

# Understanding Holocene peat accumulation pattern of continental fens in western Canada

Zicheng Yu, Dale H. Vitt, Ian D. Campbell, and Michael J. Apps

**Abstract:** Assessing carbon sink–source relationships in peatlands must be based on the understanding of processes responsible for long-term carbon accumulation patterns. In contrast with ombrogenous bogs, however, the processes in geogeneous fens are poorly understood. Here, we present high-resolution Holocene peat accumulation and macrofossil data from a rich fen (Upper Pinto Fen (UPF)) in west-central Alberta, Canada. The ~8000-year chronology of a 397 cm peat core was controlled by 20 accelerator mass spectrometry  $^{14}\text{C}$  dates. The paludified peatland initially consisted of diverse brown moss species and some *Larix* trees but was dominated by *Scorpidium scorpioides* from 6500 to 1300 calibrated years BP. The last 1300 years are characterized by the reappearance of *Larix* together with abundant woody materials and Cyperaceae, culminating in a sharp increase in *Tomenthypnum nitens* in the last several decades. During the *Scorpidium*-dominated period, the peat accumulation pattern derived from 15  $^{14}\text{C}$  dates and 260 bulk density measurements indicates declining mass accumulation rates over time (i.e., convex age–depth curve), in contrast with the standard bog growth model (i.e., concave curve). The analysis of the UPF data using an extended model incorporating variable peat addition rates (PAR) to the catotelm suggests a unidirectional sevenfold decrease in PAR from 191.8 to 26.0 g dry mass·m<sup>-2</sup>·year<sup>-1</sup> during the ~5000-year “convex period”. Decreasing vegetation production and (or) increasing acrotelm decomposition could have produced the convex pattern. Decreasing PAR might be owing to autogenically induced changes in local hydrology and nutrient availability, which are pronounced in the moisture-limited climate of the region and in peatlands that have a strong groundwater influence. The convex-pattern model, explicit to the height-induced long-term drying hypothesis, has important implications for building simulation models and for projecting future carbon dynamics of peatlands. Prior to recent human disturbance, the UPF site has a time-weighted mean carbon accumulation rate of 31.1 g C·m<sup>-2</sup>·year<sup>-1</sup>, ranging from 7.2 to 182.5 g C·m<sup>-2</sup>·year<sup>-1</sup> during the last 8000 years. This large variation results from the gradual decline of long-term accumulation and short-term climate-induced accumulation “pulses”. The results imply that in the absence of climatic change, peatlands with a convex accumulation pattern will reach their growth limit sooner and that their carbon sequestration capacity will decline faster than would be expected given the concave-pattern model.

*Key words:* carbon dynamics, moisture and nutrient availability, macrofossils, peatland model, brown moss *Scorpidium scorpioides*.

**Résumé :** L'évaluation des relations source–puit du carbone dans les tourbières doit être basée sur une compréhension des processus responsables des patrons d'accumulation du carbone, à long terme. Contrairement aux tourbières ombrogènes, les tourbières basses géogènes sont mal comprises. L'auteur présente des données à haute résolution sur l'accumulation de la tourbe et les macrofossiles, durant l'Holocène, dans une tourbière basse riche (tourbière basse de Upper Tinto; UPF) du centre-ouest de l'Alberta, au Canada. Une carotte de tourbe de 397 cm, avec une chronologie de ~8000 ans, a été caractérisée par 20 dates AMS  $^{14}\text{C}$ . La tourbière paludifiée comportait au départ diverses mousses brunes et quelques *Larix laricina*, mais était dominée par le *Scorpidium scorpioides*, entre 6500 et 1300 ans avant le présent (BP). Les derniers 1300 ans se caractérisent par la réapparition du *Larix* avec du matériel ligneux abondant et des cypéracées, avant de culminer avec une nette augmentation du *Tomenthypnum nitens*, au cours de nombreuses dernières décades. Au cours de la période dominée par les *Scorpidium*, le patron d'accumulation de la tourbe, obtenu à partir de 15 dates  $^{14}\text{C}$  et de 260 mesures de densité apparente, montre une diminution des taux d'accumulation de la masse avec le temps (i.e., courbe convexe âge–profondeur), contrairement au modèle standard de croissance des tourbières (i. e., courbe concave). L'analyse des données de l'UPF, à l'aide d'un modèle étendu incorporant les taux variables d'addition de la tourbe (PAR) au catotelm, suggère une diminution de sept fois du PAR allant de 191,8 à 26,0 g masse sèche·m<sup>-2</sup>·an<sup>-1</sup>. Au cours de la ‘période convexe’ de ~5000 ans, la production décroissante de végétation et (ou)

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la décomposition croissante de l'acrotelme pourraient avoir produit le patron convexe. Le PAR décroissant pourrait être dû aux changements autogènes induits dans l'hydrologie locale et la disponibilité des nutriments, lesquels sont prononcés sous le climat limité par l'humidité de la région, et dans les tourbières qui sont fortement influencées par les eaux souterraines. Le modèle du patron convexe, explicite selon l'hypothèse de dessèchement à long terme induit par la hauteur, a des implications importantes pour la construction de modèles de simulation et pour prédire la dynamique future du carbone dans les tourbières. Avant les récentes perturbations anthropiques, le site UPF montre un taux pondéré d'accumulation du carbone en fonction du temps de  $31,1 \text{ g C}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$ , allant de  $7,2$  à  $182,5 \text{ g C}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$ , au cours des 8000 dernières années. Cette forte variation provient du déclin graduel de l'accumulation à long terme et des vagues d'accumulation à court terme induites par le climat. Les résultats impliquent, qu'en absence de changement climatique, les tourbières ayant un patron convexe d'accumulation atteindront leur limite de croissance plus tôt et que leur capacité de séquestration du carbone diminuera plus rapidement qu'on l'attendrait selon le modèle du patron concave.

*Mots clés* : dynamique du carbone, disponibilité de l'humidité et des nutriments, macrofossiles, modèle de tourbière, mousse brune *Scorpidium scorpioides*.

[Traduit par la Rédaction]

## Introduction

Peatlands are one of the largest terrestrial carbon reservoirs. Northern peatlands have accumulated about 400–500 Gt (1 Gt =  $10^{15}$  g) of carbon during the Holocene at an average rate of  $<0.1 \text{ Gt C/year}$  (e.g., Gorham 1991; Clymo et al. 1998; Roulet 2000). Although northern peatlands have a relatively low average net accumulation rate (e.g.,  $19.4 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  for continental western Canada; Vitt et al. 2000), their extent, high-latitude location, and the large size of their carbon pool raise concerns that northern peatlands may become significant sources for atmospheric carbon under a changing climate. However, significant uncertainties exist in addressing peatland carbon responses to climate change (e.g., Moore et al. 1998). The credible assessment of carbon sink–source relationships in peatlands must be based on the understanding of processes responsible for long-term carbon accumulation patterns.

Carbon accumulation in peatlands is a function of the balance between production of living plants atop the acrotelm (surface aerobic layer) and decomposition in both the acrotelm and the catotelm (underlying anaerobic layer) (Ingram 1978; Clymo 1984, 1991). As litter and new peat in the acrotelm are exposed to oxygen and varying water levels, they are subject to a higher decay rate. Once in the catotelm, the decay rate declines sharply and becomes independent of minor climatic fluctuations. The rate of peat transfer from acrotelm to catotelm, or the acrotelm residence time, therefore largely determines net peat accumulation. Clymo (1984) proposed a conceptual model of bog growth in which constant productivity and exponential decomposition produce a concave cumulative peat mass–age curve, evidenced in most oceanic bogs. It has been assumed that the processes causing peat to accumulate in continental regions are similar to those in oceanic regions and also that fens are similar to bogs, although with a more complicated hydrology (Clymo 1984). There are, however, limited data available to test the validity of the bog model in continental fens as well as bogs (Kubiw et al. 1989; Charman et al. 1994; Kuhry and Vitt 1996).

In continental western Canada (the provinces of Alberta, Saskatchewan, and Manitoba), peatlands cover  $365\,157 \text{ km}^2$  (~20% of the land area) and store ~50 Gt of C (Vitt et al. 2000). However, the majority of these peatlands are fens (64% of peatland area, including 35% treed fens and 29%

open fens) and only 36% are bogs, with permafrost bogs accounting for 28% of the total peatland area. About half of the fens are rich fens, which thus comprise the dominant peatland type in continental western Canada.

We present in this study high-resolution accelerator mass spectrometry (AMS)  $^{14}\text{C}$  dating and palaeoecological data from an extreme-rich fen in west-central Alberta, Canada. It acts as a case study by which to investigate similarities and differences in peat growth in continental fens and oceanic bogs. The objectives of the study are to (i) derive the development history for a peatland during the Holocene, (ii) document at a high temporal resolution the pattern of peat accumulation, for the first time, in a continental fen, (iii) elucidate what processes cause the observed pattern by using an extended model incorporating variable peat addition rates (PAR), and (iv) discuss the implications of this conceptual model for simulation models and for projecting future peat carbon dynamics under either stable or changing climatic conditions.

