Drainage as a model for long term climate change effect on vegetation dynamics and carbon cycling in boreal peatlands

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Abstract

Peatlands are important components of the global carbon cycle, storing one-third of the global soil carbon. The accumulation of peat depends on two main interacting factors: the wetness and vegetation composition of a peatland. Previous studies have looked at the impact of a water table lowering on carbon fluxes in different types of peatlands. However, these studies were conducted within a time frame that did not allow the examination of vegetation changes due to the water table lowering. To be able to predict the fate of peatlands with changing climate and potentially lower water tables, the effect of a change in vegetation has to be considered. To bridge this gap, I conducted a study along a drainage gradient resulting from the construction of a drainage ditch 85 years ago in a portion of the Mer Bleue bog, located near Ottawa, Canada. According to water table reconstructions based on testate amoeba, the drainage dropped the water table by approximately 18 cm. On the upslope side of the ditch, the water table partly recovered and the vegetation changed only marginally. However, on the downslope side of the ditch, the water table stayed persistently lower and trees established (*Larix* and *Betula*). The importance of *Sphagnum* decreased with a lower water table, and evergreen shrubs were replaced by deciduous shrubs. The water table drop and subsequent vegetation changes had combined and individual effects on the carbon functioning of the peatland. Methane fluxes decreased because of the water table lowering, but were not affected by vegetation changes, whereas respiration and net ecosystem productivity were affected by both. The carbon storage of the system increased because of an increase in plant biomass, but the long-term carbon storage as peat decreased. Several steps need to be taken to allow for the appropriate representation of water table disturbances in peatland carbon modelling. The modelling of the effect of water table drop, along with vegetation changes using the Holocene Peatland Model revealed that the model captured the general behaviour of the peatland; however, the evaluation version is more resilient than the system is. The inclusion of the feedback effect that vegetation has on the carbon functioning of a peatland when a disturbance occurs is crucial to model the carbon balance of this ecosystem.

Résumé

Les tourbières sont une composante importante du cycle global du carbone, séquestrant le tiers du carbone contenu dans les sols. L'accumulation de la tourbe dépend de deux facteurs principaux: l'hydrologie et la végétation. Des études ont abordé l'impact d'un abaissement de la nappe phréatique sur les flux de carbone des tourbières. Cependant, l'échelle temporelle de ces études ne permet pas de voir de changements de végétation en réponse à un abaissement de la nappe phréatique. Pour être en mesure de prédire le futur des tourbières dans un climat potentiellement plus sec, les effets des changements de végétation doivent êtres considérés. J'ai donc utilisé un site comprenant un gradient de conditions hydrologiques résultant du creusage d'un canal de drainage sur la tourbière Mer Bleue, près de Ottawa. D'après des reconstructions hydrologiques basées sur des assemblages de rhizopodes, le drainage a abaissé de façon permanente la nappe phréatique d'environ 18 cm. Sur le côté en amont du canal, la nappe phréatique s'est partiellement rétablie et la végétation a peu changé. Par contre, sur le côté aval du canal, la nappe phréatique a été abaissée de façon permanente et des arbres se sont établis (*Larix* et *Betula*). Avec l'abaissement de la nappe phréatique, la sphaigne est devenue moins importante et des arbustes à feuilles caduques ont remplacé les sempervirents. Les changements hydrologiques et de végétation ont eu des effets individuels et combinés sur les flux de carbone de la tourbière. Les flux de méthane ont été réduits par l'abaissement de la nappe phréatique, mais n'ont pas été affectés par les changements de végétation, mais la respiration et la productivité nette de l'écosystème ont été affectées par les deux. La séquestration du carbone a ainsi augmenté due à une augmentation de la biomasse végétale, mais la séquestration à long terme du carbone dans la tourbe a diminué. La simulation des effets d'une diminution de la nappe phréatique utilisant le *Holocene Peatland Model* a révélé que le modèle capture de façon adéquate la réponse générale du système, mais que la version évaluée est plus résiliente que le système l'est en réalité. La modélisation adéquate des effets d'une perturbation sur les flux de carbone des tourbières nécessite l'inclusion de la rétroaction amenée par les changements de végétation.

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Contribution of authors

Chapters 3 to 6 are written in a format suitable for their publication in scientific journals. All chapters are co-authored by Nigel T. Roulet, who, as my supervisor, contributed to the planning of the research, provided scientific expertise in the process of analyzing the results and edited the manuscripts, as well as contributed financially to the completion of the research. The roles of the other co-authors are detailed below.

Manuscript #1 (Chapter 3) "Assessing long-term hydrological and ecological responses to drainage in a raised bog using paleoecology and a hydrosequence" by Julie Talbot, Pierre J.H. Richard, Nigel T. Roulet and Robert K. Booth (Journal of Vegetation Science, in press). Pierre Richard contributed intellectually and financially to this research by sharing his lab resources (including his personnel) and helping in the interpretation of paleoecological results. Robert Booth provided the testate amoeba transfer functions, contributed to the editing of the manuscript and produced one figure.

Manuscript #2 (Chapter 4) "Biomass and leaf area changes 85 years after drainage in a bog" by Julie Talbot, Nigel T. Roulet, Oliver Sonnentag and Tim R. Moore (to be submitted). Oliver Sonnentag participated in the planning, the execution and the analysis of the LAI component of the study and contributed to the editing of the manuscript. Tim Moore gave scientific advice from the early planning phase of this research, and will contribute to the editing of the manuscript.

Manuscript #3 (Chapter 5) "Long-term water table drawdown and vegetation changes affect carbon fluxes and stores in a North American bog" by Julie Talbot, Nigel T. Roulet, Pierre J.H. Richard and Tim R. Moore (to be submitted). Pierre Richard contributed intellectually and financially to this research by sharing his lab resources (including his personnel) and helping in the interpretation of paleoecological results. Tim Moore gave scientific advice from the early planning phase of this research, and will contribute to the editing of the manuscript.

Manuscript #4 (Chapter 6) “Modelling the long-term influence of hydrology on peatland vegetation dynamics and carbon storage” by Julie Talbot, Nigel T. Roulet and Steve Frolking (in preparation). Steve Frolking is the author of the model. He shared the model code with me and helped me interpreting the results of the simulations. He will also edit a later version of this manuscript.

Chapter 1 - Introduction

Peatlands are terrestrial ecosystems where biomass production exceeds decomposition. This imbalance results in the accumulation of peat, a carbon-rich organic material mostly made up of partly decomposed plant remains. Peat accumulates at a rate of about 16 to 80 g m^{-2} yr^{-1} (Gorham *et al.*, 2003; Turunen *et al.*, 2002) over thousands of years, leading to peat mats that can reach a thickness of several meters. The peat profile is usually described as a two-layer system: the upper, shallow and usually oxic *acrotelm* and the deeper, anoxic *catotelm* (Ingram, 1978). The boundary between the two layers corresponds approximately to the deepest level reached by the water table on an average year.

Peatlands are important components of boreal and subarctic landscapes. In Canada, they cover more than 12% of the terrestrial area (Tarnocai *et al.*, 2005). However, despite their widespread distribution, they have historically been considered as wastelands or as mysterious and daunting areas. Their economical value was limited to peat mining for use as a domestic fuel and, since the mid-twentieth century, for use as a horticultural growing media. Only in the last few decades have scientists and the general public realized that peat is not a renewable resource and that peatlands have other values than the ones obtained through their mining (Chapman *et al.*, 2003).

In addition to their aesthetic, educational and recreational values, peatlands have an important role as a unique habitat for specialized and/or rare species of flora and fauna. They can act as hydrological buffers, regulating water flow within watersheds. Their role as paleo-archives is also widely recognized: because of the slow rate of decomposition of peat, peatlands can store for thousands of years layered traces of life such as pollen, spores, seeds, plant parts and shells, and sometimes even yield buried artifacts and human remains. Combined with proper dating methods, these proxies can provide unique information about past environments, climates and cultures. Finally, peatlands play an important part in the global carbon cycle. Their role as a long-term sink for carbon has mostly been recognized since the publication of the keystone paper by Gorham (1991) that stated that boreal and subarctic peatlands store about one-third of the terrestrial carbon pool. The number of scientific papers published annually that are dealing with different aspects of the role of peatlands in the global carbon cycle has been steadily increasing since then.

1.1. Research context: peatlands in the global carbon cycle

The quantity of carbon (C) stored in a peatland results from the net imbalance between C uptake, and C emission or export. Peatland plants take up atmospheric carbon dioxide (CO_2) through photosynthesis (gross primary productivity, GPP) and plants and microorganisms respire CO_2 to the atmosphere (ecosystem respiration, ER). The balance between GPP and ER is termed net ecosystem productivity (NEP), which is equivalent to the inverse of net ecosystem exchange (NEE) in the absence of lateral movement of C (Chapin *et al.*, 2006). However, C is also lost from peatlands through methane (CH_4) emissions from methanogenic bacteria under low redox potential, although there is some uptake of CH_4 by methanotrophic bacteria in oxic surface layers. Additionally, some C is exported in runoff in the form of dissolved organic carbon (DOC), or lost through combustion. The balance of all C fluxes, imports and exports in all forms leading to net accumulation (or loss) of C in the system is termed net ecosystem carbon balance (NECB, Chapin *et al.*, 2006). On a yearly basis, C uptake is generally higher than C emissions or exports: peatlands are therefore long-term sinks for C.

Northern peatlands have accumulated C at a mean long-term rate of about 15-30 g C m^{-2} yr^{-1} since their initiation (Ovenden, 1990; Vitt *et al.*, 2000; Turunen *et al.*, 2002, 2004). As a result, it has been estimated that between approximately 250 and 500 Gt C are stored in peatlands worldwide (Vasander and Kettunen, 2006), which between a quarter and one half of the actual total atmospheric C (approx. 730 Gt). Therefore, peatland C, if released, has the potential to significantly increase the atmospheric C burden. However, peatlands are, in turn, particularly vulnerable to disturbances driven by climate change (Turetsky *et al.*, 2002). About 60 % of the peatlands in Canada are found in areas that are expected to be severely affected by climate warming (Kettles and Tarnocai, 1999). Climate change scenarios predict that although they might receive increased precipitation, northern continental regions will also experience higher summer temperatures that will increase evapotranspiration (IPCC, 2007). Depending on the timing of precipitation and on factors such as water contribution from melting snow, the overall result could be lower water tables during the growing season.

As stated earlier, the quantity of C stored in the peat depends on the imbalance between production and decomposition of organic matter. This imbalance is mainly controlled by the wetness of the peatland, usually described by the water table depth (Belyea and Malmer, 2004; Malmer and Wallén, 2004). However, long-term processes resulting from hydrological changes, such as vegetation succession, also play a major role in the biogeochemistry of peatlands (Belyea and Malmer, 2004; Bauer, 2004). Peatlands are entirely composed of organic material, mainly plant residues. The rate at which peat decomposes depends on the amount and quality of litter input, which changes as vegetation composition and productivity changes in response to changing hydrological conditions.

1.2. Research question and objectives

The relationship between vegetation communities and the physical and chemical settings of peatlands has largely been demonstrated through various studies relating environmental gradients and vegetation composition in different types of peatlands (e.g. Glaser *et al.*, 1990; Andersen *et al.*, 1995; Bridgham *et al.*, 1996; Wheeler and Proctor, 2000). However, the impact of long-term processes such as vegetation succession on peatlands' biogeochemistry has seldom been addressed. To elucidate the role of vegetation succession in C dynamics is a critical step in getting peatland ecosystem biogeochemical models to include the vegetation response to changing environmental conditions. My main research question is therefore: what is the impact of a long-term (decadal) water table drawdown on the vegetation succession and, in turn, how does vegetation succession alter the C dynamics of peatlands?

The overall objectives of my thesis are (1) to examine how a peatland vegetation community changes in response to long-term water table drawdown; (2) to assess how the changes in water table depth and vegetation community structure lead to changes the carbon functioning of the system; and (3) to investigate if the changes in vegetation communities lead to a change in the net C balance of the system.

More specifically, I explore the link between species composition and spatio-temporal water table distribution and I establish how changes in wetness relate to changes in aboveground biomass partitioning between species, lifeforms and plant parts. I relate the combined and individual effects of changes in species composition and water table depth to measured and modelled C dynamics. Finally, I assess if vegetation changes alter the amount of C accumulated in peatlands, both as peat and as living biomass.

1.3. Methodological approach

The water table of peatlands could drop by about 15 cm with a doubling of the atmospheric CO_2 concentration, due to increased evapotranspiration (Roulet *et al.*, 1992). This drop is of the same order of magnitude as the average water table drawdown following the digging of drainage ditches for forestry purposes. Hence, artificial drainage could be a reasonable empirical analog for assessing long-term effects of climate change on vegetation dynamics and C storage of peatlands (Laine *et al.*, 1995; Minkkinen *et al.*, 2002).

Some authors have studied the effect of a water table drawdown in peatlands by regulating the water level into isolated monoliths (e.g. Blodau *et al.*, 2004; Weltzin *et al.*, 2003). Although these manipulations can give an indication of the short-term response of vegetation and micro-organisms to a sudden change in environmental conditions, they do not capture many of the feedbacks that are operating on a longer term, as species replace and peat subsides. The results are also likely to be influenced by edge effects due to the relatively small size of the micro- or mesocosms generally used. In contrast, studies using drainage that was originally done for agricultural or forestry purposes occur *in situ*, hence parts of the peatland are not moved to an unrealistic physical setting. Another drawback of monolith experiments is that the artificial control of the water table does not represent the natural variability of a system open to climate. Drainage sites retain the natural variability in the distribution of water table depths that follow daily and seasonal patterns and respond to extreme weather events.

I studied the response of vegetation (using relevés, biomass plots and paleoecological reconstructions) and C dynamics (through gas fluxes and peat C content measurements) to water table drawdown along a transect perpendicular to a drainage ditch crossing the Mer Bleue bog in Eastern Ontario. The ditch was dug 85 years ago and the drained portion has been left untouched since then. I also used a peatland ecosystem model, the Holocene Peatland Model (HPM) to simulate the impact of a water table drawdown on vegetation dynamics and peat C storage based on parameters partly derived from my field experiments.

1.4. Thesis outline

In addition to this introductory chapter (Chapter 1), this thesis is composed of six main chapters. Chapter 2 synthesizes the current state of knowledge regarding peatland structure and function in the global C cycle, as well as responses of peatlands to disturbances with an emphasis on vegetation succession. Chapters 3 to 6 are the main core of my thesis and each presents a manuscript in preparation or accepted for publication to a peer-reviewed journal. Chapter 3 presents how the combined use of paleoecological reconstructions and vegetation and environmental characterizations along a hydrosequence can help us understand long-term post-drainage hydrological and vegetation dynamics in a peatland. Chapter 4 presents an evaluation of the influence of drainage on aboveground biomass and an important ecophysiological parameter, leaf area index (LAI). In Chapter 5, the C dynamics along the same hydrosequence are analyzed through CH_4 and CO_2 flux measurements, and peat and biomass C content evaluation. Chapter 6 presents how empirical observations derived from this study can help improve simulations of long-term peatland C dynamics following a disturbance using the HPM model. In conclusion (Chapter 7), I explain how my results give insights on the possible ways that peatland vegetation can change in response to a disturbance and how this might influence their role in the global C cycle. I also identify knowledge gaps highlighted by my results.

Chapter 2 – Peatlands: water, plants and carbon

Peatlands are long-term sinks for carbon (C). However, unlike fossil C deposits such as coal, oil and gas, peatlands are living ecosystems and the amount of C that they store is directly affected by the climatic conditions. Their role in the global C cycle could therefore be altered as the climate changes, even in the absence of direct exploitation by humans. The function of peatlands as long-term C sinks is regulated by their water balance and vegetation composition, and by the interaction of the two. Indeed, peatlands are amongst the ecosystems where the interconnection between life, water and biogeochemical cycles is most tightly linked. This literature review addresses the complexity of this interrelation. After defining what are peatlands (section 2.1) and outlining their extent and distribution at the global scale (section 2.2), I explain the role of peatlands in the global C cycle (section 2.3), I give an overview of the way the vegetation of these generally stable ecosystems develops over time in response to internal or external forcing (section 2.4), and I relate the possible impacts of climate change with peatlands' C dynamics as mediated by vegetation succession (section 2.5).

2.1. Peatlands: definition and terminology

All peatlands are characterized by having a living plant layer growing over accumulated plant detritus. This peat accumulation results from a permanent water excess that prevents decay processes from compensating annual biomass production. The peat mat can grow vertically and spread horizontally for millennia, reaching several meters in height and therefore can become isolated from the hydrological contributions from surrounding areas. As acidity, low nutrient content and high concentration in toxins often complete the picture, peatlands are commonly considered as extreme environments for plant growth, and they usually support highly specialized vegetation.

There is no universally agreed on definition of the term "peatland": ecologists, soil scientists or the horticultural industry, for example, might have very different ideas of what a peatland is. The Canadian Wetland Classification System defines peatlands as organic wetlands where stable water levels and decreased nutrient availability promote a peat accumulation of at least 40 cm (National Wetlands Working Group, 1997). However, this number is rather arbitrary and other definitions use different values for the minimum depth of peat (Charman, 2002).

Many criteria have been used to classify the different types of peatlands, including hydrology, floristics, acidity, alkalinity, origin of the peatland or topography (Gorham and Janssens, 1992; Wheeler and Proctor, 2000). One of the most prevalent categorizations is between bogs and fens, with fens frequently subdivided further into poor and rich. Bogs are usually defined as ombrotrophic systems, meaning that they receive all their nutrients and water from atmospheric sources. They therefore tend to be acidic and low in nutrients. Minerotrophic peatlands, or fens, receive inputs from areas outside of their own limits; they are known to be more nutrient-rich and alkaline, although poor fens are weakly minerotrophic systems that often present more similarities with bogs than with fens in terms of vegetation composition, pH and fertility.

The pertinence of the widely used bog-fen categorization has often been questioned. Several authors argue that the terms bog and fen should be used in reference to the dominant vegetation communities and acidity of the peatlands rather than their water or nutrient source or their topography (Gorham and Janssens, 1992; Damman, 1995; Bridgham *et al.*, 1996; Wheeler and Proctor, 2000). Bogs would then refer to acidic, low alkalinity peatlands dominated by *Sphagnum* mosses, ericaceous shrubs and trees, whereas fens would refer to less acidic and more alkaline peatlands dominated by graminoids, brown mosses, and sometimes, shrubs and trees. Wheeler and Proctor (2000) recommend the further subdivision of bogs and fens based on their fertility.

2.2. Peatlands in the world – extent and distribution

Peatlands are the most common wetland type in the world. However, estimates of their extent and distribution are far from precise. When peatlands are defined as soils with more than 50 % organic matter and with a peat accumulation of at least 30 cm, their global extent has been estimated to be around 400-500 million ha (Charman, 2002; Rydin and Jeglum, 2006), which represents 3-4 % or the world’s land surface. In northern areas, the most extensive peatlands are found in Canada, Alaska, Scandinavia, Russia and the Baltic states, where the cool and moist climate prevents rapid decomposition of organic matter (Vasander *et al.*, 2003; Kremenetski *et al.*, 2003; Tarnocai *et al.*, 2005). Tropical peatlands, representing approximately 15-20 % of all peatlands, are mostly present in the very wet regions of Southeast Asia, and the Amazon and Congo River basins (Page *et al.*, 2006; Rydin and Jeglum, 2006).

In Canada, peatlands cover approximately 113.6 million ha, or 12 % of the land area, with 97 % occurring in the boreal and subarctic regions (Tarnocai *et al.*, 2005). A little more than two-thirds of these peatlands are bogs (Tarnocai, 2006). Less than 5 % of the Canadian peatlands are drained or altered for agriculture or forestry, or harvested for fuel or horticulture (Rydin and Jeglum, 2006). Hence, although industrial pressure might be locally damaging to peatlands' functions (see for example Calmé *et al.*, 2002), the biggest threats to Canadian peatlands are more likely to be the direct or indirect effects of climate change, such as lowered water tables, increased fire frequency or permafrost melt (Moore *et al.*, 1998; Robinson and Moore, 2000; Turetsky *et al.*, 2002; Lavoie *et al.*, 2005). Peatlands' vulnerability to climate change is critical since they themselves play an important role in the global C cycle.

2.3. The role of peatlands in the carbon cycle

The C content of peat from pristine peatlands is usually between 45 and 55 % of the total dry weight (Gorham, 1991; Bauer *et al.*, 2006). As peatlands cover large areas and often accumulate several meters of peat, they store a substantial amount of C. Because the assessments of the global area covered by peatlands are not precise, estimates of the total amount of C stored in peat vary from 234 to 679 Pg C (Bridgham *et al.*, 2006), with a central figure of around 462 Pg C (Maltby and Immirzi, 1993). Northern peatlands hold the greater proportion of this C, between 250 and 370 Pg C (Turunen *et al.*, 2002). In Canada, ≈ 157 Pg C is stored in peatlands, which represents a considerable proportion of the total 220 Pg C stored in the plants and soils of all North American wetlands (Tarnocai *et al.*, 2005; Bridgham *et al.*, 2006). The way this major C pool will change with time is difficult to predict, as rates of C accumulation vary considerably, both spatially and temporally (e.g. Ohlson and Økland, 1998; Vitt *et al.*, 2000; Borren *et al.*, 2004; Malmer and Wallén, 2004).

2.3.1. Rates of carbon accumulation in peatlands

Most of the world's peatlands that are currently still accumulating C were initiated in the last 16.5 thousand years, with rapid extension during the early Holocene, between 12 and 8 thousands of years ago (MacDonald *et al.*, 2006). Peatland basal dates are closely related to deglaciation history in specific regions (Kuhry and Turunen, 2006; Gorham *et al.*, 2007). Since their initiation, peatlands have accumulated C at different rates, depending on their location and vegetation assemblages, and on climatic factors.

