

Impact of global change and forest management on carbon sequestration in northern forested peatlands

Martin Lavoie, David Paré, and Yves Bergeron

Abstract: Northern peatlands occupy approximately 4% of the global land surface and store about 30% of the global soil carbon (C). A compilation of C accumulation rates in northern peatlands indicated a long-term average rate of C accumulation of $24.1 \text{ g m}^{-2} \text{ year}^{-1}$. However, several studies have indicated that on a short-time scale and given the proper conditions, these ecosystems can exhibit very high rates of C accumulation (up to $425 \text{ g m}^{-2} \text{ year}^{-1}$). Peatland development is related to precipitation and temperature, and climate change is expected to have an important impact on the C balance of this ecosystem. Given the expected climate change, we suggest that most of the northern forested peatlands located in areas where precipitation is expected to increase (eastern Canada, Alaska, FSU, and Fennoscandia) will continue to act as a C sink in the future. In contrast, forested peatlands of western and central Canada, where precipitation is predicted to decrease, should have a reduction in their C sequestration rates and (or) could become a C source. These trends could be affected by forest management in forested peatlands and by changes in fire cycles. Careful logging, as opposed to wildfire, will facilitate C sequestration in forested peatlands and boreal forest stands prone to paludification while silvicultural treatments (e.g., drainage, site preparation) recommended to increase site productivity will enhance C losses from the soil, but this loss could be compensated by an increase in C storage in tree biomass.

Key words: C sequestration, forested peatland, paludification, greenhouse gases, climate change, forest management.

Résumé : Les tourbières nordiques occupent approximativement 4 % de la surface terrestre et emmagasinent environ 30 % du carbone (C) qu'on retrouve dans le sol. Une revue sur les taux d'accumulation de C, dans les tourbières nordiques, indique que l'accumulation moyenne de C à long terme est de $24,1 \text{ g m}^{-2} \text{ a}^{-1}$. Cependant, plusieurs études ont démontré que sur une courte période de temps, et dans des conditions appropriées, ces écosystèmes peuvent montrer de hauts taux d'accumulation de C (jusqu'à $425 \text{ g m}^{-2} \text{ a}^{-1}$).

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Le développement des tourbières dépend des régimes de précipitation et de température, et les changements climatiques sont susceptibles d'avoir un effet important sur la balance du C dans cet écosystème. Selon les changements climatiques prévus, nous suggérerons que la plupart des tourbières boisées en milieu nordique, où des augmentations de précipitations sont prévues (est du Canada, Alaska, ex-URSS et Fenno Scandinavie), vont continuer à être des puits de C dans le futur. À l'opposé, dans les tourbières boisées de l'ouest et du centre du Canada où les précipitations doivent diminuer, il devrait y avoir une réduction du taux de séquestration de C et/ou ces tourbières deviendront une source de C. Ces tendances pourraient être affectées par l'aménagement forestier dans les tourbières boisées, ainsi que par les changements dans les cycles des feux. Contrairement au feu, la coupe facilite la séquestration du C dans les tourbières boisées et dans les sites sujets à la paludification, alors que les traitements sylvicoles (drainage, préparation de terrain), recommandés pour augmenter la productivité des sites augmentent les pertes de C par décomposition, mais cette perte pourrait être compensée par une augmentation de C dans la biomasse végétale.

Mots clés: séquestration du C, tourbière boisée, paludification, gaz à effet de serre, changements climatiques, aménagement forestier.

1. Introduction

It is generally accepted by most scientists that the Earth's climate is changing due to anthropogenic disturbances (IPCC 2001) although others suggest that global warming could be part of the natural cycling change (Klimanov and Sirin 1997; Stauffer et al. 1998). Among the important changes in the global climate, temperature and atmospheric CO₂ concentration increases have been measured and will likely go on increasing in the future. The atmospheric concentration of CO₂ has increased by 31% since 1750 and is expected to double by the end of the 21st century, reaching 720 ppm (parts per million) (IPCC 2001). The average global surface temperature has increased over the 20th century by about 0.6 °C and is expected to reach an average of 1.4–5.8 °C by 2100. It is also suggested that precipitation may have increased by 0.5% to 1% per decade in the 20th century over mid- and high latitudes of Northern Hemisphere continents.

The boreal forest represents one of the Earth's largest biome, encompassing an area of approximately 14×10^6 km². The boreal forest is one of the ecosystems most affected by global warming and amid the boreal forest (Bhatti et al. 2003), *Sphagnum*-dominated systems have the greatest peat accumulation potential due to the extremely low decomposition rate of *Sphagnum*. Since these ecosystems hold large quantities of carbon (C), their response to climate-induced or other changes (e.g., atmospheric deposition) could have important consequences (e.g., increase in C losses from peatlands) for the global C cycle. In addition to their role in sequestering C, forested peatlands and boreal forest stands prone to paludification located in eastern Canada (Lavoie et al. 2005), Sweden (Hånell 1991), and Finland (Nuutinen et al. 2000) will become in the near future an important source of wood supply due to a strong demand for wood products as well as an increasing pressure to set land aside for conservation purposes.

In the recent literature, important reviews on climate change and the boreal forest, including peatlands, have been published. Among them, Zoltai et al. (1998) reviewed the effects of fire on carbon cycling in North American boreal peatlands. Also, Moore et al. (1998) reviewed the uncertainties in predicting the effects of climate change on Canadian peatlands. Blodau (2002) has reviewed the processes and controls over the carbon cycle of peatlands. Finally, Saxe et al. (2000) reviewed the response of tree and forest functioning to global warming. Nevertheless, we consider that a review specific to forested peatlands and boreal forests prone to paludification with special regard to forest management was needed. This synthesis thus has three main objectives: (1) review the effects of changes in climate and in atmospheric CO₂ concentration, as well as of a change in the seasonal pattern and amount of precipitation on C sequestration in forested peatlands; (2) investigate the potential effects of forest management and climate change on C sequestration for boreal forest stands prone to paludification; and (3) identify the gaps in our knowledge and understanding, and suggest research needs to improve these

predictions. To fulfill these objectives, we will first describe the geographical and functional importance of peatlands located in the Northern Hemisphere. Second, we will briefly explain the ecology of peatlands in order to understand the effect of climate change on these ecosystems. Third, data on the current C pool and C and peat accumulation rates will be enumerated. Fourth, climate change scenarios will be illustrated followed by explanations on the effect of climate change (i.e., temperature, precipitation, and CO₂) on peatland ecology. We also discuss the importance of disturbances such as wildfire and clear-cuts on peatland succession and we will complete this synthesis by discussing the outlook for future C sequestration rates on northern forested peatlands under climate change.

2. Geographical and functional importance

2.1. Definitions and terminology

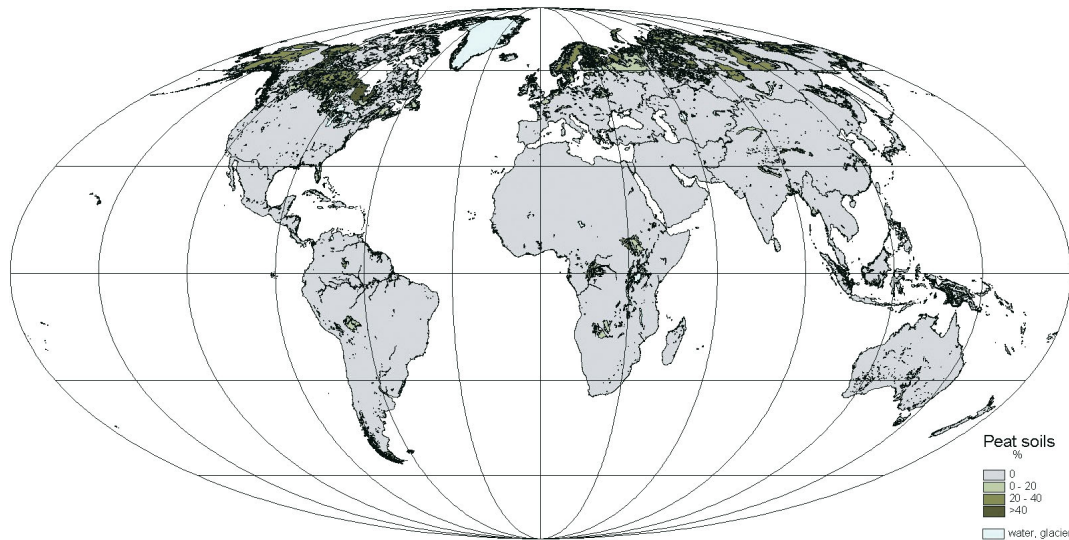
Wetlands can be subdivided into two broad categories: mineral and organic wetlands. Mineral wetlands are found in areas where an excess of water is present on the surface of the substratum and where little or no accumulation of organic matter is observed (National Wetlands Working Group 1997). Organic wetlands are more simply referred to as peatlands (synonym: mire, muskeg). In Canada, peatlands contain more than 40 cm (moderately or highly decomposed) or 60 cm (poorly decomposed) of peat accumulation on which organic soils develop. This depth limit is consistent with soil classification standards established by the Soil Classification Working Group (1998). However, in Fennoscandia, the depth limit is set at 30 cm (Pakarinen 1995). Peatlands are divided into five classes: bog, fen, swamp, marsh, and shallow water. However, for the purpose of this synthesis, only three classes will be considered: bog, fen, and swamp, which are recognized in North America as well as in Europe (Pakarinen 1995; National Wetlands Working Group 1997). For the benefit of this review, attention will also be paid to boreal forest ecosystems prone to paludification. These stands are characterized by external and internal processes suitable to peat initiation and accumulation, and also include upland sites vulnerable to *Sphagnum* lateral expansion from surrounding lowland sites.

Any peatland with a significant component of woody vegetation is named forested peatland. However, in the literature, the terms “forested, wooded, and treed” are used indistinctively to describe a bog, a peatland, or a wetland with a considerable component of woody vegetation. In only one publication, “forested” refers to bogs having more than 70% of tree cover (Halsey et al. 1997). These three words may in fact have a different meaning, which may lead to uncertainty and misinterpretation. For some, “forested” refers to dense mature trees, while “treed” is used to indicate a sparser density and generally smaller sized trees (Moore²). For others, “forested” refers to closed canopy, while “wooded” or “treed” is limited to open canopy (Jeglum 1991; Vitt et al. 2003b). Consequently, standard definitions for “wooded, forested, and treed” according to the surface area, basal area, or volume occupied by tree species must be provided given that it has a major impact on C sequestration calculation and forested peatland cover.

2.2. Distribution

To quantify the amount of C sequestered or lost under climate change, an accurate estimation of the surface area occupied by forested peatlands is essential. The current distribution and surface area of peatlands in the world is at this time not known with accuracy. There is much uncertainty underlying the C estimates for the peatland component because of the unknown degree of overlapping between forested peatland and forest inventories (Bhatti et al. 2003). With current estimates, wetlands represent 3.8% of the global land surface (Fig. 1) (Paavilainen and Päivänen 1995) with no clear distinction as to surface area occupied by open and forested peatlands or peatland classes. Boreal and subarctic peatlands are located mostly in the former Soviet Union (FSU), Canada, Alaska (USA), and Fennoscandia, with

²T. Moore. 2003. Personal communication.

Fig. 1. Approximate global peat distribution (Reprinted with permission from International Peat Society).**Table 1.** Northern peatland covers and carbon pools in peat.

	Northern Hemisphere	Canada	Quebec	Alaska	Finland	Sweden	Norway	FSU ^a
Area (Mha)								
Overall	345–525	105–170	8–12	50	10	6.5	3	165–275
Forested	NA ^b	18 ^c	3.8 ^c	41 ^c	4.4	1.8	NA	NA
Pools (Pg C)	455	103–184	13 ^d	72	13 ^d	8.7 ^d	4 ^d	215

^aFormer Soviet Union.

^bNot available.

^cForested wetlands (i.e., mineral and organic) according to Dahl and Zoltai (1997).

^dEstimated from Gorham (1991).

a total area ranging from 345 to 525 Mha (million hectares). The estimated cover of peatlands and forested peatlands for these regions are summarized in Table 1 (Van Hees 1990; Hånell 1991; Botch et al. 1995; Paavilainen and Päivänen 1995; Dahl and Zoltai 1997; Kobak et al. 1998; Nuutinen et al. 2000; Charman 2002; Conard et al. 2002). The cover of forested peatlands in the Northern Hemisphere remains uncertain due to a lack of information and of standard definitions. Thus, the area covered by forests susceptible to paludification is also unknown.