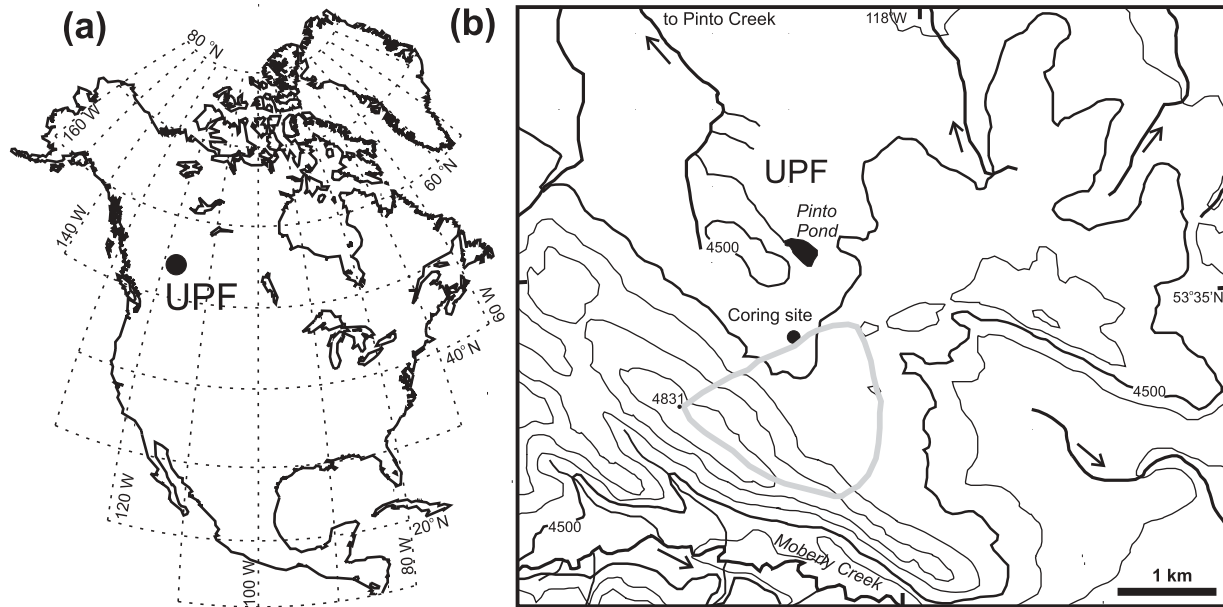
## Materials and methods

### Study area

Upper Pinto Fen (UPF) (unofficial name; previously referred to as “Hinton Fen” in Yu et al. (2000)) is located on the eastern slope of the Rocky Mountain Foothills near the northern edge of the northern Great Plains in central Alberta, Canada ( $53^{\circ}35'N$ ,  $118^{\circ}01'W$ ; elevation ~1310 m) (Fig. 1a). The region has a semihumid continental climate, with a mean annual precipitation of ~540 mm and a mean annual temperature of  $3^{\circ}\text{C}$  (Environment Canada 1993). The surficial material around the site is silty sand till, which supplies locally recharged groundwater for the peatland (Bayrock and Reimchen 1980). The site lies close to the headwater of a tributary of Pinto Creek. Local topography, its headwater position, and its small surface catchment area (~4 km<sup>2</sup>) (Fig. 1b) might make the site sensitive to changes in regional climate, particularly effective moisture.

UPF is within the Upper Foothills vegetation subregion, adjacent to the boundary of the Subalpine subregion (Beckingham et al. 1996). The upland vegetation is thus coniferous forest dominated by lodgepole pine (*Pinus contorta* Loud.). White spruce (*Picea glauca* (Moench) Voss) is

**Fig. 1.** Location maps. (a) Location of Upper Pinto Fen (UPF) in central North America; (b) Topographic map of UPF peatland showing its headwater location and small surface catchment area (gray line). Contours are at 100 ft (~30 m). The coring site is close to the 4500-ft contour line at the edge of the water-shedding topographic plateau. Hatched areas are peatlands.



common in the region, with some balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh), trembling aspen (*Populus tremuloides* Michx.), and balsam poplar (*Populus balsamifera* L.). The UPF is an extreme-rich fen dominated by the brown mosses *Tomenthypnum nitens* (Hedw.) Brid. and *Scorpidium scorpioides* (Hedw.) Limpr. and *Carex* species (Cyperaceae). There are scattered tamarack trees (*Larix laricina* (Du Roi) K. Koch) in the peatland, especially on relatively high ground (see Fig. 2).

#### Field and laboratory methods

A 397-cm peat core was collected on 22 September 1999 using a 5-cm-diameter modified Macaulay peat sampler. At the time of coring, the water table was near the peatland surface. The 50-cm-long core segments were wrapped in plastic wrap and stored in polyvinylchloride pipe during transportation to the laboratory, where they were stored at 2°C. On the same day, a second shallow core (UPF 2) was collected about 100 m further upslope to the east and was used to examine the basal clay – peat transition (Fig. 2).

The peat core was cut into contiguous 1-cm-thick slices. Subsamples from each of these slices were taken with a 1-cm-diameter brass cylinder sampler for analysis of loss on ignition. The peat subsamples were oven-dried at 100°C to estimate moisture content and then ashed at 550°C to estimate organic matter content. The peat bulk density and ash-free bulk density were calculated from the measurements of sample volume and organic matter. The UPF 2 core was also analyzed for carbonate content by measuring additional weight loss after burning at 950°C.

Twenty subsamples from selected 1-cm-thick slices at mostly 20-cm intervals were submitted for AMS radiocarbon dating. Four of these samples were prepared and dated at Beta Analytic, Inc. The other 16 samples were pretreated

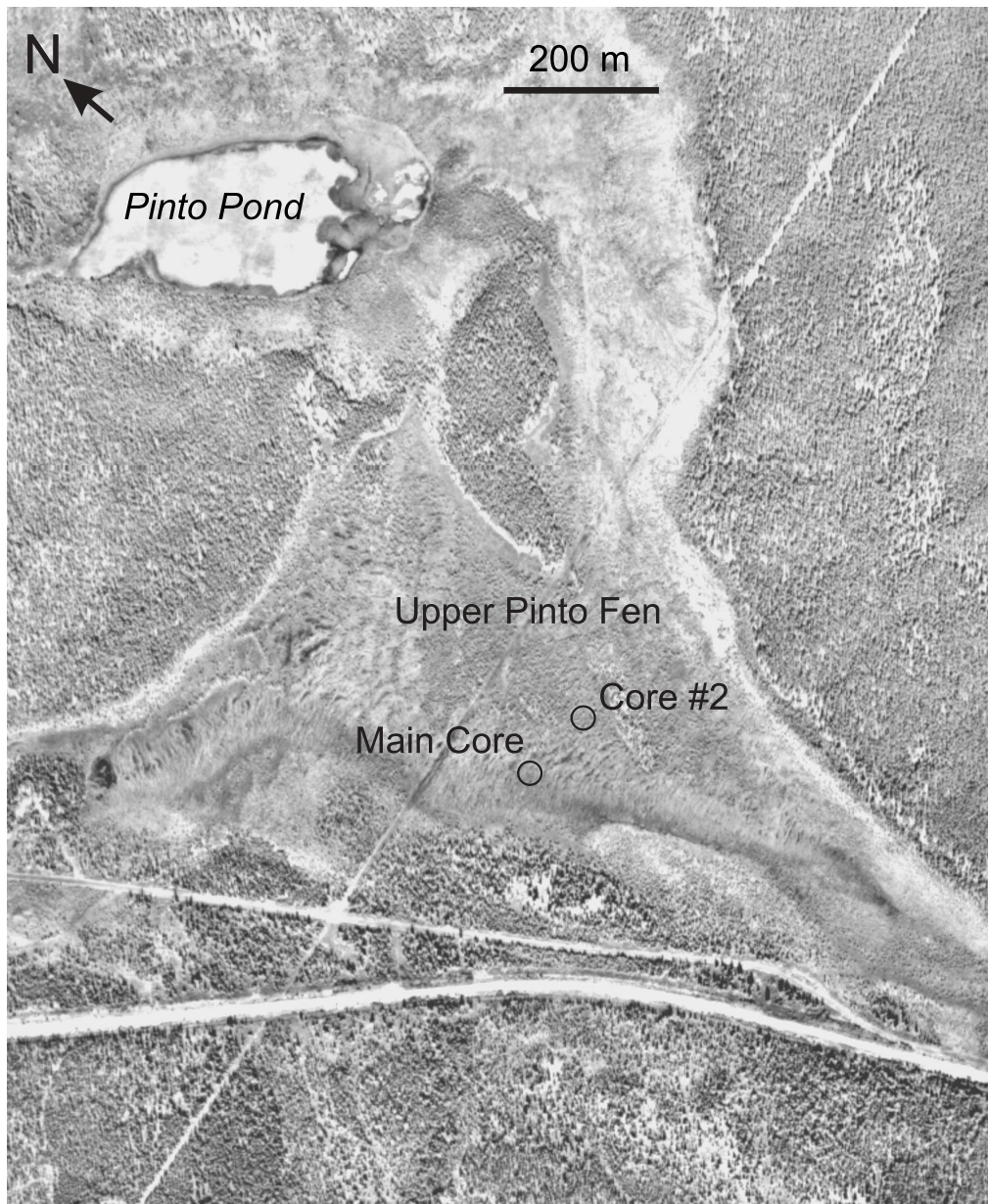
at the Limnological Research Center of the University of Minnesota and dated at the AMS Laboratory, University of Arizona. All dates were obtained on the coarse fibrous fraction remaining after a full acid–alkali–acid pretreatment.

We used a semiquantitative method for macrofossil analysis. Peat subsamples of approximately 1 cm<sup>3</sup> were taken mostly every other centimetre and dispersed into a custom-designed picking tray with channels (“channeled plexiglass template”) without chemical treatment and sieving. The subsamples were examined under a dissecting stereomicroscope to identify and estimate relative abundance of different macroscopic components, including decomposed and unrecognizable debris. The identification was aided by reference collections at the Cryptogamic Herbarium at the University of Alberta, Edmonton, Alta.

