NOTE / NOTE

Variability in organic matter lost by combustion in a boreal bog during the 2001 Chisholm fire

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Abstract: Fire directly releases carbon (C) to the atmosphere through combustion of biomass. An estimated 1470 ± 59 km^2 of peatland burns annually in boreal, western Canada, releasing 4.7 ± 0.6 Tg C to the atmosphere via direct combustion. We quantified within-site variation in organic matter lost via combustion in a bog peatland in association with the 116 000-ha Chisholm, Alberta, fire in 2001. We hypothesized that for peatlands with considerable small-scale microtopography (bogs and treed fens), hummocks will burn less than hollows. We found that hollows exhibit more combustion than hummocks, releasing nearly twice as much C to the atmosphere. Our results suggest that spatial variability in species composition and site hydrology within a landform and across a landscape could contribute to considerable spatial variation in the amounts of C released via combustion during peatland fire, although the magnitude of this variation may be dependent on fire severity.

Résumé : Le feu libère du carbone (C) directement dans l'atmosphère par la combustion de biomasse. Annuellement, on estime que 1470 ± 59 km^2 de tourbière brûle en zone boréale dans l'ouest du Canada libérant 4,7 ± 0,6 Tg de C dans l'atmosphère par combustion directe. Nous avons quantifié la variation à l'intérieur d'un site dans la perte de matière organique dans une tourbière à mousse à la suite du feu de Chisholm qui a couvert 116 000 ha en Alberta en 2001. Nous avons fait l'hypothèse que dans une tourbière avec beaucoup de variations microtopographiques à petite échelle (tourbières hautes et tourbières basses arborées), les monticules brûleraient moins que les dépressions. Nous avons observé que les dépressions brûlent plus que les monticules, libérant presque deux fois plus de C dans l'atmosphère. Nos résultats indiquent que la variabilité spatiale dans la composition en espèces et les caractéristiques hydrologiques du site à l'intérieur d'une forme de relief ou à travers le paysage peut entraîner une forte variation spatiale dans la quantité de C libéré par combustion lors d'un feu dans une tourbière. Par contre, l'ampleur de cette variation peut dépendre de la sévérité du feu.

[Traduit par la Rédaction]

Introduction

Peatland ecosystems cover an estimated 3%–4% (350 – 400 million ha) of the earth's land surface (Gorham 1991), with 101 million ha distributed in the boreal and subarctic regions of Canada (Zoltai et al. 1998). Western Canadian peatlands are ecosystems where net primary production exceeds microbial decomposition, resulting in an accumulation of organic matter, or peat (Gorham 1991). Continental western Canadian peatlands (in Alberta, Saskatchewan, and Manitoba) collectively store 42 Pg of carbon (C) as peat and another 6 Pg C in vegetation (Vitt et al. 2000). Gorham (1991) estimated that boreal and subarctic peatlands, collectively, represent a 455-Pg C pool and are sequestering atmospheric C at a rate of 23 $g \cdot m^{-2} \cdot year^{-1}$, which extrapolates to a global net sink of 76 $Tg \cdot year^{-1}$. However, the results of Turetsky et al. (2002) cast doubt on the magnitude of this claimed sink because of exclusion of disturbance in previous estimates. Previous estimates of peatland C balance generally assume a disturbance-free state and do not explicitly consider spatial heterogeneity in plant species composition and function between and within peatland landforms, which could influence the C source–sink behavior of a peatland, as well as responses to disturbance.

Fire compromises the C storage capacity of peatlands. During fire, C is lost directly through combustion of biomass, releasing, on average, 3.2 ± 0.4 kg $C \cdot m^{-2}$ from peat to the atmosphere (Turetsky et al. 2002). An estimated 1470 ± 59 km^2 of peatland burns annually in boreal, western Canada (Alberta, Saskatchewan, and Manitoba), releasing 4.7 ± 0.6 Tg C to the atmosphere via direct combustion (Turetsky et al. 2002).

Although some current estimates of C balance in peatlands have taken into account the direct effects of fire (e.g., Zoltai et al. 1998; Vitt et al. 2000; Turetsky et al. 2002), none have set out to characterize the nature of spatial variability in plant species composition and associated fire re-

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Table 1. Nested analysis of variance to evaluate hummock–hollow differences in the quantity of organic matter burned.