Long-term C accumulation rates reported in the literature for different types of peatlands can vary from less than 5 to over 100 g C m^{-2} yr^{-1} (e.g. Robinson and Moore, 2000; Vardy *et al*, 2000; Turunen *et al.*, 2002; Gorham *et al.*, 2003; Borren *et al.*, 2004), with an average between 15 and 30 g C m^{-2} yr^{-1} for northern peatlands (Ovenden, 1990; Vitt *et al.*, 2000; Turunen *et al.*, 2002, 2004). The rates depend not only on peatland characteristics, but also on the age span of the cores and methodologies used for calculating accumulation rates (for a discussion on possible error sources in accumulation calculations, see Kuhry and Turunen, 2006). For eastern Canadian peatlands, the long term apparent rate of C accumulation is on average around 19 g C m^{-2} yr^{-1} (Turunen *et al.*, 2004). A study conducted on Swedish bogs concludes that a combination of higher nitrogen deposition and drying of the surface of bogs result in a decrease in the recent C accumulation rates (Malmer and Wallén, 2004). Changes in peat accumulation over the development of peatlands or between peatlands have been related to permafrost dynamics (Robinson and Moore, 2000; Vardy *et al.*, 2000), fire frequency (Turetsky *et al.*, 2002; Robinson and Moore, 2000), latitude (Vardy *et al.*, 2000; Kuhry and Turunen, 2006), precipitation or wetness of the peatland (Mäkilä *et al.*, 2001; Gorham *et al.*, 2003; Borren *et al.*, 2004; Malmer and Wallén, 2004) and vegetation type (Borren *et al.*, 2004; Kuhry and Turunen, 2006). Bogs have generally higher rates of accumulation than fens, mostly because *Sphagnum* species are more resistant to decomposition than sedges (Kuhry and Turunen, 2006).

2.3.2. The carbon balance of peatlands

The accumulation of C in peatlands is the result of an imbalance between the C inputs (through photosynthetic uptake of CO_2 and possibly CH_4 uptake) and outputs (through autotrophic and heterotrophic respiration, CH_4 emission and DOC export). Carbon losses could also occur as a result of peat combustion or erosion, or through human withdrawal of peat (Figure 1).

Gross primary production (GPP) is the rate at which primary producers fix C through photosynthesis. When autotrophic (plant) respiration is subtracted from GPP, the result is the net primary production (NPP). Peatlands' NPP is primarily controlled by light, nutrient and water availability, temperature and plant types, which lead to great spatial and temporal variability in NPP of bogs and fens (Szumigalski and Bayley, 1996; Thormann and Bayley, 1997; Weltzin *et al.*, 2000; Lindroth *et al.*, 2007). The NPP of peatlands commonly ranges between 100 and 400 g m^{-2} yr^{-1} (Blodau *et al.*, 2002), which is generally lower than in most other ecosystems, including other types of wetlands (Thormann and Bayley, 1997; Scurlock and Olson, 2002). Hence, peat accumulation is not the result of a particularly high NPP, but of rather low rates of decomposition (Charman, 2002).

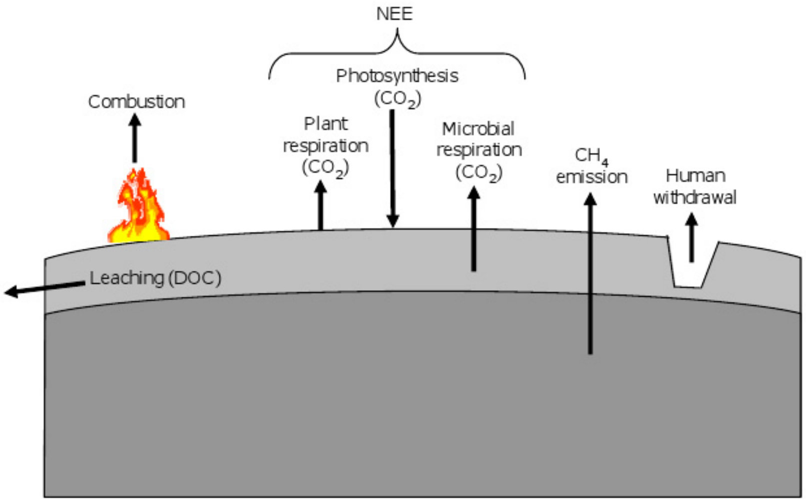

Figure 2.1 – Simplified representation of the total C balance in peatlands, including dominating fluxes and exports.

Many characteristics of peatlands or peatland environments impair the capacity of the decomposers to mineralize C, including anoxia, low pH, cool temperatures, and the input of decay-resistant litter, especially *Sphagnum* mosses and ericaceous shrubs (Aerts *et al.*, 1999; Yavitt *et al.*, 2005; Moore *et al.*, 2007). The decomposition of litter and peat is primarily conducted by the aerobic microbial community living in the acrotelm. Decay in anoxic conditions is several orders of magnitude slower than in oxic zones, with a decomposition constant (k_d) as low as 10^{-7} a^{-1} in deep catotelm compared to between $3.4 \cdot 10^{-2}$ and $7 \cdot 10^{-2}$ a^{-1} in the uppermost acrotelm (Beer and Blodau, 2007; Blodau *et al.*, 2007). The relative contribution of the different types of decomposers to total decay is not well known, but both fungi and bacteria seem to play an important role in aerobic decomposition (Thormann *et al.*, 2004). Anaerobic bacteria, active in the saturated portions of the peat, also contribute to organic matter decay, but to a much lesser extent than aerobic decomposition.

The end product of decay processes can be CO_2, CH_4 or DOC. These C forms might leave the system through gaseous emissions (CO_2, CH_4) or dissolved in water (DOC). The C balance of a system, taking into account all the inputs and outputs in any form, has recently been termed net ecosystem carbon balance (NETB) by Chapin *et al.* (2006). The difference between the CO_2 uptake by plants and the CO_2 emitted by autotrophic and heterotrophic respiration is termed net ecosystem production (NEP). Net ecosystem exchange (NEE), the CO_2 flux from the ecosystem to the atmosphere, is approximately the equivalent of [-NEP], and it is commonly measured using the eddy covariance technique (Baldocchi, 2003). NEE is therefore, by convention, negative when there is a net CO_2 uptake by the ecosystem, which is usually the case for peatlands. A peatland's annual NECB is usually positive, meaning that the ecosystem accumulates C, but can become negative depending on the climatic conditions (Roulet *et al.*, 2007). In general, peatland NEE decreases under wet conditions (thus the net CO_2 uptake by the peatland increases), mostly due to decreased respiration (Carroll and Crill, 1997; Alm *et al.*, 1999a; Bubier *et al.*, 2003a; Lindroth *et al.*, 2007; Yurova *et al.*, 2007).

Peatlands are generally known as sources of CH_4 to the atmosphere, although the magnitude and direction of CH_4 fluxes depend on the water table depth, peat temperature and vegetation composition (Bubier, 1995; Ström *et al.*, 2005; Pelletier *et al.*, 2007). Methane is produced in anoxic conditions by the methanogenic bacteria, in the portion of the peat profile that is below and slightly above the water table (capillary fringe). Part of the CH_4 produced is consumed in the oxic zone above the water table by methanotrophic bacteria. Therefore, the thickness of the unsaturated zone (as determined by the water table depth) controls the CH_4 production/consumption balance and thus, the magnitude of emissions. Vascular plants affect CH_4 emissions by increasing the C-substrate availability belowground (e.g. Ström *et al.*, 2003), by providing an oxic environment around the roots where CH_4 can be consumed (e.g. Watson *et al.*, 1997) and a rapid transit pathway for CH_4 through their vascular system that bypasses the unsaturated zone and reduces the chances of consumption by the methanotrophs (e.g. Frenzel and Rudolph, 1998).

Peatlands are an important source of C for downstream aquatic ecosystems. A small part of the C stored in peatlands is exported via the drainage water as DOC. The amount of DOC produced and exported from peatlands has been related to vegetation composition (Moore and Dalva, 2001; Turetsky, 2003), temperature (Freeman *et al.*, 2001), peatland wetness (Clark *et al.*, 2005; Worrall *et al.*, 2006), discharge (Urban *et al.*, 1989; Pastor *et al.*, 2003) and acidity (Clark *et al.*, 2005; Evans *et al.*, 2006).

Peatlands also experience potentially important C losses through the combustion of biomass and peat (Pitkänen *et al.*, 1999; Turetsky *et al.*, 2002; Ward *et al.*, 2007). Other potential C exports could result from the removal of C through peat mining (Cleary *et al.*, 2005) and peat erosion and water or wind transport following peat mining or fire (Evans *et al.,* 2006; Yeloff *et al.*, 2006). Wood harvesting on forested peatlands (Minkkinen *et al.*, 2002) and herbivory by wild animals or cattle (Ward *et al.*, 2007) also remove C from the peatland pool via living biomass losses.

The C pools of peatlands can also be affected by changes in other components of the system. The quality, and therefore, the decomposability of the organic matter accumulated in peat depend on the type of vegetation growing at the surface. Hence, although it is hard to demonstrate, it is reasonable to assume that long-term vegetation changes ultimately affect the C balance of peatlands.

2.4. Peatland dynamics: vegetation succession

Peatlands are dynamic systems that respond to various autogenic (arising from internal processes) and allogenic (arising from external processes) factors or an interaction of the two. Autogenic factors include biotic processes leading to the accumulation of the peat mat and related hydrological processes, biotic processes associated with plant types (i.e. life expectancy), and physical processes including soil movement and freeze-thaw cycles (Charman, 2002). Autogenic changes can take place under stable external conditions (e.g. pedogenic changes), but often are accelerated or inhibited by allogenic factors such as climate, fire, hydrological factors and volcanic influences.

Vegetation succession is the dynamic process of plant community change over time, in response to allogenic and/or autogenic drivers (Cowles, 1899; Clements, 1916; Schulze *et al.*, 2002). Changes in vegetation through the developmental history of peatlands and changes resulting from contemporary climatic factors are explored in this section.

2.4.1. Peatland development

Peat accumulation is initiated whenever the decomposition of organic matter becomes slower than the rate of production. This usually happens in wet and/or cold environments, and where the landscape characteristics prevent rapid drainage of surface waters. Two main processes leading to peatland formation are widely recognized. Terrestrialization is the process by which open water is gradually infilled by sediments and invaded by vegetation. Paludification is the process of peat formation over mineral soil, often following a change in the local or regional hydrological conditions, sometimes as a result of global climatic changes. Peatlands initiated through terrestrialization frequently expand laterally via paludification of surrounding lands. Therefore, a greater area of peatlands has been initiated through paludification rather than terrestrialization (Kuhry and Turunen, 2006).

Once peat accumulation is initiated, the long-term development of a given peatland can follow different trajectories, depending on site characteristics, interactions with environmental factors and chance, although common successional pathways are encountered. Hydroseral succession is probably the most prevalent autogenic peatland development pathway (Charman, 2002; Bunting and Warner, 2002). It starts when open water is gradually infilled by sediments and invaded by aquatic plants (terrestrialization) that eventually thrive in a fen stage. As the peat mat grows, the surface gets isolated from water and nutrient inputs from the surroundings, which leads to a bog phase, where the vegetation is dominated by *Sphagnum* mosses and woody vegetation. Bogs can eventually dry out to form woodlands, which are sometimes considered as the end product of hydroseral succession. This very general pattern is rarely followed entirely or in sequence (Klinger, 1996), and the course of succession can skip stages or come back to previously encountered stages (e.g. Bunting and Tipping, 2004). The later stages of hydroseral succession can also be observed in peatlands from paludified sites (Kuhry and Turunen, 2006).

Although the general development of many peatlands is dominated by autogenic factors (Payette, 1988; Zimmermann and Lavoie, 2001; Anderson *et al.*, 2003), climate or regional hydrological conditions were frequently reported in peatland paleoecological studies as primary or secondary drivers for community changes, including the transition from fen to bog (Kuhry *et al.*, 1993; Lavoie and Richard, 2000; Bauer *et al.*, 2003; Glaser *et al.*, 2004). The transition to ombrotrophy can be achieved through different pathways, either through a dry or a wet phase (Hughes and Barber, 2004). Higher vertical accumulation (wet phase) or lower water table (dry phase) could both isolate the fen from surrounding water and trigger a switch from minerotrophy to ombrotrophy. A fen-bog transition preceded by a wet phase was observed in southern Québec (Lavoie and Richard, 2000). However, drying of fen surfaces does not always lead to ombrotrophy as very alkaline conditions can prevent *Sphagnum* growth. Yu *et al.* (2003) rather observed the transition from open fen to forested fen due to an allogenic drying of a fen surface.

Many peatland development pathways culminate in bogs, with little changes in vegetation composition over centuries and even millennia (Rydin and Barber, 2001; McMullen *et al.*, 2004; Hughes and Barber, 2004). Bogs are generally known as stable ecosystems (Charman, 2002). This stability is mostly due to the dominance of the *Sphagnum* mosses, which have a clear competitive advantage over vascular plants in waterlogged and nutrient-poor environments. *Sphagnum* mosses not only outcompete vascular plants in anoxic and nutrient-poor environments, they also create their own optimal environment by building further anoxic, nutrient-poor, cold and acidic peatlands (van Breemen, 1995). However, despite their stability, bogs still can experience rapid and widespread changes as a result of important disturbances, including the direct and indirect influence of climate change (Pellerin and Lavoie, 2003).

2.4.2. Direct and indirect effects of climatic change on peatland plant communities

It is well accepted that an increase in the concentration of CO_2 and other greenhouse gases in the atmosphere results in higher average global temperatures and disturbed precipitation regimes (IPCC, 2007). Peatland vegetation communities might respond to the direct effect of an increased temperature and higher atmospheric CO_2 concentration. Other important possible impacts of climate change on peatlands are indirect, as increased fire frequency (Flannigan *et al.*, 2001; Turetsky *et al.*, 2002) and permafrost thaw (Payette *et al.*, 2004; Camill, 2005; Turetsky *et al.*, 2007). In addition to the projected changes in precipitation (which are region- and season-dependent), summer water table could drop due to higher evapotranspiration. Indeed, the lower water table observed in Swedish bogs since the 1970s is correlated to higher annual temperature (Schoning *et al.*, 2005), while lower water tables in peatlands from Estonia and England are correlated to lower precipitation and, secondarily, to higher summer temperatures (Charman *et al.*, 2004).

In order to predict the response of peatland vegetation communities to climate change, several approaches can be used. Since peatland plants, and especially bog plants, are persistent, long-term monitoring is needed to directly demonstrate any effect of climate change on vegetation (Nordbakken, 2000). Hence, long-term field-based monitoring of peatlands can give an idea of the changes occurring in the last few decades in response to climate forcing. However, very few studies have been able to demonstrate substantive contemporary changes in peatland vegetation and environments, and even less could relate those changes directly to climate warming.

The use of peatland archives to reconstruct peatland dynamics and to infer Holocene climate effects on peatlands have been the focus of many studies, especially in the northern hemisphere (Chambers and Charman, 2004). However, untangling the effect of autogenic and allogenic influences on vegetation changes from paleoecological records is a challenging task. Therefore, only a small proportion of these studies clearly relate observed patterns of vegetation succession with independent indicators of environmental variables including regional climate and water table depth.

Many studies are based on the direct manipulation of the peatland environment, either *in situ*, such as around drainage ditches, or in an artificial setting, such as microcosms. Finally, indirect approaches, mainly consisting of relating environmental gradients to vegetation communities, indicate vegetation needs in terms of environmental niches. Although each type of study has its drawbacks, taken together, they provide a glimpse of the possible fate of peatland vegetation communities following a climatic disturbance. The following sections give an overview of peatland vegetation's responses to climate change for each broad type of study.

2.4.2.1. Direct observations of climate change impacts on peatland vegetation

Paleoecological records show that an increased proportion of woody vegetation (shrubs and/or trees) can result from drier conditions in bogs (Kuhry, 1997; Bridge *et al.*, 1990; Hughes *et al.*, 2007). Conversely, a synchronous and rapid pine decline during the mid-Holocene in bogs from Ireland, England and Scotland has been linked to increased surface wetness (Mighall *et al.*, 2004; Bridge *et al.*, 1990). Drying of fens may isolate the peatland from surrounding contributions and therefore trigger or accelerate the transition to bog vegetation communities, although some fens are invaded by trees upon drying, as very alkaline conditions can prevent *Sphagnum* growth (Yu *et al.*, 2003).

Over the last 100 to 200 years, the invasion of open bogs by shrubs and increased tree growth has occurred in southern Québec (Pellerin and Lavoie, 2003) and Sweden (Malmer and Wallén, 2004). A drier climate, although potentially in combination with drainage or higher nitrogen input, might explain the shift in dominance observed in these multi-proxy studies. In a Swedish bog, Backéus (1972) found little vegetation community changes between 1910 and 1970, but observed a drying of open water surfaces due to a lowering of the water table. Gunnarson *et al.* (2003) re-investigated after 40 years a Swedish mire complex composed of a fen and a bog. Increased frequencies of shrubs were observed in both fen and bog. Tree and hummock bryophyte frequencies and overall diversity increased and *Sphagnum* cover decreased in the bog, while low-growing vascular plants frequencies and diversity decreased in the fen area. The pH in the fen area decreased significantly over the study period. According to the authors, these results are probably due to higher nitrogen deposition, acidification and increased dryness. Hughes *et al*. (2007) related *Betula* trees and *Molinia* grass invasions in Wales to increased nitrogen loading rather than desiccation. A dry year in Finland led to an apparently persistent *Sphagnum* species replacement (Alm *et al.*, 1999a). Finally, Bragazza (2006) related an increase in ericaceous shrubs and a decrease in graminoids to the lowered water table resulting from the growth of the peat mat over a 10 year period in an Italian bog.

Fire did not change the long-term vegetation development of *Sphagnum*-dominated bogs of western Canada (Kuhry, 1994). However, the successful colonization by bryophytes immediately after fire could depend on the wetness of the site (Benscoter, 2006), and in the case of severe fires, large areas may remain unvegetated several years after burning (Maltby *et al.*, 1990). A recent study identifies different phases in post-fire recolonization of bogs by bryophytes, with the most changes occurring in the first 10 years (Benscoter and Vitt, 2008). After a decade of rapid successional changes, *Sphagnum fuscum* eventually dominates the ground layer, which remains relatively stable afterwards.

Vegetation changes following permafrost thaw can be very fast (Beilman, 2001). Loss of permafrost mires in northern Europe and Canada led to changes in species distribution and structure and losses of distinct plant communities (Luoto *et al.*, 2004; Beilman, 2001; Camill, 2005). The increased wetness following the thaw of permafrost plateaus in peatlands favours the growth of graminoids, whereas the growth of trees and of some bryophyte species is suppressed (Beilman, 2001; Malmer *et al.*, 2005). Christensen *et al.* (2004) saw an increase in the wet graminoid communities at the expense of shrub-dominated, drier communities with permafrost thaw in Swedish peatlands between 1970 and 2000. Camill (2005) suggests that the current warming trend may well eliminate most permafrost peatlands in Manitoba by 2100.

2.4.2.2. Experimental observations of climate change impact on peatland vegetation

Elevated atmospheric CO_2 concentration has been simulated using mini-FACE systems in peatlands (Miglietta *et al.*, 2001). The effects of raised CO_2 concentration on plant growth are unclear. Increased CO_2 was found both to increase (Heijmans *et al.*, 2001) and to decrease (Fenner *et al.*, 2007) *Sphagnum* growth. Toet *et al.* (2006) conclude that although increased CO_2 initially stimulates *Sphagnum* growth, after one year, it inhibits *Sphagnum* growth. Although some studies show that a CO_2 “fertilization” is unlikely to occur in nutrient-poor systems (Berendse *et al.*, 2001; Jauhiainen *et al.*, 1997), other studies show that increased CO_2 increases gross photosynthesis and above- and belowground biomass (Saarnio *et al.*, 2003; Fenner *et al.*, 2007).

Increased temperature and/or water table modifications affect vegetation composition and primary production of both bogs and fens. Shrub cover increased and graminoids cover decreased in response to higher soil temperature in bog mesocosms (Weltzin *et al*., 2003). Advanced flowering and increased flower production were observed in a subarctic Swedish bog in response to increased spring temperatures in open-top chambers (Aerts *et al.*, 2004). *Sphagnum balticum*’s production decreased with increasing temperature in a greenhouse enclosure in a Swedish poor fen (Gunnarson *et al.*, 2004). Other studies show a shift in *Sphagnum* species’ relative abundance in response to warming (Breeuwer *et al.*, 2008; Robroek *et al*, 2007a) and an increase in *Sphagnum* biomass with increased summer temperature (Dorrepaal, 2004). In fen mesocosms, higher temperatures lead to increased graminoid and forb production (Weltzin *et al.*, 2000).

Water table lowering also leads to increases in shrub cover in bogs mesocosms (Weltzin *et al.*, 2003; Breeuwer *et al.*, in press). Weltzin *et al.* (2001) measured a greater increase in belowground shrub biomass (100 %) as compared with aboveground biomass (30 %). As was the case for the increased temperature treatments, a *Sphagnum* species shift was observed following water table drawdown treatments (Robroek *et al.*, 2007a; Robroek *et al.*, 2007b; Breeuwer *et al.*, in press). Another study showed an overall decrease in *Sphagnum* growth with lower water tables (Toet *et al.*, 2006). Fen communities responded to water table manipulations with increases in graminoid coverage with a higher water table and increases in shrub coverage with a lower water table (Weltzin *et al.*, 2003). In contrast, experimental flooding of a boreal basin peatland comprising a treed bog and an open bog resulted in the death of almost all trees and an 86% decrease in living biomass (Taro *et al.*, 2005).