#### Multivariate analysis

An indirect gradient (ordination) analysis was used to determine general relationships among peat components and samples (Prentice 1980) and in particular to objectively define the *Scorpidium*-dominated peatland stage. The relative abundances of 18 peat components from 215 samples were incorporated into a numerical analysis using CANOCO (ter Braak 1988). A log transformation was applied to the data because macrofossil data are “closed” compositional data (as percentages) and thus have a constant sum problem (Aitchison 1986). A detrended correspondence analysis (DCA) was carried out initially to describe the linearity of the data. DCA results show that gradient lengths of the ordination axes are less than 2.5 standard deviations (maximum 2.52 for the second axis), suggesting that most of the response curves (or surfaces) are linear or at least monotonic (ter Braak 1987). A linear analytical method such as principal components analysis (PCA) is therefore appropriate and provides more quantitative information than DCA.

**Fig. 2.** Aerial photograph of UPF. Open circles show the coring sites of UPF main core and core 2. Surface water in the peatland flows northward. The first white line from the bottom is Hwy 40 from Hinton to Grande Cache, the second white line is an adjacent railroad grade, and the oblique line is a seismic line for oil exploration. Photograph AS4834-156, taken on 20 July 1997. Courtesy of the Air Photo Services of Alberta Environment.



Log-contrast PCA is an alternative form of PCA using log transformation and centering both by samples and by component types (double centering), providing a better representation of real “ecological distance” between samples (Jacobson and Grimm 1986).

#### An extended model with variable PAR

In the peat growth model described by Clymo (1984), two variables determine long-term peat accumulation in the catotelm: the rate of peat addition to the catotelm ( $p$ ) and the catotelm decomposition rate ( $\alpha$ ). The single exponential model has the form

$$[1] \quad \frac{dM}{dt} = p - \alpha M$$

which has the analytical solution

$$[2] \quad M = \left( \frac{p}{\alpha} \right) (1 - e^{-\alpha t})$$

In both equations,  $M$  is cumulative dry peat mass and  $t$  is time. The PAR ( $p$ ) determines the general slope of the cumulative peat mass versus age curve, and the decomposition coefficient ( $\alpha$ ) determines the curvature of the curve (Clymo 1984; Yu et al. 2000). Both variables can change over time,

but the PAR is likely to be more sensitive to vegetation type and environmental conditions and thus more variable than the catotelm decomposition rate would be (see below).

Following the suggestion by Clymo (2000), we have added a PAR modifier to eq. 1, allowing exponential change in PAR. Thus, the extended model is

$$[3] \quad \frac{dM}{dt} = p e^{-bt} - \alpha M$$

where  $M$  is the cumulative peat mass in the catotelm,  $p$  is the eventual PAR,  $\alpha$  is the catotelm decomposition rate, and  $b$  is the coefficient of PAR modifier. This equation has the analytical solution

$$[4] \quad M = \left( \frac{p}{\alpha - b} \right) (e^{-bt} - e^{-\alpha t})$$

In principle, the PAR modifier could take a form other than the exponential and a function other than time, although there is no experimental or field data to support any one of these possible choices. However, eq. 3 is the only one out of several possible formulations that has an analytical solution (J. Brzustowski, University of Alberta, personal communication).

## Results

### Peat composition and macrofossil assemblages

#### Radiocarbon dates

The 20 AMS  $^{14}\text{C}$  dates were calibrated using the INTCAL98 data set (Stuiver et al. 1998) (Table 1), and an age model was based on linear interpolation between successive calibrated ages (Fig. 3). The temporal sampling resolution ranges from ~3 to 60 years for each contiguous 1-cm interval. A time scale based on this age model is used in the subsequent analysis.

#### Sediment lithology

The peat moisture content of the main core was about 90% (Fig. 4a). The remaining ~10% of material consists of ~80–90% organic matter, although there are two intervals with low organic matter values at ~4000 calibrated years BP (cal BP) and at the surface and a relatively high value of ~96% organic matter at ~1000 cal BP (Fig. 4b). The ash-free bulk density varies mostly between ~0.08 and 0.16 g/cm<sup>3</sup>, with an average of 0.127 g/cm<sup>3</sup>, excluding the first 350-year and last 50-year periods (Fig. 4c). The basal peat has lower moisture and organic matter content and higher bulk density than the rest of the core (Fig. 4).

The topmost section of the UPF core shows clear changes in the composition of organic material across the gradient from living vegetation to recently formed peat (Fig. 5). Core sections of the top 6 cm dominated by fresh brown mosses and sedge stems and from 10 to 18 cm dominated by fresh sedge roots have high moisture and low bulk density. Between these light-colored layers, a dark peat layer having lower moisture and higher bulk density was probably derived from recently decomposed mosses. Peat below ~19 cm has high bulk density, mostly >0.1 g/cm<sup>3</sup> (Fig. 4c). For bog, the acrotelm–catotelm interface can be conveniently

defined as minimum water table in late summer (Clymo 1984), but for rich fens such as UPF, the interface is most likely situated just below the root layer, where a sharp change in oxygen availability likely occurs. The mass transfer process from the acrotelm to the catotelm appears to take <50 years, suggested by the postbomb  $^{14}\text{C}$  date at 24–25 cm (Table 1).

#### Macrofossil record

The zonation of macrofossil diagram was identified by visual inspection of dominant components, with aid from multivariate analysis (Fig. 6) (also see below). The macrofossil results show that the basal peat (8000–7000 cal BP) is dominated by *Picea* needles and woody material, with some moss subfossils, including *Tomenthypnum nitens* and *Sphagnum warnstorffii* (zone 1, Fig. 6). *Picea* needles were not identified to species owing to their poor preservation. Peat composition over the succeeding 400 years includes *Sphagnum warnstorffii*, *Tomenthypnum nitens*, *Drepanocladus revolvens*, and *Calliergon* spp., together with needles of *Larix* (zone 2). Peat comprising a period from 6500 to 1300 cal BP (zone 3) is dominated by *Scorpidium scorpioides* macrofossils, with large fluctuations in its abundance. After a scattered occurrence in peat from earlier during the Holocene, *Larix* reappears around 1300 cal BP, accompanied by an increase in wood, Cyperaceae, and charcoal (zone 4). The last several decades of peat growth are recorded by a dramatic shift in species composition: the complete disappearance of *Scorpidium scorpioides* and a sharp increase in *Tomenthypnum nitens* at the coring site (zone 5), suggesting drier site conditions.

#### UPF core 2

The results from the lowest 25 cm of the shallow core (UPF 2) demonstrate a basal clay – peat transition: a sharp increase in moisture and organic matter and a slight increase in carbonate (Fig. 7a). This sharp contrast suggests a hiatus in sediment accumulation at the transition between the basal clay material and the overlying peat. The basal peat is dominated by *Drepanocladus*, Cyperaceae, *Picea* needles, and woody material and also contains charcoal (zone 1, Fig. 7b). It is succeeded by a peat horizon dominated by Cyperaceae and *Sphagnum warnstorffii* (zone 2) and, above this, one with *Calliergon* and *Scorpidium scorpioides* (zone 3).

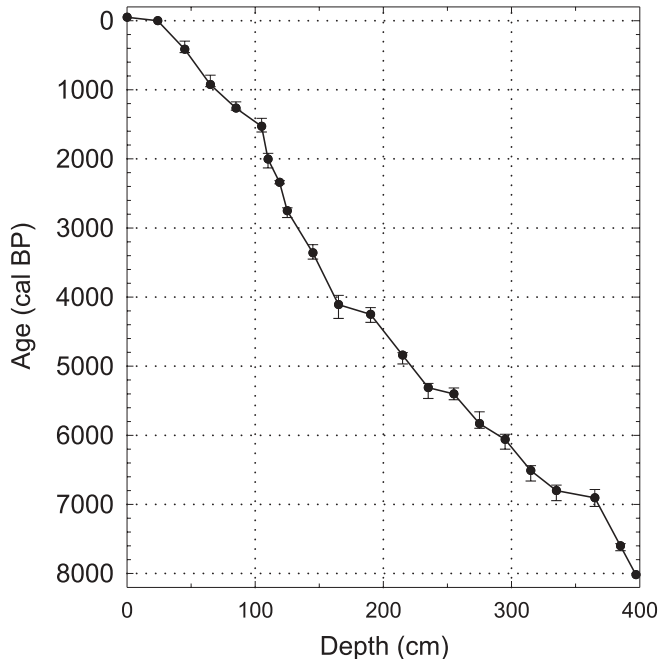
#### Multivariate analysis

The log PCA results from the ordinations of macrofossil types and samples in the UPF main core illustrate broad characteristics of the macrofossil diagram (Fig. 8). The ordination of macrofossil types suggests the importance of *Scorpidium scorpioides*, *Tomenthypnum nitens*, debris, and woody material, which lie away from the origin (bold letters in Fig. 8a). In the ordination of macrofossil samples (Fig. 8b), the first and second axes account for 45.9 and 13.7% of the variance in macrofossil data, respectively. Variation in the sample scores on these two axes represents shifts in peat composition. The DCA results (not shown here) show essentially similar patterns. Sample groupings in the ordination space as represented by the first two axes are associated with major features in macrofossil assemblages. The first PCA axis separates *Scorpidium*-dominated rich fen

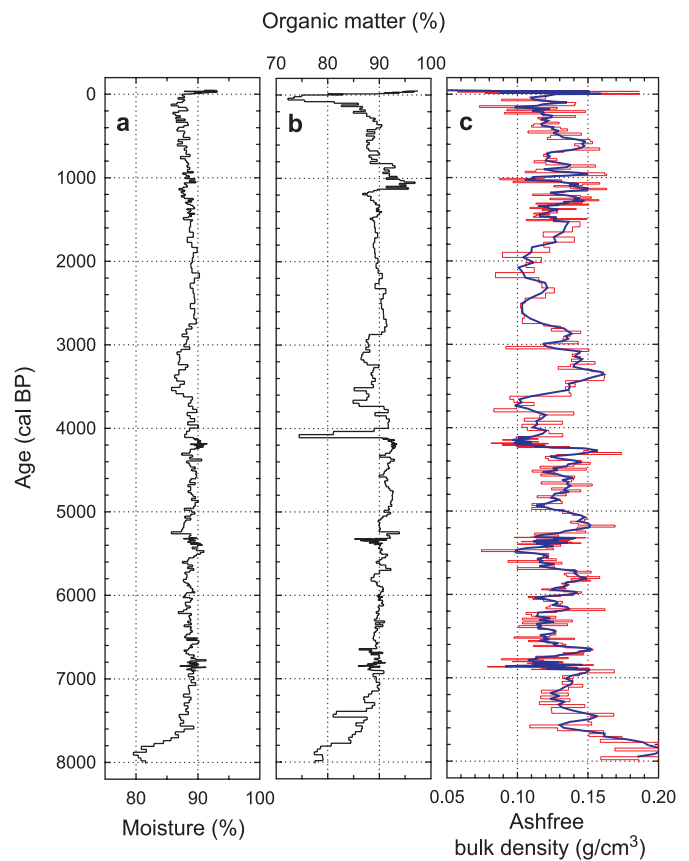
**Table 1.** AMS radiocarbon dates from the Upper Pinto Fen, Alberta, Canada.