Source	df	Sum of squares	Mean square	F	p
Total	223	600.04			
Plot	9	34.44	3.83	0.65	0.7457
Corner(Plot)	27	159.18	5.90	0.23	0.9929
Microtopography(Corner)	4	104.24	26.06	18.21	<0.0001
Error	180	257.56	1.43		

Note: The F statistic for the plot effect was calculated using the Corner(Plot) mean square, the F statistic for the Corner(Plot) effect was calculated using the Microtopography(Corner) mean square, and the F statistic for the Microtopography(Corner) effect was calculated using the Error mean square.

sponse, which could complicate assessments of fire effects. Using the excess ash approach of Turetsky and Wieder (2001), we quantified variation in organic matter lost due to combustion in the Chisholm, Alberta, fire of 2001 between microtopographic positions (hummocks vs. hollows) in an ombrotrophic bog peatland.

Peatland landforms are defined by their hydrology, vegetation, and surface water chemical composition (Malmer 1986; Vitt 1990; Gignac et al. 1991; Kuhry et al. 1993; Thormann and Bayley 1997; Ohlson and Okland 1998). Bogs are ombrotrophic (receive water only from precipitation) and oligotrophic (nutrient poor), resulting in conditions suitable for *Sphagnum* dominance (Vitt 1990; Gignac et al. 1991).

We hypothesized that significant variation exists within peatlands in degree of combustion during a fire. In particular, based on our field observations of postfire peatlands, we hypothesized that for peatlands with considerable small-scale microtopography (bogs and treed fens, the latter not included in this study), hummocks will burn less than hollows.

Materials and methods

From May to June 2001, a 116 000-ha fire occurred near Chisholm, Alberta, consuming upland and peatland landforms (DeSorcy et al. 2001). Within the area, a bog near the Tieland gas plant, approximately 15 km south of the town of Chisholm (54°55′N, 114°10′W) was chosen through analysis of prefire aerial photographs. After the fire, the bog had hummocks dominated by *Sphagnum fuscum* and extensively charred hollows (making species identification impossible, but for bogs in western Canada, the most likely species are *Sphagnum angustifolium* and (or) *Sphagnum magellanicum*), as well as *Picea mariana* exhibiting various degrees of combustion from charring to death.

Ten 1-m^2 plots were established along a stratified random transect through the burned peatland approximately 3 days after the fire burned the peatland. At each corner, a 20 cm long, 10 cm diameter peat core was collected from the nearest hummock and hollow allowing for assessment of microtopographic variation.

From each core, the upper burned portion (typically 0–10 cm) was collected based on visual inspection for evidence of charcoal or ash, along with 5 cm of the underlying unburned section. Each sample was dried at 70 °C for 72 h, weighed, and homogenized using a Cyclotec mill. Ash concentration was determined by loss on ignition at 450 °C for 4 h for three 1.0-g subsamples of each burned and unburned portion of each core. Assuming uniform ash concentration throughout an unburned peat column, a given volume of peat should generate a predictable amount of ash upon combustion, allowing for the direct calculation of organic matter lost during combustion (Turetsky and Wieder 2001).

A nested analysis of variance was used to analyze burned organic matter ($kg \cdot m^{-2}$) differences according to microtopography (between hummocks and hollows) within the bog. Statistical analyses were performed using the General Linear Model procedure in SAS V.8 (SAS Institute Inc. 1999).

Results

A significant microtopography effect (Table 1) revealed that almost twice as much organic matter was lost via combustion from hollows (2.76 ± 0.33 kg $C \cdot m^{-2}$; n = 36) than from hummocks (1.45 ± 0.11 kg $C \cdot m^{-2}$; n = 39). Comparison of C emissions from three scenarios modeling the ratio of burned peatland area (1470 ± 59 km^2; Turetsky et al. 2002) experiencing heavy (i.e., hollow) vs. light (i.e., hummock) combustion rates gave a mean direct C loss rate of 2.1 ± 0.4 $kg \cdot m^{-2}$, releasing 3.1 ± 0.5 Tg C annually from boreal, western Canadian peatlands (Table 2).