Most studies addressing the various impacts of drainage of peatlands for forestry or experimental purposes were conducted in Europe on sparsely treed fens. In fens, drainage usually results in an increased coverage of woody vegetation, both shrubs and trees, and a diminution of the coverage of species adapted to wet conditions, such as *Sphagnum* mosses (Laine *et al.*, 1995; Silvola *et al.*, 1996; Minkkinen *et al.*, 1999; Macdonald and Yin, 1999; Strack *et al.*, 2006). Strack *et al.* (2006) showed that the impact of drainage on vegetation is microform-dependent, at least in the first decade following drainage. Post-drainage conditions also lead to increases in primary production and living biomass (Laiho *et al.*, 2003). In bogs, tree biomass increases following drainage, but to a lesser extent than in fens (possibly due to a nutrient limitation), and changes in vegetation composition are less important (Minkkinen *et al.*, 1999; Vasander, 1982).

2.4.2.3. Gradient studies

Many studies related peatland vegetation composition with various environmental gradients inside and between peatlands. Although these studies are not meant to show a response of vegetation communities to changing climatic conditions, they can give an indication of the way peatland vegetation might respond to climate-driven changes, and especially to changes in the wetness of the peatlands. Water level is one of the major factors controlling the composition of plant communities between and within bogs and fens around the world (Nekola, 2004; Camill, 1999; Glaser *et al.*, 1990; Kleinebecker *et al.*, 2007). In bogs, shrub biomass dominates dry hummocks, whereas moss and sedge biomass dominates wetter microsites, such as hollows and lawns (Moore *et al.*, 2002; Thormann and Bayley, 1997; Bubier, 1995). Bryophyte species distribution also follows water table depth (Anderson *et al.*, 1995; Bubier, 1995; Belland and Vitt, 1995). Laitinen *et al.* (2008) recently identified the water table fluctuations as an important gradient explaining peatland species distribution, alongside average water table level.

2.5. Carbon cycling in peatlands and climate change: the mediating effect of vegetation

The different components of the C balance of peatlands are directly influenced by the effects of climate change, such as higher temperatures, changes in precipitation and evapotranspiration, increased fire frequency and permafrost thaw. However, as seen in the previous section, climate change also induces changes in the vegetation communities, which in turn will affect peatlands' C uptake and release. This section describes how global warming might (1) affect the production/decomposition balance of peatlands, with a special emphasis on the possible changes mediated by the plant communities; (2) modify the CO_2, CH_4 and DOC balance of peatlands, and (3) change the long-term C function of peatlands, both in peat and in living biomass.

2.5.1. Production and decomposition of organic matter

Changes in plant distribution and growth could modify the production vs. decomposition balance of peatlands in different ways. A change in vegetation composition and growth can affect (1) C uptake by plants via net primary production, (2) the rate of decomposition as a result of a change in litter quality and quantity, (3) the rate of decomposition through the indirect influence of plant types and root biomass on microbial communities, and (4) the production and decomposition rates through the indirect effect of plant community structure on the microclimate of the peatland, especially peat temperature, snow accumulation and evapotranspiration.

Any change in NPP as a result of changes in growth rates, length of the growing season or through a replacement of some species by more or less productive ones, could affect the C balance of peatlands. Higher infrared loading increased shrub aboveground NPP and decreased herb aboveground NPP in bogs and increase herb aboveground NPP in fens (Weltzin *et al.*, 2000). The NPP of the different plant functional types of bogs and fens are related to the average water table level. Total NPP (above and belowground) typically increases following drainage in peatlands (Minkkinen *et al.*, 1999; Laiho *et al.*, 2003). Herb aboveground NPP is generally higher as the water table gets closer to the surface, whereas shrubs and trees show the opposite trend (Thormann and Bayley, 1997; Weltzin *et al.*, 2000). Total belowground NPP was found to increase with lower water tables in bogs, whereas a drying treatment did not affect belowground NPP in fens (Weltzin *et al.*, 2000). Moss NPP can be primarily influenced by climatic factors (Thormann and Bayley, 1997) or by the water table level, with higher production in wetter conditions (Weltzin *et al.*, 2000; Moore *et al.*, 2002). Despite a radical change in plant species and functional groups coverage, aboveground NPP did not change following permafrost thaw in boreal peatlands of Manitoba (Camill *et al.*, 2001).

Although the production rate of organic matter might influence the C balance of peatlands in the long run, decomposition processes are the main controlling factors in peatlands' C storage capacity. Variations in organic matter decomposition are explained by litter quality, temperature and soil moisture and, to a lesser extent, soil chemistry (Walse *et al.*, 1998; Laiho *et al.*, 2004). These factors ultimately control the decomposer community, comprising microorganisms (Mitchell *et al.*, 2003) and, in drained peatlands, mesofauna (Silvan *et al.*, 2000). Litter quality, which is the direct result of the relative proportion of the dominant vegetation types (*Sphagnum* mosses, sedges, shrubs, deciduous and coniferous trees), is likely to have a major influence on peat accumulation through its variable decomposability (Bauer, 2004). Increased NPP following drainage in fens leads to changes in the quantity and quality of annual litterfall, but not necessarily on fresh litter decomposition rates (Laiho *et al.*, 2004).

Vegetation dynamics might have an effect on microbial communities, although the succession of microorganisms in response to vegetation changes has not yet been explored in peatlands. Increased root biomass may enlarge the foraging domain of microorganisms and a possible increase in root exudates may enhance microbial activities and mycorrhizal associations (Mitchell *et al*., 2003). This may lead to higher decomposition rates and hence, nutrient turnover. However, microbes encouraged by a more welcoming environment could vigorously compete with plant roots for available nutrients. The evaluation of microorganisms' importance in C cycling in peatlands, especially mycorrhizal associations, has not been addressed so far (Read *et al.*, 2004).

Vegetation affects the microclimate at the surface of the peatland and the temperature of the peat (e.g. Roulet *et al.*, 1997). Soil moisture is also very likely to be influenced by vegetation through evapotranspiration processes. Unlike vascular plants, *Sphagnum* mosses have no water transport organs. There is therefore no sustained supply of water to the surface of *Sphagnum* cushions under evaporative conditions, which limits the overall rate of water loss (Ingram, 1983). The presence and absence of trees would be particularly important in controlling evapotranspiration rates from mires (Eggelsmann *et al.*, 1993). In northern climates, the differential snow cover under contrasted vegetation structures could also have an influence on soil moisture by changing the amount of water available in spring through snowmelt. Peat temperature could also be influenced by the isolation effect of the snow mat.

2.5.2. CO_2 and CH_4 fluxes, DOC exchange

Because of the importance of peatlands as long term C sinks, several studies have measured the response of CO_2 and CH_4 production and/or exchange to changing environmental conditions through *in situ* eddy covariance and chamber measurements, inside mesocosms or through lab incubations. However, because of the short term span of many of these studies, very few have been able to pinpoint the role of changing vegetation in the C balance of the systems studied.

In general, more CO_2 is produced and emitted in peatlands under high temperatures and dry conditions. Lab incubations conducted on peats of different vegetal origin with varying temperature and moisture conditions identify all three factors as determinant in CO_2 emission rates (Moore and Dalva, 1993; Funk *et al.*, 1994). Microcosm and mesocosm studies with a living bog or fen vegetation layer or *in situ* artificial drainage generally show increased CO_2 emissions in dry conditions, as a result of increased ecosystem respiration, decreased GPP or a combination of both (Chimner and Cooper, 2003; Blodau *et al.*, 2004; Jaatinen *et al.*, 2008; Riutta *et al.*, 2007; Strack *et al.*, 2006). In contrast, although it responded to a warming treatment, ecosystem respiration did not differ between plant communities and water table treatments in a mesocosm experiment including monoliths from both bogs and fens (Updegraff *et al.*, 2001).

Vegetation changes, especially a replacement of *Sphagnum* by vascular plants, were accompanied by increased respiration and a reduction in NEE following an exceptionally warm summer in a bog in the Alps (Gerdol *et al.*, 2008). Dry summers in Canada and Europe led to decreased CO_2 uptake in bogs and fens, mostly as a result of increased respiration (Carroll and Crill, 1997; Bubier *et al.*, 2003a; Bubier *et al.*, 2003b; Lafleur *et al.*, 2003; Alm *et al.*, 1999a; Lund *et al.*, 2007). Reduced GPP was also found in dry conditions in bogs and fens, as a result of *Sphagnum* moss dessication (Alm e*t al.*, 1999a; Lund *et al.*, 2007).

Phenology and plant types are important factors to consider when trying to predict the impact of environmental conditions on photosynthesis (Glenn *et al.*, 2006; Griffis and Rouse, 2001; Bubier *et al.*, 2003a, 2003b). Early-season conditions seem to be particularly important in the growing season C budget. Griffis and Rouse (2001) showed, with a combination of field measurements and modelling, that a warm and wet spring in a northern fen, allowing an early leaf-out of vascular vegetation, has helped mitigating the effect of a mid-growing season drought on photosynthesis. Bubier *et al.* (2003a; 2003b) showed a differential response of different plant growth forms during a dry summer, where sedge photosynthesis was reduced, whereas deciduous and evergreen shrubs' photosynthesis was enhanced or, in the case of shrubs growing in an already dry bog, just slightly reduced. Riutta *et al.* (2007) measured a similar differential response of plant communities in response to drying in a fen, where shrubs' contribution to total CO_2 exchange gained importance as compared with sedges. Strack *et al.* (2006) measured increased photosynthesis in hollows and lawns of a poor fen, whereas hummocks' photosynthesis declined following long term *in situ* artificial drainage. Vegetation changes over the 20 years following drainage occurred on all three microforms, where hollows were invaded by *Sphagnum* mosses, laws were invaded by sedges and hummocks experienced a decrease in *Sphagnum* cover. A fen and a bog drained for forestry and invaded by trees had increased CO_2 emission as a result of increased respiration (Martikainen *et al.*, 1995). Ecosystem and soil respiration have been correlated with plant productivity (Bubier *et al.*, 2003a; Syed *et al.*, 2006). This is probably due to the increased microbial activity as a result of enhanced root exudation, mycorrhizal activity and CO_2 release by the roots (Tang *et al.*, 2005; Syed *et al.*, 2006).

Field and lab studies generally show that both bogs and fens with high water table (Keller *et al.*, 2004; Blodau *et al.*, 2004; Updegraff *et al.*, 2001; Funk *et al.*, 1994; White *et al.*, 2008) and increased temperature (Granberg *et al.*, 2001; Moore and Dalva, 1993; White *et al.*, 2008) produce and emit more CH_4. Similarly, within a fen or a bog, wetter microsites emit more CH_4 (Alm *et al.*, 1997; Waddington and Roulet, 1996; Bubier *et al.*, 1993; Bubier, 1995). However, relationships between environmental conditions at a daily time scale (e.g. water table fluctuations) are difficult to relate to CH_4 fluxes as a result of a time lag between CH_4 production and release (Blodau and Moore, 2003; Strack and Waddington, 2008).

Drainage has been shown to lower CH_4 emissions by about half from a fen in Quebec (Strack *et al.*, 2004) and a bog from Finland (Martikainen *et al.*, 1995), whereas drainage of a fen in Finland led to a net uptake of CH_4 (Martikainen *et al.*, 1995). A dry year in Finland decreased CH_4 emission in a bog's wet hollows and lawns (Alm *et al.*, 1999a) whereas a wet year resulted in higher CH_4 emission than average in a bog in Manitoba (Bubier *et al.*, 2005).

Methane emissions were shown to respond to changes in plant community dynamics (White *et al.*, 2008). Methane production and consumption depend on peat type (Moore and Dalva, 1993). Methane emissions are generally higher in fens than in bogs, as fens have generally higher water tables and support vegetation species that promote rapid transit of CH_4 to the surface (Strom *et al.*, 2003, 2005; Martikainen *et al.*, 1995). In contrast, a mesocosm study measured higher emission rates from a bog compared to a fen, partly as a result of higher plant productivity in the bog (Updegraff *et al.*, 2001; White *et al.*, 2008). White *et al.* (2008) showed that pore water chemistry and plant productivity, which changed in relationship to infrared loading and water table treatments in bog and fen mesocosms, were as important as the direct effects of changing temperatures and wetness in controlling CH_4 fluxes.

Permafrost thaw, as it generally results in higher water tables, increases CH_4 emissions in peatlands. Christensen *et al.* (2004) showed that permafrost thaw and vegetation changes have been associated with increases in CH_4 emissions of 22–66% between 1970 and 2000. Increased atmospheric CO_2 concentrations, as simulated through mini-FACE experiments, leads to increased CH_4 emission, although the ventilation system of the mini-FACE enclosures partly explains the increases (Saarnio *et al.*, 2000, 2003). No study was found that relates CH_4 emissions with fire in peatlands.

Most studies reporting DOC export from peatlands were conducted at the watershed scale, therefore any local change due to changing environmental conditions or plant communities is challenging to detect. Lowered water tables in bog mesocosms did not affect the rate of DOC production and release (Blodau *et al.*, 2004), which is consistent with the findings of Pastor (2003), who states that DOC movement and export in peatlands depend on discharge rate rather than temperature or water table level. Freeman *et al.* (2004) attrinuted increased DOC export from bogs (14 % increase) and fens (49 % increase) under elevated CO_2 concentration to increased microbial activity.

No study directly related DOC release from a peatland to vegetation changes. However, as DOC production depends strongly on the quality of plant litter, it is likely that a change in dominating plant functional type would affect DOC production and export (Moore and Dalva, 2001; Blodau *et al.*, 2004). Strack *et al.* (2008) measured a large DOC release pulse immediately after the drainage of a fen. The DOC concentration in pore water remained high even a decade after drainage, which, according to the authors, could be attributed to an increased plant biomass and larger water table fluctuations. Increased DOC production was measured in peat monoliths that experienced a vegetation change (from a predominant *Sphagnum* cover to vascular species), which is likely related to enhanced exudation from vascular plants roots and increased decomposition (Fenner *et al.*, 2007).

2.5.3. Long term carbon balance

As seen in the previous section, the direct and indirect effects of climate change modify the different components of the C cycle of peatlands in different directions and magnitudes (see also Moore *et al.*, 1998). Paleoecological studies generally show that the rate of accumulation of peat or C is lower when the climate is drier (Lavoie and Richard, 2000; Robinson and Moore, 2000; Yu *et al.*, 2003; Malmer and Wallén, 2004). From a spatial point of view, wetter (oceanic) climates promote higher peat accumulation rates than drier (continental) climates (Tolonen and Turunen, 1996). On the other hand, litter produced from fens is more readily decomposable than that from bogs (Thormann *et al.*, 2001). Hence, although they are drier systems, bogs are generally known to accumulate peat faster than fens (i.e. Kuhry and Turunen, 2006), although some studies have demonstrated the opposite (e.g. Bauer *et al.*, 2003), potentially due to a greater sensitivity of bogs to fire or moisture limitation in some bogs.

The impact of drainage on the C accumulation of peatlands is debated. Some studies showed a lower C accumulation after drainage in bogs and fens (Alm *et al.*, 1999b; Silvola *et al.*, 1996). Others conclude that an increase in living biomass, a decrease in CH_4 emissions and a slight increase in peat CO_2 uptake in drained peatlands leads to increased C accumulation, at least on the short to medium term (Minkkinen *et al.*, 2002; Laine *et al.*, 1996).

Increased fire frequencies generally decrease C accumulation rates (Kuhry, 1994; Pitkänen *et al.*, 1999; Turestsky *et al.*, 2002), although Turunen *et al.* (2001) did not find a significant effect of fire on peat C accumulation in Siberian peatlands. In permafrost peatlands, increased fire frequency could lower peat accumulation or lead to net peat loss through combustion and post-fire decomposition (Robinson and Moore, 2000).

In discontinuous permafrost areas, permafrost formation was found to lower C accumulation in peatlands (Robinson and Moore, 2000). However, further permafrost formation is unlikely with projected climate change (Camill, 1999). On the other hand, permafrost bog collapse could increase C accumulation rates in the scar by 45 – 72%, while collapse at peat plateau margins leading to collapse fens would not significantly change C accumulation (Robinson and Moore, 2000).

Conclusion

Peatlands are important components of the terrestrial C sink. They store C through long-term peat accumulation resulting from waterlogged conditions that prevent litter decomposition to compensate for biomass production. All the processes involved in the C balance of peatlands are likely to be directly or indirectly affected by climate change. Direct effects include increased temperatures, changes in wetness and increased CO_2 concentrations. Indirect effects include increased fire frequency and permafrost thaw.

The abiotic direct and indirect effects of climate change will not only affect the C cycling of peatlands, but will also result in changes of vegetation productivity and composition. As all the components of the C cycle are influenced by the vegetation composition, any change in vegetation will in turn affect the C balance of peatlands.

Identifying the role of vegetation in the C dynamics of peatlands represents a methodological challenge, as changes in vegetation are triggered by environmental factors that are also likely to influence the process studied. The time span over which vegetation succession occurs (decades) also limits the possibilities for studying the link between vegetation and C dynamics. Hence, the vast majority of the studies reported here focused on very short term (from a few hours to a few years) or very long term (millennia) observations. It clearly demonstrates the need for a detailed study of vegetation changes and its effects on C fluxes and pools over a time scale relevant for vegetation succession. The following chapters present, in the form of scientific journal manuscripts, how I bridged that gap by studying C cycle components and vegetation dynamics in a drained portion of a bog, 85 years after the initial water table drawdown.

Chapter 3 - Assessing long-term hydrological and ecological responses to drainage in a raised bog using paleoecology and a hydrosequence

Context within the thesis and overview

The literature review presented in Chapter 2 clearly states that the fate of peatland vegetation and its relationship to carbon cycling in drier peatlands is largely unknown, and that drainage could be a valuable surrogate to the climate change effects on peatland vegetation and carbon cycling, because of its long term nature. This chapter contributes to attain the first objective of my Ph.D., namely, to assess how a water table drawdown affects vegetation communities in a peatland. It is adapted from a manuscript specifically addressing the following questions: (1) how does bog vegetation change following a long-term lowering of water table and (2) how are the effects of drainage on hydrology and vegetation distributed temporally and spatially?

I analyzed changes in vegetation and hydrology associated with drainage spatially along a hydrosequence and temporally using paleoecological reconstructions from peat cores (testate amoebae, pollen). The relationship between modern vegetation and water table was assessed through clustering and ordination analyses of vegetation relevés. Results reveal post-drainage increases in tree cover, especially *Betula* and *Larix*, decreases in *Sphagnum* cover, and shifts in the species composition of dominant shrubs. Present-day vegetation patterns along the hydrosequence were primarily related to seasonal variability of water table depth. Paleoecological records reveal that in an area where the present-day vegetation has been impacted by drainage, a persistent water-table lowering occurred in response to drainage. However, in an area with relatively natural vegetation, a transient drop in water-table depth occurred at the time of drainage. Temporal and spatial patterns revealed by this study show that the bog response to drainage was spatially and temporally heterogeneous, and probably mediated by feedbacks among vegetation, peat structure, and hydrology. Spatial patterns along the hydrosequence were similar to those observed in paleoecological reconstructions, but the use of the two complimentary techniques provides additional insights.

3.1. Introduction

Anticipating how ecosystem structure and function will respond to future and ongoing environmental change is a critical challenge for ecologists. For example, annual precipitation is expected to increase in the coming decades over most subpolar regions (IPCC, 2007), although a shift in the relative proportions of rain and snow, and increased evapotranspiration rates (Rouse, 1998), may lead to increased summer moisture deficit in many northern peatlands (Roulet *et al.*, 1992). Given that the carbon stored in northern peatlands represents a considerable proportion of the total terrestrial carbon pool (reviewed by Vasander and Kettunen, 2006), and that cycling of carbon in peatlands is strongly influenced by hydrological conditions (Turetsky *et al.*, 2002; Belyea and Malmer, 2004; Malmer and Wallén, 2004; Strack *et al.*, 2004), it is critically important to understand the potential ecological responses of northern peatlands to a persistent water table depth drawdown. In particular, the role of long-term changes in hydrology on vegetation dynamics and subsequent changes in the biogeochemistry of peatlands is unclear (Belyea and Malmer, 2004; Bauer, 2004).

The composition of vegetation can change in response to external (e.g. climatic) and/or internal (e.g. life expectancy) drivers (Cowles, 1899; Clements, 1916; Schulze *et al.*, 2002), and these changes occur at a range of temporal and spatial scales. Unfortunately, in all but the most rapidly changing ecosystems, the rate and long-term characteristics of vegetation change are often difficult to deduce from a few years of observation, experiments and/or manipulations. Spatial analogues (chronosequences or hydrosequences) have been used in natural and managed ecosystems to infer patterns of vegetation change over extended periods of time (e.g. Amiro *et al.*, 2003; Bond-Lamberty *et al.*, 2004; Lecomte *et al.*, 2005; Laiho *et al.*, 1999). However, using only spatial patterns to draw conclusions about temporal succession can be misleading because the boundaries between different plant communities can be hard to detect (van der Maarel, 1996), transient stages, alternative trajectories and reversals may not be present (Hughes and Dumayne-Peaty, 2002), and sites may not have been similar prior to the disturbance or have a similar disturbance history (Lecomte *et al.*, 2005; Jackson *et al.*, 1988). Therefore, paleoecological techniques are an extremely valuable alternative or compliment to studies that employ space-for-time substitution, and often allow detailed reconstructions of vegetation and environmental change.

Peatlands are wetlands that accumulate partly decomposed plant residues that become the substrate (peat) on which vegetation grows. Although classification criteria vary (e.g. Wheeler and Proctor, 2000), fens and bogs are widely recognized as the two main types of peatlands. Fens are generally wet peatlands that receive some water and nutrients from outside their own limits (minerotrophic), whereas bogs are generally drier, nutrient-poor systems fed by atmospheric inputs only (ombrotrophic). The vegetation structure of boreal bogs usually comprises an extensive ground cover of *Sphagnum* mosses beneath shrubs and, sometimes, trees. This typical vegetation composition is generally considered to be fairly stable in time, sometimes over centuries and even millennia (Backéus, 1972; Rydin and Barber, 2001; McMullen *et al.*, 2004; Hughes and Barber, 2004). Bogs commonly develop from autogenically- and/or allogenically-induced drying of fens, although several different succession pathways have been identified (e.g. Payette, 1988; Kuhry *et al.*, 1993; Lavoie and Richard, 2000; Anderson *et al.*, 2003; Yu *et al.*, 2003; Hughes and Barber, 2004).