Depth (cm)	AMS laboratory No.	$^{14}\text{C}$ date $\pm 1 \sigma$ (years BP)	Age (cal BP)*	Age range at $2 \sigma$ (cal BP) (95% probability)*
24–25	AA37423	Postbomb	(1.3169 fraction of modern $^{14}\text{C}$ )	
44–45	AA37428	305 $\pm$ 40	417, 411, 314	462–297
64–65	AA37108	975 $\pm$ 40	924	955–789
84–85	AA37429	1315 $\pm$ 40	1264	1295–1174
104–105	AA37104	1630 $\pm$ 40	1529	1611–1413
109–110	Beta-144856	2060 $\pm$ 40	2005	2130–1920
118–119	Beta-144857	2320 $\pm$ 40	2340	2360–2315
124–125	AA37419	2620 $\pm$ 45	2750	2848–2707
144–145	AA37105	3125 $\pm$ 45	3357	3450–3242
164–165	AA37420	3775 $\pm$ 60	4148, 4105, 4103	4308–3974
189–190	Beta-135661	3850 $\pm$ 40	4244	4365–4152
214–215	AA37421	4270 $\pm$ 50	4837	4968–4803
234–235	AA37422	4600 $\pm$ 50	5312	5467–5249
254–255	AA37106	4690 $\pm$ 50	5452, 5377, 5330	5486–5314
274–275	AA37424	5035 $\pm$ 50	5840, 5831, 5747	5899–5661
294–295	AA37425	5325 $\pm$ 50	6169, 6145, 6110, 6070, 6058, 6042, 6027, 6009, 6002	6201–5985
314–315	AA37426	5750 $\pm$ 50	6532, 6515, 6502	6662–6438
334–335	AA37107	5990 $\pm$ 50	6848, 6840, 6797, 6766, 6762	6945–6720
364–365	AA37427	6075 $\pm$ 55	6905	7029–6783
384–385	Beta-135662	6750 $\pm$ 40	7607, 7600, 7589	7670–7568

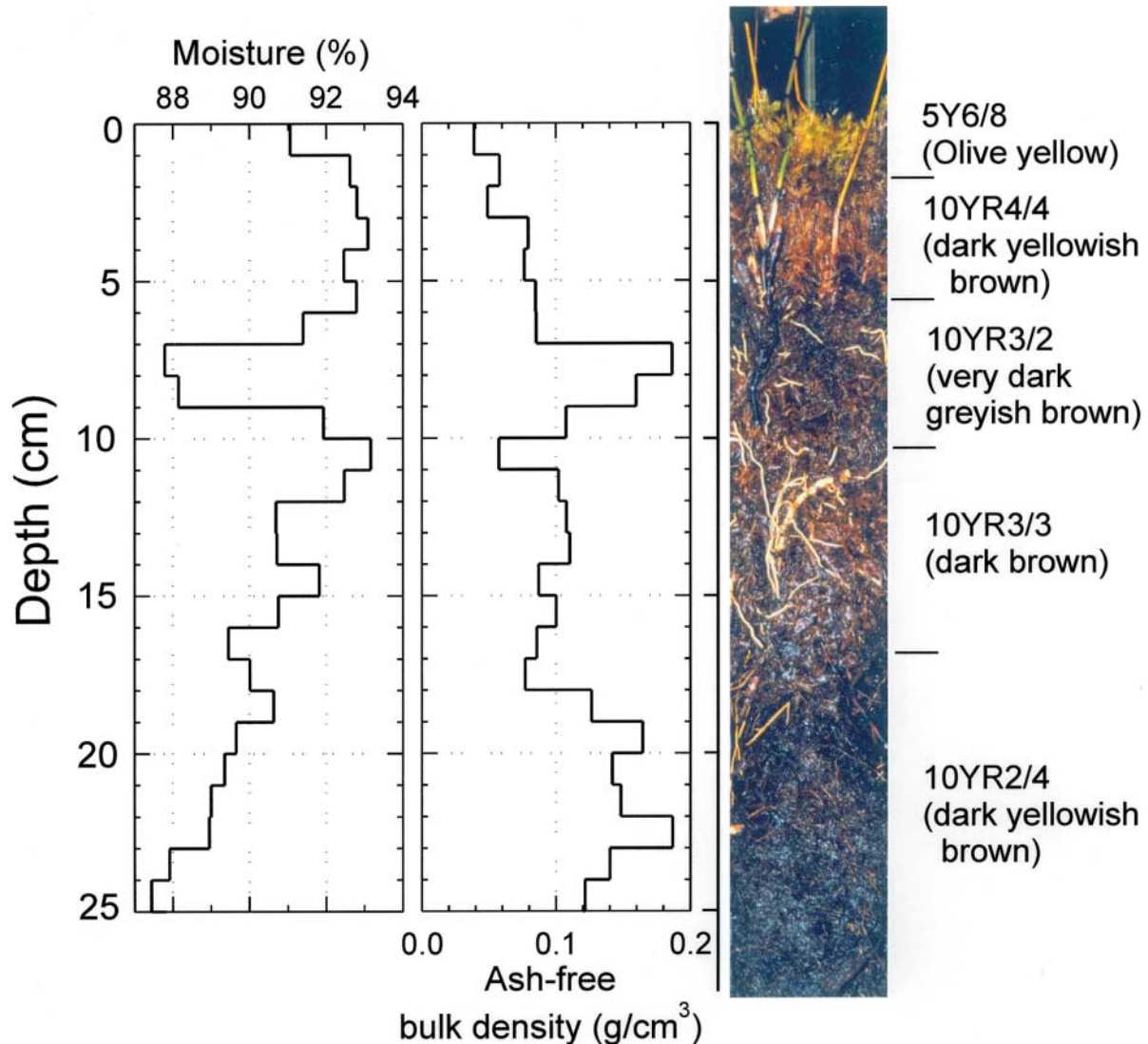
\*Calibrated ages were based on the program CALIB 4.02 using the INTCAL98 data set (Stuiver et al. 1998).

**Fig. 3.** Age–depth model of the UPF core. The  $2 \sigma$  (95% probability) error ranges are represented by vertical bars.

samples (densely clustered) on the left from woody and *Tomenthypnum*-dominated samples on the right (Fig. 8b). The first axis demonstrates the three stages of peatland development: ~8000–6500 cal BP (high scores, zones 1 and 2), 6500–1300 cal BP (low scores, zone 3), and the last 1300 years (high scores, zones 4 and 5). The second PCA axis represents fluctuations between *Scorpidium* and uniden-

**Fig. 4.** Sediment lithology of the UPF core. (a) Moisture content; (b) organic matter content; (c) ash-free bulk density (bars show raw data measured at 1-cm intervals and the heavy curve a simple three-point running mean).

**Fig. 5.** Closeup of the topmost 25 cm of the UPF core showing moisture content and ash-free bulk density on depth scale. Also shown is a core photograph with color descriptions based on the standard Munsell color chart. The boundary of the acrotelm and catotelm is presumably around 20 cm depth below the rooting zone.



tifiable organic debris during the *Scorpidium*-dominated period. The second axis also separates the *Tomenthypnum*-dominated phase (zone 5) from zones 1–2 and 4. The PCA results also provide statistical justification of the macrofossil diagram.

#### Rates and pattern of carbon accumulation

Carbon accumulation rates at UPF (Fig. 9) were calculated from ash-free bulk density measurements (Fig. 4c) and peat vertical growth rates (Fig. 3) using the average carbon content of peat organic matter (51.8%) derived from 253 measurements in peatlands in continental western Canada (Vitt et al. 2000). Excluding the last 50 years of freshly produced plant fragments and peat, the estimated rates for each dated peat interval range from 7.2 to 182.5 g C·m<sup>-2</sup>·year<sup>-1</sup>, with a time-weighted mean of 31.1 g C·m<sup>-2</sup>·year<sup>-1</sup> (a simple mean of 46.7 g C·m<sup>-2</sup>·year<sup>-1</sup>) (Fig. 9).