Discussion

Site conditions (i.e., microtopography, peat moisture, and vegetation composition; Malmer 1986; Vitt 1990; Gignac et al. 1991; Kuhry et al. 1993; Thormann and Bayley 1997; Ohlson and Okland 1998) and fire characteristics (i.e., intensity, frequency, and duration; Kasischke et al. 1995) can have implications for the quantity of organic matter burned (C lost) via direct combustion during peatland fire (Gorham 1994; Kuhry 1994; Kasischke et al. 1995; Kasischke and Bruhwiler 2003). Within peatland landforms, microtopographic variation may arise because of competition and tolerance interactions between dominant moss species (Titus et al. 1983; Foster 1984; Vitt and Slack 1984; Wagner and Titus 1984; Rydin and McDonald 1985; Rydin 1986, 1993) and the differential peat accumulation capacities of those species (Vitt 1990; Gignac et al. 1991; Wallen and Malmer 1992; Thormann and Bayley 1997). Bogs exhibit such variation, with relatively high, dry hummocks dominated by *Sphagnum fuscum* and low, wet hollows dominated by more

Table 2. Peatland carbon losses under six combustion scenarios.

Combustion (heavy:light) ratio (%)	Relative combustion	Area burned ($km^2·year^{-1}$)[a]	Estimated C loss ($Tg·year^{-1}$)[b]	Combined C loss ($Tg·year^{-1}$)	Emission rate ($kg\ C·m^{-2}$)[c]
30:70	Heavy	441±18	1.2±0.2	2.7±0.4	1.8±0.3
	Light	1029±41	1.5±0.2		
40:60	Heavy	588±24	1.6±0.3	2.9±0.4	2.0±0.4
	Light	882±35	1.3±0.2		
50:50	Heavy	735±30	2.0±0.3	3.1±0.5	2.1±0.4
	Light	735±30	1.1±0.1		
60:40	Heavy	882±35	2.4±0.4	3.3±0.5	2.2±0.4
	Light	588±24	0.9±0.1		
70:30	Heavy	1029±41	2.8±0.5	3.5±0.5	2.4±0.4
	Light	441±18	0.6±0.1		
Mean				3.1±0.5	2.1±0.4

Note: No differences were assumed in combustion between bog and permafrost peatlands (Turetsky and Wieder 2001) and in total C emissions between bogs and fens when above- and below-ground combustions were taken into account (Zoltai et al. 1998). Values represent mean ± SE.

[a]Based on percentage of 1470 ± 59 $km^2·year^{-1}$ burned (cf. Turetsky et al. 2002).

[b]Area burned multiplied by estimated carbon loss per unit area ($kg·m^{-2}$) for respective degree of combustion: Heavy, 2.8 ± 0.33; Light, 1.5 ± 0.1.

[c]Combined C loss divided by total area burned (1470 ± 59 $km^2·year^{-1}$; cf. Turetsky et al. 2002).

wet-loving *Sphagnum* sp. (i.e., *S. angustifolium*), representing up to 50 cm in vertical deviation (Vitt and Slack 1984; Malmer 1986; Rydin 1986; Vitt 1990; Gignac et al. 1991; Wallen and Malmer 1992). This inherent variation within a landform could result in certain areas burning to a greater degree than others (Hogg et al. 1992; Kasischke et al. 1995; Zoltai et al. 1998; Pitkanen et al. 1999), introducing more complexity at the site scale than has been considered in the past.

The bog hollows did exhibit greater organic matter loss due to combustion than their respective hummocks, an effect most likely related to differences in species composition. Drought-avoiding hummock species, namely *S. fuscum*, form dense mats of individuals capable of retaining water in the spaces between individuals, allowing the hummock to remain relatively moist even under periods of high stress (Titus et al. 1983; Wagner and Titus 1984; Rydin and McDonald 1985; Longton 1992). *Sphagnum* species in hollows tend to be more loosely arranged; water availability usually is relatively high because of closer proximity of the water table (Titus et al. 1983; Wagner and Titus 1984; Rydin and McDonald 1985). However, during extended dry periods, hollow species, with lower water retention abilities than hummock species, can become quite desiccated. Hummock species are therefore less likely to burn because they remain relatively moist during fire, while hollow species, lacking high concentrations of stored water, will combust more readily, especially when the ambient water is evaporated during fire. At the bog site, high degree of moisture saturation was observed in the field just below the surface (2–4 cm) of burned hummocks, while burned hollows were relatively dry and highly charred, supporting this explanation.