3. Ecology of peatlands

Most peatlands begin their existence as mineral peatland and turn into peatland over time. Peat initiation is controlled by allogenic (i.e., external to the ecosystem) and autogenic (i.e., internal to the ecosystem) factors that influence *Sphagnum* establishment and the hydrological balance at peat initiation. These factors are: climate, geomorphology (e.g., flat topography will facilitate peat initiation), geology and soils (e.g., heavy clay acts as an impermeable substrate that facilitates water accumulation), biogeography (e.g., area prone to peat initiation), natural disturbances (e.g., fire, insects), and human activities (e.g., forest management) (Kuhry et al. 1993; Halsey et al. 1997; Kobak et al. 1998; Payette 2001; Charman 2002; Crawford et al. 2003; Lavoie et al. 2005). Among these factors, climate is

probably the most important in determining whether there will likely be a surplus of water available for peat initiation. The precipitation–evaporation balance is critical here and a surplus can result from low precipitation – low temperature or high precipitation – high temperature regimes as well as high precipitation – low temperature conditions (Charman 2002). When these five main factors generate conditions promoting a surplus of water and the establishment of *Sphagnum*, it can result in two pathways of peat formation named terrestrialization and paludification (Payette 2001; Charman 2002; Lavoie et al. 2005). Terrestrialization is a process by which a shallow water body is gradually filled in with accumulated debris from organic and inorganic sources. This continues to a point where the water table is at or below the surface for at least some part of the year, and peat accumulates over the previously deposited limnic sediments. Paludification is defined as a key dynamic process of peatland expansion involving a gradual rise in the water table as peat accumulation exceeds drainage and *Sphagnum* spp. ground cover continues to grow and expand. Paludification is a much more important process than terrestrialization in terms of the proportion of peatland area that has developed (Payette 2001; Charman 2002).

The accumulation of peat is a function of the balance between the production of biomass by plants and decomposition both in the acrotelm and catotelm. The acrotelm is described as the active layer and is characterized by a variable water content and soil aeration, active microbial activity, and a high hydraulic conductivity. Below this layer is the catotelm, which is permanently anaerobic and saturated with water. Hydraulic conductivity is very low and there is also a very low biological activity and decomposition rate (Paavilainen and Päivänen 1995). Thus, the litter from each year goes through aerobic decay and is buried under the weight of younger material until eventually the main plant structure collapses. Consequently, C is sequestered over long periods of time by the submergence of organic matter at the base of the acrotelm.

4. Peat accumulation and soil C pool

Carbon and peat accumulation in peatlands is also influenced by allogenic (e.g., climate, human activities, hydrological changes, fire) and autogenic (e.g., growth, decomposition, accumulation, freeze–thaw cycle, water table) processes as well as by compaction and subsidence (Payette 2001; Charman 2002; Lavoie et al. 2005). The direct impact of climate change on forested peatlands is on (i) hydrology (e.g., warmer and drier climate will decrease the water table level); (ii) physical processes (e.g., warmer climate will increase permafrost degradation); (iii) peat accumulation rate (via soil temperature and moisture changes); and, to a lesser extent, on (iv) biotic changes (e.g., climate change can result in species migration); and (v) peatland morphology (i.e., peatland moisture balance can result in changes to the overall shape). As for C accumulation, it is the result of inputs from C sequestration from the atmosphere by primary production and by minor inputs from dissolved organic C (DOC) and inorganic C (DIC) as part of rainwater. Soil C is released to the atmosphere in the forms of CO₂ and CH₄ as a result of decomposer organisms activities. Also, fluxes of DOC, particulate organic C (POC), DIC, and dissolved gases leave the system in drainage water (Fig. 2) (Worrall et al. 2003).

To predict future C sequestration rates, it is necessary to know and understand the long-term average and actual rates of peat accumulation. These accumulation rates should preferably be associated with climatic factors (i.e., paleoecology) and environmental variables (e.g., peat moisture, vegetation composition) that control the initiation and development of peatland. There is much uncertainty underlying the C estimates for the forested peatland component because of (i) terminology and typology, (ii) the estimation of bulk density and C content, (iii) the continuum in space from mineral wetland to forested peatland, and (iv) the unknown degree of overlapping between forested peatlands and current forest inventories (Gorham 1991; Apps et al. 1993; Garnett et al. 2001; Bhatti et al. 2003). Recent studies have estimated that about 720 Pg (1 Pg = 10¹⁵ g) of C are stored in the boreal forest region, representing approximately 40% of the total amount of C stored in the terrestrial biosphere (Table 2) (Kasischke et al. 1995). Most of this large C pool (≈455 Pg) is contained in the soil of largely open peatlands (Tables 1 and 2) (Gorham 1991). The estimated sizes of peat C pools for North America, Fennoscandia,

Fig. 2. Overview of the global C system for a forested peatland and the dynamics (tendency) of accumulation and emission of greenhouse gases. Symbols: ↓, decreased emission; ↑, increased emission; WTL, water table level; DOC, dissolved organic carbon. (Illustration in Taylor et al. (2000), reprinted with permission from Northeast Science & Technology).

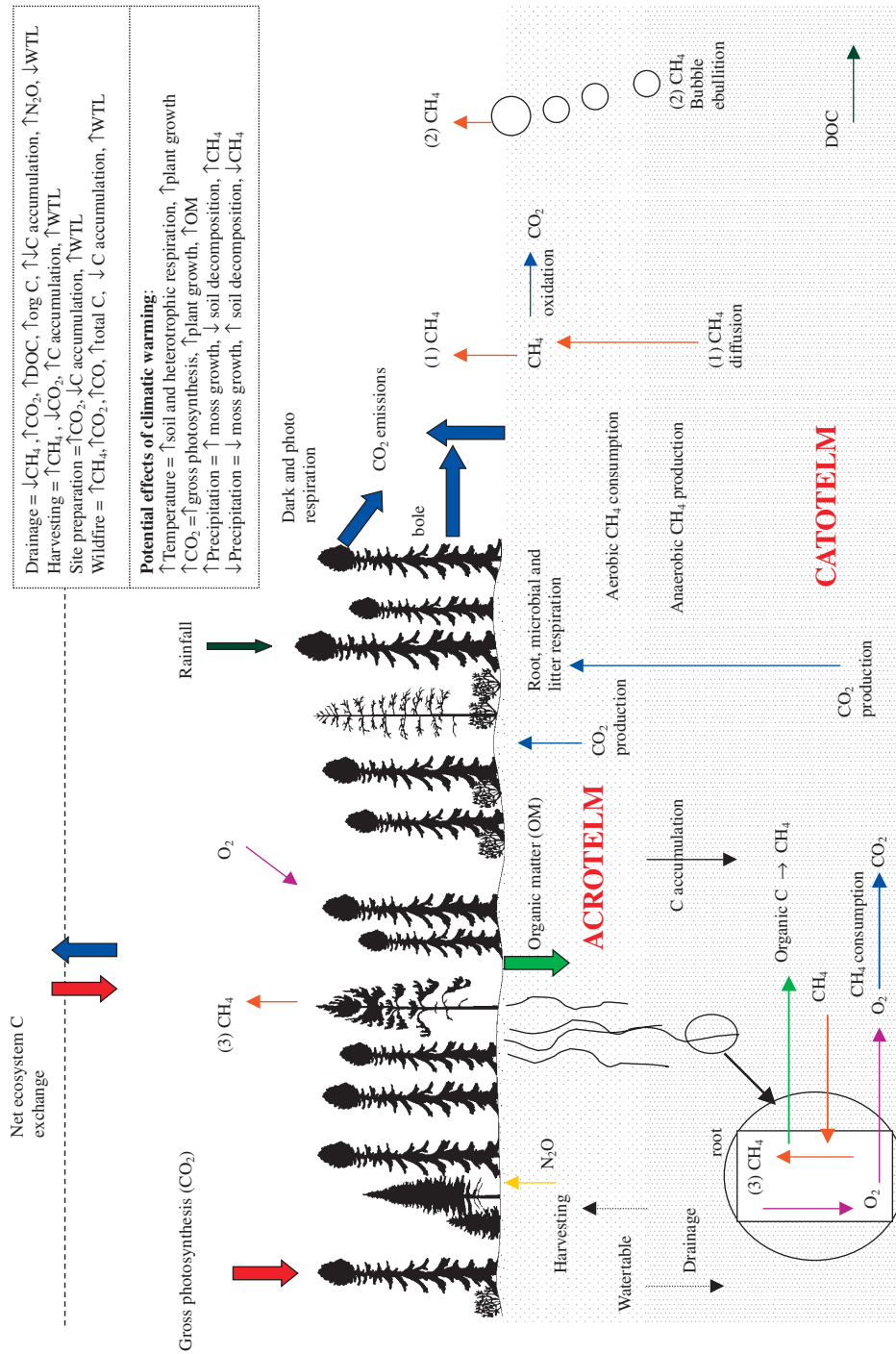


Table 2. Overview of C pools and fluxes in terrestrial systems.

	Boreal forests ^{a,b}	Boreal peatlands ^{b,c,d}	Native forests ^{a,e}	Global ^a
Area (Mha)	1370	346	4500 ^c	15 120
Pools (Pg C)				
Atmosphere	—	—	—	750
Plant biomass	88 ^f	6.9	360	470
Soil and litter	212	—	530	2 000
Peat	—	448.1 ^d	NA	NA
Total	300	455	890	3 220
Fluxes (Pg year ⁻¹)	0.6 ^g	0.07	-0.9	NA

Note: Source: Kasischke et al. 1995; Brown 1997; Gorham 1991; Clymo et al. 1998; IPCC 2000; Bhatti et al. 2003.

^aDown to a depth of 1 m.

^bCanada, Alaska, Russia, and Scandinavia.

^cOpen peatlands.

^dDown to a depth of 2.3 m.

^eTropical, temperate, and boreal forests.

^fIncludes forested peatlands.

^gFluxes represent net transfers from the atmosphere: positive = sink, negative = source; NA = not available.

and FSU are summarized in Table 1 (Ovenden 1990; Apps et al. 1993; Botch et al. 1995; Kobak et al. 1998; Halsey et al. 2000; Bhatti et al. 2003).

The long-term rate of C accumulation (LORCA) since the last glaciation might be estimated at 0.046 Pg year⁻¹ (455 Pg/10 000 year) for peatland soils. However, Gorham (1991) obtained an estimate of 0.096 Pg year⁻¹ for LORCA based on an average rate for 4600 years. On the other hand, C and peat accumulation rates may vary along the peat profile with changes in soil moisture and temperature, vegetation composition, thickness of peat, and microtopography (Lavoie et al. 2005). Moreover, the estimation of rates of C accumulation may vary according to the period of time that is considered (e.g., last 10 000 years, last 200 years, etc.), and whether it is measured by mass or height increment and what technique is used (e.g., ²¹⁰Pb versus ¹⁴C). A compilation of literature values (Table 3) illustrates that the C accumulation rate of peatland soil ranges from -7.6 up to 450 g m⁻² year⁻¹ (negative = C source), with a long-term average rate of 24.1 g m⁻² year⁻¹, and that peat accumulation rates range from 0.06 up to 3.8 mm year⁻¹, according to time span estimation and peatland types. A clear classification according to peatland types was not possible because in many references (see Table 3) peatland site description is very general or absent. In order to illustrate more clearly the C accumulation rate according to the time span that is used, we made nine classes ranging from current, short-term rates to long-term rates (Fig. 3). Figure 3 shows clearly that mean C accumulation rate decreases from 120 g m⁻² year⁻¹ for 50-year time span estimates to 24 g m⁻² year⁻¹ for LORCA estimates, and that the rate of average peat accumulation decreases from a maximum of 6 mm year⁻¹ (50-year time span estimation) to 0.5 mm year⁻¹ (time span estimation of 1000+ years). Figure 3 also illustrates that the variability is higher for shorter time span estimation. Thus, peat accumulation and long-term average rate of C accumulation are imperfect indicators of the current rate of C accumulation of a site. These indicators do not take into account (i) the effect of internal (e.g., variation in vegetation structure) and external (e.g., repeated peat fires, climate variation) processes; (ii) variations in bulk density and C content; and (iii) the declining rate of net accumulation in mature bog (Kobak et al. 1998; Vitt et al. 2000a). Although high spatial and temporal variability illustrates that peatlands can be a C sink or source, the current rate of C accumulation in northern peatlands has been estimated at about 0.07 Pg year⁻¹ (Gorham 1991; Clymo et al. 1998).

Thus, to predict future C sequestration rates, short-term variability in C and peat accumulation rates as illustrated in Fig. 3 and Table 3 will have to be better understood, and variables explaining this variability

Table 3. Carbon and peat accumulations in peatland sites in the Northern Hemisphere.