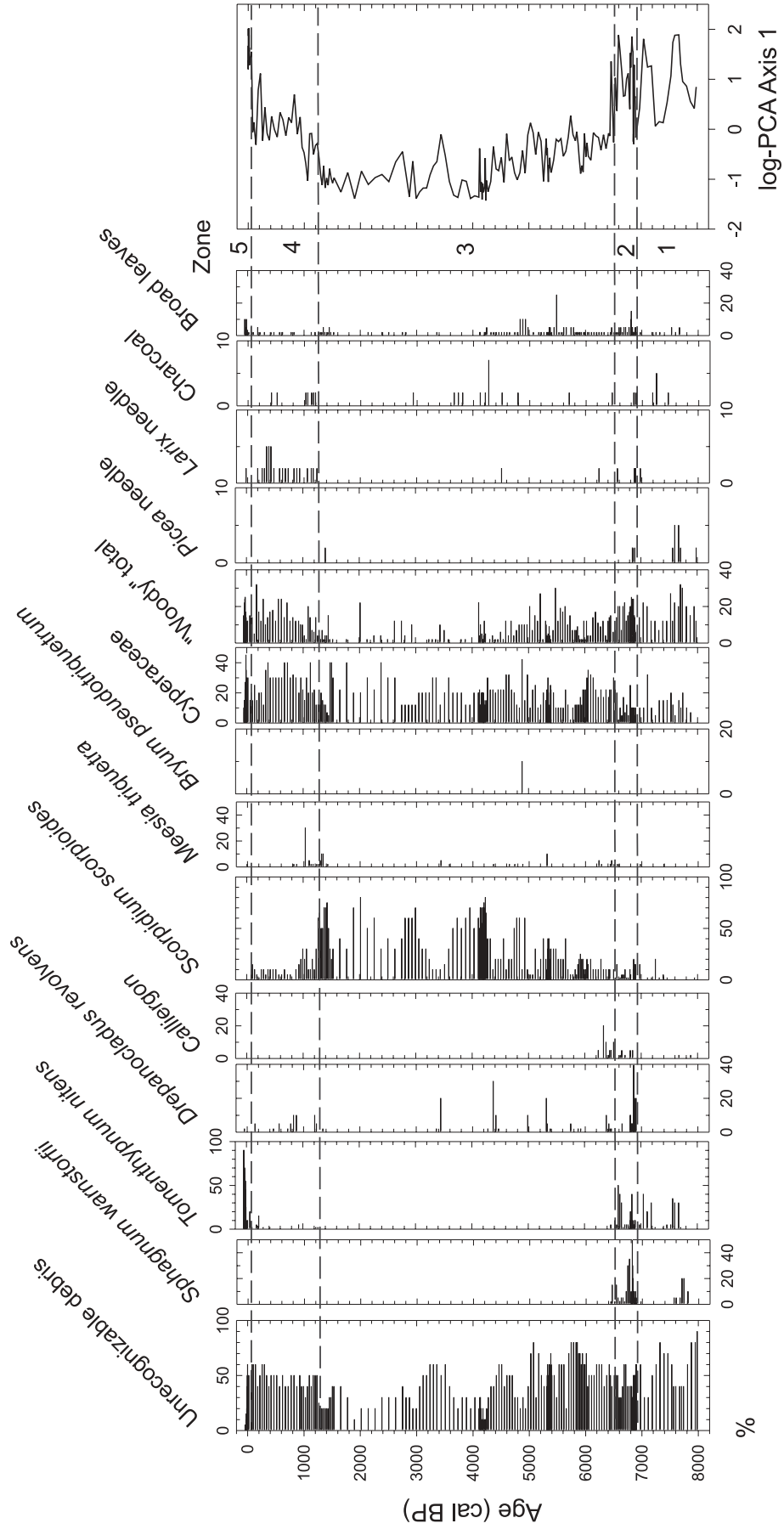
The peat accumulation pattern shown in Fig. 10 is based on 20 AMS <sup>14</sup>C dates and 398 bulk density measurements in

the UPF main core. Excluding the early (zones 1 and 2: >6500 cal BP) and late Holocene (zones 4 and 5: <1300 cal BP) woody peat (Fig. 6), the *Scorpidium*-dominated non-woody peat from 6500 to 1300 cal BP (zone 3) has a convex cumulative peat mass–age curve.

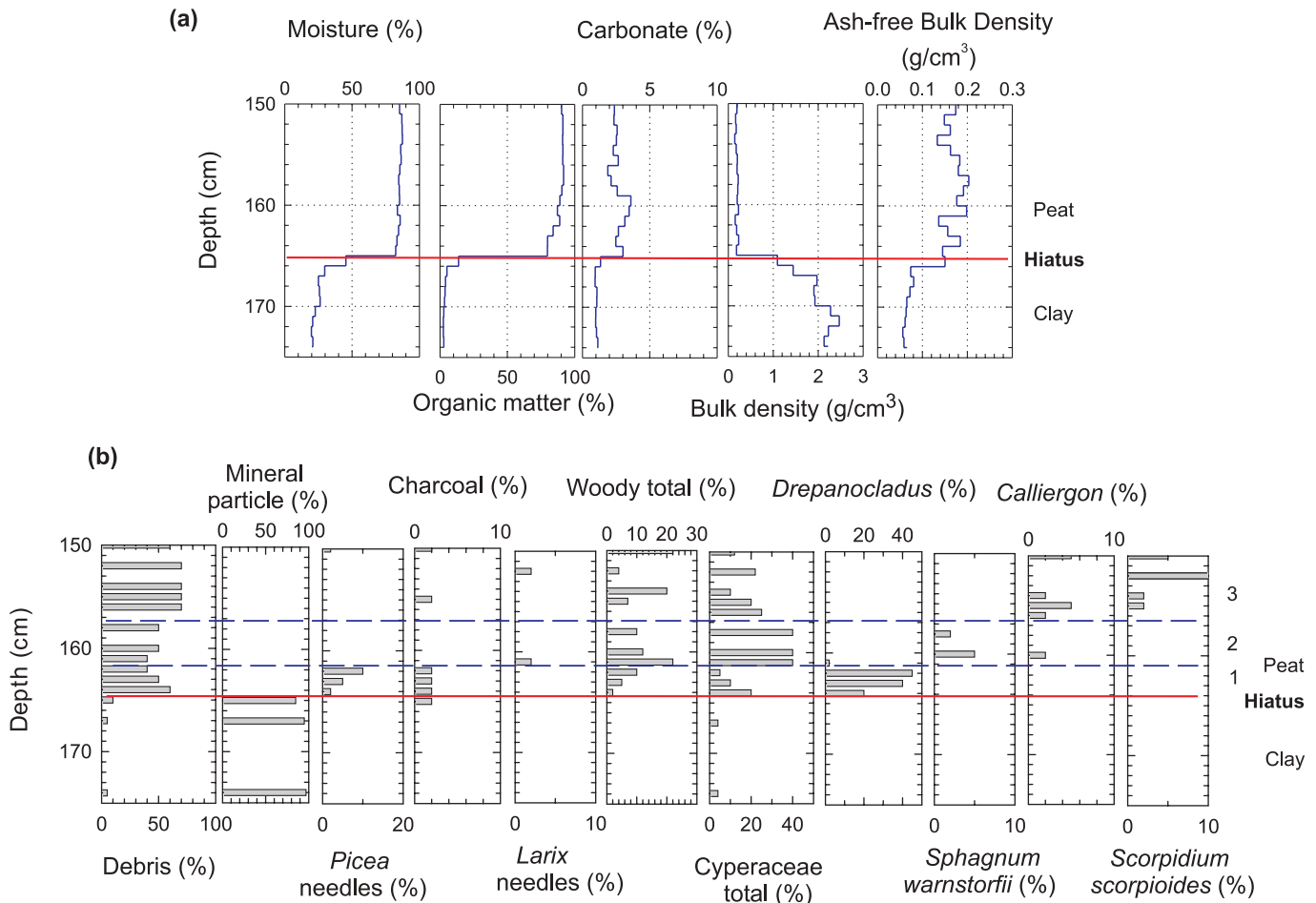
#### Extended model and sensitivity analysis

Equation 4 was fitted to the data for a 5375-year period during which peat growth was assumed dominated by *Scorpidium scorpioides* from 6905 to 1530 cal BP in the UPF main core (Fig. 11a). We used a fixed decomposition rate of 0.0002/year, an average value for the catotelm decomposition rate of peatlands in continental Canada (Yu and Campbell 1998; Vitt et al. 2000). The convex pattern (Fig. 10) is explained by the model, which suggests a unidirectional decrease in PAR from an initial value of 191.8 g·m<sup>-2</sup>·year<sup>-1</sup> at 6900 cal BP (model age of 5400 years) to an eventual value of 26.0 g·m<sup>-2</sup>·year<sup>-1</sup> at 1530 cal BP (model age of 0 years) (Fig. 11b).

**Fig. 6.** Macrofossil abundance (% in volume) diagram of the Upper Pinto Fen core together with scores of log PCA axis 1. Zonation was based on visual inspection of changes in dominant components aided by multivariate PCA scores.



**Fig. 7.** Stratigraphy of the second, shallow Upper Pinto Fen core. (a) Sediment lithology; (b) macrofossil records. Only the basal 25 cm portion (175–150 cm in depth) of the mineral–peat transition was analyzed.



A sensitivity analysis shows the effects of changing model parameters on the overall pattern of peat accumulation (Fig. 12). As with the case for the concave accumulation pattern (Yu and Campbell 1998; Yu et al. 2001), changing the decomposition rate has only relatively limited influence, especially on recently formed peat (Fig. 12a). In contrast, changing PAR has a noticeable effect on the amount of peat accumulated, including the amount of younger peat as well as older peat in the final profile (Fig. 12b). The coefficient for the PAR modifier (*b*) determines the curvature of the convex curves, with smaller values approaching a straight line (Fig. 12c).

