Distribution and habitat niches of 37 peatland Cyperaceae species across a broad geographic range in Canada

L.D. Gignac, R. Gauthier, L. Rochefort, and J. Bubier

Abstract: The presence and absence of 37 Cyperaceae species found on 498 peatlands across Canada were examined along surface water chemistry, shade, height above the water table, and climatic gradients. A canonical correspondence analysis of the species distribution along the environmental gradients indicated that surface water chemistry and climate were highly correlated with the first and second axes and were the two most important gradients distinguishing among groups. The climatic gradient was further subdivided into western oceanic continental and eastern oceanic continental gradients. Height above the water table and shade were correlated to the third canonical correspondence analysis axis and were of secondary importance in explaining species distributions. A TWINSPAN analysis of the species separated them into eight groups: (1) widespread, obligate rich fen, wet, shade-tolerant species; (2) widespread rich fen preferential species; (3) continental and eastern oceanic, rich fen preferential, wet, shade-intolerant species; (4) widespread fen, wet, shade-intolerant species; (5) widespread bog or fen, shade-tolerant species; (6) widespread subcontinental and oceanic, bog or fen, shade-intolerant species; (7) eastern subcontinental and oceanic, poor fen preferential species; (8) western oceanic, bog and poor fen preferential, shade-intolerant species. Response surfaces were generated by quantifying the frequency of occurrence of representative species in each group along pH and height above the water table, shade and mean annual temperature, and mean annual total precipitation gradients. Frequency of occurrence values for several of the rarer species indicated that they were not limited by the number of suitable habitats analyzed in this study but by other factors such as competition, failure to establish, or dispersal. This study emphasizes the importance of habitat and climate in determining the local and regional diversity and distribution of the most common Cyperaceae on peatlands in Canada.

Key words: sedges, *Carex*, peat lands, response surfaces, climate, water chemistry.

Résumé : Les auteurs ont examiné la présence ou l'absence de 37 Cyperaceae, sur 498 tourbières à travers le Canada, en relation avec la chimie de l'eau de surface, l'ombrage, la hauteur au dessus de la nappe phréatique, et les gradients climatiques. Une analyse par correspondance canonique de la distribution des espèces, le long de gradients environnementaux, montrent une forte corrélation entre la chimie des eaux de surface et le climat et les premiers et deuxièmes axes, et constituent les deux gradients les plus importants permettant de distinguer les groupements. Les auteurs ont ensuite subdivisé le gradient climatique en gradients continental océanique de l'ouest, et continental océanique de l'est. La hauteur de la nappe phréatique et l'ombrage montrent une corrélation avec le troisième axe analyses par correspondances canoniques, et occupent une place secondaire dans l'explication de la distribution des espèces. Une analyse TWINSPAN des espèces permet de les réunir en huit groupes distincts : (1) espèces largement distribuées, obligatoirement de tourbières basses et riches, de milieux humides, tolérantes à l'ombre; (2) espèces largement distribuées, préférant les tourbières basses riches; (3) espèces continentales et océaniques de l'est, préférant les tourbières basses riches, de milieux humides, intolérantes à l'ombre; (4) espèces largement distribuées, de tourbières basses, de milieux humides, intolérantes à l'ombre; (5) espèces largement distribuées, de tourbières hautes ou basses, tolérantes à l'ombre; (6) espèces subcontinentales et océaniques, largement distribuées, de tourbières hautes ou basses, intolérantes à l'ombre; (7) espèces subcontinentales et océaniques de l'est, préférant les tourbières basses et pauvres; (8) espèces océaniques de l'ouest, préférant les tourbières hautes et basses pauvres, intolérantes à l'ombre. On génère des surfaces de réaction en quantifiant la fréquence de présences d'espèces représentatives dans chaque groupe, selon les gradients de pH, de hauteur au dessus de la nappe phréatique, d'ombre, de température annuelle moyenne, et de précipitation annuelle totale moyenne. Les valeurs des fréquences de présence pour plusieurs des espèces plus rares, indiquent qu'elles ne sont pas limitées par le nombre d'habitats convenables analysés dans cette étude, mais par d'autres facteurs tels que la compétition, l'échec à l'établissement ou à la dispersion. Les auteurs soulignent l'importance de l'habitat et du

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climat dans la détermination de la diversité et de la distribution régionale et locale des espèces de Cyperaceae les plus communes, dans les tourbières du Canada.

Mots clés : carex, *Carex*, tourbières, surfaces de réaction, climat, chimie de l'eau.

[Traduit par la Rédaction]

Introduction

The Cyperaceae occur in a wide variety of habitats within their distribution range, and several species may be found in each habitat (Bernard 1990; Busch and Losch 1999). Moreover, they are often an important component of plant diversity in otherwise relatively depauperate plant communities. In some wetlands or communities, Cyperaceae dominate extensive areas (Vitt and Slack 1975). However, despite their exceptional diversity and abundance in wetlands in general and peatlands in particular, the Cyperaceae, as a group, have received relatively little attention in the ecological literature of North America. We present a detailed analysis of the habitats of 37 of the more common species of Cyperaceae found in peatlands of Canada.

The Cyperaceae are probably the seventh largest family of vascular plants with ca. 4500–5000 species in about 100 genera (Reznicek 1990). There is strong evidence that they evolved as forest-floor plants and subsequently spread into open habitats (Ball 1990). *Carex*, with about 2000 species, is by far the largest genus in the Cyperaceae and one of the most widespread and ecologically important genera of vascular plants (Bernard 1990). *Carex* is cosmopolitan in distribution, but the great majority of species are found in the north and south temperate, boreal, and arctic regions and the montane tropics (Reznicek 1990). The geographic distribution of peatlands is coincidentally very similar to the distribution of most *Carex* species (Gignac 1993). Approximately 500 species are found in North America.

Four main environmental gradients are responsible for the distribution of peatland plants: (1) surface water chemistry; (2) height of the peat surface relative to the water table; (3) shade; and (4) distance from the peatland margin (Sjörs 1952, 1963; Vitt et al. 1975a; Vitt and Slack 1975; Slack et al. 1980; Gignac and Vitt 1990; Økland 1990; Bragazza 1999; Campbell and Rochefort 2001). The distance from the margin gradient is complex and involves several factors such as greater fluctuations of the water table in the margin, higher availability of nutrients in the margin, and generally higher overstory cover and thus deeper shade in the margin (Bragazza 1999).

Descriptions of the habitat niches of many peatland sedges are often found in papers that describe mire plant communities. Only a few studies have focused specifically on the ecology of peatland Cyperaceae in general, or Carices in particular, in North America (Damman 1964; Wheeler et al. 1983; Anderson et al. 1996). However, the geographic scale in those studies is confined to a single province or state. As a result, the ecology of only a relatively limited number of species is analyzed, and the climatic and geographic distribution of most of those species is often truncated.

Our objectives were to: (1) characterize the habitats of peatland Cyperaceae across Canada; (2) identify groups of cooccurring species that have similar ecological requirements; (3) describe the environmental gradients that determine the distribution of species and groups; and (4) characterize species distributions along the most important climatic and ecological gradients.

Methods

Study sites

The abundance of vascular plants, bryophytes, and lichens was measured on 498 peatlands located in all regions of Canada except for Newfoundland, Nova Scotia, the northern limit of peatland distribution in Québec, Ontario, and the eastern Northwest Territories, and the southern limit in Ontario (Fig. 1). With the exception of 11 peatlands at five different locations in northeastern Manitoba, all sites were within 100 km of a permanent weather station in topographically homogeneous terrain or within 50 km in more heterogeneous terrain. In Canada, peatlands are defined as wetlands having a minimum accumulation of 40 cm of peat and a water table that is close to or above the peat surface (Zoltai 1988). According to that definition, the sites studied here were peatlands that can be classified as either bogs or fens. Data were collected from several sources that employed either quadrats or relevés to quantify species abundance (Table 1). At least one relevé or several quadrats were studied on each peatland.

Vegetation sampling

The presence of Cyperaceae species was noted for each quadrat or relevé. Quadrat size and sampling design varied as follows: randomly placed quadrats (25 cm × 25 cm) along a transect bisecting each plant community on a peatland (restricted random) (Vitt et al. 1990; Chee and Vitt 1989); 0.5-m^2 circular restricted random (Nicholson et al. 1996; L.D. Gignac, unpublished data; L. Rochefort, unpublished data); 50 cm × 50 cm restricted random (Bubier et al. 1993; Bubier 1995). Relevé sizes and their sampling designs also varied: systematic by peatland (S.C. Zoltai and J.D. Johnson, unpublished data) and systematic by plant community within a peatland (Gauthier 1980). Of the Cyperaceae species found on the peatlands, only species that were found on three different peatlands and on seven different relevés or quadrats were retained in this study. With the exception of *Carex sitchensis* Prescott ex Bong (Douglas et al. 2001) = *Carex aquatilis* Wahlenb. var. *dives* (T. Holm) Kukenthal in H.G.A. Engler, nomenclature follows that of the Flora of North America Editorial Committee (2002).

Environmental variables

The macroclimate was quantified for each peatland based on meteorological data averaged over 30-year means between 1951 and 1980 (Canadian Climate Program 1982a, 1982b) and obtained from the nearest permanent weather

Fig. 1. Location of 498 study sites in Canada. Some locations may have several sites in relatively close proximity and are represented by one asterisk.
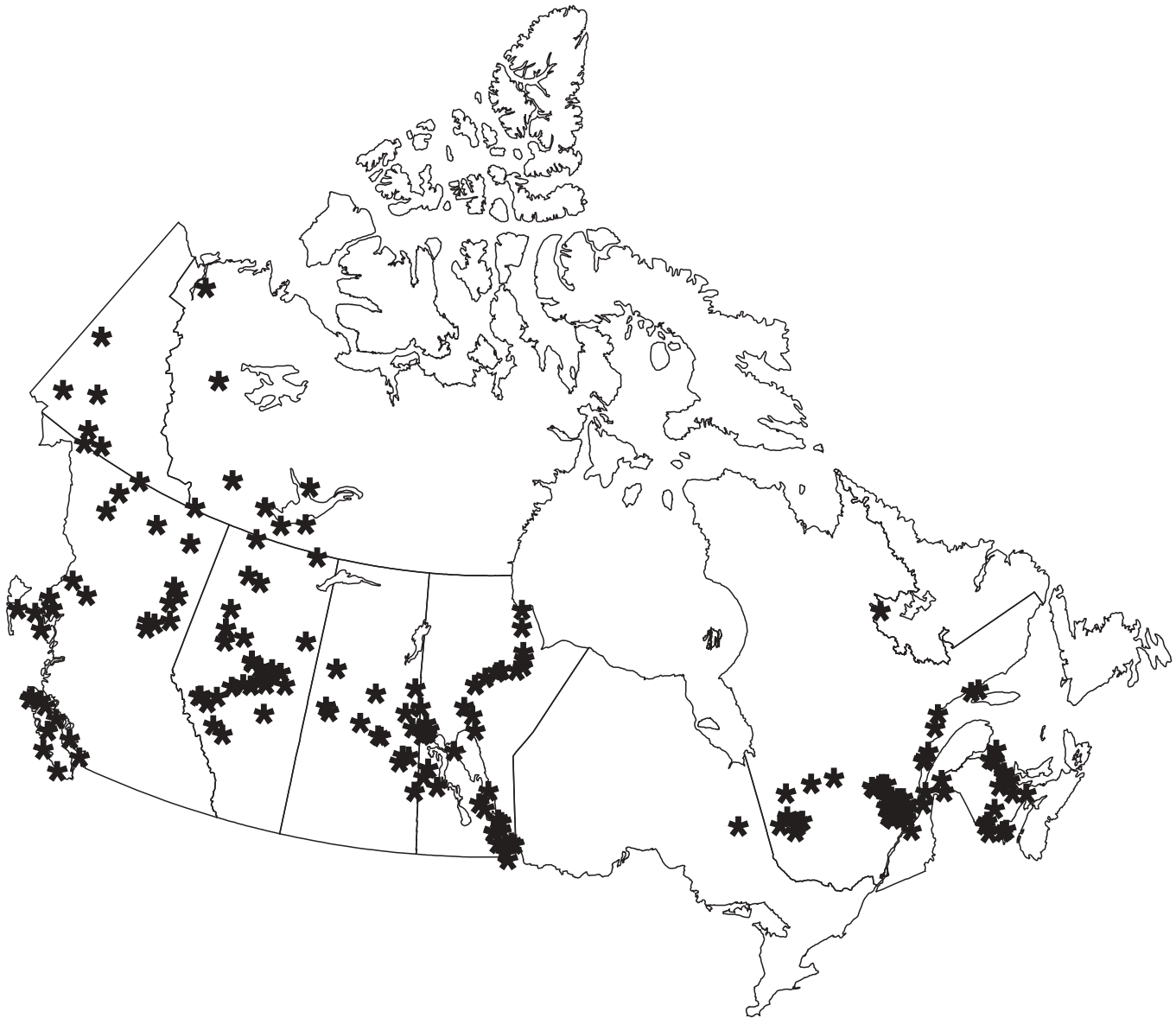
stations in proximity to each study site. Data for the 11 peatlands in northeastern Manitoba that were not within 100 km of a permanent weather station were generated by interpolating between data obtained from weather stations directly to the north at Churchill and directly to the south at Bird. This method provided relatively accurate data, since all 11 peatlands were located on the Hudson Bay Lowlands, where the terrain is topographically homogeneous (Bostock 1970). The following climatic variables were used: mean annual temperature (MAT), mean annual total precipitation (MATP), mean annual total rainfall (MATR), and length of the growing season (GS) calculated for a 2 °C threshold.