Average emissions values obtained by this study (assuming an even distribution of combustion severities across affected peatlands; Table 2) are comparable with those of other published studies (Table 3) of peatlands and forests with organic soils throughout the boreal region. However, with the exception of Turetsky and Wieder (2001), the emissions estimates of these other studies were obtained through extrapolation from remote sensing data (Cahoon et al. 1994; Kasischke et al. 1995*b*; Conard et al. 2002; Kajii et al. 2002; Kasischke and Bruhwiler 2003), map overlays (Zoltai et al. 1998), mathematical modeling (Harden et al. 2000), combinations thereof (Amiro et al. 2001; Turetsky et al. 2002), or analysis of peat profiles (Pitkänen et al. 1999); some did not explicitly include peatlands (Amiro et al. 2001; Conard et al. 2002), although mention of peatlands' unique contributions were made. More direct measurements must be made if we are to understand the reasons for the combustion variability reflected in this study.

Dry, windy conditions before and during the Chisholm fire, suggested by high Canadian Forest Fire Danger Rating System indices (buildup index, 122.5; duff moisture code, 100.8; drought code, 390; fire weather index, 42.9; Alberta Sustainable Resource Development, Provincial Fire Forecasting Centre), suggest extreme fire behavior, resulting in fast rates of fire spread (DeSorcy 2001). However, these indices give little insight into peatland fire characteristics because the indices are not calibrated for the unique nature of peatland soils and vegetation. Because bog peatlands have only sparse cover of *Picea mariana*, it is unlikely that intense crown fire conditions occurred, resulting in relatively fast moving but low severity ground fire activity through the bog. Peatlands may actually undergo more complete and extensive combustion of the organic layer during less intense, slower moving fires with higher incidence of smoldering, resulting in greater C emissions due to increased extent of heavy combustion (Table 2). Therefore, the emissions estimates obtained by this study may represent minimum values for peatlands.

Spatial variability in species composition and site hydrology within a landform and across a landscape could contribute to considerable spatial variation in the amounts of C released during fire. We acknowledge that the effects of only

Table 3. Comparison of direct C emission estimates due to combustion from worldwide boreal regions.

Study	Area burned ($km^2 \cdot year^{-1}$)	Emission rate ($kg\ C \cdot m^{-2}$)	Total C losses ($Tg \cdot year^{-1}$)
North America			
This study	1 470 ± 59[a]	2.1±0.4[b]	3.1±0.5[b]
Kasischke and Bruhwiler 2003		0.9–3.7[c]	
Turetsky et al. 2002			
Historical	580 ± 23	3.2±0.4[d]	1.9±0.2
Current	1 470 ± 59	3.2±0.4[d]	4.7±0.6
Amiro et al. 2001[e]			
Total	20 342	1.2±1.0	27±6
Boreal only[f]	11 318	1.2±0.9	15.1
Turetsky and Wieder 2001	1 470 ± 59[a]	2.2±0.5	3.2±0.9[g]
Harden et al. 2000[h]	3 300 – 8 400[g]	<1.0	3.3–8.4
Zoltai et al. 1998	6 420	1.5	9.6
Kasischke et al. 1995b[i]			
Total forest		2.5–3.0	12–18
Peat only		2.0[g]	
Mean		1.5–2.5[j]	4.4–6.2[k]
Europe and Asia			
Kasischke and Bruhwiler 2003			
Forest		0.1–1.2[l]	
Peatland[m]	5 000	4.0	40
Kajii et al. 2002[n]	1 650	12.7[h]	20.9
Conard et al. 2002[n]			59
Pitkänen et al. 1999		2.5	
Cahoon et al. 1994		1.13	
Grand mean		1.7–2.3[o]	