Site	Peatland type	C accumulation (g m ⁻² year ⁻¹)	Peat accumulation (mm year ⁻¹)	Comment	References
North-Central Finland	Aapa mire	8.0	0.2	LORCA ^a	Mäkilä et al. 2001
Northwestern Russia	Mire, bog, swamp, fen	11.4 to 50–75	0.15 to 1.0	LORCA	Kobak et al. 1998
Canada	Peatlands	10.0 to 35.0	0.1 to 1.0	LORCA	Ovenden 1990
Manitoba, Canada	Lagg – bog forest – muskeg	26.7; 18.8; 13.0 ^{b,c}	0.28; 0.41; 0.26	LORCA	Reader and Stewart 1972
North Dakota, USA	Peatlands	37.5 ^b	0.58	LORCA	Gorham et al. 2003
Minnesota, USA		21.0 to 38.4 ^{b,d}	0.41 to 0.79	LORCA	Gorham et al. 2003
Quebec, Canada		21.9 to 28.2 ^{b,d}	0.59 to 0.83	LORCA	Gorham et al. 2003
Maine, USA		21.9 to 30.0 ^{b,d}	0.47 to 0.56	LORCA	Gorham et al. 2003
New Brunswick, Canada		22.1 to 32.5 ^{b,d}	0.49 to 0.79	LORCA	Gorham et al. 2003
Nova Scotia, Canada		17.0 to 19.4 ^{b,d}	0.40 to 0.48	LORCA	Gorham et al. 2003
Newfoundland, Canada		18.9 to 41.2 ^{b,d}	0.39 to 1.05	LORCA	Gorham et al. 2003
Alaska, USA		8.1 to 16.1 ^{b,d}	0.18 to 0.38	LORCA	Gorham et al. 2003
Finland	Sedge – <i>Sphagnum</i>	4–13 to 6.7–21.2 ^b	0.18 to 1.36	LORCA	Tolonen et al. 1992
Sweden	Bog	42.6 ^c	0.83 ^c	LORCA	Belyea and Malmer 2004
Siberia, Russia	Bog, fen	19.0 to 69.0	0.35 to 1.13	LORCA	Borren et al. 2004
Alaska, USA		7.0 to 41.0		LORCA	Billings 1987
Yukon – Manitoba, Canada	Peatlands	11.0–35.0		LORCA	Tarnocai 1988 ^f
Canada	Subarctic	9.0 – 23.0		LORCA	Tarnocai 1988 ^f
Alaska, USA		7.0 – 41.0		LORCA	Tarnocai 1988 ^f
Southern Finland		6.0 to 34.0 ^b		LORCA	Tolonen 1979 ^e , 1987 ^f
Boreal		23.0 to 29.0		LORCA	Gorham 1991
Monts du Forez, France		5.7 – 7.8 ^b		LORCA	Francez 1991
Former Soviet Union	Mire, bog, fen, marsh	12.0 to 80.0		LORCA	Botch et al. 1995
Finland, Estonia, Maine	Peatlands	4.6 to 85.8		LORCA	Korhola et al. 1995
Western Canada	Bogs (9)	11.0 to 32.0		LORCA	Kuhry and Vitt 1996
Northwestern Ontario	Bog	34.0 ^b		LORCA	Belyea and Warner 1996
Finland	Bog	16.7 – 22.3		LORCA	Mäkilä 1997
Finland	Bogs (10)	13.7 to 35.2		LORCA	Tolonen and Turunen 1996
Southern Sweden	Bog	40.0		LORCA	Malmer et al. 1997

Table 3. Continued.

Site	Peatland type	C accumulation (g m ⁻² year ⁻¹)	Peat accumulation (mm year ⁻¹)	Comment	References
Finland	Fens (4)	9.6 to 24.9		LORCA	Tolonen and Turunen 1996
Northern peatland	Bog; fen	18.6; 16.0 ^b		LORCA	Frolking et al. 2001
Finland	Bog; fen	17.0 to 26.0		LORCA	Minkkinen et al. 1999
Finland	Bog; fen	12.4 – 37.2 ^{b,h}		LORCA	Clymo et al. 1998
Maine, USA	Bog; fen	10.3 – 13.4 ^b		LORCA	Tolonen et al. 1992
Southern Sweden	Bog	20.7 to 25.9 ^b		LORCA	Mattson and Kouller-Anderson 1954 ^g
England	Bog	24–36; 67–106 ^{b,i}		LORCA	Jones and Gore 1978 ^g
Finland	Fen	18.6 – 14.0 ^{b,j}		LORCA	Turunen and Tolonen 1996 ^k
Western Canada	Bogs (15)	31.5		LORCA	Yu et al. 2003 ^b
Eastern Canada	Small, medium, large is- lands	5.1 to 34.6		LORCA	Turunen et al. 2004
Sweden		6.4, 16.2, 27.3		LORCA	Wårdle et al. 2003
Alaska, USA	Bog		0.48	LORCA	Heinselman 1961 ^l
Washington, USA	Bog		0.52 to 0.62	LORCA	Rigg and Gould 1957
Western Canada	Peatland complex		0.37 to 0.94 ^m	LORCA	Bauer et al. 2003
Canada	Subarctic; Boreal		0.31 – 0.54	LORCA	Gorham 1991
Southern Sweden and Northern Germany			0.70	LORCA	Gorham 1991
Southern and Central Fin- land			0.75	LORCA	Gorham 1991
Northern Europe			0.6	LORCA	Gorham 1991
Boreal FSU			0.6 – 0.8	LORCA	Gorham 1991
Siberia Palsa Province			0.2 – 0.4	LORCA	Gorham 1991
Eurasia			0.52	LORCA	Gorham 1991
Alaska, USA	Bog		0.157 to 0.293	LORCA	Hansen and Engstrom 1996
Alaska, USA	Bog		1.4; 0.45	LORCA	Heinselman 1970
Northwestern Russia	Bogs (2)	9.0; 18.0		0–3160; 3160– 10310 year	Kobak et al. 1998
Northwestern Russia		17.0; 43.0		0–2500 year	Kobak et al. 1998
Northwestern Russia		27.0; 45.0		2500–4900 year 4900–7800 year	Kobak et al. 1998

Table 3. Continued.

Site	Peatland type	C accumulation (g m ⁻² year ⁻¹)	Peat accumulation (mm year ⁻¹)	Comment	References
Northwestern Russia		34.5; 45.0		7800–9000 year	Kobak et al. 1998
Western Canada	Fen	25.0 ^b		0–4000 year	Yu et al. 2003a
Western Canada	Fen	41.4 to 248.2 ^b	0.5	4000–8000 year (3 peaks)	Yu et al. 2003a
Western Canada	Fen	100; 140; 190; 270		0–8000 year (4 peaks)	Yu et al. 2003b
Newfoundland, Canada	Bog	17.8 ⁿ		0–7830 year	Damman 1988
Russia	Bog	7.4 to 17.2		0–6500 year	Borren and Bleuten 2004
Peatland, unknown	Peatland		0.80–0.16	0–6500 year	Aaby and Tauber 1975
Buffalo Narrows, Alberta	Bog	14.1; 10.2; 11.8	0.35; 0.12; 0.16	0–2480; 2480–5230; 5230–7870 year	Kuhry 1994
Legend Lake, Alberta	Bog	12.9; 6.1; 5.0	0.5; 0.1; 0.06	0–1180; 1180–4340; 4340–7950 year	Kuhry 1994
Slave Lake, Alberta	Bog	18.1; 21.5; 37.1	0.44; 0.36; 0.5	0–2830; 2830–6430; 6430–8240 year	Kuhry 1994
Zama, Saskatchewan	Bog	16.5; 18.5	0.45; 0.3	0–1990; 1990–6490 year	Kuhry 1994
Wathaman, Saskatchewan	Bog	25.6; 20.0	0.98; 0.47	0–1390; 1390–4380 year	Kuhry 1994
La Ronge, Saskatchewan	Bog	17.5	0.42	0–3710 year	Kuhry 1994
Beauval, Saskatchewan	Bog	24.1	0.59	0–2790 year	Kuhry 1994
Gypsumville, Manitoba	Bog	28.7	0.82	0–1790 year	Kuhry 1994
Canada	Fen	19.0; 20.0; 22.0 ^b	0.43; 0.52; 0.54	0–2350; 2350–3500; 3500–6600 year	Zoltai and Johnson 1985
Canada	Edge	23.0; 23.0; 24.0 ^b	0.60; 0.69; 0.54	0–2260; 2260–3500; 3500–6600 year	Zoltai and Johnson 1985
Canada	Island	16.0; 19.0; 29.9 ^b	0.49; 0.43; 0.58	0–2350; 2350–3500; 3500–6600 year	Zoltai and Johnson 1985
Newfoundland, Canada	Bog	11.6; 25.4; 18.3; 18.5 ⁿ		0–2065; 2065– 3375; 3375–5063; 5063–7830 year	Damman 1988

Table 3. Continued.

Site	Peatland type	C accumulation (g m ⁻² year ⁻¹)	Peat accumulation (mm year ⁻¹)	Comment	References
Northern Eurasia	Peatlands (21)		0.07 to 1.1	0–2600 year	Klimanov and Sirin 1997
Saskatchewan, Canada	Treed dry bog	18.7	0.56	0–1870 year	Kuhry 1997
Saskatchewan, Canada	Treed moist bog	35.2	0.66	1870–2790 year	Kuhry 1997
Saskatchewan, Canada	Total bog	24.1	0.59	0–2790 year	Kuhry 1997
Saskatchewan, Canada	Treed fen	45.0	1.15	2790–3260 year	Kuhry 1997
Saskatchewan, Canada	Total peatland	27.1	0.67	0–3260 year	Kuhry 1997
Saskatchewan, Canada	Pond with fen	49.6	0.85	3260–4330 year	Kuhry 1997
Saskatchewan, Canada	Pond with marsh	80.3	1.8	4330–4890 year	Kuhry 1997
Saskatchewan, Canada	Total pond	60.1	1.18	3260–4890 year	Kuhry 1997
Saskatchewan, Canada	Total wetland	38.1	0.84	0–4890 year	Kuhry 1997
Muskiki Lake, Alberta	Fen	48.6; 37.8; 32.4 ⁿ	0.68; 0.41; 0.34	2760–3670; 3670–7080; 7080–8084 year	Kubiw et al. 1989
Muskiki Lake, Alberta	Fen	37.8; 48.6; 37.8 ⁿ	0.66; 0.67; 0.34	3300–4600; 4600–6320; 6320–7850 year	Kubiw et al. 1989
Muskiki Lake, Alberta	Fen	48.6; 27; 43.2; 81 ⁿ	0.57; 0.37; 0.51; 0.79	2800–4910; 4910–6260; 6260–7530; 7530–9000 year	Kubiw et al. 1989
Marguerite Lake, Alberta	Fen	32.4 ⁿ	0.57	1810–2750 year	Kubiw et al. 1989
Marguerite Lake, Alberta	Fen	43.2 ⁿ	0.79	2670–3400 year	Kubiw et al. 1989
Western Siberia	Bog		0.3 to 1.9	1500–9500 year	Glebov et al. 2002
Southern Finland	Bog	30.1 to 9.6 ⁿ	1.13 to 0.18	200–7690 year	Tolonen 1979 ^g , 1987 ^f
Eastern Finland	Bog		0.1 to 0.15	6300–10000 year	Pitkänen et al. 2002
Western European Russia	Bog		1.3	1400–2000 year	Klimenko et al. 2001
Ontario, Canada	Swamp forest stage	0.04 – 0.07		<2000 year	Glaser et al. 2004
Ontario, Canada	Forested bog stage	0.08 – 1.0		<2000 year	Glaser et al. 2004
Ontario, Canada	Non-forested bog stage	0.04 – 0.05		<2000 year	Glaser et al. 2004
Western Canada	Boreal peatlands	292.6 ^b		<1500 year	Zoltai 1991
Western Canada	Subarctic peatlands	171.2 ^b		<1500 year	Zoltai 1991
Northwestern Canada	Northern peatlands	13.2	0.28	<1200 year	Robinson and Moore 1999

Table 3. Continued.

Site	Peatland type	C accumulation (g m ⁻² year ⁻¹)	Peat accumulation (mm year ⁻¹)	Comment	References
Canada	Northern peatlands	19.0; 24.0; 13.0	0.57; 0.68; 0.28 ^o	<1200 year	Robinson and Moore 2000
Canada	Peat plateau	22.0	0.57	<1200 year	Robinson and Moore 2000
Central Sweden	Bog		0.09 – 1.1	<1000 year	Foster and Wright 1990
Western Canada	Peatlands	19.4		<1000 year	Vitt et al. 2000a, 2000b
Southern Sweden	Bog	82.2; 89.7; 55.3 ^{b,p}		<1000 year	Malmer and Wallén 1999
Sweden	Bog (hummock)	8.2 to 52.3 ⁿ	0.15 to 1.0	<1000 year	Malmer and Wallén 1993 ^q
Quebec, Canada	Forested peatland	30.0 ^b		<700 year	Lecomte et al. ³
Norway	Bog		6.6 to 1.8 ^r	0–250 year	Jensen 1997
Sweden	Bog		4.9 to 2.0 ^r	0–250 year	Jensen 1997
Sweden	Bog		12.0 to 2.2 ^r	0–250 year	Jensen 1997
Norway	Bog		7.7 to 1.1 ^r	0–250 year	Jensen 1997
Sweden	Bog		7.9 to 2.8 ^r	0–250 year	Jensen 1997
Norway	Bog		3.8 to 1.5 ^r	0–250 year	Jensen 1997
Manitoba, Canada	Boreal permafrost peat-land	26.0 – 144.2 ^b		81 to 124 year	Camill et al. 2001
Manitoba, Canada	Boreal permafrost peat-land	114.3 – 196.5 ^b		173 to 200 year	Camill et al. 2001
Alaska, USA	Bog		2.5–3.8	<185 year	Heilman 1968
Norway	Bogs	100.0	1	50–200 year	Ohlson and Okland 1998
Eastern Canada	Bogs	40.0 to 117.0		Over the past 150 years	Turunen et al. 2004
USA	Temperate bog, swamp	13.6; 11.0; 8.0	4.5; 3.1; 2.2	Over 50- and 100-year period	Wieder et al. 1994
Scotland	Bog		3; 2.0	Over 50- and 100-year period	Clymo et al. 1990 ^s
Finland	Bog		5.4; 3.8	Over 50- and 100-year period	El-Daoushy et al. 1982
Northern Alberta, Canada	Permafrost bog	75.0–61.0 ^b	1.9; 1.3	Over 50- and 100-year period	Turetsky et al. 2000
Northern Alberta, Canada	Bog	79.0 – 58.0 ^b	4.0; 2.6	Over 50- and 100-year period	Turetsky et al. 2000

Table 3. Continued.

