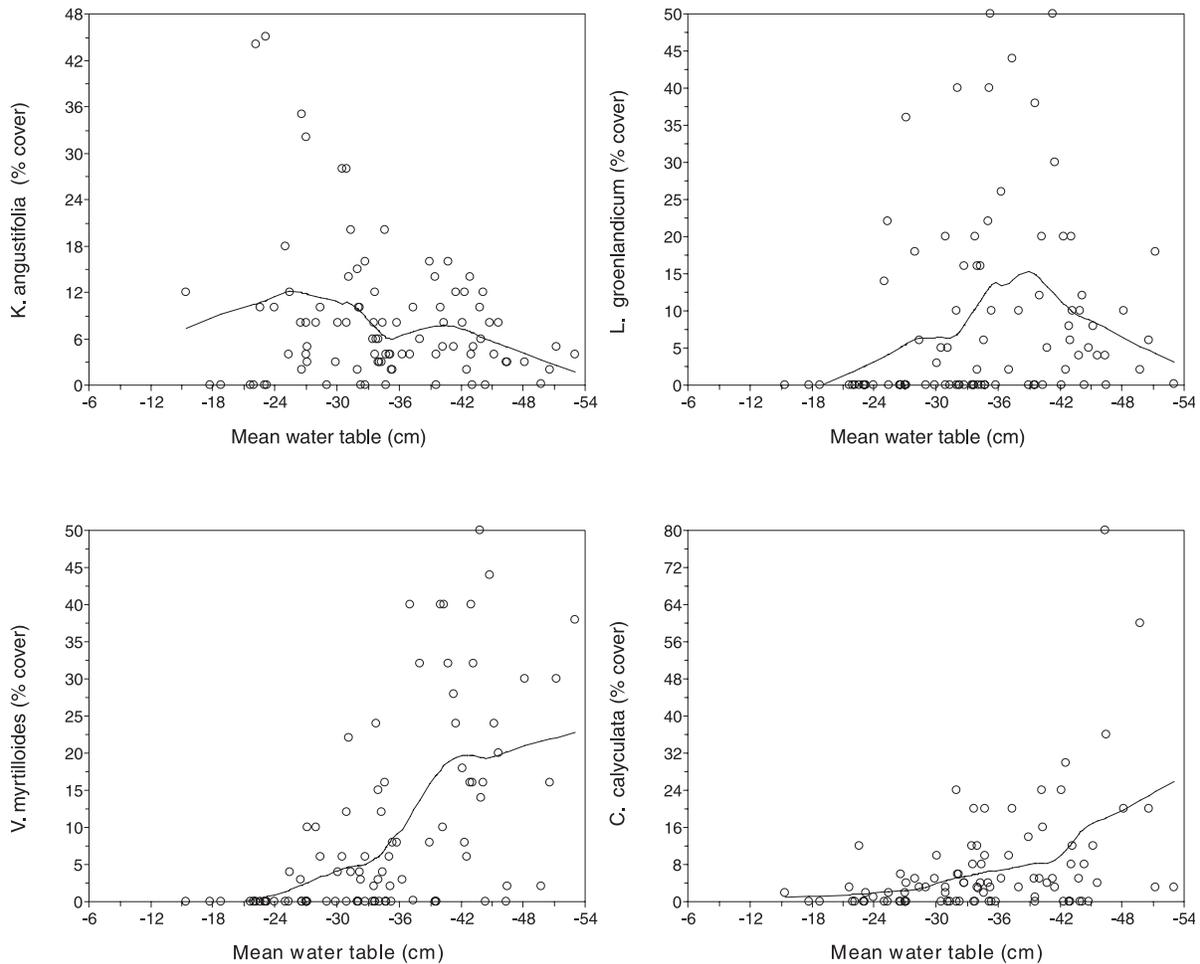
Fig. 5. Relationships between individual shrub species total and foliar biomass, and mean water table position using linear regression.