**Discussion**

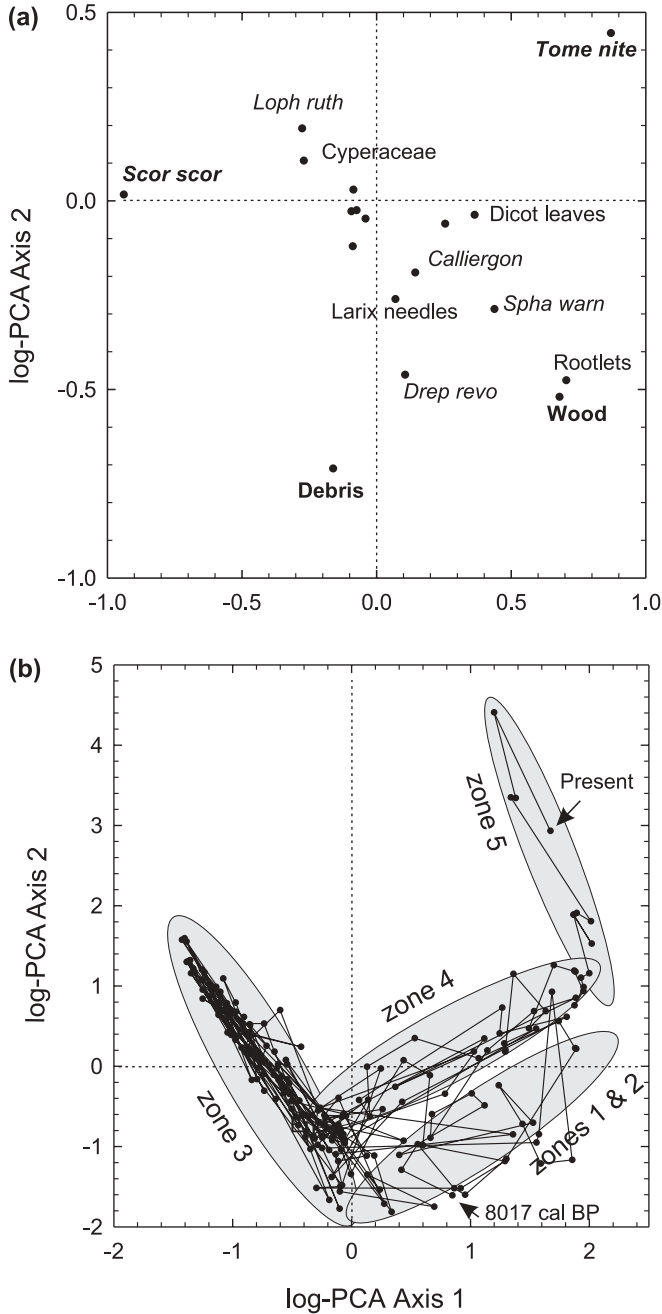
**Holocene development history of UPF**

The peatland at UPF was initiated by the paludification of a former forest, as suggested by the presence of abundant *Picea* needles and woody material in the basal peat and by the absence of lake deposits that would otherwise contain aquatic plant fossils (Figs. 6 and 7) (Kuhry et al. 1992). Paludification of forest-covered lands was the dominant process of peatland initiation in continental western Canada (Halsey et al. 1998). Peatland initiation at UPF might have been response to moist climate, occurring after the early Ho-

locene dry period in continental western Canada (Schweger and Hickman 1989; Zoltai and Vitt 1990). A gradual increase in organic matter content from 8000 to 7000 cal BP (Fig. 4b) suggests decreasing inputs of inorganic material from the surrounding mineral soils as the peatland continued to expand laterally into the surrounding uplands. Carbon accumulation rates were highest around 6850 cal BP, about 4–9 times higher than the adjacent intervals, indicating rapid vertical peat growth (Fig. 9). This period experienced widespread formation and rapid lateral expansion of peatlands in continental western Canada, suggested by basal peat dates from over 70 paludified peatlands (Halsey et al. 1998; I.D. Campbell et al. 2000).

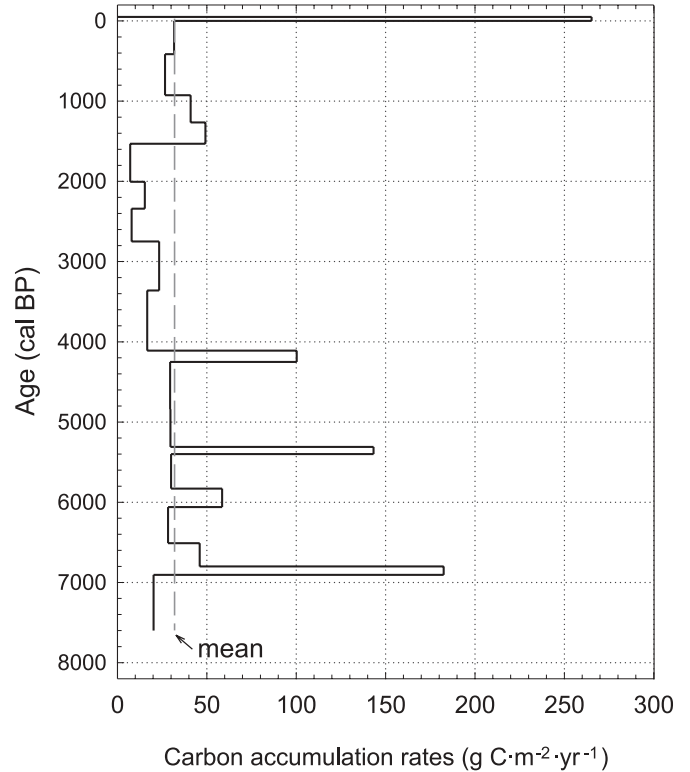
Abundant *Scorpidium scorpioides* and Cyperaceae evidence extreme-rich fen conditions from ~6500 cal BP. The transition at ~4000 cal BP from a phase with abundant woody material to a nonwoody phase might have been caused by fires, as suggested by the abundance of charcoal. Fire might have removed the shrubs from the peatland and modified the local hydrology (e.g., Tolonen 1985). Alternatively, a change in patterning or drainage regime triggered by autogenic peatland development towards more oligotrophic conditions might occur after rapid vertical peat growth. However, these two possibilities are indistinguishable without an extensive survey of the peatland. This

**Fig. 8.** Log PCA ordinations of the UPF peat macrofossil data. (a) Ordination of macrofossil types along the first two axes; (b) ordination of peat samples along the first two axes. Species: Scor scor, *Scorpidium scorpioides*; Tome nite, *Tomenthypnum nitens*; Loph ruth, *Lophozia rutheana*; Spha warn, *Sphagnum warnstorffii*; Drep revo, *Drepanocladus revolvens*.

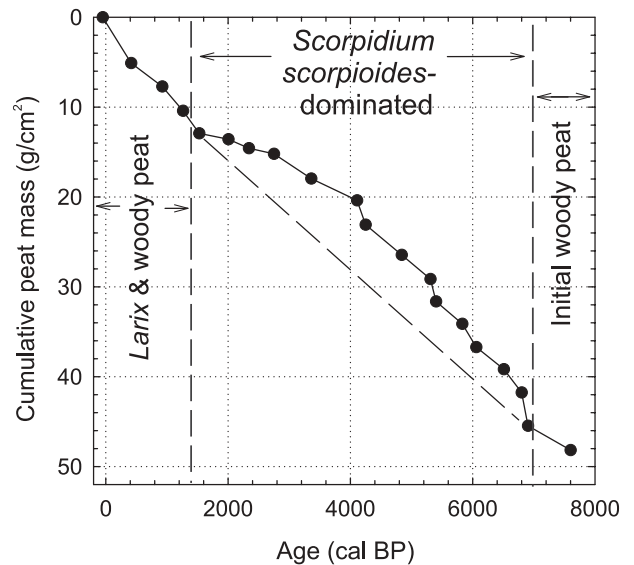


change at UPF corresponds to the establishment of permafrost under cold climate conditions in northwestern Alberta at ~3700 <sup>14</sup>C BP (equivalent to ~4000 cal BP) (Zoltai 1993). The shift from a *Scorpidium*-dominated peat to woody peat and *Larix* needles at ~1300 cal BP implies a significant change in the species composition and vegetation structure at the site. This abrupt change might have been triggered by a change in local hydrology as a result of autogenic vertical growth of the fen. This transition might relate to the “growth

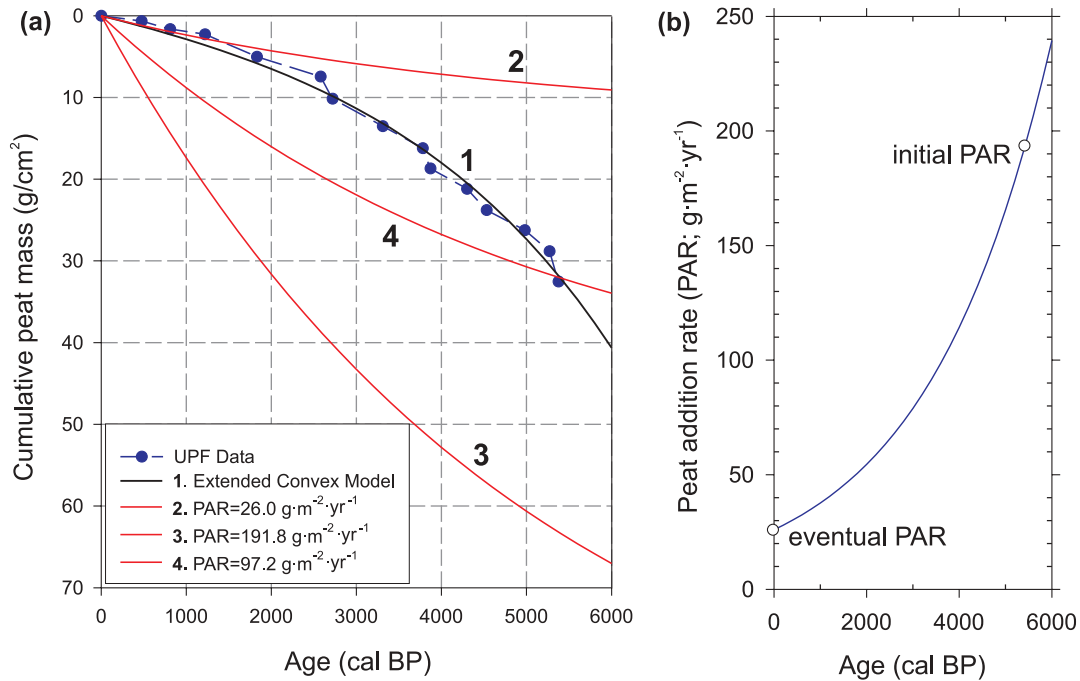
**Fig. 9.** Apparent peat carbon accumulation rates at UPF calculated using AMS dates (Fig. 3), ash-free bulk density measurements (Fig. 4c), and carbon content of peat organic matter in peatlands in continental Canada (Vitt et al. 2000). The dashed vertical line shows the time-averaged mean of 31.1 g C·m<sup>-2</sup>·year<sup>-1</sup>.