Site	Peatland type	C accumulation (g m ⁻² year ⁻¹)	Peat accumulation (mm year ⁻¹)	Comment	References
Northern Alberta, Canada	Internal lawn	119.0 – 95.0 ^b	3.8; 2.6	Over 50- and 100-year period	Turetsky et al. 2000
Central Alberta, Canada	Bog	87.0–57.0 ^b	4.1	Over 50- and 100-year period	Turetsky et al. 2000
Scotland	Bogs (3)		1.15; 0.8	Over 50- and 100-year period	Oldfield et al. 1995
Manitoba, Canada	Boreal permafrost peatland	184.0		Over 100-year period	Camill 1999
Northwestern Ontario	Bog		9.2 – 2.9	Over 50-year period	Belyea and Warner 1994
Norway	Bogs	450.0 to 25.0	3.0 to 28.0	0–50 years	Ohlson and Okland 1998
Finland	Fen	–7.0		Current year	Aurela et al. 2002
Sweden	Bog	2.0; –7.6		0–1 year	Waddington and Roulet 2000
Manitoba, Canada	Fen	28.8		Current year	Raphalee et al. 1998
Manitoba, Canada	Bog	46.0 to 17.0		Current year; 13 to >90 year	Raphalee et al. 1998
Manitoba, Canada	Bog	21.7 to 13.6		Current year; 13 to >90 year	Raphalee et al. 1998
Finland	Bogs (10)	8.1 to 23.0		Current rate accumulation	Tolonen and Turunen 1996
Alberta, Canada	Bog	34.0 – 52.0		Current rate accumulation	Wieder 2001
Finland	Fens (4)	10.7 to 17.0		Current rate accumulation	Tolonen and Turunen 1996
Finland	Fen	32.0–35.0 to 73.0		Current rate accumulation	Alm et al. 1997
Western Canada	Boreal peatland	14.3 ⁿ		Current rate accumulation	Yu et al. 2001
Manitoba, Canada	Boreal permafrost peatland	11.4; 5.1 ^b		Current rate accumulation	Camill et al. 2001
Finland	Boreal peatland	30.0 ^{b,h}		Current rate accumulation	Clymo et al. 1998

Table 3. Concluded.

Site	Peatland type	C accumulation (g m ⁻² year ⁻¹)	Peat accumulation (mm year ⁻¹)	Comment	References
Russia	Peatlands	20.0 to 100.0		Current rate accumulation	Kobak et al. 1998
Alberta, Canada	Fens; bogs; marshes	83.0; 67.0; 50.0		Current rate accumulation	Thormann et al. 1999
Russia	Bog	7.0		Current rate accumulation	Borren and Bleuten 2004

^aLong-term average rate of C accumulation.

^b51.7% C content of dry mass (Gorham 1991).

^cData transformed from the original (organic matter production in g m⁻² year⁻¹) to g m⁻² year⁻¹ of C.

^dTwo to five cores.

^eC accumulation range from 14.0 to 72.0 g m⁻² year⁻¹. Peat accumulation range from 0.37 to 6.3 mm year⁻¹.

^fData reported in Bozkurt et al. 2001.

^gBased on their Fig. 15.

^hTwo sites.

ⁱOceanic to Continental gradient.

^jData reported in Francez 2000.

^kData reported in Reader and Stewart 1972.

^l18 cores.

^m54.5% C content of dry mass.

ⁿTransects: peat plateau-transition zone-bog.

^oHummocks; hummocks; lawns.

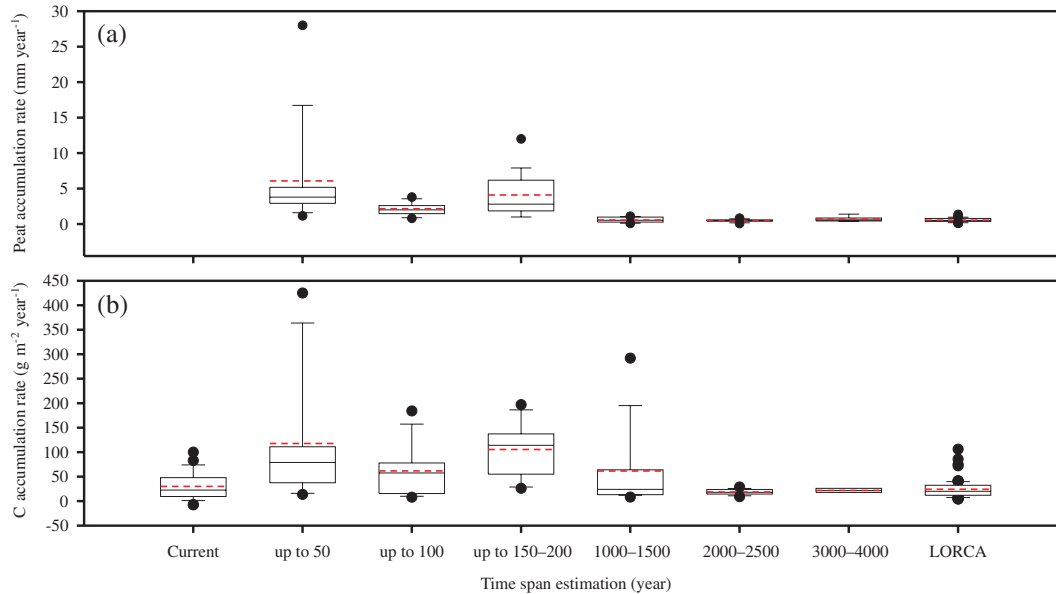
^pData reported in Ohlson and Okland 1998.

^qEstimates.

^rData reported in Turetsky et al. 2000.

^sData reported in Botch et al. 1995.

Fig. 3. (a) Peat (mm year^{-1}) and (b) C ($\text{g m}^{-2} \text{year}^{-1}$) accumulation rates in northern forested peatlands according to the varying lengths of time used for the calculation. The central crossbar represents the median; the vertical boxes, the 25th and 75th percentile; the lower and upper bars, the 10th and 90th percentiles. Dashed line, mean; solid line, median.



will have to be underlined. Currently, most of the observation data are taken from open or sparsely treed bogs and fens and very few studies have paid attention to forested peatlands (and forest stands with organic soil) or boreal stands prone to paludification. Mainly, these studies have paid attention to long-term peat and C accumulation rates and very few have estimated short-term accumulation rates (see Table 3). Previously, it was assumed that accumulation rates were linear. Nowadays, it is well recognized that peat and C accumulation rates vary with time and that different factors influence these accumulation rates. Climate is reported as one of the most important external factors explaining variability in peat and C accumulation rates. Different paleoecological methods allow to associate climate change to peat and C accumulation rates. However, the effects of temperature and precipitation on these rates are still not totally understood. Currently, all combinations between precipitation and temperature regimes seem to be favourable to peat accumulation. For example, Gorham et al. (2003) suggest that accumulation of peat in North American peatlands is favoured by dry conditions, while for peatlands located in Canada, Frolking et al. (2001) and Yu et al. (2003a) suggested respectively that warmer and wetter, and wetter and cold-warm to warm conditions are more conducive to peat accumulation. Moreover, for European mires, peat accumulation rate is reported to be favoured by cold and wet conditions (Klimanov and Sirin 1997; Belyea and Malmer 2004), while in Russia, Kobak et al. (1998) report that the rate of peat accumulation was higher during warm and wet periods. These differences in peat accumulation rate between northern Europe and North America were also related to the climate type, which is more continental in North America as opposed to being more maritime in northern Europe (Ovenden 1990). However, the influence of climate was also observed within Canada, where LORCA decreased from the west coast (oceanic) towards the east (continental) (Ovenden 1990; Zoltai 1991).

This high variability in short-term rate of peat accumulation cannot be related only to climate. Peat and C accumulation depends on a whole range of variables such as atmospheric deposition, topography, and internal factors (i.e., peatland type, species composition, evapotranspiration, substrate, surficial geology, groundwater flow and chemistry, peat fires, snow cover, permafrost), which are all reported

to affect net primary production (NPP) and decomposition rate (see section 6). The effect of each of these factors on NPP, decomposition and accumulation rates varies for each peatland site. However, it seems that changes in decomposition rate would affect more importantly peat and C accumulation rates (Clymo 1965, 1984; Malmer et al. 1997; Thormann et al. 1999; Frohking et al. 2001; Belyea and Malmer 2004).

Permafrost and wildfire, which are also affected by climate, are two important variables that can influence peat accumulation on short- and long-term perspectives. It is reported that C and peat accumulation decrease with permafrost maturity and the number of ground fires (Robinson and Moore 2000; Vitt et al. 2000b). In contrast, peat accumulation rate was also reported to increase following permafrost thaw (Camill et al. 2001). As for fire, Kuhry (1994) reports for western Canada that fire did not influence the long-term vegetation development of *Sphagnum*-dominated boreal peatlands. Vegetation response such as species composition changes in moss cover, if any, is generally limited to a few decades after the fire event. However, the influence of fire on peat accumulation rate could be more important on forested peatlands and boreal forest stands prone to paludification. Lecomte et al.³ reported that fire interval and fire severity have an important impact on the rate of accumulation of organic matter and the partition of the biomass between the trees and the soil.

Part of the accumulation rate variability could also be explained by the presence of trees. Lecomte et al.³ have shown that in paludified forests the organic carbon in young stands is mainly contained in the tree biomass but as succession proceeds the forest floor progressively becomes the main C reservoir. In Finland, Tolonen and Turunen (1996) have reported that C accumulation in the forest floor was higher in bog than in fen and higher in treeless fens and pine fens than in treed spruce-birch fens. This partition of biomass may be affected by climate change. Finally, a study by Minkinen et al. (1999) showed an important increase in tree biomass after drainage. Thus, dryer climate in northern Europe could result in higher organic matter decomposition but could largely be compensated for by C accumulation in tree biomass.

Long-term and current peat or C accumulation rates can be estimated with peat cores but modelling is needed to predict forested peatland responses to forest management, natural disturbances, and global warming. In peatland ecology, several studies have used Clymo's model to investigate rates of peat accumulation in different regions (Clymo et al. 1998; Charman 2002), but a new generation of models incorporating more variables has been developed (Clymo 1984; Korhola et al. 1996; Hilbert et al. 2000; Frohking et al. 2001; Yu et al. 2001). However, those models are still in development and still need improvement, and cannot be generally applied to the Northern Hemisphere.

Most studies have concentrated on processes occurring within the surface layer (0–0.5 m) and there are very few measurements of factors that affect the decay of deep peat (0.5–10 m) where most of the C is contained (Thomas and Pearce 2004). It is important to understand the processes involved in the preservation and accumulation of deep peat to predict future changes in net sequestration of C (Thomas and Pearce 2004). Moreover, spatial variation in the rate of C exchange between peatlands and the atmosphere is very high and this variation should be included in future models. Furthermore, data such as estimation of aboveground and belowground productivity for vascular and non-vascular plants need important improvement in order to be included in the models. Preferably, these models should (i) be applicable to all peatland classes from all regions of the Northern Hemisphere, (ii) be dynamic (as it includes both production and decay), (iii) include autogenic as well as allogenic factors, and (iv) be applicable to short-term as well as long-term predictions.

³N. Lecomte, M. Simard, N. Fenton, and Y. Bergeron. In review. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Quebec, Canada. *Ecosystems*.

5. Global change scenarios

Global atmospheric CO₂ increased from 280 ppm in 1750 to 367 ppm in 1999 and is expected to double by the end of 21st century reaching 720 ppm (IPCC 2001). During the past 250 years, the atmospheric concentration of CO₂, CH₄, and N₂O has increased by 31%, 150%, and 16%, respectively (IPCC 2001). These increases have led to modification in temperature and precipitation during the past years and future increases will potentially result in larger changes in temperature and precipitation.

Regional changes in temperature and precipitation are difficult to predict and uncertainty in modelling is relatively high (IPCC 2001). Temperature is predicted to increase by an average of 1.4–5.8 °C by 2100, but temperature increase in the Northern Hemisphere is predicted to be more than 40% higher than this (IPCC 2001). According to IPCC (2001), temperature increases are expected for Alaska, North America, Fennoscandia, and FSU. For Finland, predicted annual temperature increase reported by Karjalainen et al. (2003) is 2.5 °C between 1990 and 2050, and that reported by Jylhä et al. (2004) is 1–7 °C between 1990 and 2080. In Canada, summer temperature is expected to increase by 5 °C for western Canada (Amiro et al. 2001), and by 1–5 °C for eastern Canada (Flannigan et al. 1998; Peng et al. 2002). For FSU, Klimanov and Sirin (1997) have suggested that current warming was within the range of previous warming and may be part of natural cycling. If this warming really is part of natural cycling, cooling is expected in the 21st century.