The MAT gradient was divided as follows: <–6 °C, subarctic; –6 to 4 °C, boreal; >4 °C, temperate (Tuhkanen 1984). The MATP gradient was converted to a log scale and divided as follows: <6 (400) mm, continental; 6–6.5 (600) mm, subcontinental; 6.5–7.0 (1000) mm, suboceanic;

7.0–7.5 (2000) mm, oceanic; >7.5 mm, hyperoceanic (Tuhkanen 1984).

Water samples were collected from each site, either from surface water or, where surface water was not available, from shallow pits dug in the peat surface. Conductivity and pH were measured in situ or shortly after sampling. Conductivity (k_{corr}) was corrected to 20 °C and for H^+ ions (Sjörs 1952). Ca^{2+} concentrations were measured in each water sample either on an atomic absorption spectrophotometer or on an inductively coupled argon plasma spectrophotometer. The pH gradient was divided as follows: 3.0–4.2, bog and extreme-poor fen; 4.2–4.8, extreme-poor fen and poor fen; 4.8–5.2, poor fen and moderate-poor fen; 5.2–5.6, moderate-poor fen; 5.6–7.0, moderate-rich fen; >7.0, extreme-rich fen (Sjörs 1952).

The mean height of the peat surface relative to the water table was determined for each quadrat or relevé. With the

Table 1. General location, number of peatlands (*n*) studied by each source, sampling year, and sampling method for 498 peatlands in Canada.

Location	Source	Year	*n*	Method
Central Quebec	Gauthier 1980	1968–1972	41	Relevé
Central Alberta	S.C. Zoltai and J.D. Johnson, unpublished data	1981	55	Relevé
Central Manitoba	S.C. Zoltai and J.D. Johnson, unpublished data	1982	59	Relevé
Coastal British Columbia	Vitt et al. 1990	1983	6	Quadrat
Southern Manitoba	S.C. Zoltai and J.D. Johnson, unpublished data	1983	65	Relevé
Central Alberta	Chee and Vitt 1989	1984	14	Quadrat
Central Saskatchewan	S.C. Zoltai and J.D. Johnson, unpublished data	1984	76	Relevé
Northern Alberta	S.C. Zoltai and J.D. Johnson, unpublished data	1984–1985	33	Relevé
Northern Ontario	Bubier et al. 1993	1991	16	Quadrat
Northern Quebec, Labrador	Bubier 1995; Bubier et al. 1995	1992	4	Quadrat
Coastal British Columbia	L.D. Gignac, unpublished data	1992	12	Quadrat
Northern British Columbia	L.D. Gignac, unpublished data	1993	17	Quadrat
Central Quebec	L. Rochefort, unpublished data	1993	9	Quadrat
Northwestern Quebec	L. Rochefort, unpublished data	1993	9	Quadrat
North West Territories	Nicholson et al. 1996	1994	18	Quadrat
Eastern coastal Quebec	L. Rochefort, unpublished data	1994–1995	8	Quadrat
New Brunswick	L. Rochefort, unpublished data	1994–1995	25	Quadrat
Yukon	L.D. Gignac and B.J. Nicholson, unpublished data	1996	8	Quadrat
Northern Manitoba	L.D. Gignac, unpublished data	1997	20	Quadrat
Northern Saskatchewan	D. Bielman, unpublished data	1999	3	Quadrat

exception of the data obtained from Gauthier (1980), Vitt et al. (1990), and Chee and Vitt (1989), height measurements were taken directly by measuring the distance from the peat surface to the water table. For the remaining data, height measurements were estimated indirectly using the abundance of bryophyte species. The percent cover of each bryophyte species found on a quadrat and relevé was multiplied by each species' mean height above the water table, which was calculated from a large peatland database for North America (Gignac et al. 2000). The mean height of the water table above the peat surface for a quadrat or relevé was calculated as a weighted mean of all bryophyte species found on it. Similar methods have been used to reconstruct environmental conditions on peatlands in the past using bryophyte macrofossil abundance data obtained from peat cores (Kuhry et al. 1993; Bauer et al. 2003). The height gradient was divided as follows: <0 cm, emergent; 0–10 cm, carpet; 10–20 cm, lawn; 20–60 cm, low hummock; >60 cm, tall hummocks and peat plateaus (Vitt et al. 1975*a*, 1990; Damman 1980).

Shade was measured as percent overstory cover of trees and tall shrubs for each relevé or quadrat. Species' relative tolerance along the shade gradient were identified by the following threshold levels: species found only on quadrats or relevés having <15% cover, very intolerant; <30% cover, intolerant; <70% cover, intermediate; <85% cover, tolerant; >85% cover, very tolerant (Smith 1996).

Data analyses

The presence and absence of the 37 Cyperaceae species on each peatland was subjected to a TWINSPAN analysis, a divisive hierarchical method that divides species and stands into groups (Hill 1979). Presence and absence data and environmental variables were ordinated simultaneously using a canonical correspondence analysis (CCA) (ter Braak 1987).

Two-dimensional response surfaces were generated in climatic space along MAT and MATP and in ecological space along pH and height above the water table gradients. Linear response surfaces were produced along the shade gradient. Response surfaces were generated by dividing the range of values for each gradient into equidistant points (Gignac et al. 1991). When two gradients were used, this produced a two-dimensional grid of points, where values along each gradient met to produce nodes. For example, values on the pH gradient ranged between 8 and 3, and this gradient was divided by increments of 0.5, whereas the height above the water table gradient extended between –20 and 140 cm and was divided by increments of 10 cm. When the two gradients were used to generate a response surface, a grid node was produced wherever increment values for both gradients met. Thus, at pH 5.5 a grid node would be formed at heights of –20 cm, –10 cm, 0 cm, and so on up to 140 cm.

Frequencies of occurrence along the pH gradient (rounded to the nearest 0.5) and height above the water table gradient (rounded to the nearest 10 cm) were calculated as the number of relevés and quadrats on which a species was found at a grid node divided by the total number of relevés and quadrats found at that node. For example, if a species was found four times on quadrats and relevés that were identified by a grid node having pH 5 and height above the water table of 20 cm and there were 20 quadrats or relevés that had the same pH and height values, the frequency of occurrence of the species at the grid node was 0.20. A frequency of occurrence value was then recalculated for each node using distance-weighted means. This procedure used all values within three grid nodes of a selected node, and the mean was calculated such that values further from the node carried less weight than those that were closer (see Gignac et al. 1991 for computational details). That procedure generated estimated frequency of occurrence values for grid nodes that did

Table 2. Number of observations (*n*), mean, standard deviation (SD), minimum (min.), and maximum (max.) for nine environmental variables measured on 498 peatlands in Canada.

Variable	*n*	Mean	SD	Min.	Max.
Height (cm)	2117	23.8	18.2	–12	170
Shade (% overstory cover)	2117	31	28	0	100
pH	498	5.4	1.0	3.5	8.3
k_{corr} ($\mu S \cdot cm^{-1}$)	498	161.2	206.4	0.0	1407.0
Ca ($mg \cdot L^{-1}$)	498	15.4	23.2	0.0	146.6
MAT (°C)	230	0.8	3.2	–9.8	10.5
MATP (mm)	230	928	613	211	3943
MATR (mm)	230	658	547	115	3883
Growing season (d)	230	194	46	121	365

Note: k_{corr}, corrected conductivity; MAT, mean annual temperature; MATP, mean annual total precipitation; MATR, mean annual total rainfall.

Table 3. Correlation coefficients for relationships between height above the water table, shade, water chemistry, and climatic variables for 498 peatlands in Canada.

	Shade	pH	k_{corr}	Ca	MAT	MATP	MATR	GS
Height	0.38***	–0.32***	–0.14*	–0.18***	0.07	0.12	0.10	0.06
Shade		–0.15**	0.25***	–0.20**	–0.11	–0.21***	–0.21***	–0.16**
pH			0.50***	0.64***	–0.10	–0.27***	–0.24***	–0.08
k_{corr}				0.80***	–0.04	–0.30***	–0.25***	–0.05
Ca					–0.00	–0.26***	–0.22***	–0.02
MAT						0.51***	0.59***	0.87***
MATP							0.96***	0.59***
MATR								0.73***

Note: k_{corr}, corrected conductivity; MAT, mean annual temperature; MATP, mean annual total precipitation; MATR, mean annual total rainfall; GS, length of the growing season. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

not have data because of gaps in the sampling and also smoothed the data between adjacent nodes. The procedure also extrapolated species ranges by one grid node.

Frequency of occurrence values along the shade gradient (rounded to the nearest 10%) were calculated as the number of quadrats on which a species was present for a shade value divided by the total number of quadrats and relevés that had the same shade value. Frequency of occurrence values for each species along the MAT (rounded to the nearest 2 °C) and log(MATP) (rounded to the nearest 0.25 mm) gradients were calculated as the number of peatlands on which it occurred divided by the total number of peatlands found at the same grid node. Response surfaces were illustrated only for representatives of ecologically related species within each TWINSPAN group. Ecologically related species had similar ranges along all gradients, and representative species were selected from among related species, because their estimated (smoothed) frequency of occurrence values were closest to the observed values.

The statistical analysis system (SAS) was used for all computations and statistical analyses. Three-dimensional response surfaces were graphed using Proc G3D from SAS graph. TWINSPAN and CCA were done through PC-ORD version 4 (McCune and Mefford 1999).

Results

Environmental gradients

Height above the water table varied between –12 and 170 cm and covered the full range of habitat classes from submerged to tall hummock and peat plateau (Table 2). The height gradient was significantly positively correlated with the shade gradient and significantly negatively correlated with the three water chemistry gradients (Table 3). Percent overstory cover (shade) ranged between 0% and 100% and was also significantly correlated with the three water chemistry variables as well as MATP, MATR, and GS (Table 3). pH varied between 3.5 and 8.3 and covered the complete range of peatland types from bogs to extreme-rich fens. All three water chemistry gradients had wide ranges and were highly significantly correlated with each other. The MAT gradient ranged from low subarctic to cool temperate, while the MATP and MATR gradients ranged from continental to hyperoceanic. The four climatic variables were highly significantly correlated with each other.

Axis 1 of the CCA ordination of the 498 peatlands along with the environmental variables had an eigenvalue of 0.581 and explained 26.3% of the variation (Fig. 2). Axes 2 and 3 had eigenvalues of 0.468 and 0.452 and accounted for 14.4% and 12.5% of the variation, respectively. The water chemistry and climatic variables were negatively ($p < 0.001$) and positively ($p < 0.001$) correlated, respectively, with the first axis. The climatic gradients were also positively correlated ($p < 0.001$) with the second axis, while the height and shade gradients were positively correlated ($p < 0.001$) with the third axis. Thus, hyperoceanic temperate sites were found in the upper right corner, while continental subarctic sites were found in the lower left corner of the ordination space that was delimited by axes 1 and 2 (Fig. 2*a*). In both ordination spaces (axes 1 and 2 and axes 1 and 3), bogs were on the
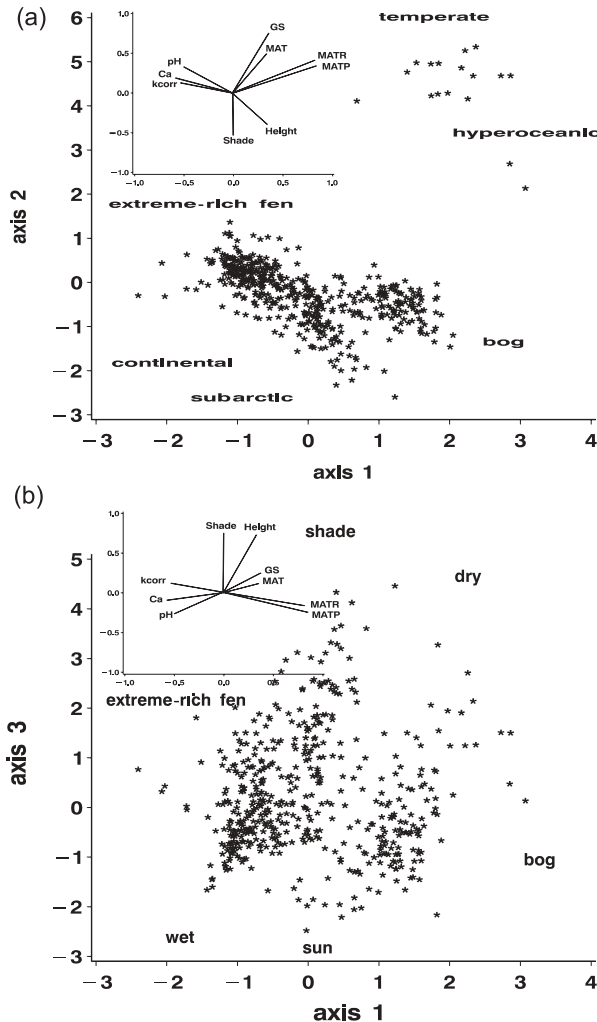
right side and extreme-rich fens were on the left side (Figs. 2*a* and 2*b*). In the ordination space bounded by axes 1 and 3, wet sunny sites are found at the bottom of the ordination, while dry shaded sites were found at the top (Fig. 2*b*).

The distribution of sites within the ordination of axes 1 and 2 revealed a sampling gap along the climatic gradient that appeared to occur in oceanic areas (Fig. 2*a*). However, sites were relatively evenly distributed along the water chemistry gradient. Sites were also relatively evenly distributed along the height above the water table and shade gradients.