Note: Estimations of error provided when available.
[a]From Turetsky et al. (2002).
[b]See Table 2.
[c]Based on 2.1 kg $C \cdot m^{-2}$ estimate of French et al. (2000) used for North American boreal forest.
[d]Averaged value from Turetsky and Wieder (2001).
[e]Estimates based on total Canadian forest fire emissions weighted by fuel characteristics and fire behavior.
[f]Estimates obtained using values for boreal shield east and west, boreal plains, and boreal cordillera.
[g]Calculated by Benscoter based on provided and (or) assumed data.
[h]Only very poorly drained (wetland) class used.
[i]Estimates from Alaska only.
[j]Excludes Turetsky et al. (2002) estimate to avoid repeated representation of values (see footnote *d*).
[k]Includes current estimated emissions from peatlands only.
[l]Assumed range of emissions from Russian organic forest soils across range of burn severities.
[m]Values for peatlands in Russian Far East. Areal extent and emissions rate are assumptions.
[n]For Siberian peatlands during 1998 fires only.
[o]Excludes values of Turetsky et al. (2002) (see footnote *k*) and Kajii et al. (2002).

one fire were examined at only one peatland site in this study, so broad generalizations of direct peatland response to fire cannot be determined from this study. However, the results provide support for the hypothesis that significant variation exists within peatland landforms in degree of combustion during relatively uniform fire conditions. While overall mean C emissions during combustion from peatlands may be comparable to upland areas during fire, variation in burn severity may affect the magnitude of the observed variation and make peatlands an even more important component to global fire emissions models. However, the true importance of peatlands to global C dynamics most likely lies in the indirect effects of fire on peatlands (i.e., changed decomposition and production dynamics) resulting in increased long-term postfire C emissions, as some studies have illustrated (e.g., Harden et al. 2000). Future attempts to model the contribution of burned peatlands to C emissions need to take this variability into account when making accurate assessments of overall C loss during peatland fire.

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References

Amiro, B.D., Todd, J.B., Wotton, B.M., Logan, K.A., Flannigan, M.D., Stocks, B.J., Mason, J.A., Martell, D.L., and Hirsch, K.G. 2001. Direct carbon emissions from Canadian forest fires, 1959–1999. Can. J. For. Res. **31**: 512–525.

Cahoon, D.J., Stocks, B.J., Levine, J., Cofer, W., and Pierson, J. 1994. Satellite analysis of the severe 1987 forest fire in northern China and southeastern Siberia. J. Geophys. Res. **99**: 18 627 – 18 638.

Conard, S., Sukhinin, A., Stocks, B.J., Cahoon, D.J., Davidenko, E., and Ivanova, G. 2002. Determining effects of area burned and fire severity on carbon cycling and emissions in Siberia. Clim. Change, **55**: 197–211.

DeSorcy, G.J., Cohen, J.D., and Partington, L. 2001. Chisholm Fire Review Committee final report. Alberta Sustainable Resource Development, Edmonton, Alta.

Foster, D.R. 1984. The dynamics of *Sphagnum* in forest and peatland communities in southeastern Labrador, Canada. Arctic, **37**: 133–140.

French, N.H.F., Kasischke, E.S., Stocks, B.J., Mudd, J.P., Martell, D.L., and Lee, B.S. 2000. Carbon release from fires in the North American boreal forest. *In* Fire, climate change, and carbon cycling in the boreal forest. Springer-Verlag New York Inc., New York. pp. 377–388.

Gignac, L.D., Vitt, D.H., Zoltai, S.C., and Bayley, S.E. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. Nova Hedwigia, **53**: 27–71.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. **1**: 182–195.

Gorham, E. 1994. The future of research in Canadian peatlands; a brief survey with particular reference to global change. Wetlands, **14**: 206–215.

Harden, J.W., Trumbore, S.E., Stocks, B.J., Hirsch, A.S., Gower, S.T., O'Neill, K., and Kasischke, E.S. 2000. The role of fire in the boreal carbon budget. Global Change Biol. **6**: 174–184.

Hogg, E.H., Lieffers, V.J., and Wein, R.W. 1992. Potential carbon losses from peat profiles: effects of temperature, drought cycles, and fire. Ecol. Appl. **2**: 298–306.