vascular foliar biomass as opposed to total biomass (Fig. 2). Most of the dominant shrubs had higher biomass with a lower water table position (Fig. 5), with the exception of *K. angustifolia*, which was sampled primarily on the wet end of this species distribution (Fig. 6a). Overall, however, the shrub foliar:wood biomass ratio decreased with a lower water table, suggesting the larger maintenance costs of shrubs in drier environments. These results also show that over this rather narrow range of water table position that there is a lot of “patchiness” to the pattern of vegetation. Nordbakken (1996a) examined the partitioning of spatial variation into water table versus random variation. That study found that water table alone explained 7% to 33% of the variation in species data, while spatial patchiness of hummocks and hollows explained 14% to 85%. The most likely sources of variation in addition to water table are biological processes such as competition and clonal growth pat-

terns, along with fine-scale disturbance. In addition, the interactions between vascular plants and mosses can contribute to the production of different microtopographic features in bogs (Belyea and Clymo 2001; Malmer et al. 2003).

When moss is included in the foliar biomass : water table relationship (Fig. 3a), there is no pattern, showing that there is very little variation in photosynthetic tissue along water table gradients. This is due to the opposite relationship of vascular plants and mosses to water table position (Figs. 2b, 2d). This result may explain the surprising lack of spatial variability in eddy flux net ecosystem CO₂ exchange data as measured during the peak mid-growing season by eddy covariance towers in these same three areas of the peatland (P. Lafleur and E. Humphreys, personal communication, 2005). However, there could be seasonal differences as mosses and vascular plants have different phenological patterns and respond differently to wet and dry conditions (Sil-

Fig. 6. Distribution of four major shrub species along the water table gradient. Curve fit is a lowess smooth function (C2 version 1.4, Juggins 2005).



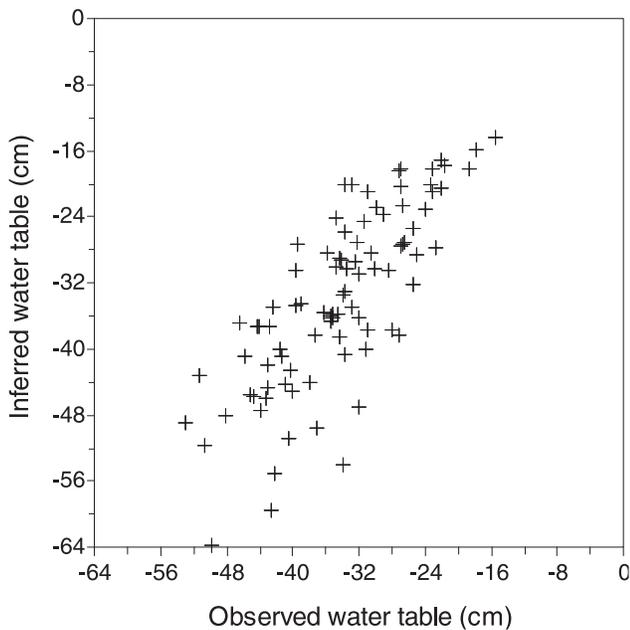
vola 1991; Bubier et al. 1998; Tuittila et al. 2004). Glenn et al. (2005) reported similar peak growing season eddy flux net CO₂ exchange for two different peatlands with contrasting vegetation types in western Canada. However, that study also showed that the whole season carbon balance of the two sites was different owing to differences in moss and vascular plant physiology in the early and later parts of the growing season.

Small (1972) has shown a strong dependence between the light-saturated photosynthetic rate and the concentration of N, ranging from 1.0% to 2.1%, in the foliage of 15 vascular species from the Mer Bleue peatland. Reich et al. (1999) and Field and Mooney (1986) have similarly shown a strong correlation between foliar N concentration and photosynthetic capacity for a wider range of vascular plants, including wetland species. At Mer Bleue, we determined summer average N concentrations ranging from 0.8% to 0.9% in *S. capillifolium* and *S. magellanicum*, through 0.9% to 1.2% in the evergreen shrubs, to 1.2% to 1.4% in sedges and *V. myrtilloides*, and 2.7% in *S. trifolia*. Chlorophyll *a* concentrations ranged from 0.3 to 3.7 mg·g⁻¹ and were correlated with N concentrations ($r^2 = 0.57$, $p < 0.001$, $n = 91$). From the perspective of CO₂ exchange in the peatland, the spatial distribution of the photosynthetic capacity is important, expressed as areal values of vascular plant leaves and