Species distribution

Of the 70 Cyperaceae species encountered, only 37 had sufficient data to permit a detailed analysis of their habitat preferences. The majority of excluded species were found in swamps, marshes, or wet meadows rather than in bogs and rich fens, and most of the remainder had subarctic and arctic distributions. Among the 37 species examined, *C. aquatilis*,

Carex limosa, and *Eriophorum vaginatum* were the most common (>400 of the 2117 quadrats or relevés) (Table 4). Both *C. aquatilis* and *C. limosa* had relatively wide ranges along the climatic gradients, while *E. vaginatum* had narrower ranges and was found in drier and warmer areas. Four species, *Carex chordorrhiza* Ehrh. ex Lf., *Carex lasiocarpa* Ehrh. (sensu stricto), *Carex oligosperma* Michx., and *Scirpus cespitosus* L. were found on between 200 and 300 relevés or quadrats. *Carex chordorrhiza* and *C. lasiocarpa* had relatively narrow ranges along the MAT and MATP gradients and were found in colder and drier areas than either *C. oligosperma* and *S. cespitosus*. *Carex angustior* Mackenz., *Carex brunnescens* (Pers.) Poir., *Carex michauxiana* Boeckl., *Carex stricta* Lam., and *Eriophorum tenellum* Nutt. were the least abundant of the species studied and, with the exception of the shade gradient, had narrow ranges along all gradients. Most species had relatively wide ranges along the three water chemistry gradients (Table 5). Among species that had relatively narrow ranges were the following: *C. angustior*, *Carex capitata* L., *C. michauxiana*, *Carex prairea* Dew. ex A.W. Wood, *C. stricta*, and *E. tenellum*. Maximum values for *C. angustior*, *C. michauxiana*, *C. stricta*, and *E. tenellum* were less than 5.9 along the pH gradient, while minimum values for *C. capitata* and *C. prairea* were above 5.8.

The TWINSPAN analysis separated the 37 species into eight groups (Fig. 3). Eigenvalues for each division ranged between 0.512 and 0.34. Groups 1 and 8 contained only *Carex* species, while Group 4 contained several *Eriophorum* species. Groups 1, 2, 4, and 7 contained more than 6 species each and accounted for the majority of the 37 species analyzed. Group 3 had the fewest species.

The ordination of the species groups identified by TWINSPAN showed that groups 1 through 7 were arranged in increasing order along the water chemistry gradient starting with species found on more alkaline sites along axis 1 (Fig. 4*a*). There was some overlap along axis 1 between groups 4 and 5, groups 5 and 6, and groups 6 and 7 (Fig. 4*b*). All of those groups were found on more acidic sites. However, the second axis, which was associated with the climatic gradient, separated group 4 from group 5 and group 6 from groups 5 and 7. Species in groups 4 and 6 were found on warmer and wetter sites than those in groups 5 and 7. Species in group 8 were completely isolated from all other species along axis 2 and were found in temperate hyperoceanic areas.

Species response surfaces

The frequencies of occurrence of the three representatives and their ecologically related species (in parentheses) that were analyzed in ecological and climatic space for TWINSPAN group 1 were the following: *Carex vaginata* Tausch (*Carex diandra* Schrank and *C. capitata*); *Carex gynocrates* Wormsk. ex Drej. (*Carex interior* Bailey); *C. prairea*. Species in this group had relatively narrow ranges along the pH gradient (Fig. 5). They reached their maximum frequency of occurrence at pH values >6 and, with the exception of *C. capitata* (not illustrated), between −5 and 30 cm above the water table. *Carex capitata* was found slightly higher above the water table. Generally, these species were not found in deep shade (>80%). With the ex-

Table 4. Mean (±1 SD) value for height above water table, shade, and climate variables for 37 common Cyperaceae species.

Species	n	Height (cm)	Shade (%)	MAT (°C)	MATP (mm)
Carex angustior Mackenz.	18	13±11	24±14	0.3±1.3	1362±149
Carex aquatilis Wahlenb. var. *aquatilis*	406	14±9	25±21	–0.5±3.2	670±635
Carex brunnescens (Pers.) Poir.	14	21±13	59±31	–0.1±2.6	582±148
Carex canescens L.	72	16±13	31±24	–0.9±2.3	947±470
Carex capitata L.	27	21±14	26±19	–4.0±2.5	420±154
Carex chordorrhiza Ehrh. ex Lf.	222	10±11	23±24	–0.5±2.1	534±197
Carex diandra Schrank	118	13±11	27±29	0.2±1.1	497±49
Carex disperma Dew.	74	24±12	60±30	0.8±1.6	506±94
Carex exilis Dew.	71	13±10	26±19	–0.3±2.3	953±199
Carex gynocrates Wormsk. ex Drej.	80	16±9	46±23	–0.7±2.7	507±111
Carex interior Bailey	92	15±11	34±30	–0.3±2.1	542±100
Carex lasiocarpa Ehrh.	222	12±13	30±30	–0.2±2.4	569±221
Carex leptalea Wahlenb.	67	17±12	37±28	0.1±4.1	661±498
Carex limosa L.	434	9±9	18±18	–0.2±2.3	827±404
Carex livida (Wahlenb.) Willd.	99	12±16	10±17	3.4±4.3	1547±1216
Carex magellanica Lam.	162	19±12	41±29	–0.6±3.0	779±380
Carex michauxiana Boeckl.	7	13±12	24±16	–0.1±0.9	1396±132
Carex oligosperma Michx.	206	21±16	29±19	1.0±1.7	1056±247
Carex pauciflora Lightf.	143	25±15	29±24	1.4±3.4	1195±619
Carex pluriflora Hult.	26	30±11	10±20	7.8±0.8	2329±887
Carex prairea Dew. ex A.W.Wood	24	22±11	26±33	3.6±4.4	697±309
Carex saxatilis L.	27	21±11	7±5	6.6±4.8	1844±640
Carex sitchensis	20	25±9	9±19	7.7±0.5	3300±488
Carex stricta Lam.	11	24±17	60±29	1.9±1.7	1169±250
Carex tenuiflora Wahlenb.	106	19±10	46±31	–0.1±1.7	508±66
Carex trisperma Dew.	129	38±29	72±27	2.3±2.1	1045±267
Carex utriculata Boott	137	11±12	16±20	0.7±3.8	1109±842
Carex vaginata Tausch	27	25±11	43±29	–0.5±4.1	976±1062
Eriophorum angustifolium Honck.	168	25±15	41±34	3.4±3.6	1293±932
Eriophorum chamissonis C.A. Meyer	69	14±13	17±24	1.5±4.5	882±542
Eriophorum gracile W.D.J. Koch	36	11±15	31±31	0.7±3.1	683±504
Eriophorum tenellum Nutt.	7	13±7	28±8	–0.0±0.9	1381±126
Eriophorum vaginatum L.	527	27±17	35±35	0.5±2.5	739±345
Eriophorum virginicum L.	165	19±20	42±34	1.7±2.5	925±350
Rhynchospora alba (L.) Vahl	147	11±9	15±18	3.8±3.4	1417±777
Scirpus cespitosus L.	286	17±15	21±22	2.2±4.0	1330±806
Scirpus hudsonianus (Michx.) Fern.	79	9±13	30±31	–1.2±2.7	648±335

Note: n, number of quadrats or relevés in which each species was found; MAT, mean annual temperature; and MATP, mean annual total precipitation.

ception of *C. prairea*, they were found in areas where the temperature was between 6 and –10 °C and log(MATP) was <7 mm. *Carex prairea* occupied a much narrower range along both the temperature and precipitation gradients.

Representative species for group 2 were the following: *C. chordorrhiza* (*Eriophorum gracile* W.D.J. Koch), *Carex disperma* Dew. (*Carex tenuiflora* Wahlenb.), and *C. lasiocarpa* (*Carex leptalea* Wahlenb.). Species in this group had broader ranges along the pH gradient than those in group 1. They were found in peatlands where the pH was below 5 (Fig. 6). However, all species attained their maximum frequency of occurrence at pH ranges >6 and were found growing on peat that was below the surface of the water. Three species, *C. chordorrhiza* (*E. gracile*) and *C. lasiocarpa*, reached their maximum frequency of occur-

rence below the surface of the water, while *C. disperma* (*C. tenuiflora*) achieved their maximum between 20 and 40 cm above the water table. *Carex leptalea* was intermediate between both those groups and reached its maximum between 0 and 20 cm. With the exception of *C. disperma* and *C. leptalea*, species in this group did not commonly occur in deep shade. *Carex disperma* (*C. tenuiflora*) were found at temperatures between 6 and –6 °C and log(MATP) values between 5.5 and 7.0 mm, while the ranges for *C. chordorrhiza* (*E. gracile*) and *C. lasiocarpa* along the MAT gradient extended to –10 °C. The ranges of *C. lasiocarpa* and *C. leptalea* along the MAT gradient extended to 10 °C and to log(MATP) values of 8 mm.

The two species in group 3 occupied wide ranges along the pH gradient (Fig. 7). Both species were found growing

Table 5. Mean, minimum (min.), and maximum (max.) values for water chemistry variables for 37 common Cyperaceae species.

Species	pH			k_{corr} (μS·cm^{-1})			Ca (mg·L^{-1})		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Carex angustior	4.8	4.0	5.6	47	16	120	1.7	0.1	9.8
Carex aquatilis	5.9	3.6	8.5	231	0	1522	26.5	0.2	146.6
Carex brunnescens	5.2	4.7	6.5	179	17	729	13.6	1.5	58.0
Carex canescens	5.1	3.8	7.2	85	16	407	6.0	0.1	39.8
Carex capitata	6.9	6.2	7.5	217	75	487	35.2	5.2	81.4
Carex chordorrhiza	6.0	4.3	7.5	198	0	1271	20.9	0.4	131.3
Carex diandra	6.3	4.8	7.4	273	12	1407	28.9	1.4	146.6
Carex disperma	6.1	4.7	7.4	318	20	1271	29.3	1.5	131
Carex exilis	5.2	3.8	6.5	16	0	144	1.8	0.3	12.8
Carex gynocrates	6.3	4.4	8.2	352	33	1407	32.6	0.4	146.6
Carex interior	6.4	4.4	7.5	297	2	1291	34.3	0.8	131.3
Carex lasiocarpa	6.0	3.6	7.5	226	0	1271	22.9	0.5	131.3
Carex leptalea	6.3	4.4	7.4	295	1	1220	31.2	2.8	93.9
Carex limosa	5.4	3.6	7.8	121	0	1407	13.1	0.6	146.6
Carex livida	5.5	3.9	7.4	196	0	1271	15.0	0.1	131.3
Carex magellanica	5.1	3.8	7.8	128	0	1163	9.2	0.1	77.5
Carex michauxiana	4.8	4.3	5.2	34	19	47	0.9	0.4	1.1
Carex oligosperma	4.4	3.7	6.0	24	0	543	1.2	0	92.2
Carex pauciflora	4.7	3.8	6.5	42	0	253	2.6	0	21.1
Carex pluriflora	4.4	3.9	6.2	42	11	89	1.1	0.1	2.5
Carex prairea	6.7	5.8	7.2	311	17	1102	31.3	3.2	92.8
Carex saxatilis	4.9	3.9	6.0	64	1	80	6.3	1.1	11.1
Carex sitchensis	5.5	4.1	6.6	36	13	81	3.4	0.1	11.2
Carex stricta	4.4	3.8	5.9	36	20	72	1.8	0.2	3.4
Carex tenuiflora	5.9	4.4	7.4	185	2	1271	16.7	0.4	131.3
Carex trisperma	4.3	3.7	6.5	76	0	395	2.9	0.1	27.0
Carex utriculata	5.4	3.9	7.4	106	2	881	11.3	0.1	94.4
Carex vaginata	5.9	5.4	7.4	393	82	1271	29.8	6.4	131.3
Eriophorum angustifolium	4.9	3.7	7.6	117	0	915	9.8	0.1	83.9
Eriophorum chamissonis	5.1	3.8	7.2	101	0	932	10.5	0.1	94.4
Eriophorum gracile	5.7	4.5	7.4	232	25	1271	18.4	0.3	131.3
Eriophorum tenellum	4.9	4.5	5.3	45	16	144	0.7	0.1	1.2
Eriophorum vaginatum	4.2	3.4	7.1	66	0	331	2.1	0.1	39.8
Eriophorum virginicum	4.7	3.7	7.5	125	0	869	9.1	0.0	94.4
Rhynchospora alba	4.7	3.8	7.4	55	0	915	3.7	0.0	69.9
Scirpus cespitosus	5.1	3.8	7.5	77	0	915	7.2	0.0	88.8
Scirpus hudsonianus	5.9	4.3	7.5	233	0	1271	22.5	0.2	131.3

**Note:** k_{corr} = corrected conductivity.

in peat that was below the surface water, but *C. aquatilis* reached its maximum frequency of occurrence at 10 cm above the peat surface. Neither species was commonly found in heavily shaded areas. The climatic range of both species extended from –10 to 6 °C along the MAT gradient. *Carex aquatilis* had a slightly wider range along the precipitation gradient than did *Scirpus hudsonianus* (Michx.) Fern.

The habitat niches of three representative species in group 4, *C. limosa* (*Eriophorum virginicum* L.), *Carex livida* (Wahlenb.) Willd. (*Carex utriculata* Boott and *Eriophorum chamissonis* C.A. Meyer), and *Eriophorum angustifolium* Honck., are illustrated in Fig. 8. Species in this group were widespread along the pH gradient but, with the exception of *C. livida*, they were found relatively more frequently on peatlands that had pH values <5 than those previously described for the other groups. They all had relatively wide

ranges along the height above the water table gradient and were found growing on peat that was below the surface water. With the exception of *E. angustifolium*, they reached their maximum frequency of occurrence below the water surface, but were also found up to 80 cm above the water table and were not commonly found in areas that have >50% shade. *Eriophorum angustifolium* was found more frequently between 30 and 40 cm above the water table and in shaded habitats. Species ranges extended to all values along the MATP gradient and between –10 and 10 °C along the MAT gradient.