Kajii, Y., Kato, S., Streets, D., Tsai, N., Shvidenko, A., Nilsson, S., McCallum, I., Minko, N., Abushenko, N., Altyntsev, D., and Khodzer, T. 2002. Boreal forest fires in Siberia in 1998: estimation of area burned and emissions of pollutants by advanced very high resolution radiometer satellite data. J. Geophys. Res. **107**(D24): 4745, doi: 10.1029/2001JD001078, 2002.

Kasischke, E.S., and Bruhwiler, L. 2003. Emissions of carbon dioxide, carbon monoxide, and methane from boreal forest fires in 1998. J. Geophys. Res. **107**: 8146, doi: 10.1029/2001JD000461, 2003.

Kasischke, E.S., Christensen, N.L.J., and Stocks, B.J. 1995*a*. Fire, global warming, and the carbon balance of boreal forests. Ecol. Appl. **5**: 437–451.

Kasischke, E.S., French, N.H.F., Bourgeau-Chavez, L.L., and Christensen, N.L.J. 1995*b*. Estimating release of carbon from 1990 and 1991 forest fires in Alaska. J. Geophys. Res. **100**: 2941–2951.

Kuhry, P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. J. Ecol. **82**: 899–910.

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.

Longton, R.E. 1992. The role of bryophytes and lichens in terrestrial ecosystems. *In* Bryophytes and lichens in a changing environment. *Edited by* J.W. Bates and A.M. Farmer. Clarendon Press, Oxford. pp. 32–65.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. **64**: 375–383.

Ohlson, M., and Okland, R.H. 1998. Spatial variation in rates of carbon and nitrogen accumulation in a boreal bog. Ecology, **79**: 2745–2758.

Pitkänen, A., Turunen, J., and Tolonen, K. 1999. The role of fire in the carbon dynamics of a mire, eastern Finland. Holocene, **9**: 453–462.

Rydin, H. 1986. Competition and niche separation in *Sphagnum*. Can. J. Bot. **64**: 1817–1824.

Rydin, H. 1993. Interspecific competition between *Sphagnum* mosses on a raised bog. Oikos, **66**: 413–423.

Rydin, H., and McDonald, A.J.S. 1985. Tolerance of *Sphagnum* to water level. J. Bryol. **13**: 571–578.

SAS Institute Inc. 1999. SAS/STAT user's guide, version 8. SAS Institute Inc., Cary, N.C.

Thormann, M.N., and Bayley, S.E. 1997. Aboveground net primary production along a bog–fen–marsh gradient in southern boreal Alberta, Canada. Ecoscience, **4**: 374–384.

Titus, J., Wagner, D., and Stephens, M. 1983. Contrasting water relations of photosynthesis for two *Sphagnum* mosses. Ecology, **64**: 1109–1115.

Turetsky, M., Wieder, K., Halsey, L., and Vitt, D. 2002. Current disturbance and the diminishing peatland carbon sink. Geophys. Res. Lett. **29**(21): 1–4. 10.1029/2001GL014000, 12 June 2002.

Turetsky, M.R., and Wieder, R.K. 2001. A direct approach to quantifying organic matter lost as a result of peatland wildfire. Can. J. For. Res. **31**: 363–366.

Vitt, D.H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical, and topographic gradients. Bot. J. Linn. Soc. **104**: 35–59.

Vitt, D.H., and Slack, N.G. 1984. Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. Can. J. Bot. **62**: 1409–1430.

Vitt, D.H., Halsey, L.A., Bauer, I.E., and Campbell, C. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. Can. J. Earth Sci. **37**: 683–693.

Wagner, D., and Titus, J. 1984. Comparative desiccation tolerance of two *Sphagnum* mosses. Oecologia, **62**: 182–187.

Wallen, B., and Malmer, N. 1992. Distribution of biomass along hummock–hollow gradients: a comparison between a North American and a Scandinavian peat bog. Acta Soc. Bot. Poloniae, **61**: 75–87.

Zoltai, S.C., Morrissey, L.A., Livingston, G.P., and de Groot, W.J. 1998. Effects of fires on carbon cycling in North American boreal peatlands. Environ. Rev. **6**: 13–24.