**Fig. 10.** Cumulative peat mass–age profile from the UPF core based on 20 AMS <sup>14</sup>C dates and 398 bulk density measurements. Excluding the basal (>7000 cal BP) and top woody peat (<1500 cal BP), the *Scorpidium*-dominated nonwoody peat shows a convex age–depth curve.



**Fig. 11.** (a) Cumulative peat mass for the UPF core during a period dominated by *Scorpidium* ( $n = 15$  data points, circles and dashed line) and modeling results. Curve 1 represents the fit for eq. 4 in the text, comprising a fixed decomposition rate of 0.0002/year, which yields an eventual peat-addition rate (PAR) of  $26.0 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  and coefficient of PAR modifier (b) of 0.00037/year. For comparison, curve 2 is the result using a concave model (Clymo 1984) (eq. 2 in the text) with decomposition rate of 0.0002/year and constant PAR of  $26.0 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (eventual PAR). Curve 3 is the same as curve 2 but with a PAR value of  $191.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (initial PAR at the beginning of the 5400-year convex period). Curve 4 shows the result with a PAR value of  $97.2 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , which would generate the same amount of peat during the 5400-year period as with the convex model. (b) Modeled change in PAR over time, showing a decrease from initial PAR of 191.8 at 5400 years ago to  $26.0 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  at the present, using a fitted exponential coefficient of 0.00037/year ( $\text{PAR} = 26.0 e^{0.00037t}$ ).



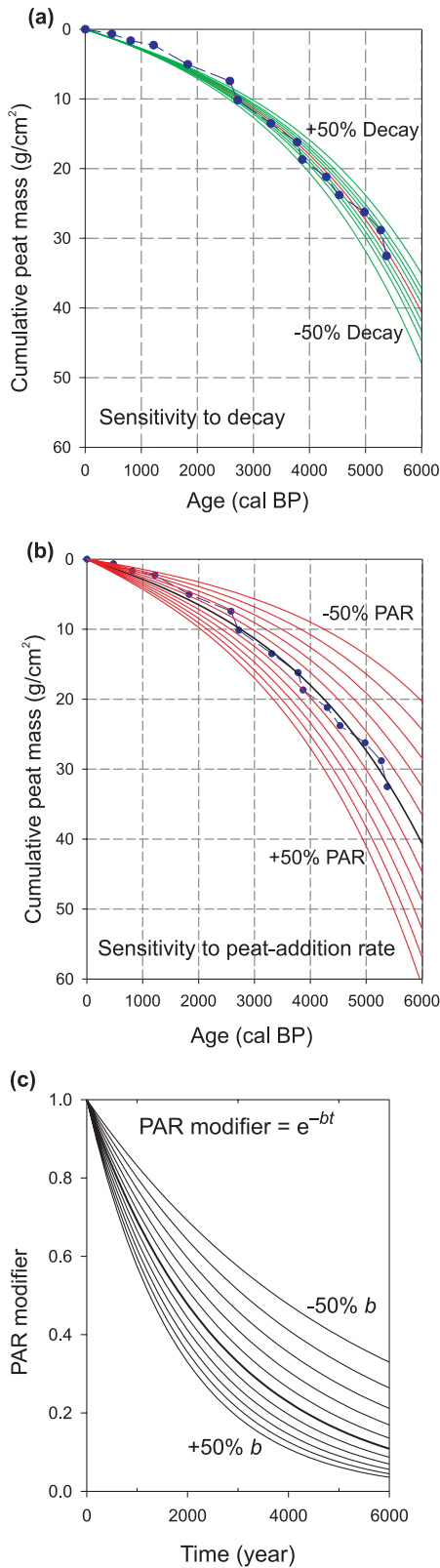
limit” of the *Scorpidium*-dominated rich fen at this time (Figs. 10 and 11). A dramatic change in species composition occurred during the last several decades, when *Scorpidium* totally disappeared and was replaced by *Tomenthypnum nitens*, a brown moss favoring drier conditions (Gignac et al. 1991). This change is associated with the most recent mineral peak (Fig. 4b), probably caused by construction of the nearby railroad and highway in the 1950s (see Fig. 2). Other intervals with high contents of inorganic mineral matter might be associated with volcanic ash-fall disturbance events (Fig. 4). The mineral peak at ~7500 cal BP concurs with ash associated with the Mazama tephra, which has recently been AMS dated at 6730 <sup>14</sup>C BP (equivalent to 7470–7620 cal BP) (Hallett et al. 1997) and dated at 7627 ± 150 cal BP from ice cores in Greenland (Zdanowicz et al. 1999). The second mineral peak at ~4000 cal BP appears to be related to St. Helens Y tephra, which has been dated between 3680 <sup>14</sup>C BP (~4000 cal BP) and 3140 <sup>14</sup>C BP (3350 cal BP) (Luckman et al. 1986). It appears that these ash falls had little influence on the peatland vegetation evidenced by macrofossil assemblages, although heavier ash falls have been suggested to have strong impacts (Zoltai 1989; Kubiw et al. 1989).

**Carbon accumulation rates and convex pattern**

The apparent carbon accumulation rates at UPF have a time-weighted mean of  $31.1 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , which is similar to reported rates from other boreal peatlands (e.g., Gorham

1991; Botch et al. 1995; Kuhry and Vitt 1996; Tolonen and Turenen 1996; Mäkilä 1997; Vitt et al. 2000) but significantly higher than for peatlands from subarctic and arctic regions (e.g., Ovenden 1990; Malmer and Wallén 1996; Vardy et al. 2000). Our high-resolution dating and bulk density measurements allow us to investigate temporal variation of carbon accumulation rates, in response to past climate change and autogenic peatland growth. In particular, the 25-fold variation from  $7.2$  to  $182.5 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  superimposed on a long-term declining trend from ~7000 to 1500 cal BP, as a result of peatland vertical growth during the convex period (Fig. 10) (see below for further discussion) and climatic fluctuations. A detailed inventory and three-dimensional modeling of a raised bog in southern Finland also showed large variations in carbon accumulation rates during the Holocene that resulted from autogenic bog development and climatic shifts (Korhola et al. 1996).

The *Scorpidium*-dominated nonwoody fen period from ~6500 to 1300 cal BP at UPF is not the only evidence from western Canadian peatlands for a convex peat mass–age curve. Three cores from Muskiki Fen in central Alberta (Kubiw et al. 1989) also show convex peat mass–age curves (Yu et al. 2000). Both Muskiki Fen and UPF are located in the Rocky Mountain Foothills, near the edge of extensive continental peatlands (Vitt et al. 1992). As reviewed by Yu et al. (2000), convex patterns have also been observed in continental bogs, e.g., Slave Lake Bog in central Alberta (Kuhry and Vitt 1996) and Beauval Bog in west-central



**Fig. 12.** Sensitivity analyses of the extended convex model. (a) Influence of changing decomposition rate using the base value of 0.0002/year (thick line) showing changes from 50% less (0.0001/year) to 50% more (0.0003/year). (b) Effect of changing PAR with an eventual PAR of 26.0 g·m<sup>-2</sup>·year<sup>-1</sup> as base case (50% increase to 39.0 g·m<sup>-2</sup>·year<sup>-1</sup> and 50% decrease to 13.0 g·m<sup>-2</sup>·year<sup>-1</sup>). (c). Change in PAR modifier over time as a function of  $b$ , which determines the curvature of curves (bold curve for the base value of 0.00037/year for  $b$ , changing from 0.00019 to 0.00056/year).

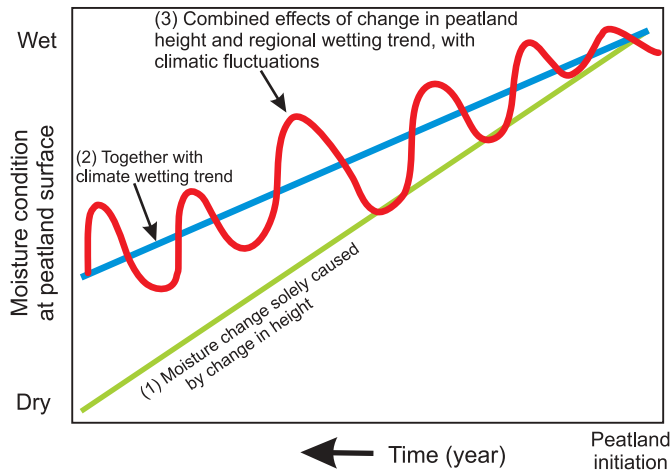
mass accumulation pattern between 9000 and 1000 cal BP based on eight calibrated radiocarbon dates in a peat profile. Clearly, peat accumulation is more complex than assumptions underlying the conceptual model of oceanic bog growth (Clymo 1984; Warner et al. 1993), which generates concave age–depth curves. Kilian et al. (2000) suggested that the concave age–depth relations as reported from raised bogs (Clymo 1984) might have resulted from variable botanical composition and consequent different accumulation rates of peat sections, or simply from dating errors. In contrast, the convex period at UPF was dominated by a single moss species, without significant change in species composition.