Sphagnum capitulum or mass of N or chlorophyll *a* contained in these tissues. These values are small (photosynthetically active biomass ranged from 114 to 672 g·m⁻², N ranged from 1.5 to 6.7 g·m⁻², and chlorophyll *a* ranged from 0.1 to 0.9 g·m⁻²) compared with other ecosystems, although the N mass per vascular leaf area (average N of 1.7 g·m⁻² leaf) is similar to that observed in boreal forest stands (e.g., Dang et al. 1988). More importantly, there was no significant relationship of leaves and *Sphagnum capitulum* or mass of N to water table position, showing that within this peatland, water table is of limited value in predicting this ecosystem function. The relationship of chlorophyll *a* mass to water table position arises from its small concentration in *Sphagnum capitulum*, compared with that of vascular plant leaves.

Although the relationships among species associations, biomass, photosynthetically active tissues, and water table are not strong owing to the factors described above, individual vascular plant species relationships to water table position are stronger. We found that unimodal responses of species cover to mean water table position (Fig. 6) were stronger than linear relationships (Fig. 5). Maximum likelihood calibration (Fig. 7) predicted optimum water table niches of individual species with a high degree of confidence ($r^2 = 0.61$; Table 3). Of the four dominant shrubs in terms of

Fig. 7. Observed versus inferred water table position using plant species cover data and maximum likelihood calibration model (C2 version 1.4, Juggins 2005; $r^2 = 0.61$, RMSE = 6.98). See Table 3 for species optima and tolerances relative to mean water table position.



biomass, *Chamaedaphne* and *Vaccinium* are found on the driest hummocks while *Ledum* occupies intermediate locations, and *Kalmia* prefers the wetter hollows. It must be noted, however, that our sampling of *Chamaedaphne* and *Vaccinium* does not include the complete water table gradient (Fig. 6), and the tolerance for *Chamaedaphne* is large (Table 3), suggesting that our data may overestimate the dry end of the species gradient. *Carex oligosperma* is found in wettest poor fen environments, which is in agreement with other studies of North American sedges (Gignac et al. 2004). The tolerance or width of each species niche varies almost twofold, suggesting that some species have stronger competitive advantages in different microhabitats (Table 3; Nordbakken 1996b). Species with larger niche widths may have stronger competitive advantages because they can tolerate a wider range of water table positions, enabling them to survive periods of drought or flood better than species with smaller niches. Also, since there is considerable microtopographic and spatial variability in water table position throughout most peatlands, a species with a wider niche can occupy more microsites than one with narrow niche widths.

We have focused on the role of summer water table position as the main driver of species composition and biomass in this system, but winter conditions may also play a role. Shrub height above the peat surface ranges from 10 to 30 cm, average 18 cm, with a weak negative dependence on water table position (data not shown). Mid-winter snow thickness ranges from 30 to 60 cm (P. Lafleur, personal communication, 2005), but for much of the winter, the upper part of shrubs is exposed to cold, windy conditions above the insulating snow layer. Moreover, wind redistribution of snow from hummock to hollow, as well as faster sublimation rates and denser snow in the former, result in a snowpack 15 to 20 cm thicker in the hollows than in the hummocks

Table 3. Optima and tolerances for water table depth (cm) below peat surface for dominant vascular plant species using percent cover data and maximum likelihood calibration (C2 version 1.4, Juggins 2005; $r^2 = 0.61$, RMSE = 6.98).

Species	Count*	Max [†]	Optimum	Tolerance
<i>Chamaedaphne calyculata</i>	69	80	-50.50	17.46
<i>Vaccinium myrtilloides</i>	54	50	-48.85	8.82
<i>Carex trisperma</i>	40	1	-45.52	15.85
<i>Kalmia polifolia</i>	22	8	-43.54	10.82
<i>Smilicina trifolia</i>	10	8	-41.01	10.42
<i>Ledum groenlandicum</i>	49	50	-39.07	7.81
<i>Eriophorum vaginatum</i>	56	25	-38.54	10.20
<i>Andromeda glaucophylla</i>	15	50	-33.70	6.77
<i>Vaccinium oxycoccus</i>	40	3	-27.01	12.68
<i>Kalmia angustifolia</i>	79	45	-21.89	19.03
<i>Carex oligosperma</i>	24	20	-8.28	11.83

*Number of observations.