Changes in precipitation are more difficult to forecast, but several models suggest regional changes in summer and winter precipitation of ±20% for the boreal region (Bhatti et al. 2003). According to IPCC (2001), increase in precipitation all year round are expected for Alaska and FSU, while precipitation increases are expected only in winter for Fennoscandia and eastern North America. On the other hand, other studies report that growing season precipitation will decrease by 10% to 20% for western and central Canada (Amiro et al. 2001; Peng et al. 2002), increase by 20% in eastern Canada (Flannigan et al. 1998), while parts of Fennoscandia will experience an increase in annual precipitation of 5% to 15% (Karjalainen et al. 2003). Jylhä et al. (2004) report for Finland that annual mean precipitation is projected to increase 0%–40% by 2080. These studies expose the difficulty in predicting future precipitation changes and clearly demonstrate the numerous uncertainties of regional climate scenarios.

There are numerous models that provide a range of climate change scenarios but most of them still suffer from many limitations. All the models predict significant change, but they differ in the details. In general, climate and vegetation models tend to agree more on broad regional patterns than on details at the local scale. Therefore, results from these models should be taken as indicative, but not as conclusive. Also, annual variation in temperature and precipitation is important to predict C sequestration, but spatial (latitude and longitude, altitude) and temporal (day and night; summer and winter; throughout the season, length of the growing season) variability must also be taken into account. Moreover, the effect of temperature and precipitation variations on evapotranspiration should be seriously evaluated since the ratio precipitation/evapotranspiration (ratio > 1) is a good indicator of peat accumulation (Hånell 1991; Gignac and Vitt 1994; Payette 2001). Finally, for the purpose of this paper, we will consider only one temperature scenario (i.e., increase in temperature) and two precipitation scenarios (i.e., decrease and increase).

6. Effect of global change on forested peatland dynamic, structure, and composition

Forested peatland net C sequestration is affected by changes in net primary production (NPP) (section 6.1), organic matter decomposition (section 6.2), species migration and permafrost (section 6.4.), wildfire (section 7.1), and anthropogenic disturbances (sections 7.2 and 7.3) (Fig. 2). In the following section, the influence of temperature and CO₂ increases as well as seasonal changes in precipitation on NPP and organic matter decomposition will be reviewed.

The processes of photosynthesis, respiration, and decomposition are the links between C in the atmosphere and C in terrestrial ecosystems. Plants remove CO₂ from the atmosphere through the process of photosynthesis, which results in the production of living plant tissue. Carbon is lost (DOC, POC, DIC) and also returned to the atmosphere (CO₂ – CH₄) through plant respiration and decomposition of dead organic matter in the soil (Fig. 2). Any change in the global balance between photosynthesis and respiration and (or) decomposition will alter the amount of C that is sequestered in or released by forested peatlands and boreal forest stands prone to paludification.

6.1. Net primary production

Although difficult to estimate precisely, productivity of wetlands and peatlands has been looked at in many studies (Charman 2002). Productivity is affected by light and nutrient availability, as well as by soil temperature, moisture, and aeration. The spatial and temporal variances in NPP are relatively large (Blodau 2002). For marshes and swamps, aboveground productivity ranges from 125 to 2590 g m⁻² year⁻¹, while belowground productivity ranges from 150 to 1800 g m⁻² year⁻¹ (Charman 2002). In bog and wet tundra, aboveground productivity ranges from 40 to 1400 g m⁻² year⁻¹, while belowground productivity ranges from 60 to 1460 g m⁻² year⁻¹ (Thormann et al. 1999; Vitt et al. 2000a; Blodau 2002; Charman 2002; Lecomte et al.³). *Sphagnum* mosses and, to a lesser extent, feathermosses (mainly *Pleurozium schreberi*) are significant contributors (30%–50%) to the total primary productivity in many forested peatlands (Bond-Lamberty et al. 2004; see also Table 4). Aboveground productivity of bryophytes ranges from 5 to 1660 g m⁻² year⁻¹ (Charman 2002; Bond-Lamberty et al. 2004). *Sphagnum*, which has a key role in controlling peat accumulation, has a wide distribution and the maximum abundance occurs between 630 and 1300 mm of annual precipitation and between –2 and 6 °C of mean annual air temperature (Gajewski et al. 2001). *Sphagnum* growth and production are highly variable in the Northern Hemisphere (Table 4). Height growth can vary from less than 1 to up to 60 mm year⁻¹, while *Sphagnum* production ranges from 3 to 414 g m⁻² year⁻¹. The variability is influenced by water table level, mean temperature, light availability, peat characteristics and species (Lavoie et al. 2005).

Carbon dioxide fertilization can increase tree growth of some species, partly because of higher photosynthesis rates and greater nutrient and water-use efficiency (Moore 1996; Bhatti et al. 2003). Carbon dioxide fertilization allows trees to remove more C from the atmosphere. However, any direct effect of CO₂ fertilization on tree growth may not be apparent because of nutrient limitation, low pH, and excess of moisture, especially in bogs as opposed to fens (medium to rich). Moreover, tree and soil respiration must be taken into account before concluding to an increase in C sequestration following CO₂ fertilization (Moore 1996). Results of CO₂ fertilization on *Sphagnum* growth are inconclusive. Increase (Jauhiainen et al. 1998; Heijmans et al. 2001), decrease (Heijmans et al. 2002), and no significant effect (Berendse et al. 2001; Hoosbeek et al. 2001) have been reported.

Increase in temperature can enhance tree growth because of higher photosynthesis, longer daily and seasonal growing period, and higher soil nutrient availability (see also section 6.2) (Saxe et al. 2000). Higher temperature will increase evapotranspiration and evaporation and therefore decrease the water-table level. Consequently, it can result in an increase in organic matter decomposition and in a reduction in *Sphagnum* growth. But, the effects of increased temperature on trees and *Sphagnum* mosses also depend on the modifications in the precipitation regime.

Changes in the amount of precipitation in forested peatland will directly influence the water-table level and tree and moss species. Dry period combined with higher temperature can result in an extended period of deep drawdown of the water-table (Lafleur et al. 2005). A reduction in precipitation can increase tree growth because of better root and soil aeration, but it can also have a significant impact on NPP by reducing the photosynthesis of mosses (Griffis et al. 2003). In contrast, increased precipitation can reduce tree productivity and enhance *Sphagnum* growth, which can indirectly affect tree growth by seedling engulfment and by reducing soil nutrient availability. Since *Sphagnum* has a tendency to

Table 4. Growth and primary productivity of moss species.

Species and location	Growth (mm year ⁻¹)	C production (g m ⁻² year ⁻¹)	References
<i>Sphagnum angustifolium</i>			
Norway (south)	14.7	250	Pedersen 1975
Quebec, Canada	4–17	15–64 ^a	Moore 1989
Finland	20–60	80–200	Lindholm and Vasander 1990
Ontario, Canada	20–39	49–99	Rocheffort et al. 1990
<i>Sphagnum magellanicum</i>			
England	1.4–1.49	35 ^a	Forrest and Smith 1975
Norway (south)	10	35	Pedersen 1975
Minnesota, USA	36	155 ^a	Grigal 1985
Sweden	16–22	NA	Wallén et al. 1988
Finland	8–20	105–115	Lindholm and Vasander 1990
Ontario, Canada	11–34	26–120	Rocheffort et al. 1990
France	42	126–174	Francez 1992
Italy	34–41	74–86 ^a	Gerdol 1995
Minnesota, USA	NA	2.7–3.8–6.5 ^{a,b}	Weltzin et al. 2001
<i>Sphagnum capillifolium</i>			
Quebec, Canada	9	38 ^a	Moore 1989
France	19–27	64–103	Francez 1992
Italy (Alpes)	20–23	186–235 ^a	Gerdol 1995
<i>Sphagnum fuscum</i>			
Manitoba, Canada	NA	3.6 ^a	Reader and Stewart 1972
Quebec, Canada	6.8	39–43 ^a	Moore 1989
Finland	6–18	135–160	Lindholm and Vasander 1990
Ontario, Canada	7–13	35–152	Rocheffort et al. 1990
Central Alberta, Canada	NA	54–78 ^a	Li and Vitt 1997
Central Alberta, Canada	NA	74–86 ^a	Szumigalski and Bayley 1997
Central Alberta, Canada	NA	81–138 ^a	Thormann and Bayley 1997
British Columbia, Canada	21.3	214 ^a	Asada et al. 2003a
British Columbia, Canada	16	169 ^a	Asada et al. 2003b
<i>Sphagnum rubellum</i>			
England	9–38	67 ^a	Clymo and Reddaway 1974
England	NA	3–7 ^a	Forrest and Smith 1975
British Columbia, Canada	19.4	145 ^a	Asada et al. 2003a
British Columbia, Canada	15	119 ^a	Asada et al. 2003b
<i>Sphagnum</i> sp.			
Alaska, USA	0.6–1.7	NA	Heilman 1968
England	38–43	55–220	Clymo 1970
Sweden	7–23	NA	Wallén et al. 1988
Unknown	NA	78–256–414 ^{a,b}	van Breemen 1995
Saskatchewan, Canada	NA	77	Bisbee et al. 2001
Minnesota, USA	NA	85–124–162 ^{a,b}	Weltzin et al. 2001
Quebec, Canada	2–14	NA	Heijmans et al. 2002
<i>Pleurozium schreberi</i>			
Manitoba, Canada	NA	56 ^a	Reader and Stewart 1972
British Columbia, Canada	20.4–23	148–166 ^a	Asada et al. 2003a
<i>Polytricum strictum</i>			
Minnesota, USA	NA	14–19–26 ^{a,b}	Weltzin et al. 2001

Note: NA, not available.

^aTransformed (g m⁻² year⁻¹ to g m⁻² year⁻¹ of C) = 54.5% C content of dry mass.

^bRelated to hummocks, lawn, and hollows.

increase water storage and peat accumulation in bogs, a rise in *Sphagnum* growth could lead to greater C sequestration in forested peatlands and boreal forest stands prone to paludification.

We consider that further investigations on the effect of climate change on the precipitation/evapotranspiration ratio, *Sphagnum* dynamics, composition and distribution, and the interaction (and feedbacks) between *Sphagnum* and tree species could bring a better understanding of these processes.

6.2. Organic matter decomposition

Decomposition rates are controlled by soil pH, temperature, degree-day, moisture and aeration, and by chemical and physical characteristics of peat and living *Sphagnum* (Bubier et al. 1993, 1995; Whiting and Chanton 1993; Szumigalski and Bayley 1996; Clymo et al. 1998; Yavitt et al. 1997; Charman 2002). As litter and new peat in the acrotelm are exposed to more oxygen and varying water table levels, they are subject to a higher decay rate. Once in the catotelm, the decay rate becomes independent of small climatic fluctuations and it declines sharply because of slow anaerobic decomposition processes (Clymo et al. 1998). As a matter of comparison, Yu et al. (2001) estimated a peat decay constant in the range of 0.01–0.8 year⁻¹ for the acrotelm and 0.7–5.5 × 10⁻⁴ year⁻¹ for the catotelm of forested peatland if a single exponential model is used (Clymo 1984). The rate of peat transfer from the acrotelm to catotelm therefore largely determines net peat accumulation. Several authors have suggested that peat accumulation is controlled by slow decomposition rates rather than rapid NPP (Clymo 1965; Damman 1979, 1988; Malmer 1986; Farrish and Grigal 1988; Clymo et al. 1998). This affirmation is mainly applicable to bogs or poor fens where high peat accumulation rates appear to be maintained by low rates of decomposition, but in rich fens peat accumulation takes place because of greater production (Thormann et al. 1999). Peat accumulated since the last glaciation will eventually reach a steady state when addition from the acrotelm to the catotelm equals material losses from the catotelm due to decomposition (Clymo et al. 1998; Thormann et al. 1999).

The efflux of CO₂ to the atmosphere from peatland soils is a function of plant root respiration and decomposition of plant material and peat in the soil profile. Control of the rates of CO₂ production from organic soils depends on the availability of oxygen associated with the depth of the water table, microbial activity in the peat, soil temperature, type of vegetation, and peat chemical characteristics (Blodau 2002). In general, higher temperature, lower and fluctuating water tables, minerotrophic conditions, and the predominance of vascular plants seem to sustain larger C mineralization rates (Blodau 2002). Hobbie et al. (2000) pointed out that winter activity accounts for roughly 20% of annual soil respiration, although estimates range between 3% and 50% across different arctic and tundra and boreal forest communities. Unfortunately, most of the studies measuring the effect of climatic change on CO₂ effluxes were conducted only during the growing season.