#### Possible cause of convex pattern

What could have caused the convex age–depth shape of peat accumulation curves at UPF and other peatlands? PAR and decomposition rates determine long-term peat accumulation in the catotelm (Clymo 1984; Clymo et al. 1998). Both variables can change over time, but the PAR is likely to be more sensitive to vegetation type and environmental parameters and thus more variable than the catotelm decomposition rate. The PAR is determined by production and aerobic decomposition above the acrotelm–catotelm interface that usually lies at 50 cm or less below the peat surface, where environmental conditions (e.g., temperature, moisture, and chemistry) vary greatly. In contrast, the catotelm decomposition is determined by conditions within the catotelm, and deeper peat is less susceptible to environmental influences acting from the surface. For example, in a detailed study of five contrasting peatlands (including bog, poor fen, and rich fen) in central Alberta, Vitt et al. (1995) found that seasonal temperature variations at 1.5 m depth are smaller (3–5°C) in all cases than at the peatland surface (up to 20°C), even though bogs and fens have a characteristic difference in temperature regime. They also noted differences in peat porewater chemistry at different depths. The surface temperature of a bog in Finland varies 15°C seasonally but at > 4 m depth remains constant at 6°C (Puranen et al. 1999). Yu et al. (2000) carried out sensitivity analyses using the bog growth model by modifying the PAR to explore the possible consequences, suggesting that either a continuously decreasing PAR or an increasing decomposition rate would cause convex peat mass–age curves. Decreasing PAR, with or without decomposition, produces a simple convex curve, but increasing decomposition produces a sigmoidal (S-shaped) curve due to the differential influence of decomposition on the older and younger strata of the peat profile (Yu et al. 2000).

Saskatchewan (Kuhry 1997). In the European literature, the most convincing convex pattern is described using 123 radiocarbon dates at Pesänsuo, a raised bog in southwest Finland (Ikonen 1993). Mäkilä et al. (2001) studied an aapa mire (fen) in north-central Finland and found a convex peat

**Fig. 13.** Schematic diagram showing the different effects of peatland vertical growth and climatic change on moisture conditions of a continental fen: (1) Moisture change solely caused by change in peatland vertical growth, (2) moisture as superimposed on a possible wetting climatic trend, and (3) eventual moisture variation with combined effects of height-reduced change, regional wetting climate, and millennial-scale climatic fluctuations. See text for further explanation.



The results from the extended model (Figs. 11 and 12) provide a quantitative evaluation that suggests that a seven-fold decrease in PAR would generate the observed pattern at UPF. Assuming that the catotelm decomposition rate is relatively constant over this 5400-year period (Fig. 12a), the extended model suggests that PAR was  $191.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  initially, decreasing exponentially at a rate of  $0.00037/\text{year}$  to  $26.0 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  at the end of the period (Fig. 11b). It is likely that a newly initiated fen on a mineral-rich landscape would have much higher plant production, or lower acrotelm decomposition.

Is there any evidence to support the actual values of PAR suggested by this modeling analysis? The net primary production (NPP) of peatlands is usually only measured for the aboveground portion, with belowground production being estimated (C. Campbell et al. 2000). Such measurements tend to show large variation, which may relate to history or substrate of corresponding peat deposits. Recently reported NPP values from boreal fens indicate that belowground production, mostly from fine roots, could contribute over 70% of the total NPP of over  $1000 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (Sjörs 1991; Saarinen 1996). The modeled initial PAR of  $191.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  at UPF is <20% of these reported total NPP values, providing a reasonable proportion of the NPP (Clymo 1984; Gorham 1991).

### The height-induced long-term drying hypothesis

Why would the rate of peat addition to the catotelm show a unidirectional decrease over time in continental fens? We suggest here that such a decline is related to the moisture-limited continental climate and to the particular hydrology of fens and some continental bogs having groundwater (geogeneous water) influences (Glaser et al. 1997; Lamers et al. 1999). Both autogenic and allogenic processes control the hydrology of peatlands and peatland development (e.g., Damman 1986; Foster and Wright 1990; Almquist-Jacobson and Foster 1995; Mäkilä 1997). Local moisture conditions

on a peatland surface are determined by a combination of three factors at different temporal and spatial scales (Fig. 13): (i) long-term growth of the peatland and associated progressive isolation from the surrounding regional water table (autogenic), (ii) regional climatic trends and fluctuations (allogenic), and (iii) noise from local site disturbances and short-term hydrologic events. We argue that the first factor is more important in determining surface moisture conditions in groundwater-dependent continental fens than in the classic raised and blanket bogs of oceanic regions. Year-round high rainfalls (e.g., >3000 mm) in oceanic regions flush the peat column and maintain high and relatively stable water tables (Ingram 1982). Thus, bog growth does not change the hydrological configuration with regard to the surrounding uplands and does not significantly alter water and nutrient availability, as it can only affect water losses to lower ground, and over time, self-adjustment of bog shape and size can compensate for such losses (Ingram 1982). In contrast, fens and some continental bogs experience changes in hydrology and nutrient availability in response to growth (Siegel et al. 1995; Kuhry and Vitt 1996; Glaser et al. 1997; Moore 1997). Furthermore, bogs (and poor fens) are typically dominated by *Sphagnum* whose capacity for water retention acts to stabilize local water levels, whereas rich fens are dominated by brown mosses that have little or no such capacity to retain water; these rich fens are accordingly extremely sensitive to local water inputs. Given stable water input, growth of rich fens above the groundwater will gradually decrease surface moisture.

We hypothesize that a long-term drying trend is caused solely by vertical growth of continental rich fens and that this reduces the production of moisture-sensitive mosses or increases the acrotelm decomposition or both, causing a decrease in the PAR. Although this phenomenon might also occur in ombrotrophic bogs because continuous bog growth will accelerate drainage and limit *Sphagnum* production (Damman 1986) or increase acrotelm decomposition (Aaby 1976), it will be more pronounced in continental fens or groundwater-fed bogs due to greater dependence of these peatlands on local hydrology as a water source. On fens, height growth leads to a decrease in the water budget because the change in hydraulic gradients and groundwater flow patterns means less water is gained from, and more water is lost to, surrounding areas.

Two conditions are required for this mechanism to work: (i) productivity must be positively related to moisture and (ii) the height-induced drying trend must not be reversed by a wetter climate. *Scorpidium scorpioides*, the dominant brown moss at UPF, is a characteristic species of extreme-rich fens. It is most common at or just below the water surface and rarely occurs more than 10 cm above the water table (Gignac et al. 1991; Vitt et al. 1993; Zoltai et al. 2000). Kooijman and Whilde (1993) found that productivity of *Scorpidium scorpioides* is quite sensitive to moisture conditions. High water levels result in high growth rates, and growth rates are strongly reduced when the plants are exposed to prolonged summer drought. The autogenically induced drying trend at this site did not result in a classic community succession from fen to bog (e.g., Almquist-Jacobson and Foster 1995), as alkaline, calcium-rich fen waters are too severe for invading *Sphagnum* species to tolerate

(Vitt 2000). The UPF data, however, show rapid transition from a nonforested to a forested fen, possibly triggered by gradual and autogenically induced change in environmental conditions. This nonlinear response of peatland ecosystems to gradual and minor environmental change has been documented in a peatland model with coupled peat depth and water table depth (Hilbert et al. 2000).

Continuous upward peatland growth (4 m over the last 8000 years at UPF) increases the distance of the peatland surface from the regional water table and reduces nutrient inputs derived from groundwater to living plants, thus limiting their growth, especially for moisture-sensitive *Scorpidium scorpioides*. Climatic fluctuations are superimposed on this long-term autogenic trend. Multiple proxy data from Beauval Bog in Saskatchewan indicate progressively decreasing on-site local moisture over the last 4000 years (Kuhry 1997), which is at odds with the general regional climate history of increasing moisture during the late Holocene (Schweger and Hickman 1989). This contrast demonstrates the interaction between autogenically induced local moisture reductions and regional climate on peatland development and peat accumulation.

In summary, we propose the following height-induced long-term drying hypothesis to explain the convex peat accumulation pattern observed in some continental rich fens. In groundwater-fed fens under a continental climate, autogenic vertical growth causes a long-term drying trend on the peatland surface owing to progressive isolation from surrounding upland water tables. In cases where progressive, long-term drying is not sufficient to cause species change, dry conditions decrease NPP, especially for moisture-sensitive rich fen mosses, and increase litter and peat decay in the acrotelm, consequently reducing the PAR to the catotelm. This unidirectional decrease in the PAR would in turn produce a convex peat mass–age curve. Climatic fluctuations superimposed on this drying trend determine the eventual peat accumulation pattern and also produce the wiggles often seen in peat cores (Clymo 1984).

The convex pattern and related conceptual model have important implications for building simulation models and for projecting future peat carbon dynamics. A simulation model based on the concave-shaped accumulation pattern (e.g., Frolking et al. 2001) could provide erroneous results for continental fens that have convex patterns. Our extended model also suggests that the continued decrease in PAR caused by peatland vertical growth in continental fens would eliminate their carbon sequestration capacity over time, even in the absence of climate change. These peatlands will reach their growth limit faster than the previous model (Clymo 1984) suggested, if succession of vegetation or peatland type does not occur, because of decreasing production over time and continued decomposition in the catotelm.

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