The long-term effects of drying on bogs have seldom been explicitly studied. Paleoecological records show that drier conditions in bogs are characterized by an increase in the proportion of woody vegetation, both shrubs and trees (Kuhry, 1997; Bridge *et al.*, 1990; Booth and Jackson, 2003). For example, over the last 100-200 years, invasions of open bogs by shrubs and increased tree growth have been observed in southern Québec (Pellerin and Lavoie, 2003) and Sweden (Gunnarson *et al.*, 2002; Malmer and Wallén, 2004). A decrease in *Sphagnum* ground cover has also been observed in Sweden (Gunnarson *et al.*, 2002). These changes may have been related to drier climatic conditions in these regions.

Artificially drained peatlands may provide a valuable surrogate to study the impact of surface drying on vegetation succession and ecosystem processes in peatlands. Most studies describing the impacts of drainage on peatland processes have been conducted in northern Europe on sparsely treed fens that were drained for forestry purposes. Drainage usually initiates a succession towards forest vegetation (Laine *et al.*, 1995; Silvola *et al.*, 1996; Minkkinen *et al.*, 1999), leading to an increase in primary production and living biomass (Laiho *et al.*, 2003). An augmentation of shrub and tree proportions and a reduction of species adapted to wet conditions have been observed on drained fens (Laine *et al.*, 1995; Minkkinen *et al.*, 1999; Macdonald and Yin, 1999). On bogs, similar changes in tree and shrub biomass have been observed following drainage, but perhaps to a lesser extent, and changes in vegetation composition may be less important (Minkkinen *et al.*, 1999; Vasander, 1982; Weltzin *et al.*, 2003).

The goal of this study was to investigate the effect of water table drawdown on vegetation succession in bogs, as a model for understanding potential consequences of climate warming. My approach was to describe vegetation along a water-table gradient perpendicular to a drainage ditch in a bog and compare it to reconstructed vegetation sequences from peat cores. Peat cores were collected from an area with no obvious drainage effects and from within the most severely drained area. The drainage ditch was dug 85 years ago and the area was left untouched since drainage. The ditch has not been maintained in the last few decades, hence it is now filled with debris and its water is mostly stagnant. These particular conditions allow us to describe the temporal dynamics of vegetation and hydrology, and the end-products (modern hydrosere), following a relatively ancient hydrological change. My specific objectives were (1) to reconstruct vegetation and surface wetness changes following drainage in a bog using paleoecological methods, (2) to describe the current relationships among spatial patterns of vegetation, vegetation physiognomy, and hydrology along a drainage gradient (hydrosequence) at the same site and (3) to compare the results from the two approaches and evaluate the use of a hydrosequence to study the possible impacts of climate change on vegetation in bogs.

3.2. Study area

The study site was Mer Bleue peatland (Figure 3.1a), located 5 km east of Ottawa, Canada (45.40°N lat., 75.50°W long.). The climate is cool continental, with a mean annual temperature of 6.0°C and annual precipitation of 943.5 mm (1971 – 2000 average for Ottawa International Airport; Environment Canada; http://www.climate.weatheroffice.ec.gc.ca/climate_normals). This 28 km^2 peatland complex is dominated by a central raised bog. The peatland started developing about 8500 years ago in a postglacial river channel, and switched from an initial fen phase to a bog phase around 6000 years ago (Roulet *et al.*, 2007). Surface topography of the bog consists of hummocks and small hollows, with a maximum relief between hummock tops and hollow bottoms of 0.5 m. Hummock vegetation is dominated by evergreen (*Chamaedaphne calyculata*, *Kalmia angustifolia*, *Ledum groenlandicum*) and deciduous (*Vaccinium myrtilloides*) ericaceous shrubs, and *Sphagnum* mosses (*S. capillifolium, S. fuscum*). Hollows are dominated by *K. angustifolia*, *Sphagnum* species (*S. magellanicum*, *S. angustifolium*) and the sedge *Eriophorum spissum* (Moore *et al.*, 2002).

A drainage ditch dug in 1922 in the eastern part of Mer Bleue led to a visible change in the dominant vegetation from *Sphagnum* mosses and evergreen ericaceous shrubs to trees and deciduous ericaceous shrubs, within a few hundred meters of the ditch on the downslope (east) side of the drainage ditch. Typically, the water table drawdown around a drainage ditch on forested peatlands is most pronounced within a few meters from the ditch and is attenuated for distances extending 15-25 m (Prévost *et al.*, 1997; Berry and Jeglum, 1991). The large extent of the water table drawdown downslope from the Mer Bleue drainage ditch (as observed from the extensive vegetation changes) is explained by the unusual depth of the ditch (up to approximately 2 m) and its orientation, perpendicular to the flow of subsurface water.

3.3. Methods

3.3.1. Paleoecological analyses

Two 10 x 10 x 100 cm long cores were extracted along the study transect using a box corer in September 2004. The two cores were located approximately 150 m apart and on opposite sides of the drainage ditch (Figure 3.1b). The upslope core, MBU, was sampled at an intermediate microform (*Sphagnum capillifolium* lawn) and the downslope core, MBD, was sampled in a small, flat clearing in a relatively dense *Betula populifolia* patch where the bog microtopography had disappeared. The cores were placed in plastic boxes, transported to the lab within 6 hours and kept at 4^oC until further analyses.

A chronology for the two profiles was established using ^{210}Pb. Ten samples of 1 cm thickness were taken from each core at 6 cm intervals. Samples were analysed at the GEOTOP radioisotopes laboratory (Montreal, Canada), where ^{210}Pb activity was estimated by measuring the α emission of ^{210}Po (a ^{210}Pb granddaughter isotope), after spiking with a ^{209}Po tracer. The constant rate of supply (CRS) model was applied to calculate the age of the peat layers (Appleby and Oldfield, 1978). The chronology was refined using a palynostratigraphic marker, the *Ambrosia* rise after early European settlers arrived in 1820, and a charcoal layer corresponding to a known event, the Carleton County fire (or Green's Creek fire), in 1870.

The stratigraphy of the cores was described every 5 cm (or less, in case of transition zones) following the Troels-Smith (1955) nomenclature. The cores were divided into 1 cm thick slices, except for the first 5 cm to the surface that comprises loose *Sphagnum* moss, which was kept intact. A subsample of 2 cm^3 was taken from the center of approximately every second slice for pollen analyses from the surface down to a depth of 50 cm. Another subsample of 2 cm^3 was taken for testate amoebae analyses every cm from the surface down to 30 cm.

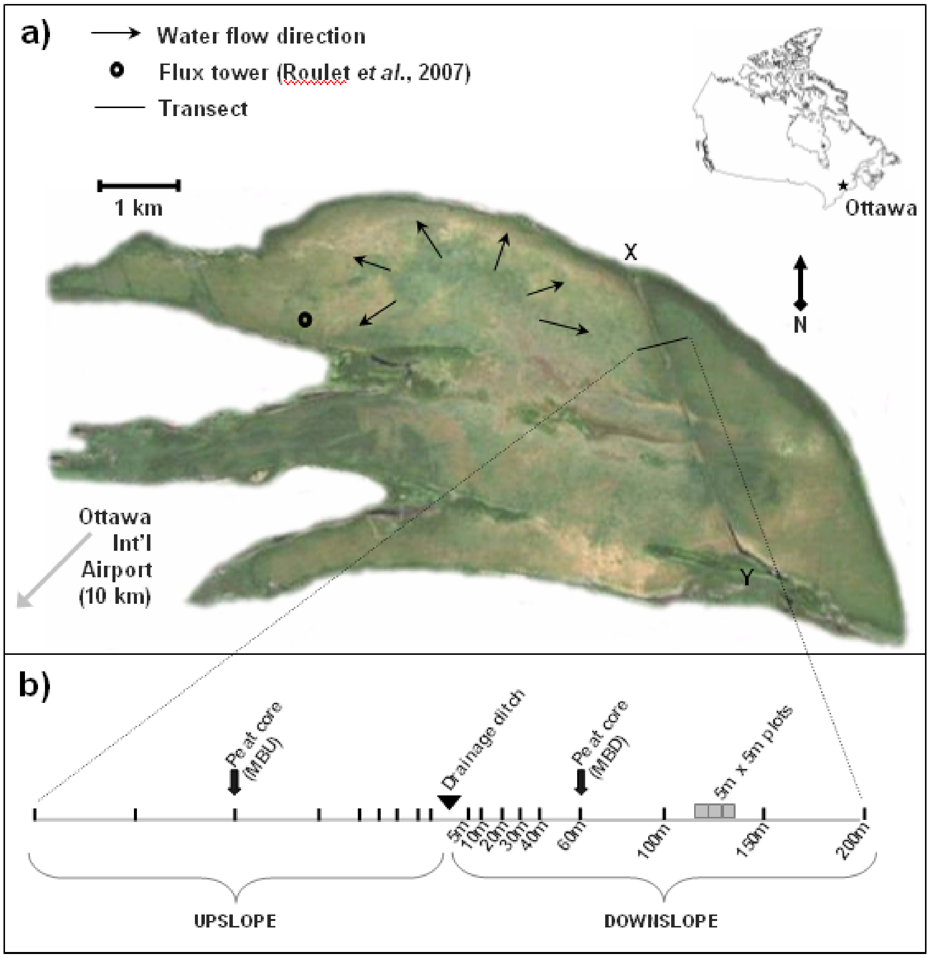

Figure 3.1 – (a) Mer Bleue peatland, located near Ottawa.The study transect was laid perpendicular to the drainage ditch that runs approximately north-south (from point X to point Y), in the eastern part of the peatland. (b) The transect consists of 80 adjacent 5 x 5 m plots and 18 water table wells symmetrically located on both sides of the ditch. The two peat cores were taken 60 m downslope from the ditch and 100 m upslope from the ditch.

Pollen samples were prepared using a standard protocol (Faegri and Iversen, 1989), but without the hydrofluoric acid treatment since no silicate particles were present in the peat. The minimum number of pollen grains counted per sample was 500. Pollen influx was calculated by multiplying peat accumulation rate (in cm/yr) with pollen concentration (in grains/cm^3). Testate amoebae were isolated from the peat following Charman *et al.* (2000) and taxonomy followed Charman *et al.* (2000), except as detailed by Booth

(2007). Individuals were tallied until a count of at least 150 was reached with the exception of the uppermost sample of MBD, where that number could not be reached. Transfer functions were applied to the data to reconstruct changes in water-table depth, using a weighted average partial least squares model (WA-PLS) (Booth, 2007).

3.3.2. Vegetation surveys and water table monitoring

Vegetation was described along a 400 m transect set perpendicular to the drainage ditch (Figure 3.1). The transect was randomly located along a portion of the ditch that was far enough from the margin of the peatland to avoid edge effects, as estimated by eight point-intercept transects conducted prior to the study (data not shown). Eighty adjacent plots of 5 x 5 m were surveyed using the Braun-Blanquet abundance/dominance scale (Braun-Blanquet, 1932). The relevé method was chosen because of the combined rapidity of execution and the fact that we did not need fine-scale estimates of each species' cover to describe general patterns of vegetation change along the transect. Relevé area (25 m^2) was chosen so that it encompassed the largest microforms of the upslope sector. Cover estimates were recorded for each species of the four main plant functional types present along the transect: trees, shrubs, herbs and mosses/lichens. In addition, the average height of each species of the shrub and the tree functional types were recorded based on three random samples inside each relevé.

Water table depth was monitored approximately biweekly along the transect, from June to November 2005 and from May to November 2006, using 18 water table wells that were spaced closer together nearer to the ditch, where the water table was expected to change the most (Figure 3.1b). They were installed at intermediate microform locations in the upslope sector, and at least 2 m away from a tree trunk in the drained sector. To allow comparison with the vegetation relevés, the water table values were linearly interpolated between the wells. The distance between the surface of the peat and a common datum was also recorded every 10 cm along the 400 m main transect, using a line level.

3.3.3. Statistical analyses

The structure of the vegetation data was characterized by cluster and ordination analyses of the relevés, using PC-ORD v4.5 (McCune and Mefford, 1999). Three plots that were very close to the ditch and dominated by aquatic vegetation were omitted. Species abundance scores were converted prior to analyses into the middle percentage value of each Braun-Blanquet class (1-2.5; 2-15.0; 3-37.5; 4-62.5; 5-87.5), ignoring the lower classes (r, +). Although this type of transformation artificially transforms the data into quantitative values (Podani, 2006), it allows the assessment of broad-scale community patterns relevant to ecosystem functions and facilitates the use of common ordination methods.

Hierarchical clustering (flexible-β linkage method, β=-0.25) was applied using Sørensen's distance measure (McCune and Grace, 2002). The dendrogram was used to define groups, and the pruning was done at the level where 30% of the information was retained, which resulted in the plots being separated in three main groups. Indirect gradient analysis was done through non-metric multidimensional scaling (NMDS) using Sørensen's distance measure (McCune and Grace, 2002), with 250 runs using random starting configurations. The dimensionality of the dataset was assessed through a visual examination of the scree plot, and two dimensions were retained for the final solution. A Monte Carlo test was conducted to assess the probability that the final stress of 15.1 would have been obtained by chance (p=0.0040). Ordination results were related to water table descriptors (average, standard deviation, maximum and minimum water table depth over growing seasons 2005 and 2006) through linear correlation, expressed by Pearson's r coefficient.

Linear regressions between water table characteristics and the average height of trees and shrubs canopies were conducted with SAS v9.1 (SAS Institute Inc.). Linear models were chosen as no theoretical reason pointed towards any other type of model, considering the limited range of water table depths represented along the transect compared to other types of ecosystems (i.e. no upper limitation of height was attained).

3.4. Results

3.4.1. Paleoecological reconstructions

Paleostratigraphic markers (*Ambrosia* rise, charcoal layer) and ^{210}Pb-derived chronologies are generally in good agreement for the top 20 cm of the cores. However, deeper in the profiles, the dates derived from the markers and ^{210}Pb diverge, especially for the MBD core. The error associated with the ^{210}Pb reconstruction also increases with depth in the profile, reaching 32 % and 45 % for MBU and MBD, respectively. As both paleostratigraphic markers are in good agreement with each other for both cores, we adjusted the ^{210}Pb chronologies accordingly (Figure 3.2a). In general, palynostratigrapic events (dated and undated) are in good agreement between cores MBD and MBU, with MBD markers found comparatively shallower in the profile than MBU markers, with this trend increasing with depth in the cores (Figure 3.2b).

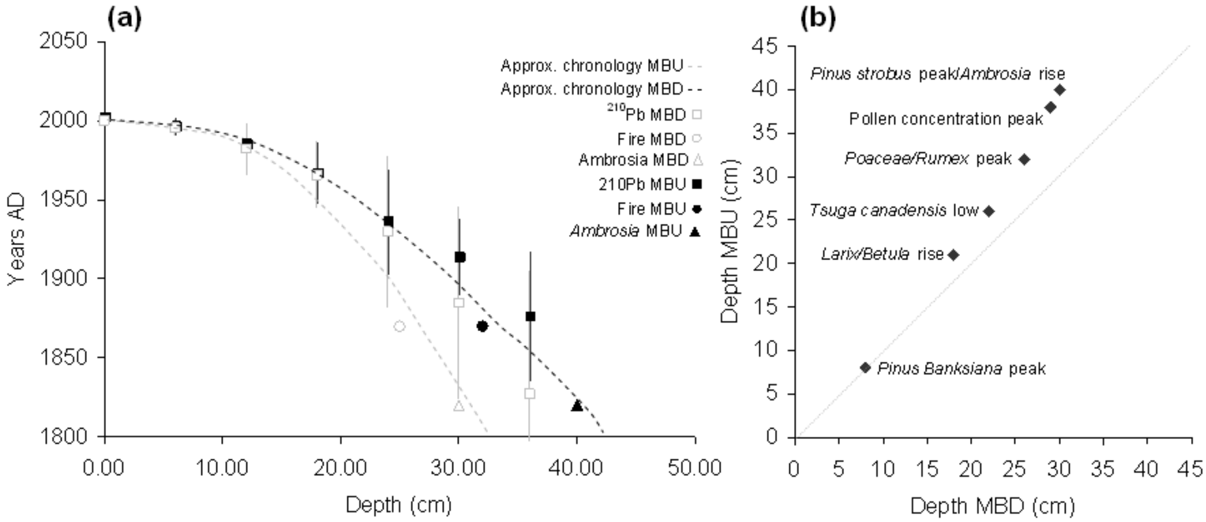

Figure 3.2 – (a) Summary of chronological indicators for cores MBU and MBD, estimated chronology based on a combination of known events and ^{210}Pb (error bars represent one standard deviation), and (b) depth-depth relationship of the cores MBU and MBD based on palynostratigraphic indicators.

The MBD core has more distinctive stratigraphic layers than MBU (Figure 3.3), with more humified material occurring closer to the surface. A pre-drainage sedge dominated layer occurs about 25 cm earlier for MBD than for MBU. Pollen percentages of the local taxa *Betula* and *Larix* more than doubled following drainage in MBD (Figure 3.4a). A similar change was observed in the MBU core, but to a lesser extent and lower down in the profile. Ericaceous shrubs show a trend of increasing percentage following drainage in MBD, but it decreases again in the upper 10 cm. Hence it is not clear if that signal can be interpreted as a local increase in ericaceous shrubs representation. *Sphagnum* mosses, almost absent in the lower part of the MBU core, show the exact opposite pattern for MBD, where the spores were virtually absent in the upper 20 cm. Total pollen influx from MBD and MBU are of the same order of magnitude and show comparable patterns, with values varying between 6000 and 50 000 grains cm^{-2} year^{-1} (Figures 3.4b). The influx of regional species (including species not represented on the Figures, such as *Abies balsamea*, *Populus tremuloides*, *Acer rubrum*, *Fraxinus nigra*, *Salix* spp. and *Rumex* spp.) have similar patterns for both cores and are generally in the same order of magnitude, with the exception of *Quercus* spp., *Ambrosia* and *Poaceae* influx, which are clearly higher in MBD.

Testate amoeba assemblages within the MBD and MBU cores were relatively similar in composition just prior to drainage, and were both dominated by *Hyalosphenia subflava* and *Nebela militaris* (Figure 3.5). However, differences did occur between the two sites prior to drainage, with *Cyclopxis arcelloides* type and *Arcella discoides* more common at MBU whereas *Difflugia pulex* was more common at MBD. At about the time of drainage at MBU, *Hyalosphenia subflava*, a taxon indicative of dry and probably variable conditions (Booth, 2007; Booth *et al.*, 2008) reaches its highest percentages in the core. However, *H. subflava* percentages quickly return to pre-drainage levels. In contrast, the shift in testate amoeba community composition at about the time of drainage at MBD appears to have been more persistent, with increasing percentages of taxa characteristic of relatively dry conditions (Booth, 2007), such as *Assulina muscorum* and *Cyclopyxis arcelloides* type. Percentages of *Nebela militaris* also peak at about the time of drainage in the MBD core.

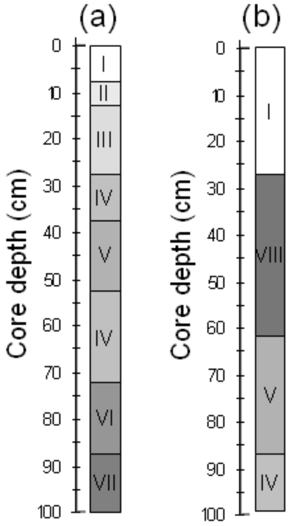

Figure 3.3 – Peat stratigraphy of (a) core MBD and (b) core MBU. I – Intact or slightly decomposed material, mostly *Sphagnum*; II – Fragmented material > 2 mm, mostly *Sphagnum*; III – Fragmented material > 2 mm, mostly ericaceous shrub roots and aerial parts and *Sphagnum* (some fragments < 2 mm); IV – Material < 2 mm, mostly sedge stems and roots, and *Sphagnum* (some fragments > 2 mm), some ericaceous shrub roots; V – Mix of material of all sizes, mostly sedges; VI – Material < 2 mm, mostly herbaceous (some fragments > 2 mm); VII – Mix of material of all sizes, mostly ericaceous shrub roots and aerial parts; VIII – Mix of material of all sizes, mostly *Sphagnum* and sedges, some ericaceous shrub roots.