Methane (CH₄) is the second most important gas for global warming. Forested peatlands act as a greenhouse gas source by emitting CH₄ that contributes to the atmospheric absorption of infrared radiation (Whiting and Chanton 1993). Methane emissions by wetlands represent 5% to 10% of CH₄ produced globally (Blodau 2002). Average emissions of 5 to 80 mg m⁻² d⁻¹ are most common in northern peatlands (Blodau 2002) but they can range from 3 to 2000 mg m⁻² d⁻¹ (Huttunen et al. 2003). Although CH₄ atmospheric abundance is less than 0.5% that of CO₂, it is an important greenhouse gas on a molar basis. Rates of CH₄ production and consumption by peat soils are influenced directly by microbial activity and indirectly by availability of oxygen (i.e., influenced by soil moisture, peat depth, microtopography), soil temperature, type of vegetation, and peat chemical characteristics (Whiting and Chanton 1993; Bubier et al. 1995; Moore and Dalva 1997; Blodau 2002; Huttunen et al. 2003). Methane emissions from peatlands decrease with lower watertable levels and emissions are expected to reduce with increasing temperature and decreasing precipitation. Methane emissions are expected to be higher in open bog than in forested peatlands and boreal stands prone to paludification due to the generally lower water table found in forested stands (Minkinen et al. 2002). Current estimates of CH₄ are highly variable, temporally and spatially.

Dissolved organic C in peatland waters results mainly from precipitation, leaching, and decomposition of plant material and soil organic matter (Moore 2003; Moore et al. 2003). Dissolved organic C is primarily composed of organic acids generally characterized as fulvic or humic acids (Charman 2002; Moore et al. 2003). The DOC concentrations in northern peatlands range between 10 and 60 mg L⁻¹ (Blodau 2002; Moore 2003; Moore et al. 2003; Worrall et al. 2003). Peatlands export DOC to discharging streams at rates between 1 and 50 g m⁻² year⁻¹ (Blodau 2002; Worrall et al. 2003; Moore et al. 2003; Billett et al. 2004). The controls on DOC production and export in peatlands are still poorly understood but temperature, runoff, topography, water table level, and plant exudation seem to be important controlling factors (Fraser et al. 2001; Blodau 2002; Freeman et al. 2004). The loss of C from peatlands in the form of DOC increases slightly by leaching after water level drawdown (Laine et al. 1996). A decrease in runoff rates would decrease DOC discharge but this DOC would accumulate in the peat matrix and would be available for CO₂ and CH₄ emissions (Pastor et al. 2003).

Although rates of microbial decomposition, NPP, and evapotranspiration are temperature dependent, soil moisture directly or indirectly determines (i) the pathways and rates of transport of nutrients, gases, and heat into and out of the soil; (ii) whether microbial decomposition will proceed via aerobic or anaerobic pathways; (iii) the composition and structure of the overlying vegetation community; and (iv) susceptibility of the vegetation and surface peat to fire (Zoltai et al. 1998). If climate change does not significantly alter soil moisture content, peat accumulation and soil C sequestration should remain unchanged or be favoured. By contrast, where higher temperature and precipitation reductions are expected, soil moisture content in forested peatland should be significantly altered with a much lower precipitation/evapotranspiration ratio and water table level. As a result, a shift from anaerobic to aerobic processes for the upper part of the peat profile is likely, and higher decomposition rates should occur. This shift to aerobic decomposition will increase CO₂ emission and decrease CH₄ production. Moreover, soil decomposition should result in higher soil nutrient availability and thereby higher NPP and tree growth (Bonan and Van Cleve 1992). However, it must be noted that higher soil temperature does not necessarily result in greater tree growth (Bonan et al. 1990; Lahti et al. 2005).

6.2.1. Nitrogen deposition

The rates of atmospheric deposition of N have increased considerably in the past 150 years in North America and Europe as a result of acid precipitation and may have influenced the rates of plant production and decomposition and C cycling (Lamers et al. 2000; Aerts et al. 2001; Aldous 2002a; Moore et al. 2005). At present, the results of N deposition in forested peatlands are inconclusive. Nitrogen deposition can have an influence on vegetation and moss production, and also on soil dynamics. Nitrogen deposition can increase litter decomposition, tree growth, and soil nutrient availability (Mäkipää et al. 1999; Limpens and Berendse 2003). The effect of N deposition on organic matter decomposition depends of the N status of forested peatlands and may be limited by soil microbial activity and excess of moisture.

The effect of N fertilization on *Sphagnum* growth is also very variable (Alban and Watt 1981; Gunnarsson and Rydin 2000; Limpens and Berendse 2003; Malmer et al. 2003) and responses to N deposition are related to N and P status, the extent of the experiment, the water table level, microtopography (i.e., hummock, hollow), and species composition (Alban and Watt 1981; Williams et al. 1999; Gunnarsson and Rydin 2000; Berendse et al. 2001; Aldous 2002a; Blodau et al. 2004, 2005; Moore et al. 2005). At low levels of N deposition (<0.5 g m⁻² year⁻¹), *Sphagnum* mosses remove close to 100% of the N from natural precipitation and this additional N can increase *Sphagnum* growth. At the other extreme, *Sphagnum* mosses under conditions of high N deposition (>1.5 g m⁻² year⁻¹) decrease their capacity to assimilate N from aerial deposition and this excess N can reduce *Sphagnum* growth (Gunnarsson and Rydin 2000; Aldous 2002a). As an example of reduced production under treatment with the highest N application (10 g m⁻² year⁻¹), Gunnarsson and Rydin (2000) have showed in two sites that *Sphagnum fuscum* had only 50% and 79% of the control plot production. In regions with intermediate levels of N deposition, *Sphagnum* moss responses to N deposition are more variable. Moreover, it has been shown

that if N is not immediately taken up by *Sphagnum* mosses it can also be retained within the system and cycled through the microbial pool or vascular plants and eventually returned to the mosses through the process of translocation (Aldous 2002b). In a review on N deposition, Vitt et al. (2003a) calculated a critical N deposition value between 14.8 and 15.7 kg ha⁻¹ year⁻¹ for NPP of *Sphagnum* species. On the other hand, Williams and Silcock (1997) and Bragazza et al. (2004) suggest a critical load in Europe of 10 kg ha⁻¹ year⁻¹ above which *Sphagnum* change from being N limited to being K + P colimited. Nitrogen assimilation without concomitant growth leads to moss tissues with decreased C:N ratios, which will enhance their decomposition at senescence (Aerts et al. 1992). The greater turnover of C and nutrients in the surface peat horizons that could result would increase nutrient availability, and therefore could eventually reduce the rates of peat accumulation. Furthermore, N input above the *Sphagnum* critical load can increase the availability of N to the rooting system of vascular plants with consequent shifts in the plant competitive equilibria (Berendse et al. 2001; Bragazza et al. 2003) and higher potential decay rates of plant litter with effects on the carbon balance of peat ecosystems (Aerts et al. 2001; Limpens and Berendse 2003; Malmer et al. 2003). Thus, a future increase in N deposition combined with N input above the critical value for *Sphagnum* species could lead to a decrease in peat accumulation. Finally, to improve our understanding of the effect of N deposition, we believe that a long-term experiment measuring the effect of N deposition on the interaction (and feedbacks) between tree and moss species is needed.

6.3. Net primary production versus organic matter decomposition

What is more difficult to predict is whether following climatic change the increase in C storage in the living biomass (if it occurs) and the input of organic matter in the soil as litter will exceed the C lost through higher organic matter decomposition. Very few studies have measured this aspect, especially in mature and old-growth forested peatlands and forests prone to paludification. Bonan and Van Cleve (1992) have shown that following soil warming in a young black spruce stand, C sequestration in trees and mosses offsets C loss during soil decomposition (sum of C over 25 years: 46 g m⁻² more than the control) for the first 25 years of simulation. On the other hand, Mäkipää et al. (1999) have observed in a simulation experiment that the changed climatic conditions (over a 100-year rotation) in a Scots pine stand resulted in a 12% increase in gross primary production, but respiration increased even more (22%) thereby leading to a loss in total C. Recent studies on net ecosystem exchange have also indicated a net CO₂ release in winter, early spring, and late fall when the vegetation is inactive but soil respiration continues, and a net CO₂ uptake in summer when photosynthesis is strong (Blodau 2002). The lack of year-round measurements in most studies complicates the prediction of the effect of global change on the net C exchange of these ecosystems.

Because drainage of forested peatlands produces effects that are closely related to those of a drought, monitoring drained peatlands provides valuable information on the effect of a change in the precipitation regime on the C balance (see also section 7.2.2). It has been shown that drainage increases forest growth and NPP (Paavilainen and Päivänen 1995; Laine et al. 1996; Lavoie et al. 2005). Although C losses after drainage have been reported by Sakovets and Germanova (1992) and by Braekke and Finér (1991), the increased tree biomass plays an important role in storing new C (Laine et al. 1996; Minkkinen and Laine 1998) and suggests that after a few decades drained peatlands could remain a C sink. Results from Hargreaves et al. (2003) showed that afforested drained peatlands acted as a higher C sink (3 t ha⁻¹ year⁻¹ 4 to 8 years after tree planting) for 90 to 190 years but after that time the ecosystem would act as a C source. Therefore, as Cannell et al. (1993) illustrated, to regain their sink role, afforested peatlands would have to be returned to their previous form. Their results (under different scenarios) showed that if rates of oxidation are less than 100 g m⁻² year⁻¹, then afforestation will give a net benefit for about 200 years. If rates of oxidation are in the range 100–200 g m⁻² year⁻¹, afforestation will give a net benefit for only one rotation (50–100 years) but if rates of oxidation are 300 g m⁻² year⁻¹ or more, there may be no benefit from afforestation.

It should be noted, on the other hand, that most of the studies monitoring the effect of drainage on the C cycle were conducted in Europe and FSU. Thus, the results of drainage on NPP and tree growth may not be applicable to North American tree species. For example, in eastern Canada, premature and mature stands that had been drained generally showed little growth improvement following drainage (Sundström 1992; Sundström and Jeglum 1992; McLaren and Jeglum 1998). Thus, water level drawdown caused by drainage may not be sufficient to increase tree growth and NPP, and thereby insufficient to increase C stored in tree biomass. For many years, it was also assumed that increases in peat decomposition would lead to an increase in C loss. Recent findings in Finland have indicated that C density and storage in peat soil can increase after drainage, even when soil respiration has clearly increased (Minkkinen and Laine 1998). One of the reasons that might explain this situation is the higher C input in the system via NPP, especially through the fine roots of trees (Minkkinen et al. 2002; Laiho et al. 2004).

Thus, the current information available suggests to us that peatlands will keep acting as a C sink for the first few decades following climate warming but could become a C source afterwards. On the other hand, these results are based on short-term studies (<300 years) and on a limited type of peatland. Thus, we consider that the effect of climate change on total C sequestration rate in forested peatlands located in the Northern Hemisphere is still uncertain and among the factors responsible for this uncertainty one finds the lack of research on different peatland types (and tree species) and stand structure (i.e., age), the lack of long-term studies monitoring the effect of climate warming (or indirectly by drainage) on the C cycle in forested peatlands, and the shortage of studies in some specific areas (e.g., Canada, Alaska).

6.4. Species migration and permafrost

Climate change can influence the distribution of tree and moss species. Under global warming the distribution of major vegetation zones and species is expected to be significantly altered and a shift northward is expected. Migration of deciduous tree species in well-established forested peatlands located in southern boreal forest is unlikely due to the presence of *Sphagnum* and a thick organic layer. On the other hand, migration of deciduous trees in boreal forest stands prone to paludification is more probable due to a more receptive environment (e.g., lower peat depth, *Sphagnum* cover, and soil moisture). Climate change will also have an important effect on the ecotone between forests, forested peatlands, and open peatlands. Precipitation can play a key role in the future dynamics of these ecosystems. Increase in precipitation will likely increase peat accumulation in boreal forest stands prone to paludification and facilitate forested peatlands expansion into upland forest while a diminution in precipitation will probably favour the succession of forested peatlands to upland boreal forests. In cases where upland forest ecosystems take over forested peatlands, higher release of C by CO₂ is probable even if these stands become more productive (Hartshorn et al. 2003).

Change in climate may also alter permafrost depth. Higher temperature, increased growing season degree-days, change in fire frequency and snow thaw can lead to the thawing of extensive regions of permafrost (Jorgenson et al. 2001; Turetsky et al. 2002a; Yoshikawa et al. 2003; Christensen et al. 2004). Increase in depth of thaw and altered soil moisture will affect root depth, root respiration, and soil microbial community activity and composition. Under such a scenario, peat accumulation should increase (Robinson and Moore 2000; Turetsky et al. 2000; Vitt et al. 2000 b; Camill et al. 2001; Jorgenson et al. 2001).