The representative species for group 5 were *Carex magellanica* Lam. = *Carex paupercula* Michx. (*Carex canescens* L.) and *E. vaginatum* (*C. brunnescens*) (Fig. 9). Species in this group also had wide ranges along the pH gradient, but they were more commonly found on peatlands that had

Fig. 3. Dendogram of TWINSPAN generated species groups based on presence and absence data for 37 Cyperaceae species. Numbers on the dendogram indicate eigenvalues for each division.
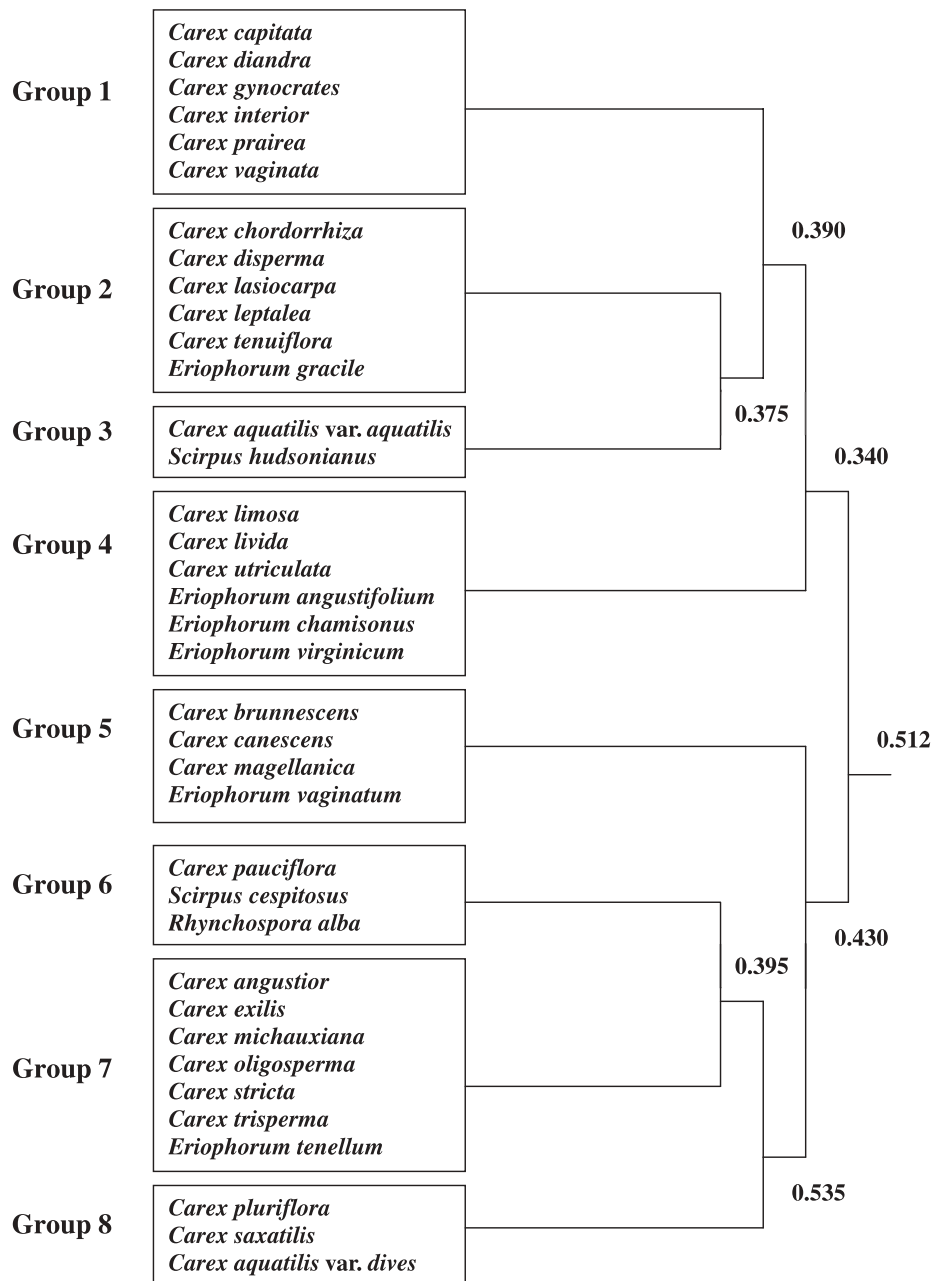

pH values <6 than on sites that had values >6. Although they were all found in areas where the peat was below the surface of the water, they reached their maximum frequency of occurrence between 10 and 40 cm above the water table. *Eriophorum vaginatum* had the widest range along the height gradient and was found up to 1 m above the surface water. *Eriophorum vaginatum* (*C. brunnescens*) were more commonly found in heavily shaded rather than sunny areas, while *C. magellanica* (*C. canescens*) were more commonly found in less-shaded areas. Species ranges along the log(MATP) gradient extended from 5.25 to 7.75 mm. With the exception of *E. vaginatum*, species in this group ranged

between –6 and 8 °C. The range for *E. vaginatum* extended to slightly colder temperatures.

Species in group 6 had wide ranges along the pH gradient (Fig. 10). All of the species reached their maximum frequency of occurrence at values between 5 and 5.5, but both *S. cespitosus* and *Rhyncospora alba* (L.) Vahl were commonly found on peatlands that had pH values >6.5. All three species in this group also commonly occurred on sites that had pH values below 4.5. They were found on peat that was at or below the surface water, but they had different ranges along the microtopography gradient. *Rhyncospora alba* had the narrowest range and was generally found between –10

Fig. 4. Canonical correspondence analysis plot of 37 Cyperaceae species identified by TWISPAN group along axes 1 and 2 (*a*). Mean and range of values for each group (*b*).
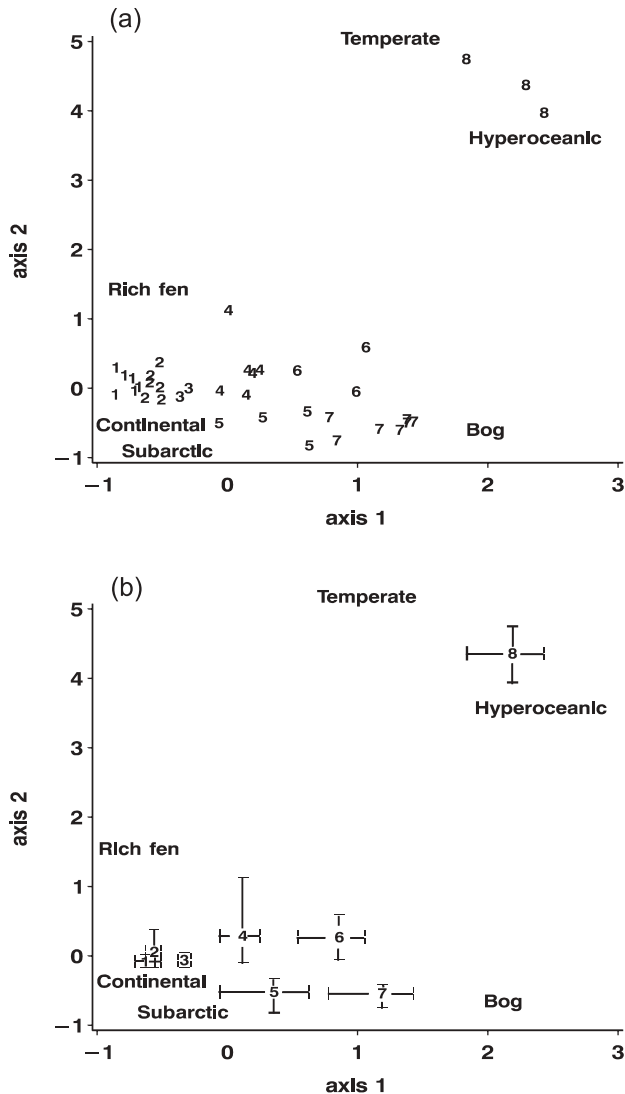
and 20 cm above the water level. *Carex pauciflora* was more commonly found between 0 and 50 cm above the water, while *S. cespitosus* had a relatively wide range and was found between –20 and 80 cm above the water. The three species in this group were rarely found in areas where the shade was >70%. *Scirpus cespitosus* had the widest range of the three species along the log(MATP) gradient and was found between 6 and 8.25 mm. The remaining species were found between 6.25 and 8.25 mm. The ranges of both *S. cespitosus* and *C. pauciflora* were found between –4 and 10 °C, while *R. alba* was found between –2 and 10 °C.

The five representative species for group 7 were the following: *Carex exilis* Dew. (*C. angustior*, *C. michauxiana*, and *E. tenellum*), *C. oligosperma*, and *Carex trisperma* Dew. (*C. stricta*). The seven species in this group were found on peatlands having pH values >6, but all of them reached their maximum frequency of occurrence at pH values equal to or less than 5 (Fig. 11). They occupied widely different ranges above the water table. *Carex exilis* (*C. angustior*,

C. michauxiana, and *E. tenellum*) reached their maximum frequency of occurrence between 0 and 5 cm above the water table and had narrow ranges along the height gradient. *Carex oligosperma* had a wider range but was most commonly found on peat that was below the surface water level. *Carex stricta* also had a relatively wide range along the height gradient but reached its maximum frequency of occurrence between 20 and 30 cm. *Carex trisperma* had an exceptionally wide range along the height gradient and was generally found on the highest hummocks on peatlands. *Carex exilis* (*C. angustior*, *C. michauxiana*, and *E. tenellum*) were not commonly found in areas that had >60% shade. *Carex trisperma* on the contrary was found almost exclusively in shaded areas.

The representative species for group 8 were *C. sitchensis* (*C. pluriflora* and *Carex saxatilis* L.) (Fig. 13). The three species in this group had relatively wide ranges along the pH gradient and they reached their highest frequency of occurrence at values <5.5. The ranges of *C. saxatilis* and *C. sitchensis* along the height gradient extended below the surface water but reached their greatest frequency of occurrence between 10 and 30 cm above the water table. *Carex pluriflora* was found at higher elevations along the microtopographical gradient, and its maximum frequency of occurrence was between 30 and 60 cm above the water table. None of the species were found in habitats that had >60% shade, and only *C. pluriflora* was found in areas having >40% shade. All three species were restricted to areas where the temperature was >4 °C and log(MATP) values >7.

Values of maximum frequency of occurrence for several species were very low (<0.1), particularly along the shade gradient. Several species including *C. prairea* and *C. vaginata* (Fig. 5) as well as *C. angustior*, *C. brunnescens*, *C. michauxiana*, *C. stricta*, and *E. tenellum*, which are not illustrated, had low maximum frequency of occurrence values along all gradients. *Carex sitchensis* (Fig. 12) as well as *C. pluriflora* and *C. saxatilis* had low maximum frequency of occurrence values on the shade, height, and pH gradients but not along the climatic gradients.

Discussion

Environmental gradients

Climate and surface water chemistry were primarily responsible for the distribution of Cyperaceae on peatlands in Canada, since they were both highly correlated with the first CCA axis (Fig. 2*a*). Height above the water table and shade played a secondary role in the distribution of the 37 species that were analyzed, since they were significantly correlated with the third axis.

The climatic gradient covered the full range of values from continental to hyperoceanic and from temperate to subarctic. However, the CCA analysis of the sites (Fig. 2*a*) indicated a gap in the distribution between hyperoceanic and oceanic sites. This gap was an artifact of the geographic distribution of the study sites. This gradient was in fact two gradients and not one. There was a Pacific coastal gradient from temperate hyperoceanic to subarctic continental and an Atlantic coastal gradient from temperate oceanic to subarctic continental. Since the gradient between the hyperoceanic Pa-