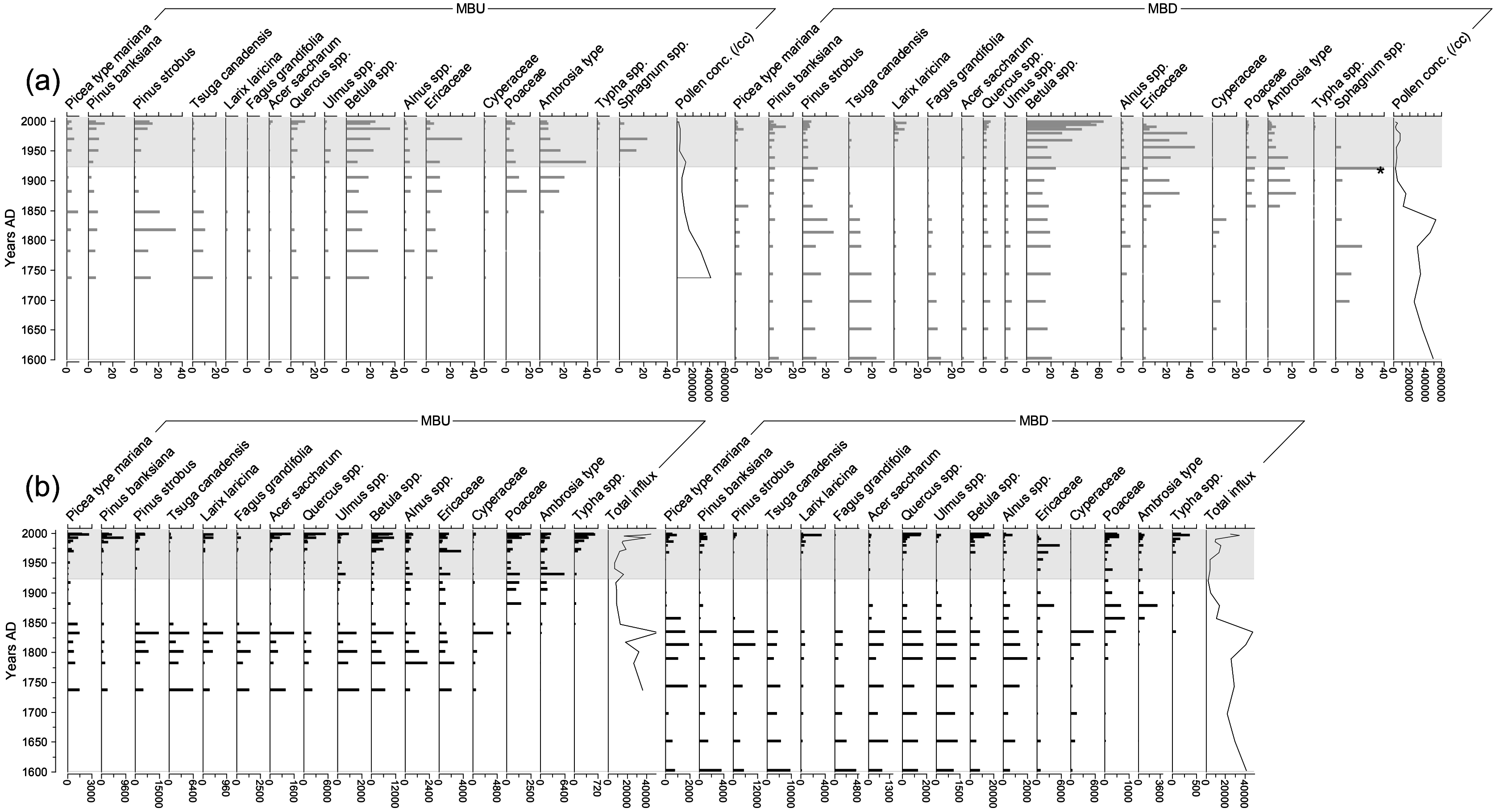

Figure 3.4 – (a) Pollen percentage (%) and (b) influx (grains/cm^2/year) of selected taxa from the first 50 cm of cores MBU and MBD. Chronology is extrapolated from the model presented in Figure 2. Shaded area represents the pollen accumulation that occurred after drainage. Taxa are represented only if at any point in time they represent more than 5 % of the pollen, or if their influx is of 1000 grains/cm^2/year or more. *Maximum value of *Sphagnum* percentage in MBD: 143%.

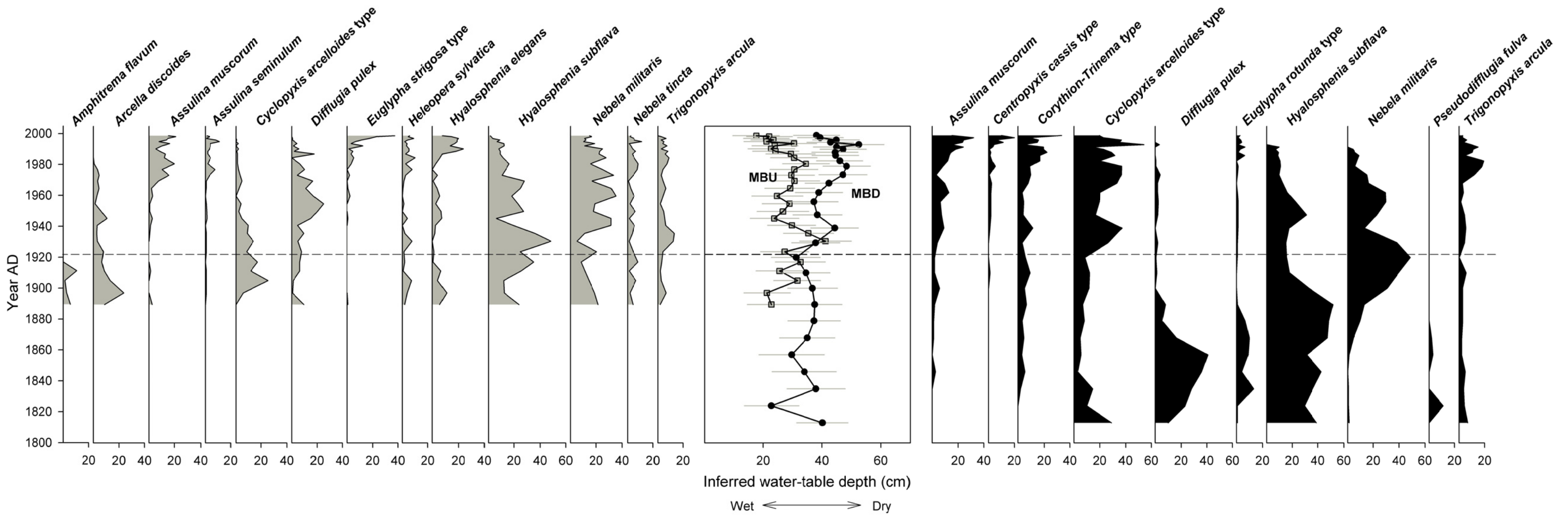

Figure 3.5 – Percentage testate amoeba diagrams of the upper 30 cm of cores MBU and MBD, vs chronology. Species that represented less than 10 % of the totals for the entire profiles were excluded. Inferred water table depths are presented in the center of the diagram.

Inferred water table depths at both sites indicate peatland drying at about the time of the drainage event (Figure 3.5). However, the drying at MBU was transient, with water-table depths recovering to pre-drainage levels within about a decade, whereas at MBD the water-table depths remained generally low throughout the rest of the century. Although the two sites record different long-term patterns associated with the drainage event, the decadal-to-multidecadal fluctuations are highly coherent between the two records after the drainage event, which is the portion of the cores where the age models are best constrained.

3.4.2. Hydrosequence

Peat surface is much lower on the downslope side of the drainage ditch where it was more severely affected by drainage (Figure 3.6). Seasonal patterns show that the water table was generally closer to the surface starting 100 m away from the drainage ditch (Figure 3.7, section A), with the exception of the first 10 m upslope and the first 30 m downslope from the ditch, which behaved like a flood plain (Figure 3.7, section C). Hence, the ditch starts affecting the water tables somewhere between 60 m and 100 m upslope (Figure 3.7, section B) and starting at around 30 m downslope of the ditch (Figure 3.7, sections D and E). Occasional measurements conducted farther away from the ditch on both sides (data not shown) confirm these general trends and after 300 m downslope of the ditch, any drainage effect gets confounded with the effect of the peatland border.

The water table depth of the most affected section of the transect (40 – 150 m downslope) averaged 34.4 (15.4) cm, whereas the undrained component of the transect (200 – 100 m upslope) averaged 16.8 (7.0) cm over the two measurement seasons, a difference of 17.6 cm. This difference was even larger during the drier months: the average difference between these two sections increased to 32.5 in August 2005. Hence, the drained upslope and, most importantly, the downslope water tables showed higher variation than the "pristine" water tables, especially during the drier periods (July 2005, August 2005, September-November 2005, July 2006 and August 2006).

The coverage of the most common plant species as expressed by Braun-Blanquet scores was clearly related to the position along the transect, and hence, the position of the water table (Figures 3.8 and 3.9). Most tree species' coverage (besides the very sparse *Picea mariana*) was higher on the more severely drained area downslope of the ditch and near the ditch (sections C, D, E on Figure 3.7). *Betula populifolia*, completely absent in the undrained or less severely drained portion of the transect, became dominant 40 m downslope from the ditch (Figure 3.8). The coverage of ericaceous shrubs changed along the drainage gradient as well, with a clear increase in *Vaccinium myrtilloides* and a decrease in *Ledum groenlandicum* and *Kalmia polifolia* in drained portions of the transect. The creeping shrub *Vaccinium oxycoccos* was largely absent from drained areas and the coverage of the sedge *Eriophorum spissum* greatly diminished in these areas (Figure 3.9). With the exception of *Polytrichum strictum*, which is frequent, although rarely abundant, along the entire transect, non-sphagna brophytes were more abundant in drier areas. The dominance of *Sphagnum* species changed along the drainage gradient, although most species were well represented along the entire transect, with the exception of *S. girgensohnii* which was present only at drier sites. Overall, species richness as expressed by the number of species counted per relevé seemed to be more spatially variable in the drained portions of the transect (Figure 3.10a).

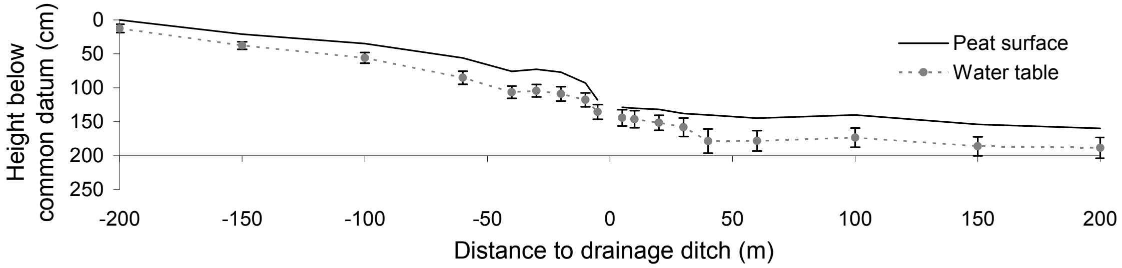

Figure 3.6 – Peat surface and average water table depth (± standard deviation) over growing seasons 2005 and 2006, along the main transect, from upslope to downslope.

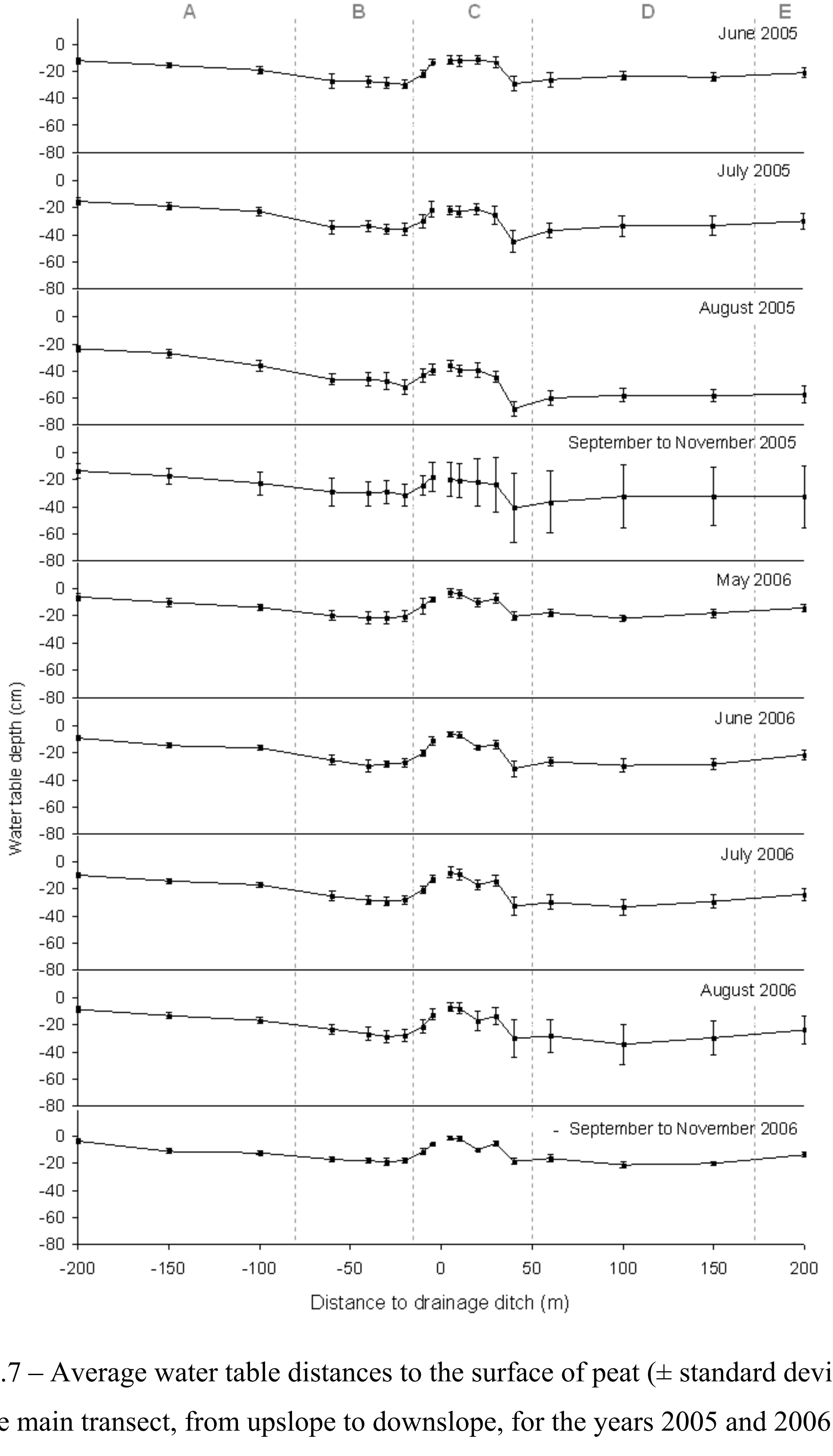

Figure 3.7 – Average water table distances to the surface of peat (± standard deviation) along the main transect, from upslope to downslope, for the years 2005 and 2006.

The average height of trees and shrubs between the upslope and downslope parts of the transect was different (Figure 3.10b). Trees and shrubs canopies height were closely related to water table descriptors, particularly average water table depth and standard deviation, and the maximum depth reached by the water table over two growing seasons (Table 3.1). Standard deviation of water table depth explained most of the variance of both tree and shrub canopy heights.

Table 3.1 – Linear regressions between trees and shrubs average height (in m) and water table variables (average, standard deviation, maximum and minimum water table values for growing seasons 2005 and 2006, in cm) based on 80 relevés.

Water table variable	Tree canopy height				Shrub canopy height			
	slope	intercept	r^2	Pr > F (model)	slope	intercept	r^2	Pr > F (model)
Average	0.26	-3.34	0.50	<0.0001	0.03	-0.17	0.30	<0.0001
Standard deviation	0.63	-3.63	0.75	<0.0001	0.08	-0.36	0.67	<0.0001
Minimum	0.23	1.17	0.11	0.0022	0.02	0.40	0.03	0.1395
Maximum	0.15	-4.46	0.67	<0.0001	0.02	-0.41	0.54	<0.0001

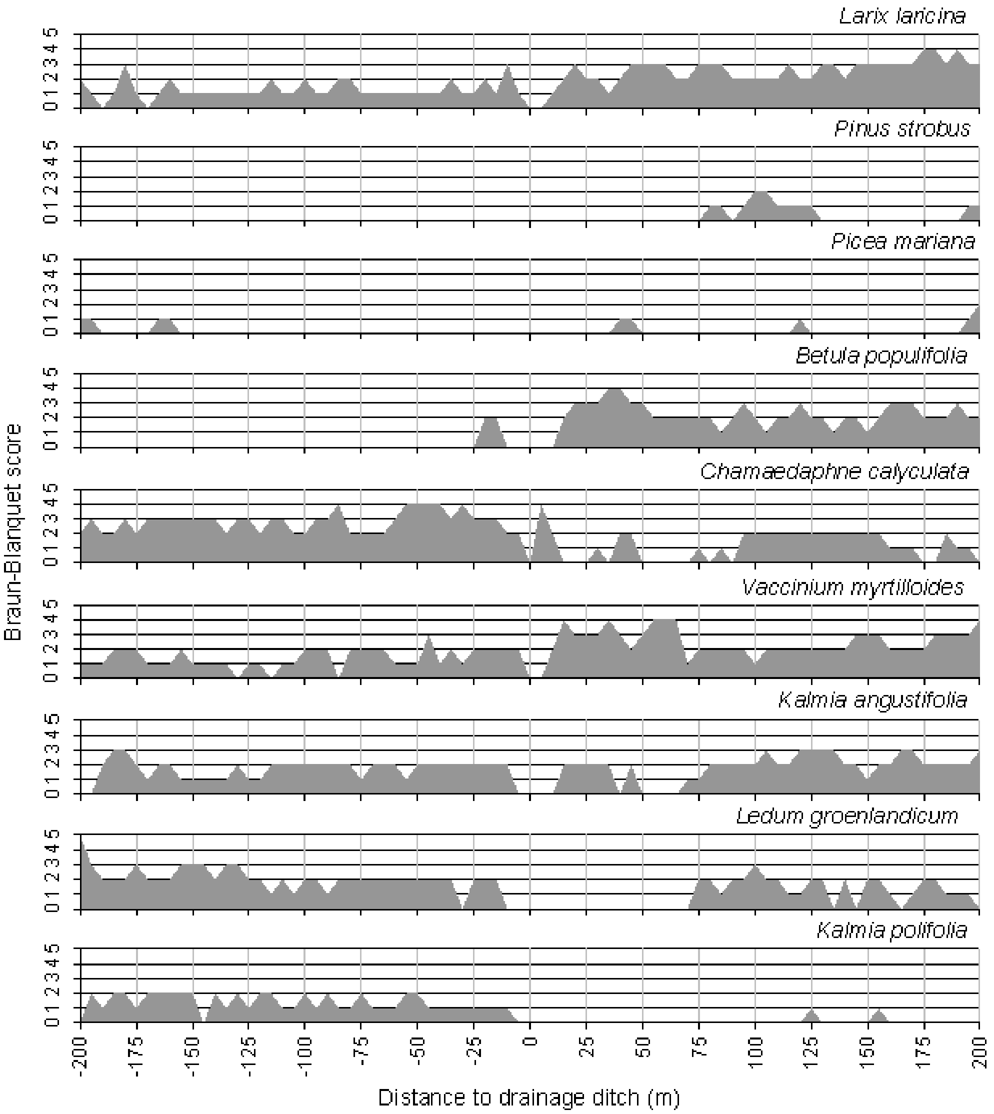

Figure 3.8 – Braun-Blanquet scores (omitting "r" and "+") for 80 vegetation relevés along the main transect, from upslope to downslope, for a selection of trees and shrubs species (1: Covering <5%, 2: Covering 5-25%, 3: Covering 25-50%, 4: Covering 50-75%, 5: Covering 75-100%).

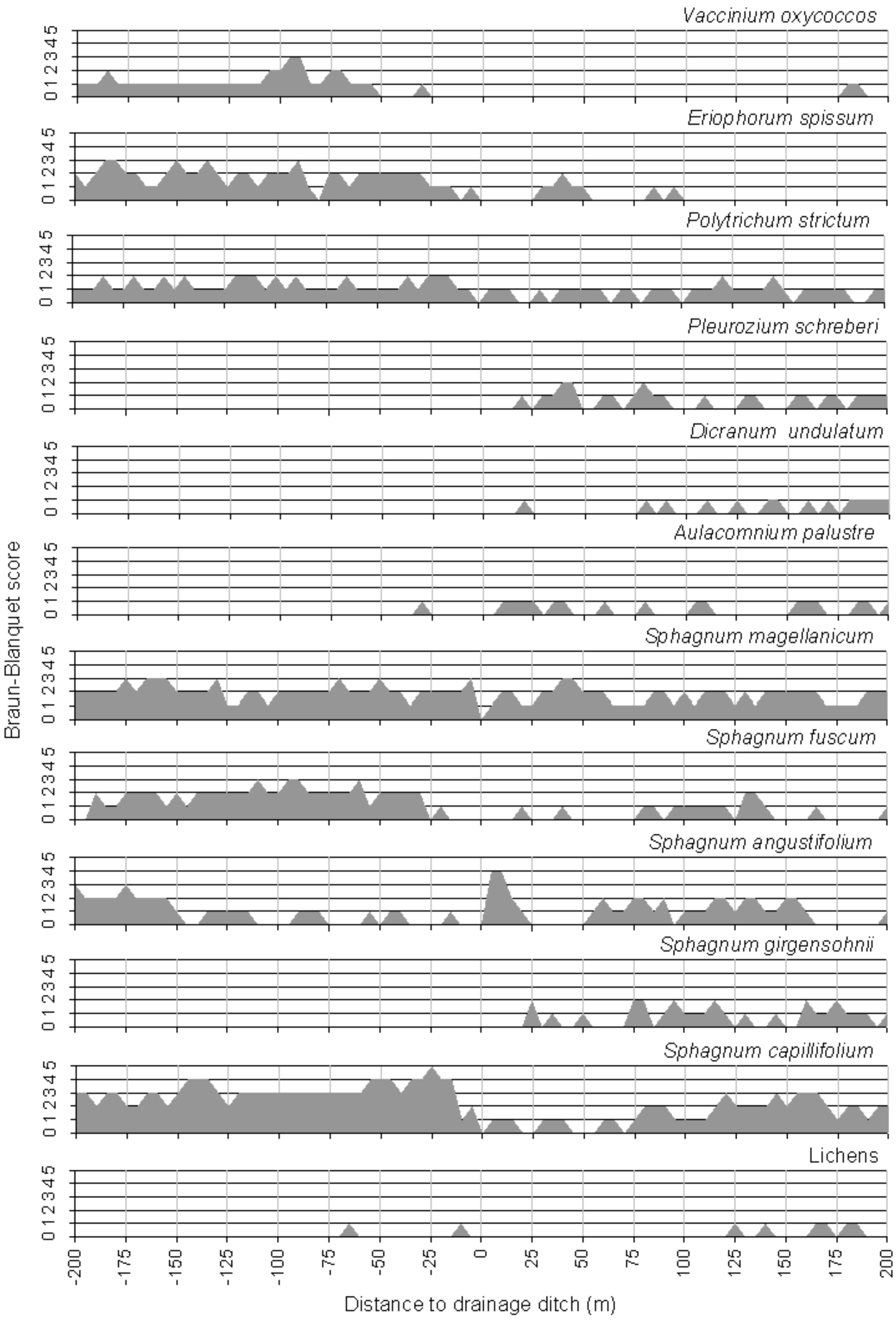

Figure 3.9 – Braun-Blanquet scores (omitting "r" and "+") for 80 vegetation relevés along the main transect, from upslope to downslope, for a selection of crawling shrubs, sedges and mosses species, and lichen (1: Covering <5%, 2: Covering 5-25%, 3: Covering 25-50%, 4: Covering 50-75%, 5: Covering 75-100%).