[†]Maximum abundance in percent cover.

(P. Lafleur and R. Smith, personal communication, 2005). The thinner snowpack and greater exposure on hummocks, especially during the coldest part of mid-winter, may contribute to the occurrence of the tough-leaved evergreen *Chamaedaphne* and the deciduous *Vaccinium* in the driest, hummock locations (Table 3) and the larger foliar:wood biomass ratios with lower water tables.

When we examined more general relationships for purposes of spatial scaling, we found that LAI was a good indicator of vascular foliar biomass and shrub cover (Figs. 8, 9). We also found a strong relationship between foliar biomass and cover values of the four dominant shrub species. In addition, the maximum likelihood calibration models for predicting WT optima for individual vascular plant species showed that using biomass was nearly as predictive as using percent cover. This has important practical implications for estimating biomass over large spatial scales. It takes about 3 h to harvest, sort, dry, and weigh aboveground plant tissues in a 0.25 m² quadrat for biomass, compared with 15–30 min to visually estimate percent cover for the same size quadrat. This suggests that the less labour-intensive estimates of percent cover can be used to predict the foliar biomass and LAI measurements, which are more relevant to the carbon modeling and eddy flux measurements.

Most models of climate change predict warmer temperatures for continental North America in which peatlands such as Mer Bleue occur. This warmth probably entails a lowering of the water table, through increased rates of evapotranspiration compensating for any increase in precipitation (Roulet et al. 1992). Weltzin et al. (2003) found that an increase in temperature along with a lowering of the water table produced a 50% increase in shrubs and 50% decrease in graminoid cover, and Thormann and Bayley (1997) also found an increase in shrub cover in fens under drier conditions. Bubier et al. (2003b) found that shrub production increased, while sedge production decreased in as little as one

Fig. 8. Relationship between leaf area index and water table position (a) and total vascular foliar biomass (b).