Fig. 5. Habitat niches for representative species in TWISPAN group 1: *Carex gynocrates* (top), *Carex prairea* (middle), and *Carex vaginata* (bottom). *F*, frequency of occurrence; MAT, mean annual temperature; MATP, mean annual total precipitation.
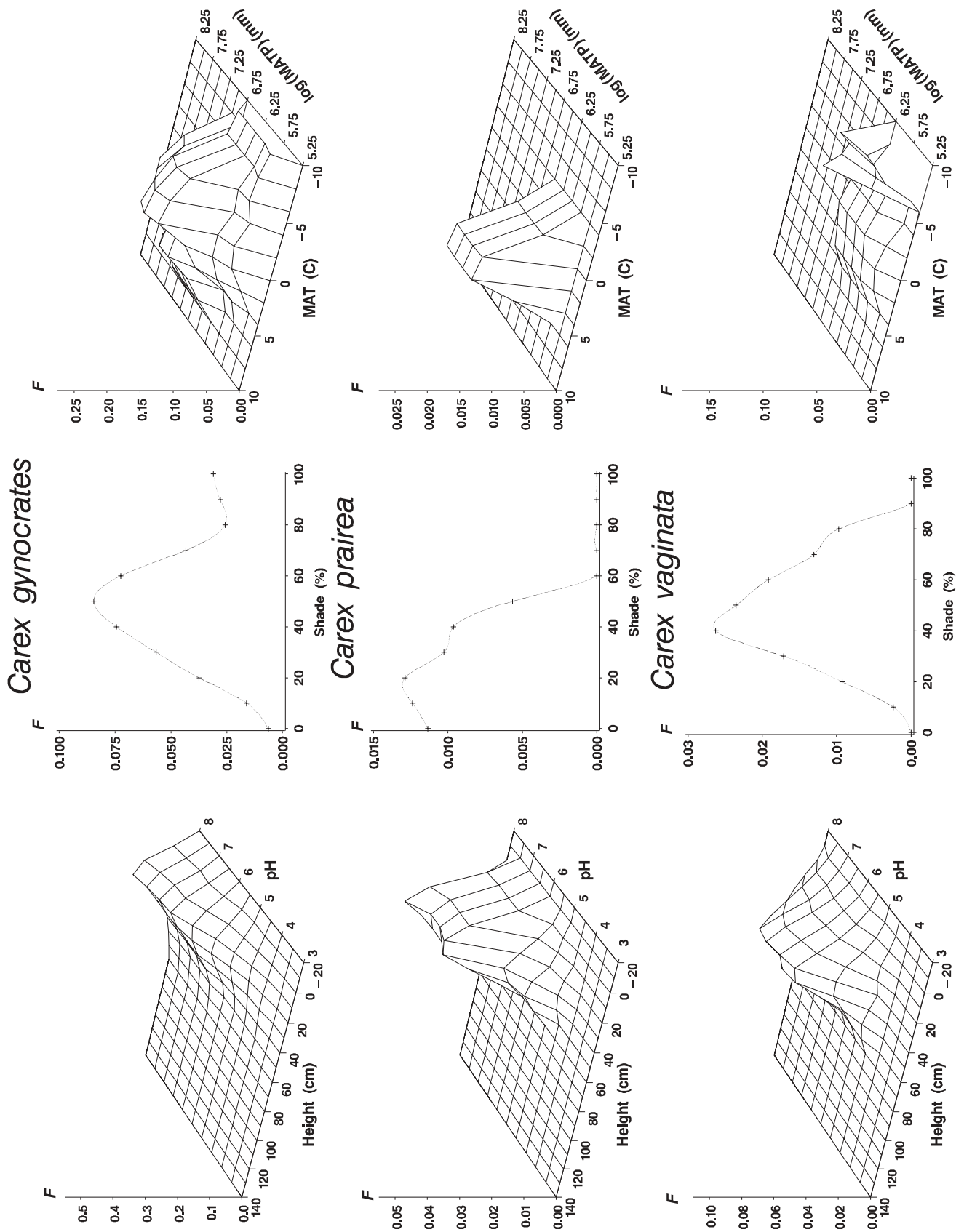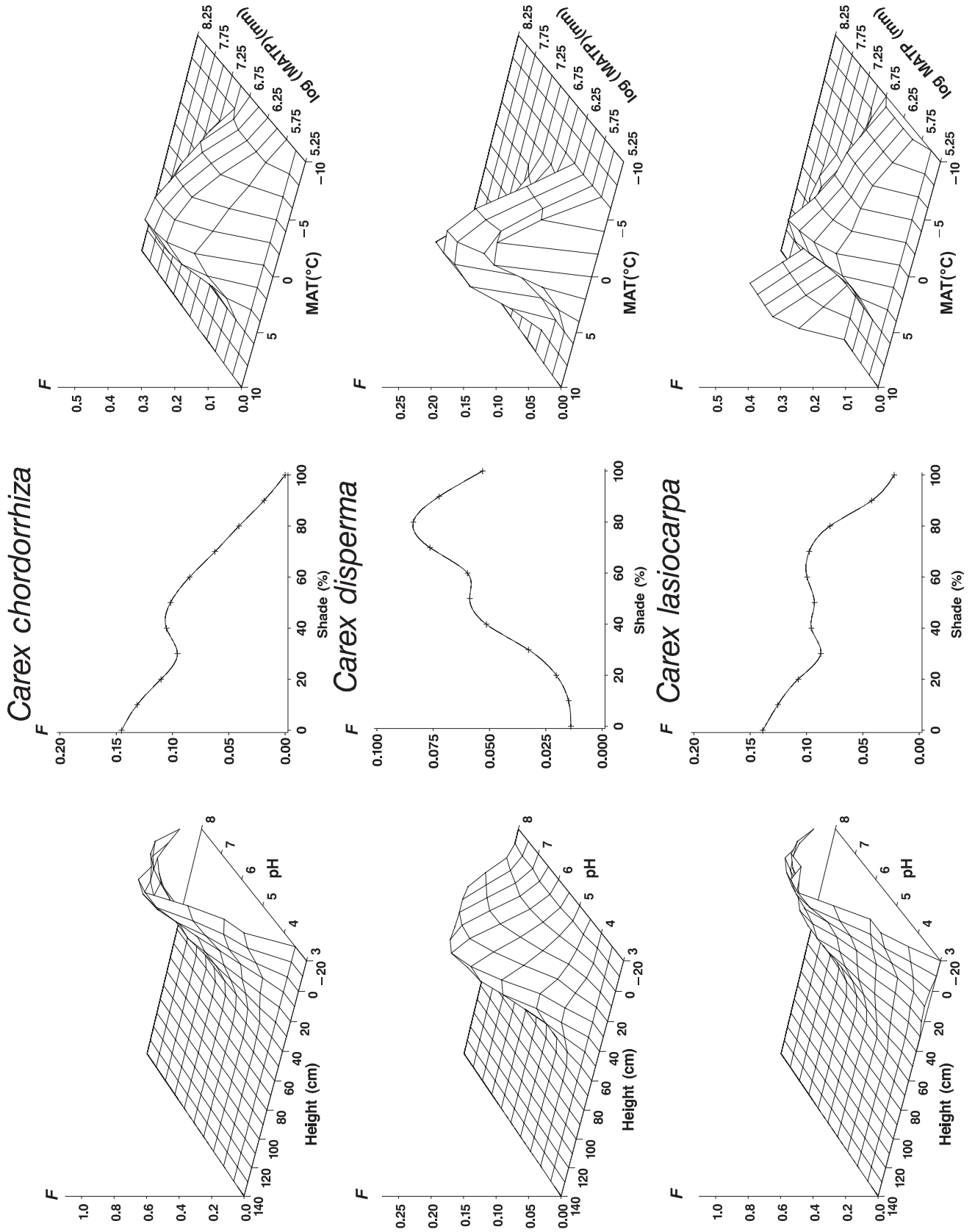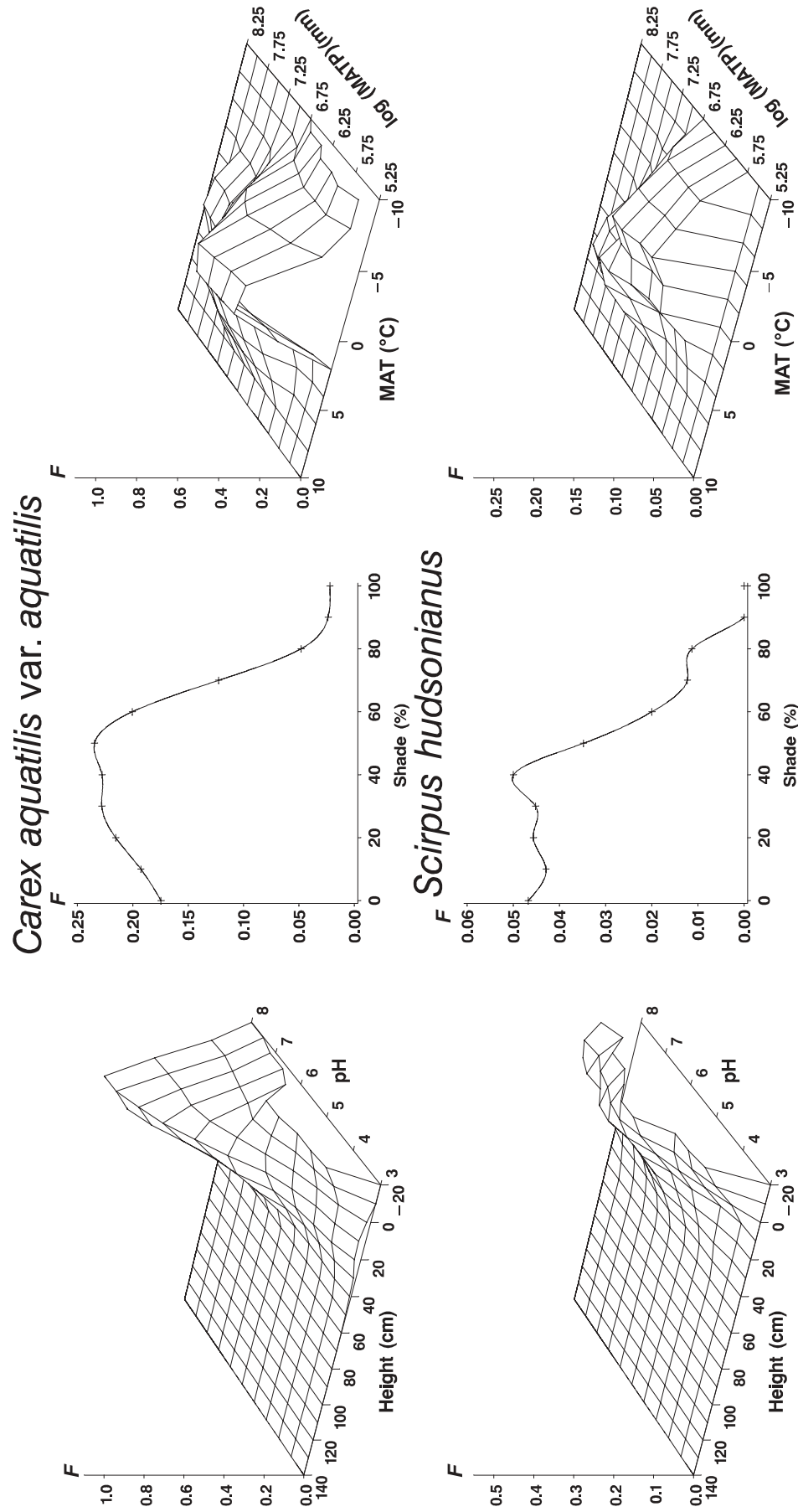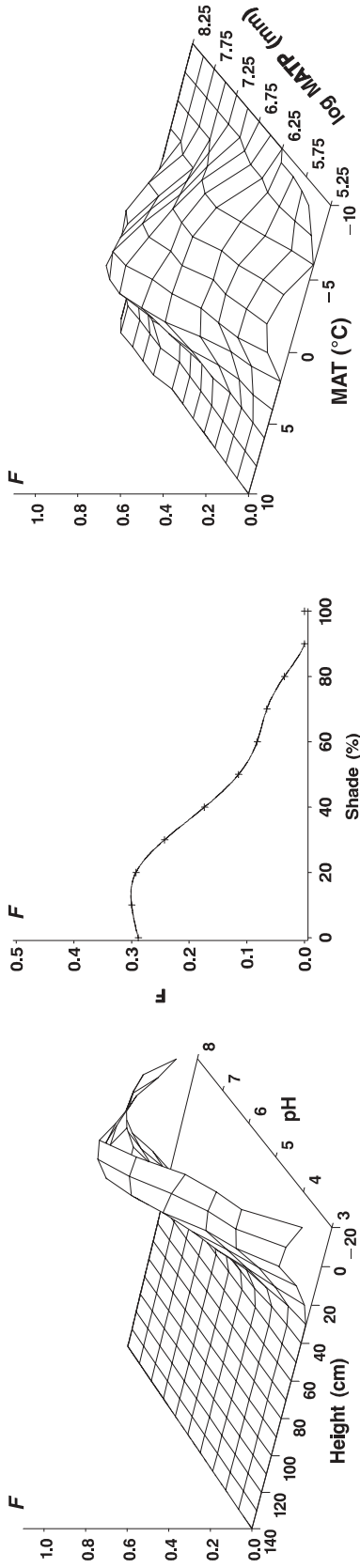
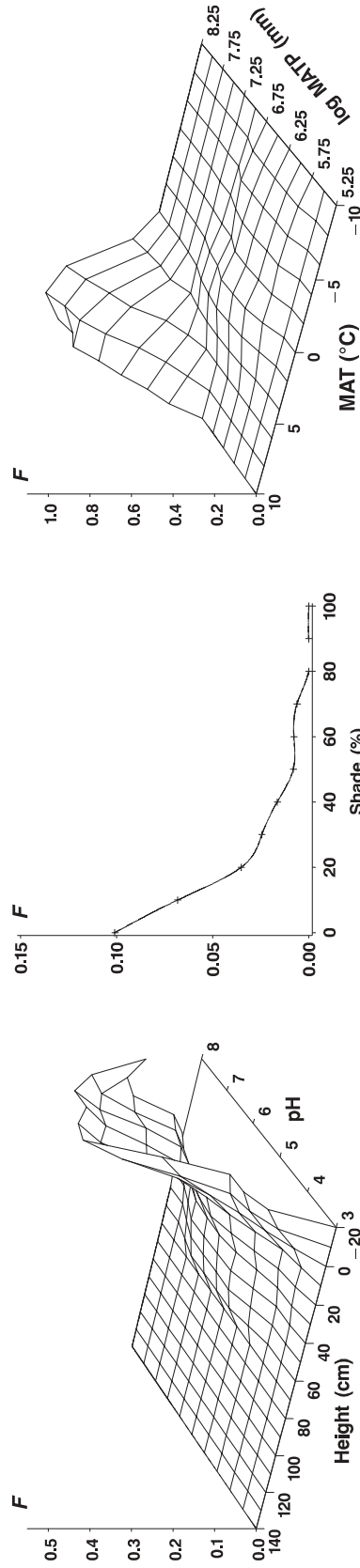**Fig. 6.** Habitat niches for representative species in TWINSPAN group 2: *Carex chordorrhiza* (top), *Carex disperma* (middle), and *Carex lasiocarpa* (bottom). *F*, frequency of occurrence; MAT, mean annual temperature; MATP, mean annual total precipitation.

Fig. 7. Habitat niches for representative species in TWINSPAN group 3: *Carex aquatilis* var. *aquatilis* (top) and *Scirpus hudsonianus* (bottom). *F*, frequency of occurrence; MAT, mean annual temperature; MATP, mean annual total precipitation.