Two major gradients represented most of the variance in the vegetation communities, with these two dimensions containing 31 % and 59 % of the variance (Table 3.2). Cluster analysis identified three main vegetation communities, roughly corresponding to (A) open, low-statured shrub vegetation (including all the upslope relevés up to 15 m away from the ditch); (B) partly open tree canopy with underlying high shrubs (including relevés starting 75 m downslope of the ditch to the end of the transect and the remaining upslope relevés); and (C) closed tree canopy with underlying high shrubs (downslope relevés, up to 70 m away from the ditch) (Figure 3.11). As was the case for trees and shrub canopy height, both axes of variation represented by the ordination are correlated with the standard deviation of water table depth, followed by the maximum value of water table depth (Table 3.2 and Figure 3.11).

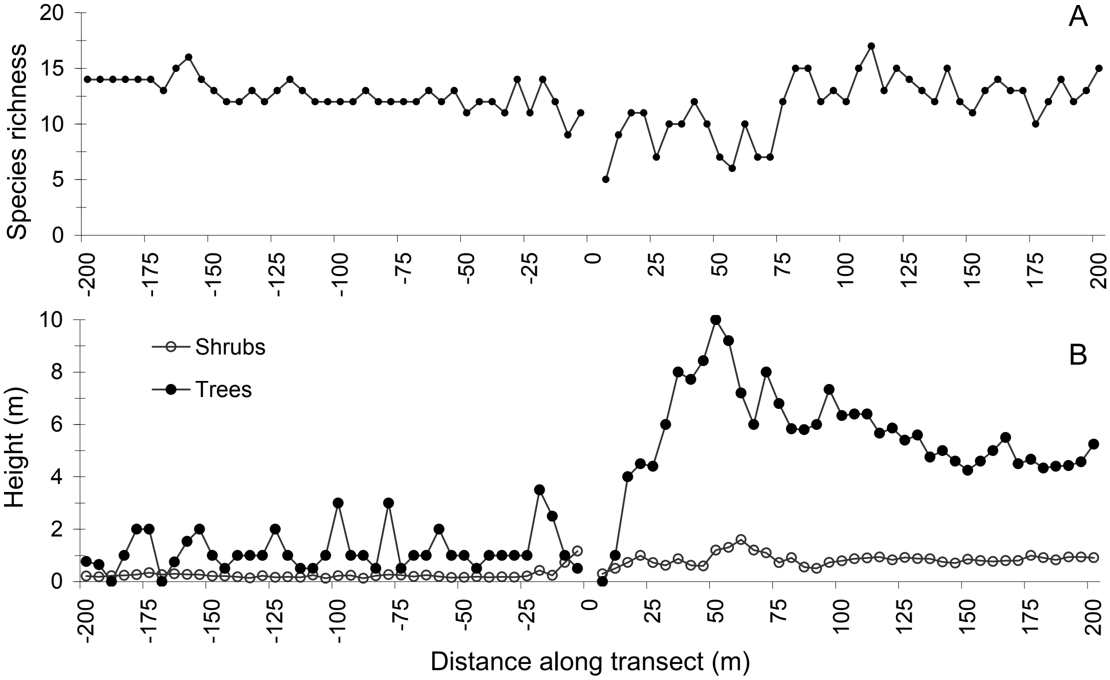

Figure 3.10 – (A) Number of species per plot and (B) average height of the shrub and the tree canopy along the main transect, based on 80 plots, from upslope to downslope.

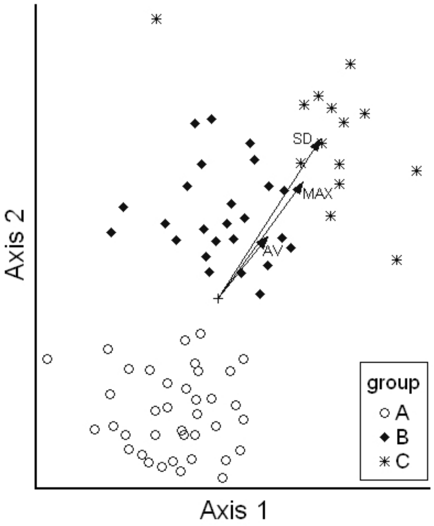

Figure 3.11 – Joint plot of NMDS ordination of 77 vegetation relevés in species space showing direction and strength of the relationships with water table variables (SD = standard deviation; MAX = maximum water table depth; AV = average water table). Distance between sample units approximate dissimilarity in species composition. The 3 main groups resulting from flexible-β clustering are overlaid (A = upslope, low-statured shrub vegetation; B = downslope, partly open tree canopy; C = downslope, closed tree canopy).

Table 3.2 – Statistics of NMDS ordination of 77 vegetation relevés and correlations with water table variables (average, standard deviation, maximum and minimum water table values for growing seasons 2005 and 2006).

	Variance represented in data reduction (r^2)	Relationship with water table variables (r^2)			
		Average	SD	Min	Max
Axis 1	0.31	0.22	0.45	0.06	0.37
Axis 2	0.59	0.27	0.69	0.00	0.50
Total	0.90	n/a	n/a	n/a	n/a

3.5. Discussion

3.5.1. Age models

The ^{210}Pb derived dates are underestimated for both profiles when compared to dates derived from chronostratigraphic markers, with the error increasing as going deeper in the cores. Such an underestimation was reported by Belyea and Warner (1994). However, the ^{210}Pb-derived chronologies properly reflect the impact of drainage on the age-depth relationship of the cores. For a given depth, the MBU core is consistently younger compared to MBD, reflecting the increased decomposition and compaction of peat following drainage on the downslope side of the ditch (Figure 3.2). Increased decomposition in MBD is also reflected in the stratigraphy of the cores, with peat layers comprising small fragments occurring much closer to the top of the core in MBD than in MBU. The overall effect of the water table drawdown on peat accumulation would require the measurement of bulk density and peat carbon concentration. Both increases and decreases in carbon storage following drainage have been documented (Laiho, 2006).

3.5.2. Bog drainage and spatiotemporal patterns of water-table dynamics

The testate amoeba-inferred water tables indicate that both MBD and MBU became drier after drainage, although the persistence of this drying differed between the sites. At the 'pristine' location upslope of the drainage (MBU), a transient drying event occurred at the time of drainage and water levels recovered within approximately a decade. However, at the site near the drainage ditch where vegetation was altered (MBD) the drop in water-table depths was persistent. Interestingly, even though the long-term patterns of water-table response to drainage differed between the two sites, decadal-scale moisture fluctuations since drainage were remarkably similar, providing additional support for the reliability of the testate amoeba-based reconstructions.

Several possible factors may have caused the different long-term responses to drainage between the two sites. One possibility is that the water-level drawdown was severe enough to increase peat decomposition rates and alter peat structure near the drainage ditch but not further upslope, and this change may have permanently affected water-holding capacity and drainable porosity. Another complementary possibility is that the vegetation changes were persistent in the area adjacent and downslope of drainage ditch, whereas transient or little vegetation change occurred at the more pristine site. The change in vegetation may have led to a positive feedback that promoted drier surface-moisture conditions and higher water table fluctuations, through increased evapotranspiration of woody plants (Eppinga *et al.*, 2008) and/or additional changes in peat composition and structure, including compaction.

Drainage of the bog probably not only resulted in lower water-table depths in the impacted area, but also may have led to increased seasonal variability in moisture conditions due to changes in vegetation and peat structure. Consistent with this hypothesis, the drained portion of the hydrosequence was characterized by enhanced seasonal variability in water table depth. More data is needed on the role of seasonal hydrologic variability in structuring testate amoeba assemblages, so it is unclear to what degree the downcore changes in testate amoeba assemblages are the result of increased seasonal variability versus changes in the mean condition after drainage. However, we note that the main indicator for a water table drawdown in MBU is an increase in *Hyalosphenia subflava*, a taxon that has been suggested as an indicator of dry yet variable conditions (Booth *et al.*, 2008). Other patterns, such as the increase in *Cyclopyxis arcelloides* type at MBD may also be indicative of variable conditions.

Immediately prior to drainage, inferred water-table depths at the two sites were similar (Figure 3.5). However, the reconstructions are increasingly different with depth in the cores. This difference may be related to poorly constrained age models or differences in microhabitats between the sites, although the latter is not supported by the core's stratigraphic description (figure 3.3). Another potential explanation for the difference might be differential preservation of testate amoeba and the resultant effect on water-table depth estimates. Differential preservation of testate amoebae has been suggested by some studies (Wilmshurst *et al.*, 2003; Jauhiainen, 2002; Caseldine and Geary, 2005), although the effect on bog water-table depth reconstructions has generally been minimal (Mitchell *et al.*, 2008). Also, the composition of the pre-drainage assemblages in MBD and MBU does not support this hypothesis, as taxa with more fragile tests are not more abundant prior to drainage at the pristine site than the drained site. Water table depth reconstructions were also made after removing particularly fragile species from the dataset and percentage calculations (e.g., *Euglypha* spp.) and these reconstructions were not significantly different than the reconstructions using all taxa.

3.5.3. Vegetation responses to drainage: hydrosequence and paleoecological perspectives

Pollen assemblages tend to confirm that the vegetation composition was similar prior to drainage at the sites where the cores were taken. One of the most obvious pollen signals observed after drainage is the peak and subsequent decrease in *Larix laricina* percentages, mostly observed in the MBD core, although a weak signal can also be detected in MBU. *Betula populifolia* percentage also increased after drainage, and still seems to be increasing.

Drainage or drier climatic conditions has been suggested as one of the main factors contributing to tree cover increase in bogs over the twentieth century (Linderholm and Leine, 2004; Pellerin and Lavoie, 2003; Frankl and Schmeidl, 2000; Gunnarsson *et al.*, 2002). Our results provide additional support for this hypothesis, as we observed similar patterns along the hydrosequence. For example, a maximum in *Larix laricina* cover is observed in the intermediate drainage location (section E, Figure 3.7), and the greatest percentage of *Betula populifolia* is found where the water table is the lowest. *Betula populifolia* also proliferated in a harvested peatland in Quebec due to a persistently low water table (similar to the one from this study) and the absence of microtopography (Lavoie and Rochefort, 1996). Hence, *Betula populifolia*, which is commonly associated with disturbed peatland conditions and has a wide ecological range (Lavoie and St-Louis, 1998), seems to have competitive advantage over *Larix* trees as conditions get drier or stay dry for a longer period of time.

Shrub cover generally increases with water table drawdown in bogs (Weltzin *et al.*, 2003; Gunnarsson *et al.*, 2002; Bragazza, 2006). In my study, the pollen of ericaceous shrubs peaks after drainage, but this is unlikely to be related to drainage as the same peak is present in the undrained core. However, vegetation patterns along the hydrosequence suggest that drier conditions led to a shift in shrub species rather than a net increase in shrubs. Shrub species replacement was also observed following drainage in a drained peatland in Finland (Laine *et al.*, 1995), although in that case, the typical peatland shrubs were gradually replaced by forest succession species. As Mer Bleue peatland has for a long time been a dry peatland with a continuous cover of shrubs, it is not surprising that shrub cover did not increase following drainage. However, shrubs biomass probably increased following drainage considering how taller the shrubs are in the most impacted section of the hydrosequence. The only deciduous shrub species present (*Vaccinium myrtilloides*) has a competitive advantage over the other ericaceous shrub species as water table gets deeper, although all species are present over the entire transect. One exception is *Kalmia polifolia* that generally grows no higher than 30 cm and therefore probably suffered from competition for light. This switch towards deciduous shrubs dominance might be due to an increased nutrient turnover in the drained site since evergreen species loose their competitive advantage when nutrients are available to faster-growing and taller deciduous species (Tilman, 1984; Aerts and Berendse, 1989; Aerts, 1995; Dorrepaal *et al.*, 2007).

The observed decrease in *Sphagnum* spores in the peat core after drainage corresponds to a general decrease in *Sphagnum* cover with water table depth along the hydrosequence, although lower *Sphagnum* spores percentages do not necessarily mean lower *Sphagnum* abundance. *Sphagnum* decline was observed in bogs and poor fens on higher microforms following water table drawdown (Minkkinen *et al.*, 1999; Strack *et al.*, 2006; Toet *et al.*, 2006). An increase in non-sphagna bryophyte cover was observed in parallel to the *Sphagnum* cover decrease. A similar increase was also observed by Laine *et al.* (1995).

Multivariate analyses of vegetation relevés showed that the main axes of variation of the species assemblages are mostly explained by the water table variability, rather than by the average growing season value. A recent study also emphasizes the importance of water level fluctuations in explaining the vegetation community composition in peatlands (Laitinen *et al.*, 2008). These authors suggested that the differential tolerance of species to drought conditions (expressed through fluctuations) rather than an optimal water table niche (expressed through average water table depth) better explains vegetation assemblages. Shrub and tree canopies average heights relationships to water table characteristics also show the same patterns. As stated earlier, our testate amoebae assemblages do not give clear indications about how the water table variability evolved following drainage, hence, it is not possible to assess if increased water table variability led to the current vegetation assemblages, or if the vegetation assemblages are a direct or indirect cause for increased water table variability.

Conclusion

Paleoecological reconstructions and observations of contemporary vegetation along a hydrosequence provide a detailed description of post-drainage succession in an ombrotrophic peatland in southeastern Ontario, Canada. These descriptions reveal that bog response to drainage was spatially and temporally heterogenous, and reveal potential feedbacks among vegetation, peat structure, and hydrology that result from drainage. Results from paleoecology and the modern transect reveal post-drainage increases in tree cover, especially *Betula* and *Larix*, and decreases in *Sphagnum* cover. Multivariate analyses of vegetation communities showed that they are closely correlated with water table depth, and even more with water table depth variability. An area of the bog that currently has no observable effects of drainage was found to have experienced a transient water-table depth lowering at the time of drainage, whereas an area that presently has obvious drainage effects was found to have undergone a persistent water-table depth lowering. The severity of the water-table depth lowering, and feedbacks among vegetation, peat structure, and hydrology, likely explain the temporal differences at the two sites.

Water table drawdown is a possible consequence of climate change in northern peatlands. Peatland vegetation communities exert a strong control on peatland carbon cycling and therefore it is important to understand how a persistent water table drawdown might affect vegetation communities and the implications that these changes may have on the global carbon cycle. Our results show that, in some conditions, peatlands might shift to forest-like ecosystems, altering their role as a sink for carbon.

Chapter 4 - Biomass and leaf area changes 85 years after drainage in a bog

Context within the thesis and overview

Chapter 3 describes the changes in water table and vegetation composition following drainage. This chapter builds on the knowledge gained in Chapter 3 to detail the changes in biomass distribution between species and plant parts, and to relate changes in biomass to changes in leaf area. The results presented in this chapter are directly related to my first thesis objective (assess how a peatland vegetation community changes in response to long-term water table drawdown). The biomass values detailed in this chapter are also going to be used later in the thesis to attain part of my third objective and determine the changes in the amount of carbon that is stored in the living biomass upon drainage.

My results show a 10-fold increase in aboveground biomass between the reference site and the site that has been affected the most by drainage. The change is mostly due to the appearance of a relatively dense tree layer and a slight increase in shrub biomass. The increase in aboveground biomass is dominated by an increase in woody biomass, whereas the total leaf biomass increases very little as a result of drainage. Leaf area index approximately triples when trees are present, and as a result of a much higher specific leaf area at the drier sites. *Sphagnum* mosses, accounting for close to 20% of all aboveground biomass at the reference site, decrease to less than 1% of aboveground biomass as the drainage effect increases, although it remains present at all sites. The percentage of deciduous shrubs increases as the water table depth gets lower. The changes in vegetation structure could affect the carbon cycling of the system through changes in litter input amount and quality. The observed changes in vegetation structure and composition suggest that there may be two alternative stable states following drainage.

4.1. Introduction

Peatlands are important components of northern landscapes, covering more than 12% of the terrestrial area of Canada (Tarnocai et al. 2005). As a result of a persistent water saturation that keeps the decomposition rate of dead organic matter lower than that of plant production, peatlands can accumulate up to several meters of partly decomposed organic matter (peat), which contains between 45 and 55 % carbon (Gorham, 1991; Bauer *et al.*, 2006). Peatlands are therefore important long-term sinks for carbon. Changes in the magnitude and timing of precipitation or increases in evapotranspiration resulting from higher temperatures are possible consequences of climatic change that can lead to the drying of peatland surfaces (Rouse, 1998; Bragazza, 2008), which, in turn, could affect their role in the global carbon cycle.

A water table drawdown can affect the carbon functioning of peatlands in various ways. Methane emissions generally decrease as the peat surface gets drier (Bubier *et al.*, 2005; Strack and Waddington, 2007), whereas carbon dioxide emissions might increase due to an increased heterotrophic respiration (Alm *et al.*, 1999a; Yurova *et al.*, 2007). However, changes in the composition, distribution and productivity of peatland plant communities would also be expected with a change in peatland wetness, as determined by the water table depth and peat moisture content. As vegetation is at the interface between the peat and the atmosphere, changes in vegetation structure can have a profound effect on the carbon cycling in peatlands (Christensen *et al.*, 2004; Malmer *et al.*, 2005; Ward *et al.*, 2009). Changes in the biomass allocation within and between different plant functional types can change the production vs. decomposition of organic matter dynamics, the pathways of methane transport and the peat aeration through root activity (Belyea and Malmer, 2004; Strack *et al.*, 2006; Laiho, 2006).

A change in the amount of photosynthetic material available might affect the net primary production (NPP) of ecosystems. Total NPP (above and belowground) typically increases following drier conditions in peatlands (Minkkinen *et al.*, 1999; Laiho *et al.*, 2003). The rate at which peat decomposes depends on the amount and quality of litter input, which is, in turn, a function of vegetation composition and biomass allocation to different parts of the plants (Belyea and Malmer, 2004; Bauer, 2004). Decomposability can generally be predicted based on plant growth form, with decomposition following the general pattern, from highest to lowest rates: sedges > deciduous shrubs and trees > evergreen shrubs and trees > *Sphagnum* mosses (Aerts *et al.*, 1999; Thormann *et al.*, 2001; Scheffer *et al.*, 2001; Dorrepaal *et al.*, 2005).

Some studies have used artificial *in situ* drainage of peatlands for forestry or experimental purposes as a surrogate to study the possible consequences of a climate-driven water table drawdown on peatland plant communities. In fens, drainage usually results increased biomass and coverage of woody vegetation (both shrubs and trees), and a diminution of the coverage of species adapted to wet conditions, such as *Sphagnum* mosses (Laine *et al.*, 1995; Silvola *et al.*, 1996; Minkkinen *et al.*, 1999; Macdonald and Yin, 1999; Laiho *et al.*, 2003; Strack *et al.*, 2006). In bogs, tree biomass increases following drainage, but to a lesser extent than in fens (possibly due to a nutrient limitation), and changes in vegetation composition seem less important (Minkkinen *et al.*, 1999; Vasander, 1982).

I studied the changes in vegetation biomass and leaf area index along a water table gradient resulting from the 85 years-old drainage of a portion of an ombrotrophic peatland, the Mer Bleue bog, located in the cool temperate region of Eastern Canada (Chapter 3). Leaf area index (LAI), representing the total single-sided area of leaves per ground unit area (Chen and Black, 1992), is an important parameter expressing the control of photosynthetic material on NPP. My goal is to explore how changes in vegetation structure caused by changes in peatland wetness might affect peatland carbon functioning. My objectives are to (1) quantify the change in biomass and LAI following drainage, (2) determine if biomass allocation changes in different plant functional types and different plant components and (3) quantify the relationship between biomass and leaf area.

4.2. Study area

The Mer Bleue peatland is a 28 km^2 ombrotrophic mire complex located in eastern Ontario, Canada (45.41° N, 75.48° W). The climate of the area is cool continental, with a mean annual temperature of 6.0^{o}C and annual precipitation of 943.5 mm (1971 – 2000 normal for Ottawa International Airport; Environment Canada). The mire complex includes a central open raised bog, several treed sectors and poor fen areas at the margin. The study site is located in an open bog portion located in the eastern part of the peatland, where a drainage ditch was dug in 1922. The bog surface pattern consists of hummocks and small hollows, with a maximum relief between hummock tops and hollow bottoms of 0.5 m. Extended, more or less flat areas are also present and are referred to as lawns in this paper. S*phagnum* mosses cover the entire surface of the open bog and are overlain by a mostly evergreen shrub canopy, sparsely distributed sedges and a few small trees. The drainage led to a notable increase in tree (*Larix laricina*, *Betula populifolia*) and deciduous shrub (*Vaccinium myrtilloides*) coverage and a decrease in *Sphagnum* coverage (Chapter 3). Six sampling sites were selected to cover different levels of disturbance as indicated by the vegetation changes, the surface peat density, the average water table depth and the position relative to the drainage ditch (Figure 4.1, Table 4.1).

Table 4.1 – General description of the sampling sites and quadrats. Water table depth is the average of growing seasons 2005 and 2006, taken at an intermediate microtopographic location (see Chapter 3). Electrical conductivity and pH of the peat pore water is the average of seven measurements taken over growing seasons 2005 and 2006.