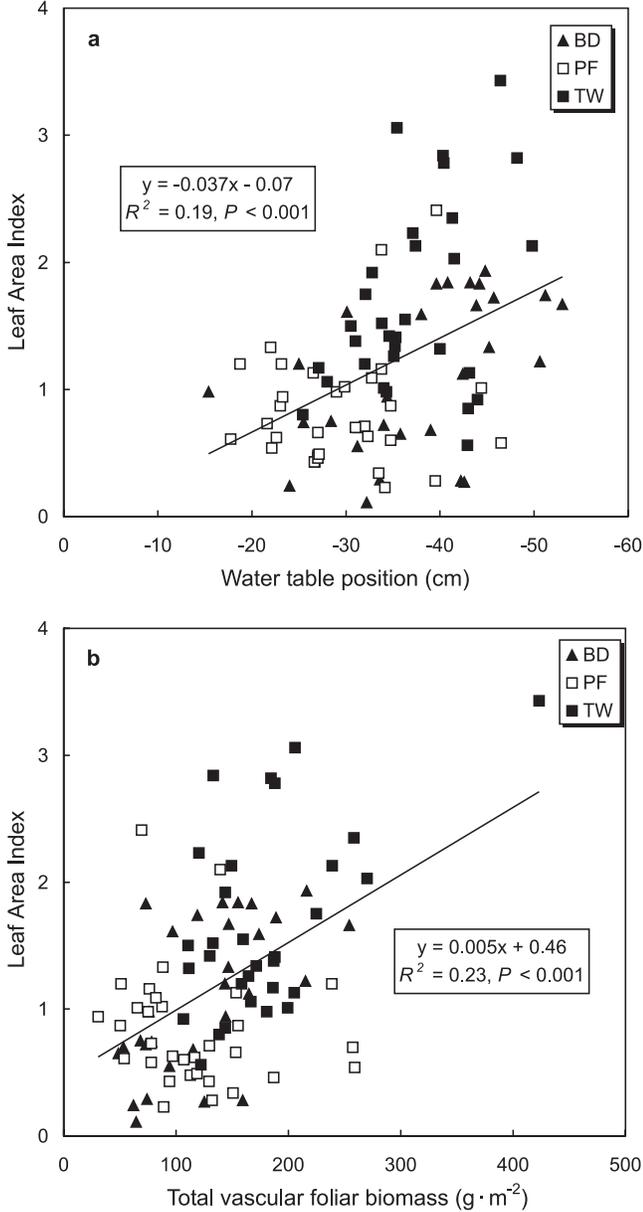
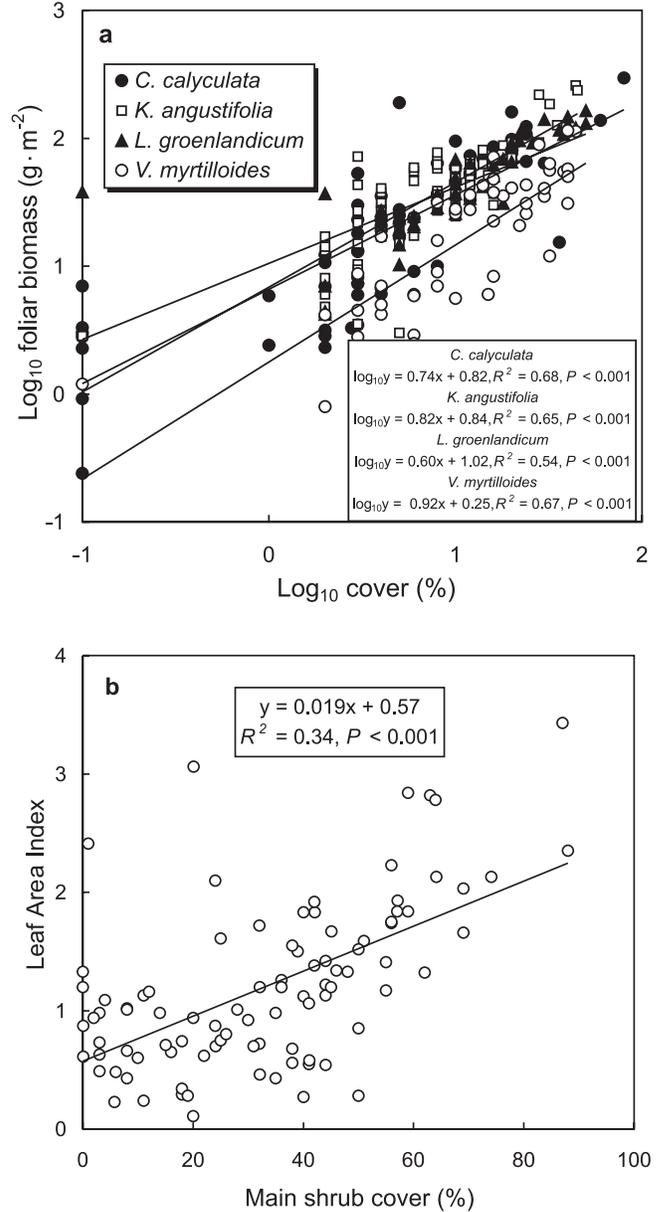


Fig. 9. Relationship between shrub cover and shrub foliar biomass (a) and leaf area index (b).



dry growing season as measured by automatic CO₂ chambers. At Mer Bleue, the bog is already dominated by ericaceous shrubs, so a drier climate may not result in major changes; however, a lowering of the summer water table in our peatland may result in species shifts, such as an increased coverage of those shrubs that occupy the highest hummocks (*V. myrtilloides*, *C. calyculata*), an increase in tree cover, a decrease in sedge cover within the fen, and an overall replacement of the wetter sphagna, such as *S. papillosum* and *S. fallax* by those tolerant of lower water tables, such as *S. capillifolium* and *S. magellanicum*.

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