Fig. 8. Habitat niches for representative species in TWINSPAN group 4: *Carex limosa* (top), *Carex livida* (middle), and *Eriophorum angustifolium* (bottom). *F*, frequency of occurrence; MAT, mean annual temperature; MATP, mean annual total precipitation.
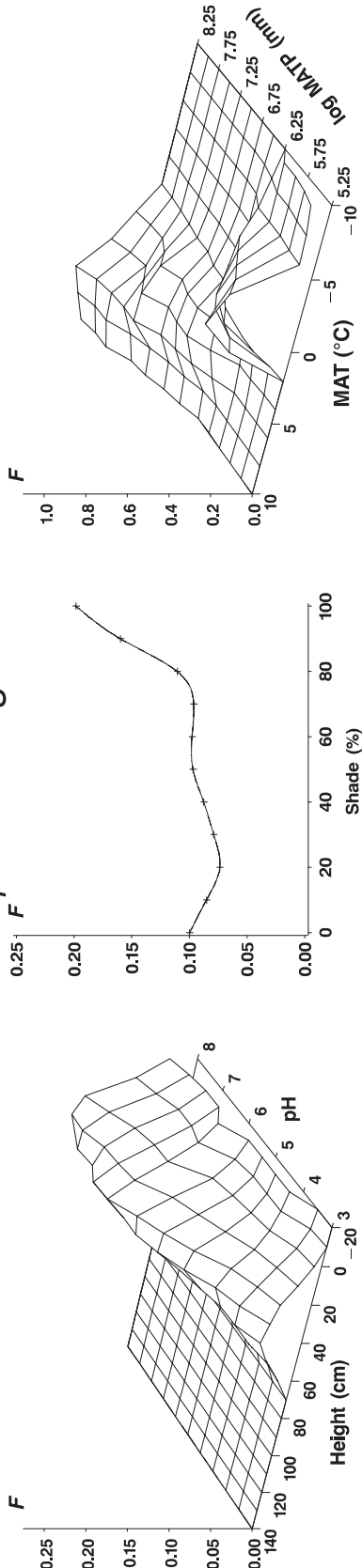
Fig. 9. Habitat niches for representative species in TWINSPAN group 5: *Carex magellanica* (top) and *Eriophorum vaginatum* (bottom). *F*, frequency of occurrence; MAT, mean annual temperature; MATP, mean annual total precipitation.
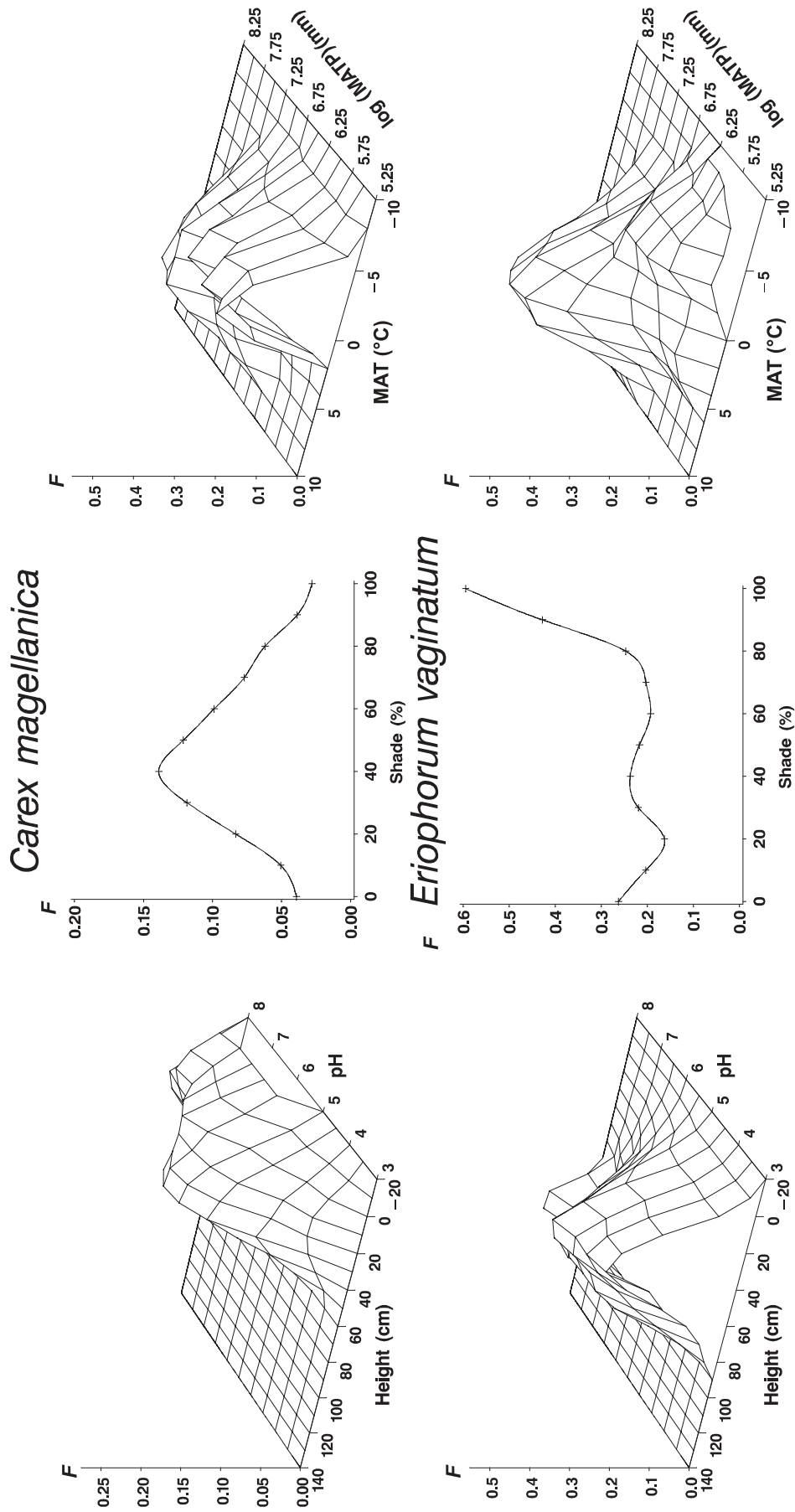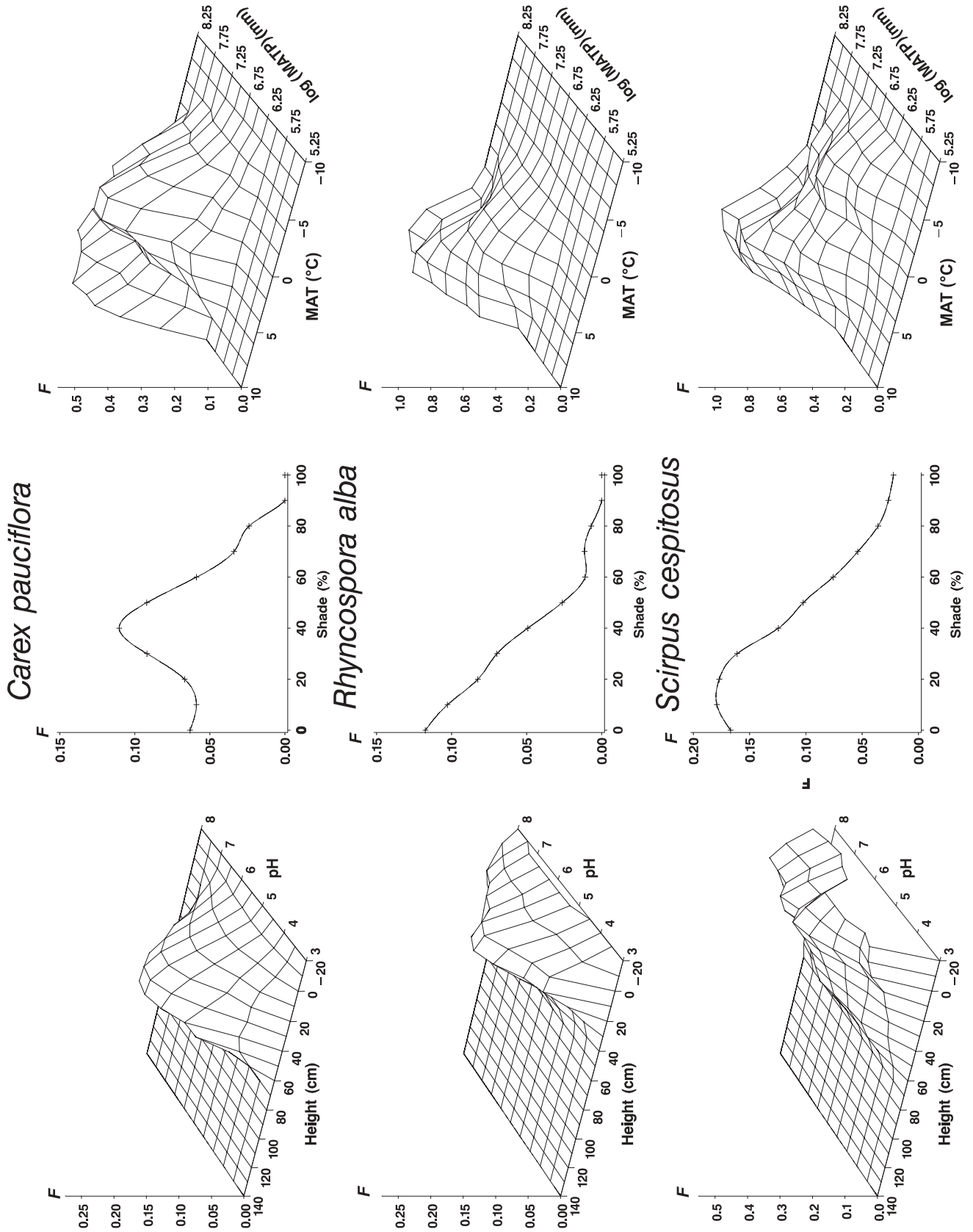
Fig. 10. Habitat niches for representative species in TWINSPAN group 6: *Carex pauciflora* (top), *Rhyncospora alba* (middle), and *Scirpus cespitosus* (bottom). *F*, frequency of occurrence; MAT, mean annual temperature; MATP, mean annual total precipitation.

cific Coast and the continental prairies was steep and topographically very heterogeneous, few sites were located in Pacific oceanic and suboceanic temperate areas (Gignac et al. 2000). Thus, Pacific coastal sites were isolated on the CCA ordination. As a result, the variables affecting the CCA ordination were redrawn to show a geographic as well as a climatic distribution (Fig. 13). The geographic distribution separated Pacific coastal hyperoceanic and oceanic sites from Atlantic coastal oceanic sites, and it became clear that the gap in the distribution of the sites was caused by a lack of Pacific oceanic and suboceanic sites.

The water chemistry gradient from acidic bog to alkaline extreme-rich fen was extensively surveyed. Although there were no gaps in the sampling of this gradient, the distribution of sites was significantly negatively correlated with the climatic (geographic) gradient (Table 3). There were many extreme-rich fens in continental subarctic and boreal areas (Zoltai et al. 1988) and very few in hyperoceanic and oceanic temperate areas (Banner et al. 1988; Wells and Hirvonen 1988). Water chemistry in fens is related to the buffering capacity of the mineral soil through which the ground water flows. In western continental areas, the mineral soil is mostly sedimentary and contains a relatively high concentration of bases, while in eastern boreal regions and coastal areas the bedrock is mostly granite (Bostock 1970), and water flowing over that substrate contains low concentrations of buffers and can thus easily become more acidic as a result of the acidifying properties of *Sphagnum* mosses. As a result, there was also a geographic rather than a climatic component to the distribution of the different peatland types.

Although the mineral soil in continental areas was circumneutral or alkaline, bogs and poor fens may form in recharge areas along drainage divides or as islands in rich fens (Kuhry et al. 1993). The height above the water table and shade gradients were highly positively correlated, indicating that wetter sites were generally open and drier sites were treed. Both gradients were negatively correlated with the water chemistry gradient. Thus, extreme-rich fens had relatively high water tables and were open when compared with bogs, particularly in continental areas, since the peat surface in bogs was elevated above the water table, thus creating drier conditions suitable for tree growth (Glaser and Janssens 1986; Zoltai et al. 1988). The shade gradient was also negatively correlated with the climatic gradient. Therefore, oceanic and hyperoceanic peatlands were generally open, while continental sites, with the exception of extreme-rich, moderate-rich fens, and some poor fens, were treed. The shade gradient was thus related to the climatic gradient.

Species habitat niches

Group 1 was composed of species that were restricted to rich fens (Fig. 5), and several species in this group were considered to be rich-fen indicators in the Hudson Bay Lowlands (Sjörs 1963), Minnesota (Wheeler et al. 1983), Newfoundland (Damman 1964), and Maine (Anderson et al. 1996). These calciphiles were found relatively close to the water table in such wet habitats as emergent, carpet, and lawn communities and were, with the exception of *C. prairea*, shade tolerant. All species appeared to be confined to continental, subcontinental, and suboceanic areas and absent from temperate regions. However, this relatively

narrow climatic range was misleading, since they have been found in eastern North America in temperate and oceanic conditions (Crow and Hellquist 2000). The climatic distribution observed in this study was due to scarcity of rich-fen study sites in eastern Canada and along the Pacific Coast. All species in this group had a widespread climatic distribution. Members of group 1 can thus be labeled as widespread, obligate rich-fen, wet, shade-tolerant species.

Species in groups 2, 3, 4, 5, and 6 were mostly found in fens. However, species within each group were generally separated from those in other groups along the pH gradient by their frequency of occurrence in poor-fen habitats (pH < 5.0). Species in groups 2 and 3 were infrequently found in poor fens (Fig. 6), but the frequency of occurrence of species in each subsequent group in those habitats gradually increased up to group 6 (Fig. 10).