Site	Distance relative to ditch[1] (m)	Treatment	Number of Quadrats	Quadrat size (cm)	Water table depth (cm) (±SD)	pH (±SD)	Conductivity (mS/m) (±SD)
1	US 200	Control	9	50x50	12.6 (6.3)	3.7 (0.5)	69.1 (4.3)
2	US 60	Drained	12	50x50	25.2 (8.8)	4.0 (0.2)	64.1 (8.8)
3	US 30	Drained	12	50x50	31.4 (9.1)	4.1 (0.3)	55.3 (6.6)
4	DS 30	Drained	6	75x75	38.6 (17.7)	3.7 (0.1)	155.9 (24.2)
5	DS 60	Drained	6	75x75	33.2 (15.0)	4.0 (0.1)	127.7 (13.2)
6	DS 200	Drained	6	75x75	28.6 (15.3)	4.1 (0.4)	150.1 (28.1)

[1] US = upslope, DS = downslope

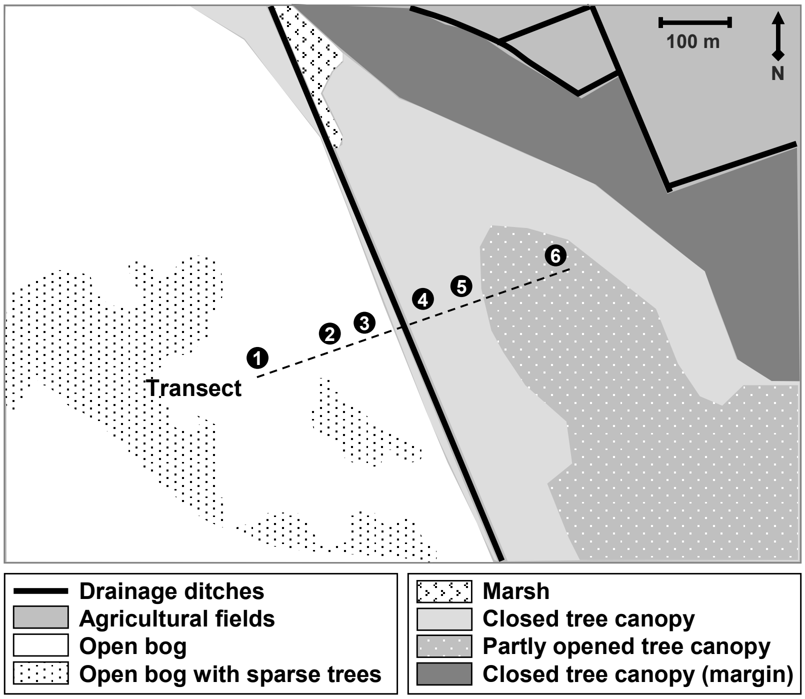

Figure 4.1 - Location of the 6 sampling sites along the study transect, with the main vegetation types and drainage ditches from the eastern portion of the peatland.

4.3. Material and methods

The aboveground parts of shrubs, tree seedlings, herbs and mosses were clipped in 51 quadrats distributed among the six sampling sites. To insure that all major components of the landscape were included in the sampling, the number of quadrats per site was dependent on the presence and extent of microforms and the dominant vegetation types (Table 4.1). The quadrats in sites 1 to 3 were randomly distributed between pre-identified microforms, comprising 3 hummock, 3 hollows and 3 lawn plots each. In addition, sites 2 and 3 had 3 quadrats each representing a taller form of hummocks, mostly dominated by deciduous shrubs. Sites 4 to 6 had 6 randomly distributed quadrats each. The shrub layer of the sites located downslope from the drainage ditch was much taller (approx. 1.0 m high) compared to the upslope shrubs (approx. 0.2 m high). Quadrats had therefore to be larger on that side to allow a better estimation of shrub biomass, hence quadrats 4 to 6 were 0.75 x 0.75 m, whereas quadrats 1 to 3 were 0.50 x 0.50 m.

Each quadrat was identified using bamboo posts and nylon strings one month prior to clipping. During that period, water tables were measured at least once per week using a PVC tube installed at one corner of each quadrat. Clipping was conducted inside a period of 2 weeks at the end of August 2005. After assessing the percent cover of all species present in the quadrats and the average height of all shrub species, the living vegetation was clipped and sorted by species into plastic bags. As there is no clear distinction between the living and dead parts of *Sphagnum* mosses' stems, we clipped the stems at the base of the capitula for all species of all quadrats (Moore *et al.*, 2002). In the lab, plants were sorted into leaf and woody components, when applicable. Each component was oven-dried at 80^{o} C for 48 hours and weighed.

The biomass of the trees on the downslope side of the drainage ditch was evaluated using allometric relationships based on non-destructive measurements within three sampling parcels of a radius of 5 m, randomly located within each site (4 to 6). Within each radia, I measured the diameter at breast height of all living trees (breast height is defined as 1.37 m above the forest floor on the uphill side of the tree). In addition, I measured the total height, crown width and crown height of three trees randomly selected from the dominant tree layer. The total aboveground and belowground (coarse roots only) biomass, as well as the partitioning between foliage and wood biomass were determined based on the equations of Ker (1980) and Bond-Lamberty *et al.* (2002) for above-ground biomass and Jenkins *et al.* (2003) for belowground biomass. I also present estimates of the belowground biomass conducted close to sites 1 and 3, based on 3 hummock and 3 hollow cores of 0.10 x 0.10 m each, the depth of the cores depending on the rooting depth (Murphy, 2009). A less rigorous estimate of fine root biomass based on one core only conducted close to site 5 is also presented (A. McKinley, pers.com.), to complement the coarse root biomass calculated from allometric relationships. Total aboveground biomass per site was calculated by weighting the average of each microform depending on its importance in the landscape. Weighting was based on data derived from a microtopographic transect, where each section was assigned to the microform "hollow", "lawn", "high hummock" or "low hummock" (data not shown).

We measured understorey and overstorey LAI for all 51 biomass quadrats using a combination of optical measurements and plot-specific allometric relationships based on specific leaf area (SLA), the ratio of leaf area to leaf dry mass. Understorey LAI was calculated by scanning and weighing a portion of the clipped leaves for each quadrat. Based on this SLA estimate and the total weight of all leaves clipped per quadrat, we calculated a species-based LAI (for details, see Sonnentag *et al*., 2007a). Overstorey LAI above each quadrat was calculated from effective LAI measurements under diffuse sky conditions using the LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, NE, USA). Effective LAI was converted to overstorey LAI as outlined in Sonnentag et al. (2007b).

Statistical analyses were conducted using the SAS software. Biomass, LAI, SLA and ratios were related to each other and to the water table depth via regression analyses. Curve fitting was done based on theoretical considerations rather than on goodness of fit statistics. The influence of site or microform on different biomass parameters and LAI was tested using an ANOVA test, followed by post-hoc multiple comparisons using the Dunnett-Tukey-Kramer pairwise test, adjusted for unequal variances and unequal sample sizes.

4.4. Results

Relative to the reference site, all sites experienced changes in water table following drainage (Table 4.1). However, the total aboveground biomass dry weight is significantly different from the reference site only at sites 4, 5 and 6 located downslope from the drainage ditch, mostly due to the establishment of a tree layer (Table 4.2). Site 4, where water table experienced the greatest impact of drainage (Table 4.1), is also the site that has the highest biomass (5720.6 ± 454.6 g m^{-2}), compared to the reference site 1 (688.2 ± 234.1 g m^{-2}) (Table 4.2, Figure 4.2). The shrub biomass varies according to microform, with hollows and lawns having a significantly lower shrub biomass than low and high hummocks (Table 4.3). However, total biomass differs significantly only for the downslope, “flat” sites 4 to 6, because of the confounding effect of increasing *Sphagnum* biomass in microforms that have a lower shrub biomass (Table 4.3).

Although I do not have enough belowground biomass data to get a precise figure of the drainage effect on roots, the data shown in Figure 4.2 indicates that there is an increase in root biomass in the drained upslope (3) and downslope (5) sites, and that the proportion of the total biomass (above and belowground) occupied by roots decreases with an increase in aboveground biomass.

The partitioning of the aboveground biomass between different plant functional types changes along the transect, with trees being the dominant component in sites 4, 5 and 6, comprising 88, 78 and 69 % of total aboveground biomass, respectively. The main tree species present are *Larix laricina* (89, 61 and 33 % at sites 4, 5 and 6, respectively) and *Betula populifolia* (11, 38 and 17 % at sites 4, 5 and 6, respectively). Evergreen shrubs dominate at sites 1, 2 and 3, occupying 89, 81 and 72 % of total biomass, respectively (Figure 4.3). When compared to the coverage of evergreen shrubs, the importance of deciduous shrubs also increases with decreasing water tables, whereas *Sphagnum* mosses biomass goes from representing 18 % of the total biomass in site 1 to less than 1 % in sites 4, 5 and 6 (Figure 4.3).

Table 4.2 – Comparisons among sites for different biomass descriptors and total LAI. The leaves vs. total biomass fraction corresponds to the shrub leaf biomass over shrub total aboveground biomass. Standard deviations are in brackets. For all columns, the treatment effect was significant as tested by an ANOVA (all $p < 0.001$). For each column, the averages followed by the same letters are not significantly different from each other.

Site number	Total biomass ($g\ m^{-2}$)	Shrub biomass ($g\ m^{-2}$)	*Sphagnum* biomass ($g\ m^{-2}$)	Leaves vs total biomass fraction (-)	Total LAI (-)
1	688.2^{a} (234.1)	505.7^{a} (233.5)	120.42^{a} (41.0)	0.41^{a} (0.09)	1.58^{a} (0.78)
2	671.8^{a} (201.6)	491.6^{a} (245.6)	119.36^{a} (56.53)	0.40^{a} (0.07)	1.45^{a} (0.51)
3	699.3^{a} (355.0)	537.9^{a} (398.2)	99.17^{ab} (50.24)	0.37^{ab} (0.11)	1.25^{a} (0.67)
4	5720.6^{b} (454.6)	674.7^{ab} (291.4)	20.61^{b} (19.71)	0.19^{b} (0.06)	5.77^{b} (0.53)
5	4908.6^{c} (2018.1)	1026.2^{b} (434.5)	7.59^{b} (9.67)	0.12^{b} (0.04)	7.25^{c} (0.80)
6	3174.9^{d} (1619.0)	938.7^{ab} (257.9)	17.39^{b} (15.48)	0.18^{b} (0.02)	5.31^{b} (0.90)

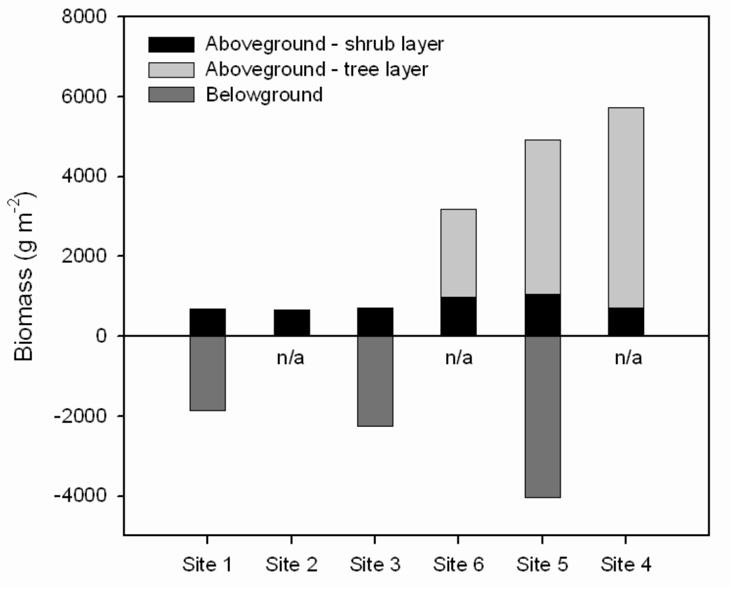

Figure 4.2 – Total biomass of the aboveground tree layer, shrub layer (including herbs and mosses) and belowground biomass (estimate available for plots 1, 3 and 5 only). Sites are in order of their level of disturbance by drainage.

Table 4.3 – Comparisons among microforms for different biomass descriptors and total LAI. The plots 4 to 6 do not have microforms - they are averaged together as “flat”. For all columns, the treatment effect was significant as tested by an ANOVA (all $p < 0.001$). Standard deviations are in brackets. The averages followed by the same letters are not significantly different from each other.

Microform	Total biomass (g m^{-2})	Shrub biomass (g m^{-2})	*Sphagnum* biomass (g m^{-2})	Leaves vs total biomass fraction (-)	Total LAI (-)
Hollow	470.47^{a} (109.77)	258.10^{a} (90.81)	147.73^{a} (21.88)	0.40^{ab} (0.07)	0.77^{a} (0.31)
Lawn	535.05^{a} (85.76)	353.41^{a} (99.53)	125.72^{ab} (42.56)	0.46^{a} (0.03)	1.21^{ab} (0.53)
Low hummock	907.35^{a} (114.38)	766.13^{b} (143.99)	82.46^{bc} (50.88)	0.33^{bc} (0.07)	1.92^{c} (0.40)
High hummock	1065.95^{a} (185.86)	937.26^{b} (207.24)	56.53^{cd} (32.63)	0.26^{c} (0.07)	2.18^{c} (0.28)
Flat (upslope)	4601.38^{b} (1141.80)	879.89^{b} (374.32)	15.20^{d} (15.64)	0.17^{d} (0.05)	1.81^{bc} (0.63)

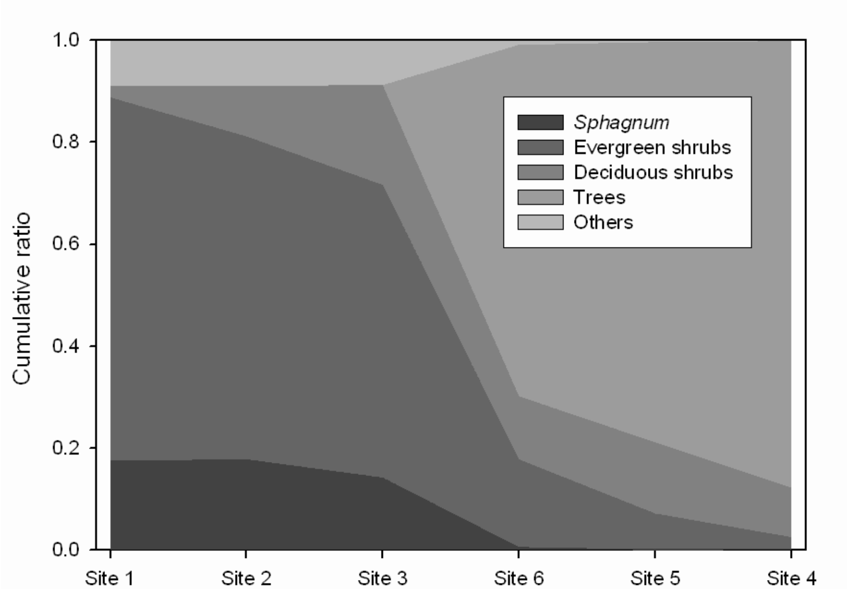

Figure 4.3 – Cumulative proportion of the main plant functional types to the total aboveground biomass of all sites, showed by order of level of disturbance of the peatland wetness (from the least affected by drainage to the most affected by drainage).

Total LAI is significantly higher in sites 4, 5 and 6 ($p < 0.001$), mostly due to the contribution of the tree layer (Figure 4.4, Table 4.2). Within site 1, 2 and 3, LAI increases with the height of the microforms, with hollows < lawns < low hummocks < high hummocks, although hollows and lawns and low and high hummocks are not significantly different from each other (Table 4.3). Shrub LAI is significantly ($p < 0.001$) related to leaf biomass, shrub biomass and total biomass of upslope sites (r^2 of 0.88, 0.83 and 0.80, respectively) (Figure 4.5). The LAI of the shrub layer of the downslope plots is also significantly ($p < 0.001$) related to leaf biomass, shrub biomass and total understorey biomass of the plots, but the relationships are less tight (r^2 of 0.49, 0.46 and 0.42, respectively).

Both total biomass and LAI are significantly related to water table depth ($p < 0.001$, r^2 of 0.60 and 0.36, respectively), for the plots of sites 1 to 3 (Figure 4.6A, C). Biomass and LAI of sites 4 to 6 are not significantly related to water table depth (Figure 4.6B, C). The water table averages of the plots from sites 4 to 6 are within the range of the driest extremes from sites 1 to 3. SLA values are generally higher for the plots from sites 4 to 6, as they are mostly related to the relative importance of deciduous vs. evergreen shrub biomass (Figure 4.7).

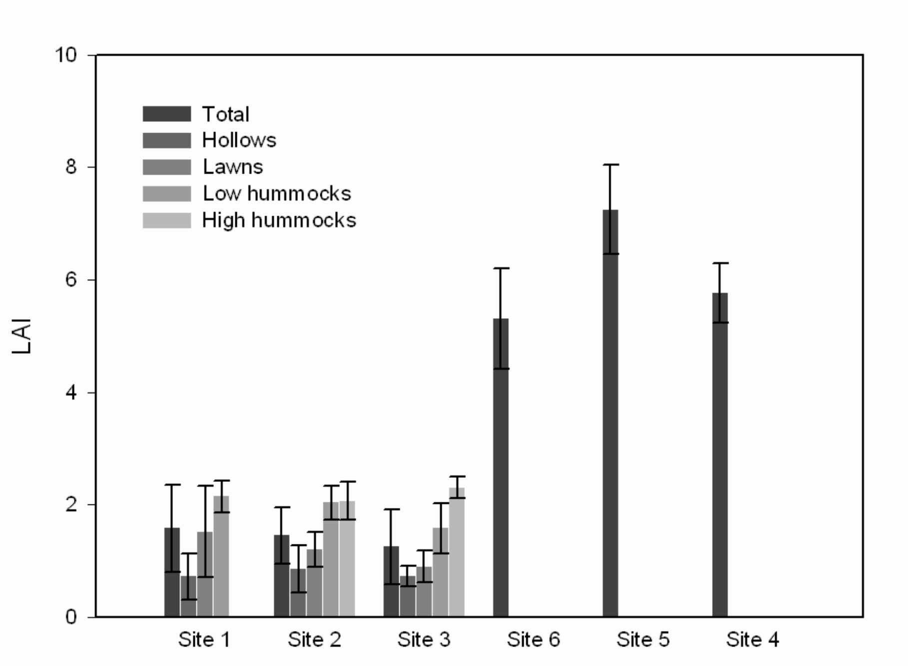

Figure 4.4 – Total LAI for each site, and partitioning of LAI per microform for site 1 to 3. Error bars are one standard deviation. Sites are presented in order of their level of disturbance by drainage.

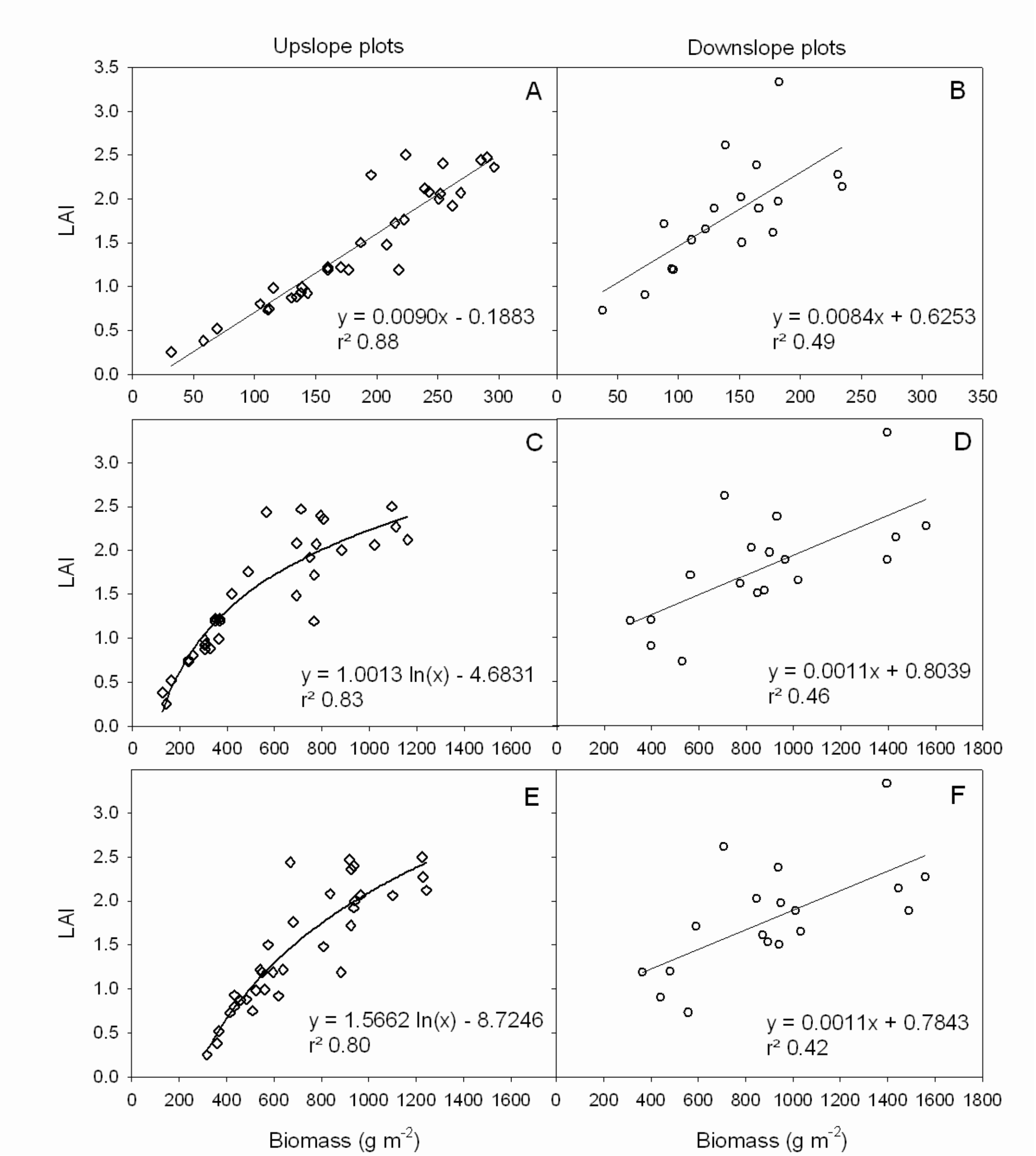

Figure 4.5 – Relationships between shrub LAI and shrub leaf biomass (A, B), total shrub biomass (C, D) and total biomass of all species from the shrub layer (E, F) for upslope 1 to 3 (left) and downslope 4 to 6 (right) plots. The LAI for downslope plots is for the shrub layer only.