7. Effects of disturbances

7.1. Wildfire

Fire is known for driving much of the boreal forest C balance in North America and Russia (Amiro et al. 2001). Forest fires affect the global C cycle in several ways (Kasischke et al. 1995; Bhatti et al. 2003; O'Neill et al. 2003). First, fire directly releases large quantities of C into the atmosphere through combustion of plant material and surface soil organic matter. Fire releases most C as CO₂, but quantities

of CO, CH₄, and nitrogen oxides are also produced (Amiro et al. 2001). Second, fire converts plant material into charcoal, which is an inert form of C that does not break down via decomposition (Carcaillet et al. 2002). Third, the direct and indirect effects of burning strongly influence the pattern of secondary succession on fire-disturbed landscapes, which in turn control the patterns of C storage in aboveground biomass. Fourth, fire significantly alters (i.e., increases) the thermal regime of the organic and mineral soil layers. Fifth, through the reduction of plant biomass to ash, the melting of the permafrost layer and increased decomposition, fire increases the amount of soil nutrient available for plant growth. All of these processes could contribute to an increase in NPP in the aboveground vegetation layer. Finally, for several years or decades after a fire, the vegetation on newly burned sites may not fix as much C from the atmosphere as did the pre-fire vegetation. In addition, it can take many years before the peatland C stocks (in vegetation and in soil) return to their pre-fire levels (Benscoter et al. 2005). Thus, in general, increase in fire frequency causes a short-term net reduction in C sequestration (Zoltai et al. 1998; Bhatti et al. 2003).

The ignition and spread of wildfire is determined by fuel (e.g., presence of small coarse woody debris will facilitate fire ignition), weather, topography, soil moisture, timing of fire (e.g., wildfire that occur during spring are often less severe due to higher soil moisture), organic mat depth at the time of the fire, and fire management efforts. The position of the water table in peatlands relative to the surface is of major importance when assessing the susceptibility of peatlands to fire, because it has a direct bearing on the moisture content of the surface peat (Zoltai et al. 1998). Therefore, changes in temperature and precipitation may have a direct effect on fire frequency. For example, under a warmer or drier climate, we can expect an increase in fire frequency and severity. Other factors such as ignition agents, length of the fire season, peatland classes (i.e., bog, fen), vegetation characteristics, and human activities such as fire exclusion and landscape fragmentation may greatly influence the fire regime over the next century (Weber and Stocks 1998).

7.1.1. Extent and severity of wildfires

Future C emission from fire is difficult to predict because the effect of wildfire on C emission is influenced by the extent (i.e., area burned over time) and the severity (i.e., organic matter removal) of fire. These two factors can be correlated under specific weather conditions, but in other conditions, both will respond differently. For example, spring conditions can lead to large wildfires with low severity because peat is still frozen. On the other hand, summer and early fall conditions can result in many small wildfires or in one large wildfire with more severe effects on organic matter removal. Wildfires in boreal forest appear to show tremendous interannual variation in both the extent and the severity of burning. For example, in Canada, about 2 Mha of forest have burned annually on average from 1959 to 1999, with extreme fire years burning more than 7.5 Mha (Weber and Stocks 1998; Amiro et al. 2001). Mean direct C emissions from combustion in forest fires have been estimated at about 27 Tg year⁻¹ (1 Tg = 10¹² g) for this period (Amiro et al. 2001). For western Canada peatlands, Turetsky et al. (2002b) reported that, on average, 3.2 kg m⁻² of C is lost directly through combustion of biomass from peat to the atmosphere. Benscoter and Wieder (2003) report that total C losses by combustion range from 1.9 to 27 Tg year⁻¹ (mean 4.4–6.2) in North America and from 20.9 to 59 Tg year⁻¹ in Europe and Asia. Unfortunately, no extensive long-term studies have been done in FSU. Thus, the current C release rate from fire in the boreal forest of FSU is not accurate. However, Conard et al. (2002) have reported that the estimated C emissions for the 1998 fire season range from 135 to 190 Tg for the Russian boreal forest.

Within the boreal forest, fire severity shows a discrepancy and is correlated to forest types. Wildfires are reported to occur in uplands up to twice as frequently as in peatlands (Zoltai et al. 1998; Sukhinin et al. 2004), although Cyr et al. (2005) report the fire cycle as low as 36 years in forest stands with peaty soil. The difference (in percentage) in fire interval between forest stands on mineral soil and forest stands on organic soil or on forested peatland may be questionable, but one can surely claim that fire

severity will be lower and the fire cycle will be on average longer on organic soil because of higher soil moisture content and moss cover. Seasonality is also important because of the direct change in fuel moisture that affects flammability (Lynch et al. 2004). Most often, only surface and shallow peat fires occur in forested peatlands. Peat surface fires only slow down paludification and C sequestration and do not influence the long-term vegetation development of *Sphagnum*-dominated boreal peatlands (Kuhry 1994; Zoltai et al. 1998; Charman 2002). However, in very dry years or after drainage in forested mineral wetland, in peatland with permafrost, and in boreal stands prone to paludification, a shallow or deep peat fire may burn to a considerable depth, sometimes down to the underlying mineral soil.

7.1.2. Fire and the carbon budget

Several recent studies have estimated total C emissions from fires in boreal forest (Amiro et al. 2001; Conard et al. 2002; Kasischke and Bruhwiler 2003), but very few of them estimated total C balance after wildfire (i.e., total C emission, CO₂, CO, CH₄, increase in organic matter decomposition, conversion of C into charcoal). Early studies as well as recent analyses have concluded that circumpolar boreal forest fires contributed a relatively small portion of global annual emissions of these gases from biomass burning (<1%–3%). However, these conclusions have been confronted with research showing that during large fire years, boreal forest fire emissions contribute as much as 15%–20% of total global emissions from biomass burning (see French et al. 2003). The C balance after wildfires is difficult to estimate since C losses depend on the extent and severity of wildfires, as well as on the quality of drainage in the forest. For example, Harden et al. (2000) have estimated that over the last 6500 years in Manitoba 10%–30% of the annual CO₂ that is fixed as NPP was likely consumed by fire, while 40%–80% of NPP was released through decomposition and 8%–30% was fixed as soil C. On the other hand, Kasischke and Bruhwiler (2003) estimated emissions of CO₂, CO, and CH₄ from boreal forest fires in 1998. Their results show that the average level of C released from biomass burning according to different severity and biomass burning (flaming and (or) smoldering) scenarios ranges from 11.9 to 30.4 t ha⁻¹. They also estimated that total C, CO₂, CO, and CH₄ emissions could range (according to different fire scenario) from 183 to 458 Tg (10¹² g), 105–1328 Tg, 18–149 Tg, and 0.6–4.7 Tg, respectively. In a 50-year average estimation in Alaska, French et al. (2003) showed that emissions of total C, CO₂, CO, and CH₄ released during fires are 4.49 Tg, 12.5 Tg, 1.65 Tg, and 0.014 Tg, respectively. Meanwhile, Bond-Lamberty et al. (2004) and Wang et al. (2003) have shown that the vegetation C pool (above-ground + below-ground) steadily increase from 1.3 to 83.3 t ha⁻¹ for the dry chronosequence (i.e., 3 to 151 years), and from 0.6 to 37.7 t ha⁻¹ in the poorly drained chronosequence stands and that the rate of C sequestration in tree biomass peaked at 37 years before declining in the oldest stands due to a change in the soil conditions. Their results also showed that total NPP was low (50–100 g m⁻² year⁻¹ of C) immediately after fire, highest 12–20 years after fire (332 and 521 g m⁻² year⁻¹ of C in the dry and wet stands, respectively) but 50% lower than this in the oldest stands. Finally, another important issue with respect to fire and C emissions in the boreal forest is the changes in surface soil properties such as pH and albedo (Simard et al. 2001) that generally favour organic matter decomposition and respiration. Thus, permafrost melting and an increase in soil temperature might greatly stimulate the decomposition rate and result in even higher CO₂ emissions for up to a decade after fire has occurred (Kasischke and Bruhwiler 2003). Amiro et al. (2001) have estimated that post-fire release of C due to decomposition is equivalent to direct emissions during combustion in some boreal ecosystems. This indirect effect of wildfire on soil temperature and soil respiration will result in even higher levels of variability in emission of C and more research will be needed to quantify these emissions.

7.1.3. Regional predictions

7.1.3.1. North America

Overall, the fire weather index is expected to increase in many areas by more than 20%, indicating weather more conducive to fire activity in western and central Canada (Hogg et al. 1992; Weber and

Flannigan 1997). Turetsky et al. (2002b) reported that a 17% increase in the area of peatlands burned annually and intensity of organic matter combustion would convert these peatlands into a regional net C source. On the other hand, where permafrost is present, a reduction in local fire frequency is possible since an increase in temperature will increase soil moisture following permafrost thaw. In contrast to western Canada, it is highly probable that parts of eastern Canada may experience less fire because of increased precipitation in a warmer climate (Flannigan et al. 1998, 2001; Amiro et al. 2001; Bergeron et al. 2001; Carcaillet et al. 2001). With expected increases in precipitation, fire frequency in Alaska should also decrease or remain unchanged.

7.1.3.2. *Fennoscandia*

As opposed to Canada, Alaska, and FSU, wildfires in Finland, Sweden, and Norway play a minor role in influencing the forest C balance because of efficient fire prevention in the last decades (Parviainen 1996). Thus, climate change effects on fire frequency are not expected to have a major influence on the C balance. Nevertheless, an increase in precipitation should result in a decrease in natural wildfire occurrence.

7.1.3.3. *Former Soviet Union*

No extensive studies on past and future fire frequency have been carried out in FSU (Conard et al. 2002). The lack of accurate data in the estimation of forested peatlands introduces large potential errors in predictions. However, climate change scenarios for FSU predict an overall increase in temperature and precipitation (IPCC 2001) or cooling (Klimanov and Sirin 1997). Thus, a decrease in fire frequency is apparent under both scenarios. The FSU contains a huge amount of forested peatlands spread over a large area and, like in Canada, temporal and spatial variability in fire frequency is high.

7.2. Forest management

Forest management decisions on fire exclusion, harvesting methods, and silvicultural treatments have an important impact on C sequestration. To increase tree productivity, site preparation, drainage, and fertilization are currently recommended. These silvicultural treatments increase soil temperature, organic matter decomposition, nutrient availability, and also the amount of C released by respiration. With the growing interest in international agreements on the C cycle, forest management in boreal forest will also have to cope in the future with the objective of increasing C sequestration.

7.2.1. *Harvesting*

Harvesting in boreal forest stands prone to paludification can enhance peat accumulation and thereby C sequestration by rising the water table depth while maintaining the cover of *Sphagnum* mosses and ericaceous shrubs intact. Careful logging is often used as a harvesting method in the boreal forest, which means more time since the last fire is needed before the next rotation. For an additional protection of soil and advance regeneration, harvesting in these stands is often carried out during winter (Tanttu and Sirén 2001; Lavoie et al. 2005). Moreover, careful logging increases soil rutting and in doing so promotes paludification because in small depressions, *Sphagnum* establishment is facilitated (Asada et al. 2004). Lastly, tree removal reduces evapotranspiration rates and causes a rise of the water table (i.e., watering-up) in the surface layers and a greater range in week-to-week fluctuations, as a result of increased peat accumulation (Lavoie et al. 2005). Therefore, using careful logging in boreal forest stands prone to paludification may, in a long-term perspective, enhance C sequestration to the detriment of site productivity.

There is currently a strong interest in forest management that maintains forest composition and structure in an attempt to emulate natural disturbance regimes and natural vegetation patterns (Bergeron et al. 2002; Holgén and Hånell 2000; Harvey et al. 2003; Mielikäinen and Hynynen 2003), and alternative

harvesting methods such as partial cutting and shelterwood harvesting are currently experimented. Partial harvesting could favour paludification because it prevents soil disturbance (as opposed to fire) and because the amount of light available to *Sphagnum* or ericaceous shrubs would be higher as opposed to unharvested stands (Lavoie et al. 2005). However, paludification should be less problematic following partial harvesting than following conventional harvesting because (i) the proportion of trees removed would be lower, thus reducing watering-up; (ii) the amount of light available to *Sphagnum* would be lower, potentially favouring feathermoss growth over *Sphagnum*; and (iii) the amount of rainfall interception would be higher, thereby keeping the water table lower.

7.2.2. Silvicultural treatments

7.2.2.1. Drainage

Over 90% of drainage occurred in Fennoscandia and FSU (Laine et al. 1997). Drainage of peatlands in Fennoscandia will no longer be done to any significant degree due to environmental issues (Minkkinen et al. 2002; Jeglum⁴). To ensure that drained peatlands continue to produce timber, the ditches are cleaned. However, forest drainage requirements have been revised on the basis of experience, and some of the most nutrient-poor drained peatlands will be left to return to a natural state (Finnish Forest Industries Federation 2000).