Species in group 2 had a marked preference for rich fens, since their maximum frequency of occurrence was found at pH values of 6 or greater (Fig. 6). They were found along a wide range of habitats on the depth to the water table gradient from emergent to low hummock. However, none were found on tall hummocks. These results were consistent with those of Wheeler et al. (1983), who found *C. chordorrhiza*, *C. lasiocarpa*, and *C. tenuiflora* in all habitats along the pH gradient, with the exception of bogs and extreme-poor fens. However, Wheeler et al. (1983) found *C. disperma* and *C. leptalea* in rich fens exclusively, whereas in the present study their range extended into moderate-poor fens. Several species including *C. chordorrhiza*, *C. lasiocarpa*, and *E. gracile* were found most frequently in the wettest environments and were rarely found on low hummocks. Thus, group 2 was composed of species that were widespread and rich-fen preferential.

Species in groups 2 and 3 were ecologically closely related, as indicated by the TWINSPAN division that separated them (Fig. 3). The distinguishing feature between both groups was that members of group 2 had wider ranges along the climatic and pH gradients than species in group 3. Species in group 3 were not found in hyperoceanic areas along the Pacific Coast, while the ranges for all species in group 2 extended to that region. Both species in group 3 were found more frequently in poor-fen habitats than species in group 2. In fact, in some regions of eastern Canada, *C. aquatilis* was even considered to be poor-fen preferential (Gérardin and Grondin 1984). However, when peatlands across Canada were considered, *C. aquatilis* was definitely more commonly found on rich fens than on poor fens. Both species in group 3 were restricted to wet, relatively open environments and were rarely found in hummock and heavily treed habitats, whereas some of the members of group 2 were more frequently found in those habitats. Therefore, group 3 species are continental and eastern oceanic, rich-fen preferential, wet, and shade intolerant.

Species in group 4 were found in all peatland habitats but were generally associated with fens across North America (Sjörs 1963; Wells 1981; Wheeler et al. 1983; Banner et al. 1988; Anderson et al. 1996). With the exception of *E. angustifolium*, species in this group attained their highest frequency of occurrence in wet open habitats and were only occasionally found on low hummocks or in deep shade (Fig. 8). These habitat preferences were consistent with re-

Fig. 11. Habitat niches for representative species in TWINSPAN group 7: *Carex exilis* (top), *Carex oligosperma* (middle), and *Carex trisperma* (bottom). *F*, frequency of occurrence; MAT, mean annual temperature; MATP, mean annual total precipitation.
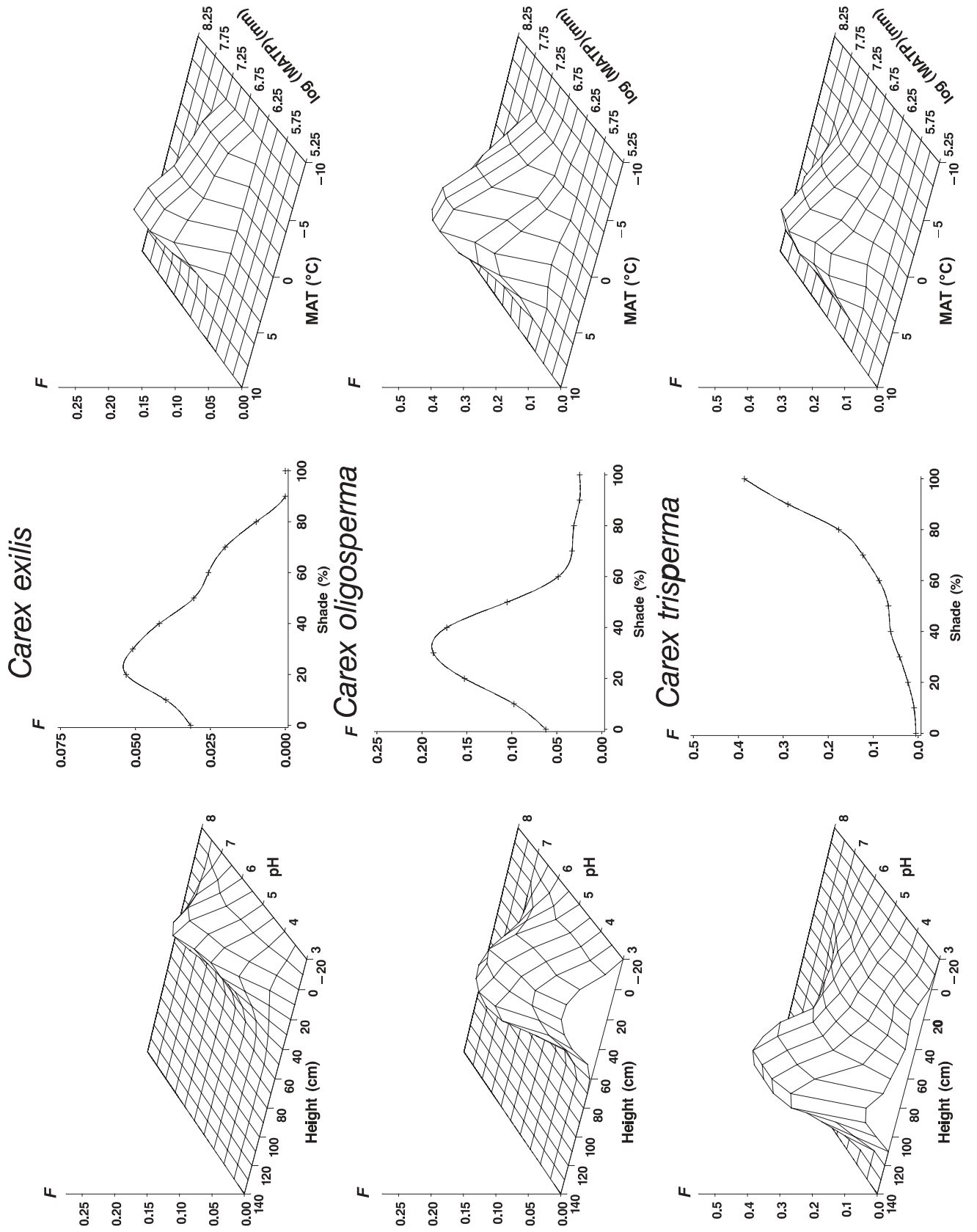
Fig. 12. Habitat niches for representative species in TWINSPAN group 8: *Carex sitchensis. F,* frequency of occurrence; MAT, mean annual temperature; MATP, mean annual total precipitation.
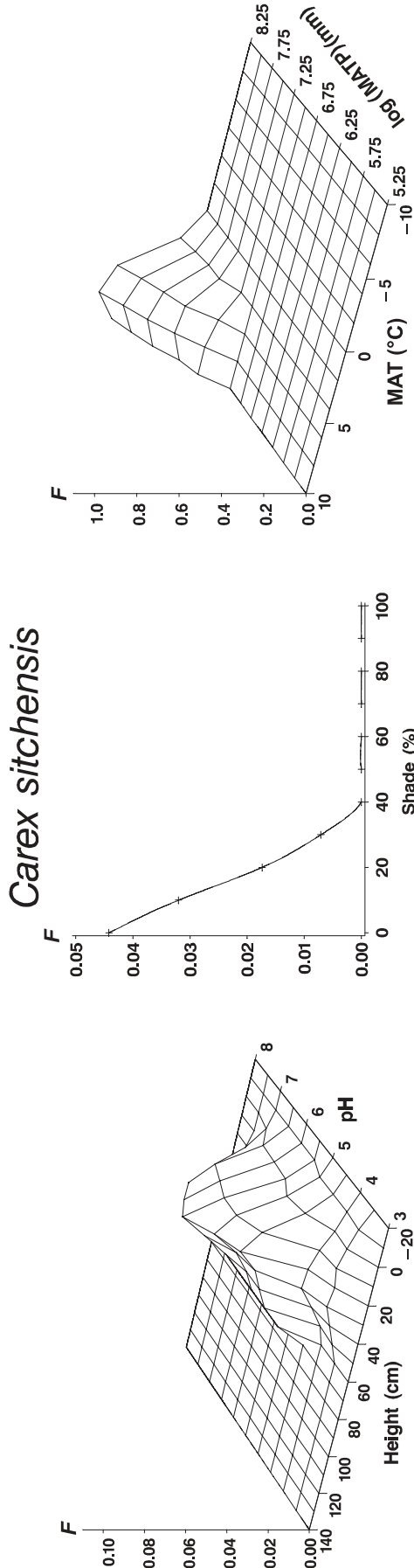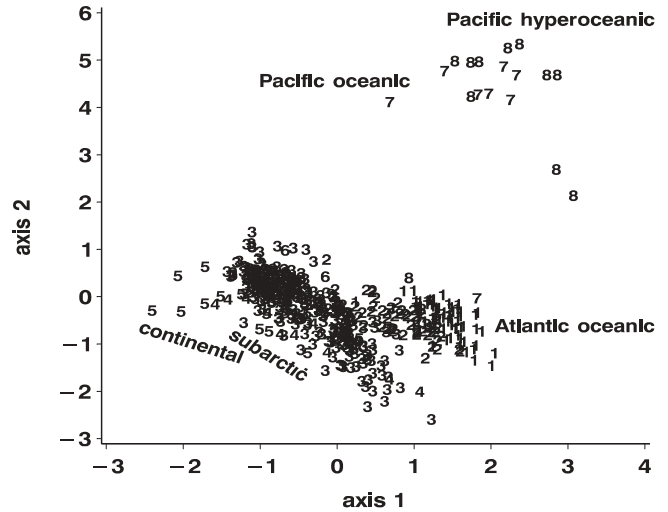
Carex sitchensis

Fig. 13. Canonical correspondence analysis plot of 498 study sites along axes 1 and 2 showing the geographic position of the sites. 1, Atlantic oceanic; 2, Atlantic suboceanic; 3, subcontinental; 4, subarctic; 5, continental; 6, Pacific suboceanic; 7, Pacific oceanic; 8, Pacific hyperoceanic.

sults from other studies (Sjörs 1963; Wells 1981; Wheeler et al. 1983; Banner et al. 1988; Anderson et al. 1996). Group 4 members can thus be labeled as widespread, fen, wet, shade-intolerant species.

With the exception of *C. pauciflora*, the frequency of occurrence of species in groups 5 (Fig. 10) and 6 (Fig. 10) showed no preference for either bog or rich-fen habitats. In this study, *C. pauciflora* showed a slight preference for poor-fen habitats but was also common on bogs. Elsewhere, this species was found on poor fens in the Hudson Bay Lowlands (Sjörs 1963), Alberta (Vitt et al. 1975b), and Minnesota (Wheeler et al. 1983) and on flat and raised bogs in coastal British Columbia (Banner et al. 1988).

Species in group 5 reached their maximum frequency of occurrence on low hummocks, although they could also be found in wetter habitats. With the exception of *C. brunnescens*, they ranged over the entire shade gradient but reached their maximum at 40% or greater. *Carex brunnescens* was not found in open habitats and is known to have a distinct preference for drier forested and thinly wooded areas (Wheeler et al. 1983). Species in group 5 were only found in continental and oceanic areas and not in hyperoceanic regions. However, Ball (1990) indicated that the phytogeographic distribution of *C. canescens* included hyperoceanic coastal British Columbia, but Banner et al. (1988), who surveyed the vegetation on many peatlands in that area, only found it in elongated wet depressions between beach ridges and not on bogs or fens. Group 5 was therefore labeled as having widespread, bog or fen, lawn, carpet and low hummock, shade-tolerant species.

Species in group 6 were found in all climatic regions, with the exception of colder continental areas. All the species in this group had relatively wide ranges along the height above the water table and pH gradients but reached their maximum abundance in carpet and lawn habitats and in poor fens. However, both *S. cespitosus* and *R. alba* may be consistently present or even dominate all other vegetation in

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spring-fen channels, where the pH is greater than 7.0 in the Hudson Bay Lowlands (Sjörs 1963) and Minnesota (Glaser et al. 1990). *Carex pauciflora* was generally associated with carpets and lawns (Sjörs 1963; Vitt et al. 1975*a*) but had been found on low hummocks (Wells 1981). Species in this group were rarely found in heavily shaded habitats. Group 6 can thus be identified as having widespread subcontinental and oceanic, bog or fen, shade-intolerant species.

In light of the geographic interpretation of the climatic gradient (Fig. 13), it is possible to reinterpret the regional distribution of groups 7 and 8. Group 7 was almost exclusively found in eastern North America, while group 8 was composed of species that were restricted to the Pacific Coast. Among the species in group 7, *C. oligosperma* and *C. trisperma* had the widest geographic distribution. *Carex oligosperma* had been found as far west as Great Bear Lake, Northwest Territories, while *C. trisperma* had been found in Saskatchewan (Scoggan 1978). However, the southern portions of their ranges in North America only extended to Minnesota (Wheeler et al. 1983; Glaser 1992). The geographic distribution of *C. exilis* (*C. angustior*, *C. michauxiana*, *C. stricta*, and *Eriophorum tenellum*) was mostly restricted to eastern warm temperate regions, as mapped by Ball (1990) for *C. michauxiana*. Although all species in this group were found on acidic peatlands (pH < 4.5), only *C. trisperma* was consistently found on bogs. The remaining species showed a preference for more minerotrophic habitats such as those found on poor fens, although their ranges also extended to rich fens. *Carex exilis* and *C. stricta* attained relatively high frequency of occurrence values on rich fens in the study area (Fig. 11) and in Minnesota (Glaser et al. 1990).