The purpose of drainage is to increase tree productivity and to dry out peat for peat harvesting. Drainage reduces the water table level and thereby improves soil and root aeration. By doing so, drainage generally increases CO₂ emission as a by-product of the decomposition of a larger pool of decaying biomass (Silvola et al. 1996; Moore and Dalva 1997; Cui et al. 2005). Simultaneously, drainage may increase CO₂ sequestration in living biomass by improving tree growth. Recent findings in Finland have indicated that C density and storage in peat soil can increase after drainage, even when soil respiration has clearly increased (Minkkinen and Laine 1998). This increase in C content is possibly due to a decrease in peat pH, peat temperature, litter quality, and to higher C input in the system via NPP, especially through the fine roots of trees (Minkkinen et al. 2002; Laiho et al. 2004). Studies report that drainage usually reduces CH₄ emissions (Martikainen et al. 1995; Nykänen et al. 1997; Cui et al. 2005), given that only a small persistent decrease in water table depth may be necessary (Roulet et al. 1993). This diminution in CH₄ emissions may sometimes be partially compensated by emissions measured from drainage ditches. However, CH₄ fluxes from the ditches would be a considerably small contribution to global warming since the proportion of ditches to total peatland area is rather small (Minkkinen et al. 1997). Another C loss in drained peatlands may come from DOC (Laine et al. 1996; Freeman et al. 2004; Nieminen 2004). Freeman et al. (2004) have shown that under elevated CO₂, the proportion of DOC derived from recently assimilated CO₂ was 10 times higher than that of control cases. Finally, particularly in N-rich and fertilized peat soils, drainage can lead to greater emissions of N₂O and NO by increasing N mineralization (Nykänen et al. 1997; Regina et al. 1998, 2004). In the end, when newly and old drained forested peatlands turn into C sources, they can switch back to C sinks if drainage ditches are blocked, thus facilitating *Sphagnum* growth and peat accumulation.

7.2.2.2. Fertilization

Low nutrient status in forested peatlands suggests that nutrient elements supplied by fertilization should be an essential tool for improving tree productivity for peatland conifers.

Higher soil nutrient content can be attributed to direct addition of nutrient but also to higher soil decomposition and microbial activity (Wells and Williams 1996). Fertilization may also increase biological drainage by increasing tree stand growth, which would result in increased evapotranspiration and precipitation interception (Paavilainen and Päivänen 1995). Thus, fertilization in forested peatlands

⁴J. Jeglum. Personal communication. 2003.

can reduce or increase C sequestration depending on whether C stored in the living biomass will or will not exceed the C lost through higher organic matter decomposition. However, it should be noted that the effects of fertilization on C sequestration in northern peatlands are currently considerably small since forest fertilization is minimal.

7.2.2.3. Mechanical site preparation and prescribed burning

In a short-term perspective, both site preparation techniques definitely reduce C sequestration and turn peatlands into C sources. Like a wildfire, mechanical site preparation and prescribed burning can reduce the cover of feathermosses and *Sphagnum* mosses and the thickness of the organic layer. By doing so it will affect soil moisture, soil temperature, organic matter decomposition rate, and nutrient availability, and it will reduce competitive vegetation (Johansson 1994; Sutherland and Foreman 1995, 2000; Trettin et al. 1996; McLaughlin et al. 2000; Alcàzar et al. 2002; Prévost and Dumais 2003). Furthermore, elevated microsites shaped by mechanical site preparation cannot be created without also generating wetter depressions. Thus, small depressions can also revegetate with *Sphagnum* and other mosses (Asada et al. 2003a), thus facilitating *Sphagnum* invasion and leading to peat and C accumulations. In a long-term perspective, paludification can only be controlled or reversed in boreal stands prone to paludification if site preparation is severe. Mechanical site preparation and prescribed burning are alternatives to natural wildfire. On the other hand, in a situation where wildfire and site preparation are both present, it could become problematic for future C emissions.

7.3. Other natural and anthropogenic disturbances

Forested peatland damage caused by extreme weather incidents (e.g., storm, extensive dry period) or insect disturbances will probably change with climate change (Bhatti et al. 2003). However, very few data exist on the future frequency of these perturbations in forested peatlands. As for insect outbreaks, it is generally expected that they will become increasingly intense with climate change as a consequence of both temperature warming and CO₂ enrichment (Bhatti et al. 2003). Severe insect attacks are thought to increase fire hazard. When the forest canopy is removed, increased solar radiation and wind speed rapidly dry out the potential fuel. However, data records are needed to test this hypothesis (Bonan and Shugart 1989) and, to our knowledge, there are no studies reporting on the effect of insect outbreaks and pathogens on C cycle in forested peatlands.

Peat harvesting continues to represent a net removal of C from peatlands, since trees and *Sphagnum* are removed and peat is harvested, hence destabilizing peatland dynamics. However, peatland restoration (i.e., *Sphagnum* and ground-vegetation re-colonization) may well contribute to sequester C again in the future (Price and Waddington 2000), but it cannot restore peatland C sinks to their pre-disturbed state for several years.

Besides logging and peat extraction, mining, oil and mineral prospecting or hydroelectric dams are other examples of major disturbances caused by human activities. Regardless of climate change, these disturbances severely affect the ecosystem. Carbon and peat accumulations are reduced after mining and oil exploitation, but peatlands can be restored to C sinks after several years. However, following the construction of a hydroelectric dam, all (or part of) the peatland is flooded, which creates a new ecosystem (e.g., lake, pond, or marsh).

8. Future carbon sequestration

Throughout this synthesis, the effect of climate change on NPP, organic matter decomposition, and fire regime frequency, as well as the effects of forest management on C sequestration in forested peatlands have been discussed. Because of the lack of information and the significant amount of uncertainty only tendencies (summarized in Table 5 and Fig. 2) can be outlined, and quantification of future C sources

Table 5. Tendencies in future C sequestration rates in the Northern Hemisphere.

	North America		Fennoscandia	FSU
	Eastern Canada, Alaska	Western and Central Canada		
Temperature	+ ^a	+	+	+
Precipitation	+	— ^b	+	+
Fire frequency	—	+	—	—
Forest management	+	NA ^c	+	NA
C sequestration	+	— ^d	+	+

^aIncrease.^bDecrease.^cNot available.^dReduction in C sequestration rate or C source.

or sinks cannot be determined with precision. Although, we consider this exercise important to reveal the main differences between the northern regions.

In general, total C sequestration potential has not been reached yet, and many forested peatlands are still at a relatively early stage of development. Furthermore, additional mineral wetlands may turn into forested peatlands and boreal stands susceptible to paludification may also increase C sequestration while increasing their thickness from mineral soil. Recent modelling efforts have shown that if global warming occurs, part of the Earth currently covered by tundra will shift to boreal forest, thus suggesting that permafrost thaw with increase in soil moisture and bryophyte primary production will increase paludification. As it was previously noted, soil moisture is possibly the most important factor defining the response of forested peatlands to a changing climate. Thus, the effect of climate change and forest management on the C balance may differ according to peatland types. Bogs, which are more numerous (Natural Resources Canada 2005), are generally characterized by a lower water table level and a higher percentage of *Sphagnum* cover than fens (medium to rich). Thus, the potential for a positive feedback of CH₄ radiative forcing is reduced but the potential rate of C accumulation may be lower.

8.1. Regional tendencies

8.1.1. North America

We suggest that for eastern Canada, C sequestration will increase because (1) precipitation is expected to increase and fire frequency to decrease; (2) current harvesting techniques (e.g., clear-cut, careful logging, partial harvesting) prevent soil disturbance and facilitate paludification of boreal forest stands; (3) of fire exclusion policies; and (4) of peat accumulation increment following permafrost thaw in northern forested peatlands. However, if site preparation and logging increase significantly, the C sequestration rate will be reduced even if tree productivity increases due to soil organic matter decomposition. Peat extraction also occurs primarily in eastern Canada and may have a significant impact on the C balance of this region (Bhatti et al. 2003). However, forested peatlands of eastern Canada should remain C sinks in the upcoming years. In Alaska, an increase in precipitation and a reduction in fire regime frequency and severity, concomitant with an increase in permafrost thaw, should result in higher C accumulation, and forested peatlands in Alaska should remain C sinks.

For western and central Canada, we suspect that C sequestration rate will initially be reduced but that eventually most of the forested peatlands will turn into a C source because higher temperature and lower precipitation are predicted, and also because fire frequency is predicted to increase as well. As opposed to eastern Canada, there are actually very few peatland areas in western Canada that are

currently harvested (Liefvers⁵, for Alberta) or drained. Thus, the impact of forest management on future C sequestration rates will be minimal. The impact of permafrost thaw on peat accumulation rate should be in opposition to that of eastern Canada and Alaska because higher temperature with a significant decrease in precipitation should result in a drying of the peat profile. Finally, the surface area occupied by forested peatlands could potentially decrease at the southern limits of peatland distribution. In these regions, many peatlands and boreal forest stands prone to paludification may become dry enough to support upland boreal forest vegetation and be colonized by deciduous tree species (Gignac and Vitt 1994).

8.1.2. *Fennoscandia*

We believe that Fennoscandia will respond similarly to eastern Canada and Alaska. An increase in C sequestration should be expected because (1) precipitation is expected to increase; (2) fire has a minor role in influencing the forest C balance; (3) current harvesting techniques prevent soil disturbance; and (4) a certain percentage of drained peatlands will be returned to a natural state (Minkkinen et al. 2002). We assume that C sequestration will be favoured in peatlands where permafrost (very low percentage cover) thaw will occur and, as mentioned for eastern Canada, increase in site preparation should release more C for a short period of time. Overall, Fennoscandia should remain a C sink in the future.

8.1.3. *Former Soviet Union*

Because of the lack of information, future C sequestration tendencies in FSU are difficult to forecast. Nevertheless, with the small amount of information we hold, we suggest that C sequestration should also increase in FSU because annual precipitation is predicted to increase (or cooling according to the other scenario), with a concomitant reduction in fire frequency. Expansion of forested peatlands and increase in peat accumulation in tundra should also occur because of permafrost thaw. Finally, we presume that boreal forest stands prone to paludification cover an important surface area in FSU since this region has large areas of boreal forest that overlap large areas of open and forested peatlands. Thus, an increase in precipitation or cooling should greatly enhance C sequestration.

9. Conclusions

Peatlands, and among them forested peatlands, have always been long-term accumulators of C. The accumulation rate of C appears to be highly variable both in time (within a single site) and in space (in relation to site microtopography and peatland type). The conditions that are conducive to peat accumulation are strongly linked to the water balance, which is determined both by climate and topography. Also, both man-made and natural disturbances such as wildfire can have important impacts on the C accumulation rates of forested peatlands.

Current climatic trends suggest conditions that may favour peat accumulation in some regions where warmer and wetter conditions are expected, as well as conditions that may slow down peat accumulation in some other regions where dryer conditions are expected. Nevertheless, some studies on drained peatlands have suggested that the drying of accumulated peat may not necessarily be linked to high C and that the catotelm once formed may still be resistant once submitted to aerobic conditions. These conditions therefore suggest that peatlands could continue acting as a net sink of C. The large variability in short-term rates of C accumulation that was encountered indicates that predictions on the rates of peat accumulation are difficult to make. A better classification of sites and of the variability in peat depth and *Sphagnum* composition as well as a classification of sites undergoing paludification are required before making any attempt to quantitatively address this question.

⁵V. Liefvers. 2003. Personal communication.

Boreal forested peatlands are likely to sustain more forest management in the future. Forest management options have the potential to either increase or decrease peat accumulation. Management options that stimulate forest growth will generally decrease the rate of peat accumulation.

To make progress towards predicting the impact of climate change on C sequestration in forested peatlands and boreal stands prone to paludification, further research is needed to improve these predictions through the search for (1) basic information: the first priority should be the improvement of estimates of (i) forested peatland cover and boreal stands prone to paludification and (ii) depth of organic matter. The second priority, should be paleoecological studies in northern forested peatlands. It remains crucial to understand the past and current C balance (C sink, source, or steady state) of these forested peatlands to be able to predict future responses to global warming and natural and anthropogenic disturbances; (2) modelling: better predictions of regional changes in climate are needed. Also, the development of dynamics models that will integrate external and internal factors such as geographical location, vegetation composition, and variable decomposition rate is necessary; (3) monitoring: we suggest further investigations on the effect of climate change on (i) the precipitation/evapotranspiration ratio, (ii) *Sphagnum* dynamics, composition, and distribution, and (iii) the interaction (and feedback) between *Sphagnum* and tree species in forested peatlands and in boreal forests prone to paludification. We also consider that more studies monitoring CO₂ and CH₄ variations following climate change are necessary, especially long-term, year-round and field experiments. The long-term impact of atmospheric deposition on the C cycle and on the interaction between *Sphagnum* mosses and trees in forested peatlands still needs to be addressed; (4) disturbances: an important amount of work dealing with the effect of fire on C sequestration in the boreal forest has already been published but, nevertheless, (i) more quantitative data monitoring changes in C storage and fluxes during fire and in post-fire succession are needed, (ii) several areas (e.g., FSU) still appear to be poorly represented and therefore more studies measuring the effect of fire on C cycling are needed at the regional and national levels, and (iii) most of the previous research did not make the distinction between upland and lowland stands, and therefore studies specific to forested peatlands and boreal forests susceptible to paludification are required. Finally, we would like to point out that research is needed to monitor the effect of natural disturbances (e.g., storms, extensive dry periods, insect disturbance) and anthropogenic activities (e.g., forest harvesting, various silvicultural treatments, peat harvesting, mining, hydroelectric dam) on C cycling in forested peatlands and boreal stands prone to paludification.

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