Group 7 contained a subgroup that included *C. exilis* (*C. angustior*, *C. michauxiana*, *C. stricta*, and *E. tenellum*) and *C. oligosperma*, which were shade intolerant, and the latter species has been described as heliopholous by Wheeler et al. (1983). A second subgroup composed of *C. trisperma* was shade tolerant and was found almost exclusively in shaded habitats (Wheeler et al. 1983).

Species in group 7 occupied a wide range of habitats along the height above the water table gradient. *Carex oligosperma* and *C. exilis* were dominant in wet habitats as emergent or carpet species in areas that surround lakes in bogs and poor fens (Vitt and Slack 1975) or mud bottoms in oceanic sites (Glaser 1992). The distribution of *C. exilis* on the different types of peatlands was limited by the necessity for wet habitats rather than pH (Santelmann 1991). For example, *C. exilis* was found to be locally abundant in wet-fen channels that were classified as rich fens (Glaser et al. 1990). *Carex trisperma* was mostly found on the highest hummocks, where it occasionally dominated the herbaceous layer (Wheeler et al. 1983; Anderson et al. 1996). The remaining species were intermediate between those two extremes. As a result, group 7 species are labeled as eastern, subcontinental and oceanic, poor-fen preferential.

Species in group 8 were found relatively close to the water table in carpets, lawns, and low hummocks along the sides of bog pools, bog pool rivulet systems, and fens along streams (Banner et al. 1988). They were shade intolerant, since they were found only in areas where shade is <40%. Although *C. saxatilis* was only found on peatlands in west-

ern hyperoceanic areas in the present study, it also occurs in *Sphagnum* bogs in the Arctic (Aiken et al. 1999). It would appear that in more southerly habitats east of coastal British Columbia, *C. saxatilis* may not compete well with temperate species and may be reliant on water level fluctuations to eliminate competing vegetation. Those conditions are generally associated with shorelines rather than peatlands. Group 8 is thus composed of western oceanic, bog and poor-fen, shade-intolerant, lawn, carpet and low-hummock species.

Factors limiting the occurrence of the least common species in peatlands

Carex angustior, *C. brunnescens*, *C. capitata*, *C. michauxiana*, *C. pluriflora*, *C. prairea*, *C. saxatilis*, *C. sitchensis*, *C. stricta*, *C. vaginata*, *E. gracile*, and *E. tenellum* were the least common species found in this study (Table 4). With the exception of *C. capitata* and *E. gracile*, all of those species had low maximum frequency of occurrence values along the height and pH and shade gradients. Low maximum frequency of occurrence values (<0.1) are indicative of species that do not occupy a large proportion of the habitats available to them. However, maximum frequency of occurrence values increased >0.7 along the height and pH gradients for three species, *C. pluriflora*, *C. saxatilis*, and *C. sitchensis*, when only quadrats or relevés that were located within each species climatic or geographic range were analyzed. Thus, the number of occurrences of *C. capitata*, *C. pluriflora*, *C. saxatilis*, *C. sitchensis*, and *E. gracile* was limited by the number of relevés or quadrats analyzed in each species' climatic range.

The remaining species had relatively low frequency of occurrence values (<0.25), even when quadrats or relevés that were not found within their climatic or geographic range were removed from the analysis. Therefore, factors other than the number of peatlands analyzed must be affecting their rarity in the study area. There are three possible causes for the low probabilities of occurrence for those species: (1) habitat factors other than those analyzed in the present study; (2) such life-history traits as dispersal, germination, or establishment (Vellend et al. 2000; Campbell et al. 2003); and (or) (3) competition with other vascular and bryophyte species.

Acknowledgements

References

Aiken, S.J., Boles, R.L., and Dallwitz, M.J. 1999. Cyperaceae of the Canadian Arctic Archipelago: descriptions, illustrations, identification, and information retrieval [online]. Available from http://www.mun.ca/biology/delta/arcticf/ [updated November 2000].

Anderson, D.S., Davis, R.B., Rooney, S.C., and Campbell, C.S. 1996. The ecology of sedges (Cyperaceae) in Maine peatlands. Bull. Torrey Bot. Club, **123**: 100–110.

Ball, P.W. 1990. Some aspects of the phytogeography of *Carex*. Can. J. Bot. **68**: 1462–1472.

Banner, A., Hebda, R.J., Oswald, E.T., Pojar, J., and Trowbridge, R. 1988. Wetlands of Pacific Canada. *In* Wetlands of Canada. National Wetlands Working Group. Ecological Land Classification Series No. 24. Sustainable Development Branch, Environment Canada, Ontario and Polyscience Publications Inc., Montréal. pp. 307–346.

Bauer, I.E., Gignac, L.D., and Vitt, D.H. 2003. Development of a peatland complex in Boreal Western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation. Can. J. Bot. **81**: 833–847.

Bernard, J.M. 1990. Life history and vegetative reproduction in *Carex*. Can. J. Bot. **68**: 1441–1448.

Bostock, H.S. 1970. Physiographic subdivisions of Canada. *In* Geology and economic minerals of canada. *Edited by* R.J.W. Douglas. Geologic Survey of Canada. Economic Geology Report No. 1. 5th ed. Ottawa. pp. 9–30.

Bragazza, L. 1999. Spatial patterns of plant species in a poor mire on the southern Alps (Italy). Plant Biosyst. **133**: 83–92.

Bubier, J.L. 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. J. Ecol. **83**: 403–420.

Bubier, J.L., Moore, T.R., and Roulet, N.T. 1993. Methane emissions from wetlands in the midboreal region of Northern Ontario, Canada. Ecology, **74**: 2240–2254.

Bubier, J., Moore, T., and Juggins, S. 1995. Predicting methane emissions from bryophyte distribution in northern Canadian peatlands. Ecology, **76**: 677–693.

Busch, J., and Losch, R. 1999. The gas exchange of *Carex* species from eutrophic wetlands and its dependence on microclimatic and soil wetness conditions. Phys. Chem. Earth Ser. B, **24**: 117–120.

Campbell, D., and Rochefort, L. 2001. La végétation : gradients. *In* Écologie des tourbières du Québec–Labrador. *Edited by* S. Payette and L. Rochefort. Presses de l'Université Laval, Québec, Que. pp. 129–140.

Campbell, D.R., Rochefort, L., and Lavoie, C. 2003. Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands, Québec. J. Appl. Ecol. **40**: 78–91.

Canadian Climate Program. 1982*a*. Canadian climate normals. Temperature 1951–1980. Vol. 2. Published by the Canadian Climate Program, Atmospheric Environment Service, Environment Canada, Ottawa. pp. 551–582.

Canadian Climate Program. 1982*b*. Canadian climate normals. Precipitation 1951–1980. Vol. 3. Published by the Canadian Climate Program, Atmospheric Environment Service, Environment Canada, Ottawa. pp. 551–582.

Chee, W.L., and Vitt, D.H. 1989. The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada. Wetlands, **9**: 227–261.

Crow, G.E., and Hellquist, C.B. 2000. Aquatic and wetland plants of northeastern North America. Vol. 2. Angiosperms: monocotyledons. The University of Wisconsin Press, Madison.

Damman, A.W.H. 1964. Key to the *Carex* species of Newfoundland by vegetative characteristics. Department of Forestry Publication No. 1017. Queen's Printer, Ottawa.

Damman, A.W.H. 1980. Ecological and floristic trends in ombrotrophic bogs of eastern North America. *In* La végétation des sols tourbeux. Colloque Phytosociologique, Lille, 1978. Colloques Phytosociologiques. VII. *Edited by* J.M. Gehu. J. Cramer, Vaduz, Liechtenstein. pp. 61–79.

Douglas, G.W., Meidinger, D., and Pojar, J. 2001. Illustrated flora of British Columbia. Vol. 6. Monocotyledons. British Columbia Ministry of Environment, Lands and Parks, Ministry of Forests, Victoria.

Flora of North America Editorial Committee (*Editors*). 2002. Flora of North America. Vol. 23. Oxford University Press, New York.

Gauthier, R. 1980. La végétation des tourbières et les sphaignes du Parc des Laurentides Québec. Études écologiques. No. 3. Laboratoire d'écologie forestière, Université Laval, Québec.

Gérardin, V., and Grondin, P. 1984. Distribution et description des tourbières de la Moyenne-et-Basse-Côte-Nord. Série de l'inventaire du capital-nature, No. 4.

Gignac, L.D. 1993. Distribution of *Sphagnum* species, communities, and habitats in relation to climate. Adv. Bryol. **5**: 187–222.

Gignac, L.D., and Vitt, D.H. 1990. Habitat limitations of *Sphagnum* along ecological and climatic gradients. Bryologist, **93**: 7–22.

Gignac, L.D., Vitt, D.H., and Bayley, S.E. 1991. Bryophyte response surfaces along ecological and climatic gradients. Vegetatio, **93**: 29–45.

Gignac, L.D., Halsey, L.A., and Vitt, D.H. 2000. A bioclimatic model for predicting the distribution of *Sphagnum*-dominated peatlands in North America under present climatic conditions. J. Biogeogr. **27**: 1139–1151.

Glaser, P.H. 1992. Raised bogs in eastern North America — regional controls for species richness and floristic assemblages. J. Ecol. **80**: 535–554.

Glaser, P.H., and Janssens, J.A. 1986. Raised bogs in eastern North America: transitions in landfroms and gross stratigraphy. Can. J. Bot. **64**: 395–415.

Glaser, P.H., Janssens, J.A., and Siegel, D.I. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, northern Minnesota. J. Ecol. **78**: 1021–1048.

Hill, M.O. 1979. TWINSPAN — A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Section of Ecology and Systematics, Cornell University, Ithaca.

Kuhry, P., Nicholson, B.J., Gignac, L.D., Vitt, D.H., and Bayley, S.E. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Can. J. Bot. **71**: 10–22.

McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4 [computer program]. MJM Software Design, Gleneden Beach, Oregon.

Nicholson, B.J., Gignac, L.D., and Bayley, S.E. 1996. Peatland distribution along a north–south transect in the Mackenzie River Basin in relation to climatic and environmental gradients. Vegetatio, **126**: 119–133.

Økland, R.H. 1990. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. II. Identification of gradients by detrended (canonical) corrrespondence analysis. Nord. J. Bot. **10**: 79–108.

Reznicek, A.A. 1990. Evolution in sedges (*Carex*, Cyperaceae). Can. J. Bot. **68**: 1409–1432.

Santelmann, M.V. 1991. Influences on the distribution of *Carex exilis*: an experimental approach. Ecology, **72**: 2025–2037.

Scoggan, H.J. 1978. The flora of Canada. Part 2. National Museums of Canada, Ottawa.

Sjörs, H. 1952. On the relation between vegetation and electrolytes in Swedish mire waters. Oikos, **2**: 241–258.

Sjörs, H. 1963. Bogs and fens of the Attawapiskat River, northern Ontario. Natl. Mus. Can. Bull. **186**: 45–133.

Slack, N.J., Vitt, D.H., and Horton, D.G. 1980. Vegetation gradients of minerotrophic rich fens in western Alberta. Can. J. Bot. **58**: 330–350.

Smith, R.L. 1996. Ecology and field biology. 5th ed. Harper Collins College Publishers, New York.

ter Braak, C. 1987. CANOCO — a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis (Version 2.1). TNO Institute of Applied Computer Science, Wageningen, Netherlands.

Tuhkanen, S. 1984. A circumboreal system of climatic-phytogeographical regions. Acta Bot. Fenn. **127**: 1–50.

Vellend, M., Lechowicz, M.J., and Waterway, M.J. 2000. Germination and establishment of forest sedges (*Carex*, Cyperaceae): tests for home-site advantage and effects of leaf litter. Am. J. Bot. **87**: 1571–1525.

Vitt, D.H., and Slack, N.G. 1975. An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. Can. J. Bot. **53**: 332–359.

Vitt, D.H., Crum, H., and Snider, J.A. 1975*a*. The vertical zonation of *Sphagnum* species in hummock-hollow comples in Northern Michigan. Mich. Bot. **14**: 190–200.

Vitt, D.H., Achuff, P., and Andrus, R.E. 1975*b*. The vegetation and chemical properties of patterned fens in the Swan Hills, north-central Alberta. Can. J. Bot. **53**: 332–359.

Vitt, D.H., Horton, D.G., Slack, N.G., and Malmer, N. 1990. *Sphagnum*-dominated peatlands of the hyper-oceanic British Columbia Coast: patterns of surface water chemistry and vegetation. Can. J. For. Res. **20**: 696–711.

Wells, E.D. 1981. Peatlands of Newfoundland: distribution, morphology, vegetation, and nutrient status. Can. J. Bot. **59**: 1978–1997.

Wells, E.D., and Hirvonen, H.E. 1988. Wetlands of Atlantic Canada. *In* Wetlands of Canada. National Wetlands Working Group. Ecological Land Classification Series No. 24. Sustainable Development Branch, Environment Canada, Ontario and Polyscience Publications Inc., Montréal. pp. 251–303.

Wheeler, G.A., Glaser, P.H., Gorham, E., Wetmore, C.M., Bowers, F.D., and Janssens, J.A. 1983. Contributions to the flora of the Red Lake Peatland, northern Minnesota, with special attention to *Carex*. Am. Midl. Nat. **110**: 63–96.

Zoltai, S.C. 1988. Wetland environments and classification. *In* Wetlands of Canada. National Wetlands Working Group. Ecological Land Classification Series No. 24. Sustainable Development Branch, Environment Canada, Ontario and Polyscience Publications Inc., Montréal. pp. 1–26.

Zoltai, S.C., Taylor, S., Jeglum, J.K., Mills, G.F., and Johnson, J.D. 1988. Wetlands of Boreal Canada. *In* Wetlands of Canada. National Wetlands Working Group. Ecological Land Classification Series No. 24. Sustainable Development Branch, Environment Canada, Ontario and Polyscience Publications Inc., Montréal. pp. 99–154.