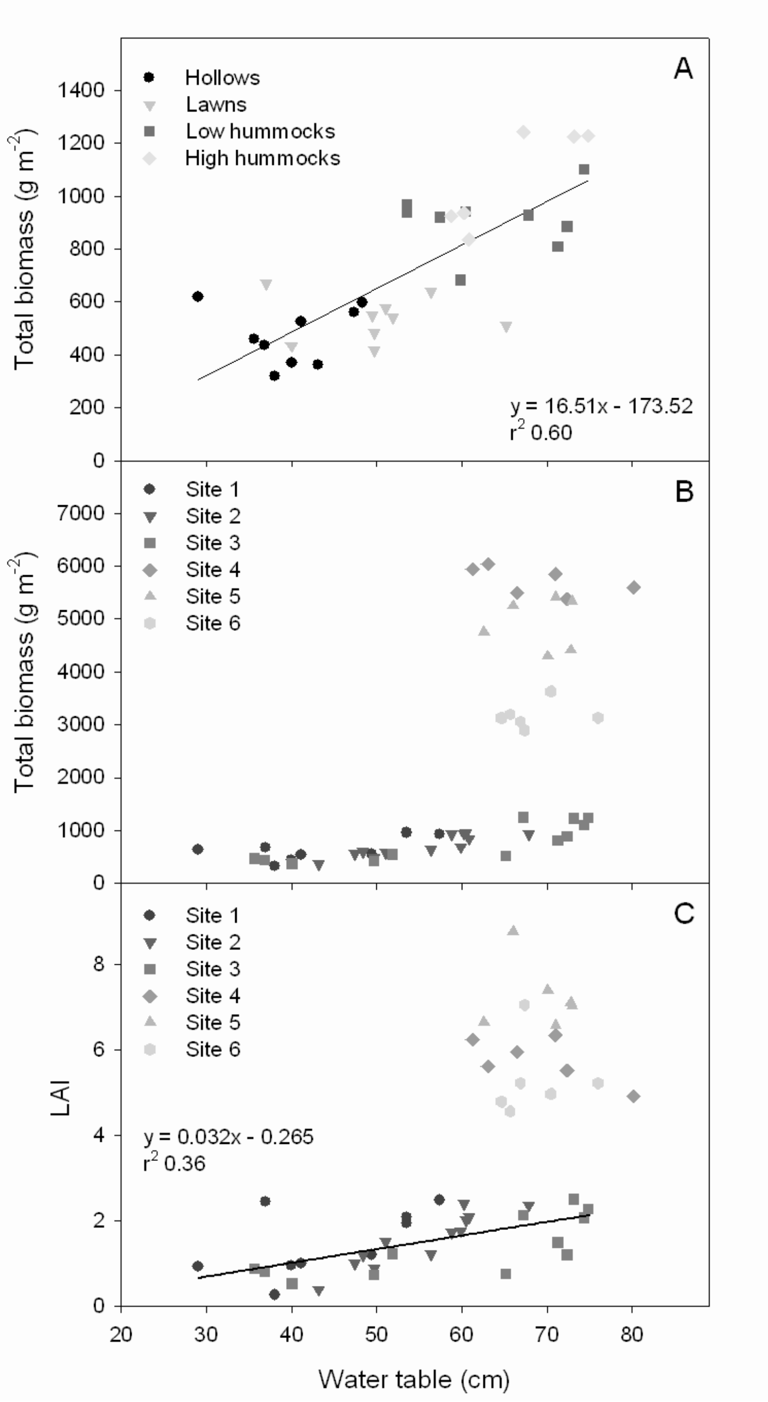

Figure 4.6 – Relationships between (A) total biomass and water table depth for sites 1, 2 and 3, by microform; (B) total biomass and water table depth for all sites, by site; and (C) total LAI for all sites, by site.

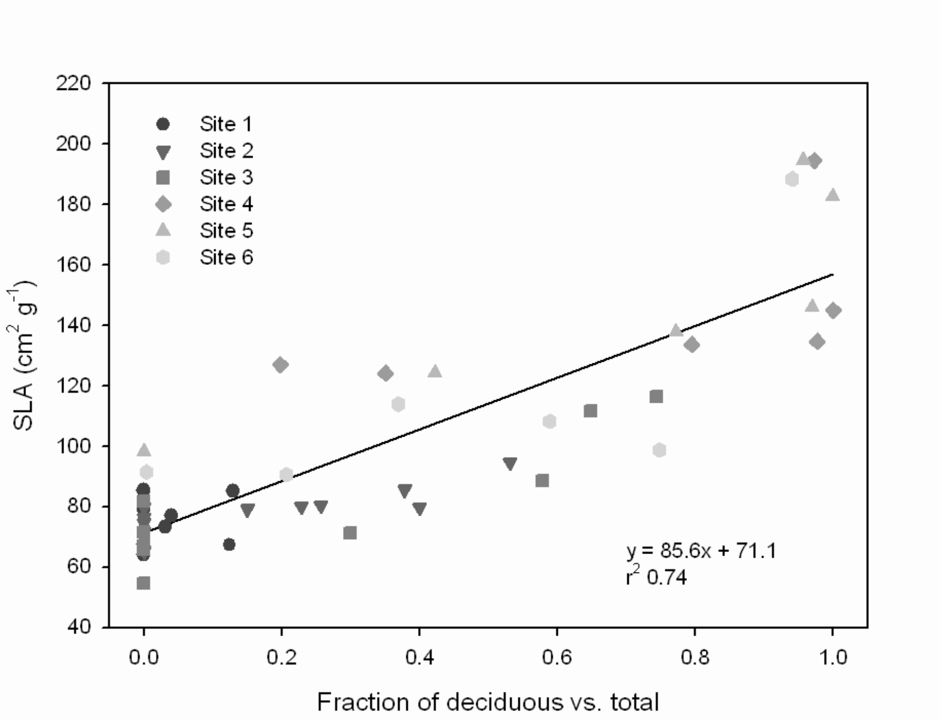

Figure 4.7 – Relationship between specific leaf area (SLA) of the shrubs and the fraction of deciduous shrubs over total shrub biomass.

4.5. Discussion

Depending on the magnitude of the impact of drainage on water table, and perhaps on other related factors not studied here such as nutrient dynamics and peat porosity, post-drainage conditions might lead to subtle or radical changes in the structure of the vegetation. The vegetation of the upslope sites (2 and 3) that experienced a mild lowering of water tables due to drainage (around 10 and 15 cm on average for sites 2 and 3, respectively) has not changed notably. The amount of aboveground biomass in these sites as well as the reference site are similar to the ones reported by Moore *et al.* (2002) for another open bog section of Mer Bleue. However, the shrub layer of sites 2 and 3, although still dominated by evergreen shrubs, has a higher deciduous shrub biomass and a slightly (albeit not significantly) lower LAI. Another study at the same site showed that *Sphagnum* total coverage did not change substantially between site 1 and sites 2 or 3, but that the proportion of species changed (Chapter 3). Most studies looking at community changes upon drying in peatlands have concentrated on either fen communities or bog communities where graminoids are present. In drier conditions, graminoids do not compete well with, and are generally replaced by shrubs (Weltzin *et al*., 2003). Communities that are already dominated by shrubs might therefore be less responsive to a lowering of the water table. However, a change of a small proportion of species for plants that produce more or less decomposable litter, or that are more or less productive, could affect a peatland's capacity to sustain carbon accumulation in the long run, especially in combination with lower water tables and hence, potentially increased respiration rates.

On the downslope side of the drainage ditch (sites 4, 5 and 6), the establishment of a tree layer in the most severely drained sites, the replacement of evergreen shrub species by deciduous shrub species, and the decrease in the contribution of *Sphagnum* species to the total biomass are the most notable difference in vegetation. An increase in the tree biomass following drainage has commonly been observed, but mostly in nutrient-rich sites (Laiho and Laine, 1997; Laine *et al.*, 1995; Silvola *et al.*, 1996; Minkkinen *et al.*, 1999; Macdonald and Yin, 1999; Strack *et al.*, 2006). These shifts imply changes in the quality of the litter, as leaves from deciduous shrubs are generally more decomposable than the litter from evergreen shrubs and *Sphagnum* (Dorrepaal *et al.*, 2005). In combination with a lower water table, this could affect the capacity of the ecosystem to accumulate peat. However, the litter production of deciduous species is higher, as they loose all their leaves yearly. This potential increase in net primary production, or an increased production of fine roots because of the presence of a tree layer (Minkkinen and Laine, 1998) might offset the effect of an increase in the decomposability of the litter.

The experimental design, with the sampling plots stratified by microform, was chosen in order to measure the maximum variability within each site. However, because of this design, the standard deviation within each site is higher than what it would have been if the sampling was completely randomized. Hence, although shrub biomass was not significantly higher in most of the drained sites, there is a clear trend towards an increase in shrub biomass with lower water tables, despite the concurrent presence of a tree layer. This increase is mostly due to an increase in the woody components of the shrubs, as the biomass allocation to leaves gets lower in drier conditions. The decrease in the percentage of shrub leaves can be explained by the replacement of evergreen shrubs by deciduous shrubs upon drainage. Evergreen shrubs that have to compete with *Sphagnum* mosses have been shown to allocate more biomass to leaves (Luken *et al.*, 1985). Deciduous shrubs generally have a higher SLA (when expressed as unit area per dry mass) and hence, leaf vs. total biomass ratio than evergreen shrubs, corresponding to different ecological strategies (DeLucia and Schlesinger, 1995; Givnish, 2002). A study also showed that along a bog – upland transect, shrubs generally have a higher specific leaf area at the center of a bog, and it gradually decreases as going upland (Burns, 2004).

The presence of an apparent bimodal distribution of vegetation biomass along the transect suggests that there are two alternative stable states of vegetation structure upon drainage. Paleoecological reconstructions conducted on the downslope side of the ditch indicate that trees established just a few years after drainage (Chapter 3). The positive effect of the establishment of trees on their microsite growing conditions could explain the persistence of trees on the downslope site even though the hydrological conditions prevailing now are not substantially different from the upslope sites (Figure 4.8). The establishment of the tree layer could have been promoted by a slightly lower water table on the downslope side of the ditch, perhaps in combination with other factors such as a differential exposure to fire, although this is not supported by paleoecological evidences (Chapter 3). This type of dynamic, where, once established, a community persists through positive feedbacks, could explain the dominance of the two alternative stable vegetation states, even though the hydrological niche of the two systems now overlap (Scheffer and Carpenter, 2003; Scheffer *et al.*, 2005).

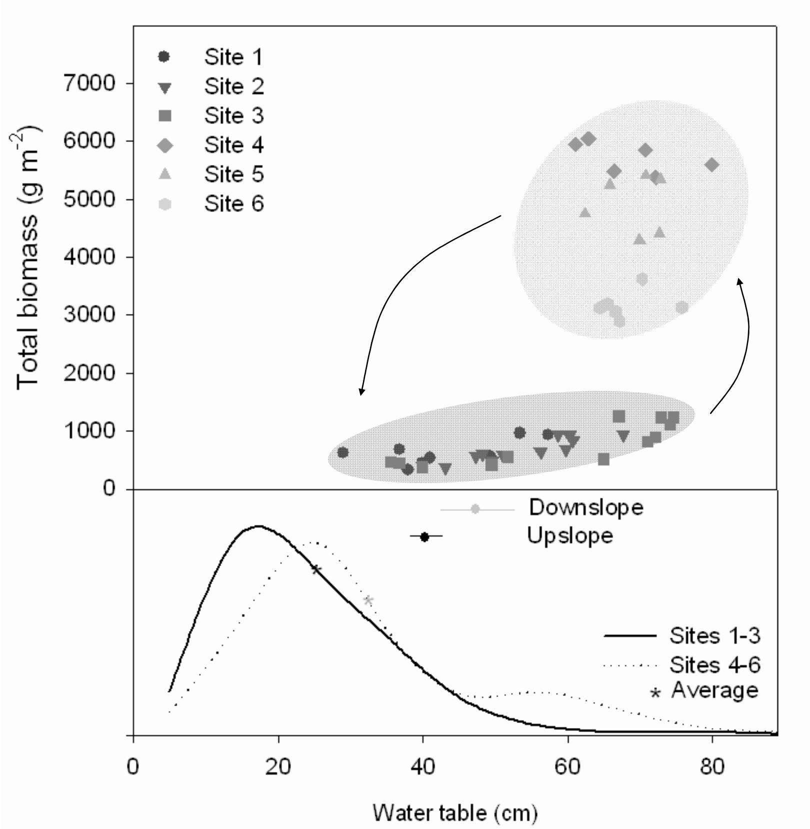

Figure 4.8 – Relationship between total biomass and water table depth (water table measurements limited to the driest weeks of the 2005 growing season), with a conceptual model of multiple equilibrium overlain (top) and water table frequency distributions of the average of upslope and downslope sites over the growing seasons 2005 and 2006 (bottom). The dots on top of the frequency distributions represent the water table depth right after drainage as inferred from testate amoeba reconstructions (Talbot *et al.*, in press), with their associated uncertainty.

Conclusion

The water table drawdown created the drainage ditch at the center of this study enabled us to study a wide range of post-drainage conditions and their impact on the vegetation structure, 85 years after the drainage occurred. In the most severely drained sites, a tree layer appeared and the shrub layer changed from being dominated by evergreen shrubs to being dominated by deciduous shrubs.

Changes in the structure, biomass and biomass allocation of the vegetation all have the potential to affect the carbon functioning of peatlands. However, the depth of the water table alone might not be the only factor that allows the most dramatic responses of a peatland to drying as observed here. A more in-depth study of the mechanisms leading to a tree invasion of bogs would allow a better understanding and prediction of the impacts of climatic changes on the carbon functioning of northern peatlands.

Chapter 5 - Long-term water table drawdown and vegetation changes affect carbon fluxes and stores in a North American bog

Context within the thesis and overview

This chapter uses a similar approach to Chapter 4 (the use of sampling areas along the hydrosequence) to characterize the effect of a water table drawdown and subsequent vegetation changes on different components of the carbon cycle of peatlands, and on its capacity to store carbon. This chapter therefore contributes to attain my second and third thesis objective, to assess how the changes in water table depth and vegetation community structure lead to changes the carbon functioning of the system, and to investigate if the changes in vegetation communities lead to a change in the net C balance of the system. The carbon content of biomass uses the biomass data detailed in the preceding chapter.

My results show that the different components of the carbon cycle are affected by the combined and individual effects of water table lowering and vegetation changes. Methane emissions decrease with a lower water table but are not affected by vegetation changes, whereas ecosystem respiration increases as a result of both water table lowering and vegetations changes. Mid-day net ecosystem exchange is closely related to the vegetation type, with deciduous shrubs > evergreen shrubs > *Sphagnum* mosses, but the impact of the water table lowering alone is hard to assess as vegetation assemblages and water table depth are correlated. As a result, the carbon storage by the system increased because of a 10-fold increase in the vegetation biomass, although amount of carbon sequestered as peat is lower in the drained site, as a result of a combination of a lower rate of accumulation since drainage and an oxidation of the deeper layers of peat following drainage.

5.1. Introduction

The quantity of carbon (C) stored in peatlands depends on the balance between net ecosystem exchange (NEE), methane (CH_4) fluxes and dissolved organic carbon (DOC) export. As organic matter production generally exceeds decomposition, CH_4 emissions and DOC exports, peatlands are long-term sinks for C. Northern peatlands have accumulated C at a mean long-term rate of about 20-30 g C m^{-2} yr^{-1} since their initiation (Turunen *et al.*, 2002, 2004). However, the role of peatlands in the global C cycle may change as climate changes at higher latitudes. A recent multi-year NEE study based on eddy covariance and chamber flux measurements, along with CH_4 flux measurements and DOC export estimates, shows a high year-to-year variability in the annual net ecosystem carbon balance (NECB, Chapin *et al.*, 2006) between years, indicating that peatlands might switch from a source to a sink of C from one year to the other depending on climatic and environmental conditions (Roulet *et al.*, 2007).

The C balance of peatlands is closely related to hydrological conditions, which affect each of the C balance components at different magnitudes and in different directions (Moore *et al.*, 1998; Trettin *et al.*, 2006). In general, NEE gets more negative under wet conditions (thus the net CO_2 uptake by the peatland is larger) in both bogs and fens (Carroll and Crill, 1997; Alm *et al.*, 1999a; Bubier *et al.*, 2003; Yurova *et al.*, 2007), mostly due to decreased ecosystem respiration (ER). CH_4 emissions from peatlands also depend on hydrological conditions as the thickness of the unsaturated zone (as determined by the water table depth) controls, in part, the CH_4 production/consumption balance. Hence, drier conditions are commonly associated with lower CH_4 emissions from bogs and fens (Moore and Knowles, 1993; Bubier *et al.*, 2005; Pelletier *et al.*, 2007; Strack and Waddington, 2007). DOC movement and export from peatlands could also depend on the water table depth (Fraser *et al.*, 2001), although the relationship between peatlands' hydrology and DOC export is debated (Pastor *et al.*, 2003; Freeman *et al.*, 2004).

Long term and secular changes to climatic conditions will not only affect peatland carbon fluxes, but will also affect vegetation composition, and this can in turn modify the carbon balance (Belyea and Malmer, 2004). The rate at which organic matter decomposes is strongly dependent on litter quality, and can generally be predicted based on plant growth form, with decomposition rates following the general pattern sedges > deciduous shrubs and trees > evergreen shrubs and trees > *Sphagnum* mosses (Aerts *et al.*, 1999; Thormann *et al.*, 2001; Dorrepaal *et al.*, 2005).

Roulet *et al.* (1992) estimated that the water table in peatlands could drop by around 15 cm with a doubling of the atmospheric CO_2 concentration, and this is of the same order of magnitude as a water table drop due to drainage conducted for forestry purposes. Hence, it has been suggested that forestry drainage is a reasonable model for assessing long-term effect of climate change on vegetation dynamics and carbon storage of peatlands (Laine *et al.*, 1995). Drainage generally results in increased woody vegetation biomass and a decrease in species adapted to wetter conditions in fens and, to a lesser extent, in bogs (Vasander, 1982; Laine *et al.*, 1995; Minkkinen *et al.*, 1999; Laiho *et al.*, 2003; Prévost *et al.*, 2005; Hillman and Roberts, 2006). However, the impact of drainage and corresponding vegetation changes on the carbon balance of peatlands is variable and depends on a multitude of interacting factors that are not well understood yet (see review of Laiho, 2006). Some studies show an increase in CO_2 emissions after drainage (Silvola *et al.*, 1996; Alm *et al.*, 1999b), while others conclude a slight increase in peat CO_2 storage follows drainage (Minkkinen *et al.*, 2002). According to Minkkinen *et al.* (2002), this increase in peat CO_2 storage, in combination with an increase in living biomass and a decrease in CH_4 emissions, could lead to increased NECB in drained peatlands, at least on the short- to mid-term (Minkkinen *et al.*, 2002).

To examine the association between changes in vegetation structure in a peatland ecosystem and its carbon function, I studied the variation of carbon fluxes and stores along a water table and vegetation composition gradient resulting from the 85 years-old drainage of a portion of an ombrotrophic peatland (Chapter 3). My goal in this paper is to explore the interacting influences of water table and vegetation change on components of the carbon balance of a northern peatland. My objectives are to evaluate the direction and magnitude of changes of part of the carbon fluxes (CH_4, NEE, ER) and on the vegetation and peat carbon pools in a peatland, using chamber exchange, biomass, and detailed peat carbon measurements.

5.2. Material and methods

5.2.1. Study area and sampling sites

The Mer Bleue peatland is located 5 km east of Ottawa (Figure 5.1). This 28 km^2 mainly ombrotrophic complex formed about 8500 years ago in an abandoned postglacial river channel and to date has accumulated up to 6 m of peat in some parts (Roulet *et al.*, 2007). The climate is cool continental, with a mean annual temperature of 6.0°C and annual precipitation of 943.5 mm (1971 – 2000 average for Ottawa International Airport; Environment Canada; http://www.climate.weatheroffice.ec.gc.ca/climate_normals). The bog surface pattern consists of hummocks and small and shallow hollows. *Sphagnum* mosses cover the surface and are overlain by a mostly evergreen shrub canopy. Sparse sedges and small trees are also present.

A drainage ditch was dug in 1922 in the eastern part of Mer Bleue. The drainage led to a shift of vegetation dominance from *Sphagnum* mosses and evergreen ericaceous shrubs to trees and deciduous ericaceous shrubs, observed up to a few hundred meters away from the ditch on the downslope (east) side of the drainage ditch (Chapter 3). Six experimental sites were established along a transect perpendicular to the ditch to cover different levels of disturbance as indicated by the water table depth, the vegetation differences, and the density of the surface peat (Figure 5.1, Table 5.1).

Sites 1-3 are located upslope from the drainage ditch. Sites 1 and 2 are 200 m and 60 m away from the drainage ditch and the vegetation and peat decomposition level (as indicated by the Von Post scale) were apparently not affected by drainage, although the water table was temporarily affected by drainage at site 2 (Chapter 3). Both have similar vegetation assemblages to pristine open bog sections located elsewhere in the peatland. Site 3 is located 30 m away from the drainage ditch, and although the vegetation has only been slightly affected by drainage, the water table and peat decomposition were different from sites 1 and 2.

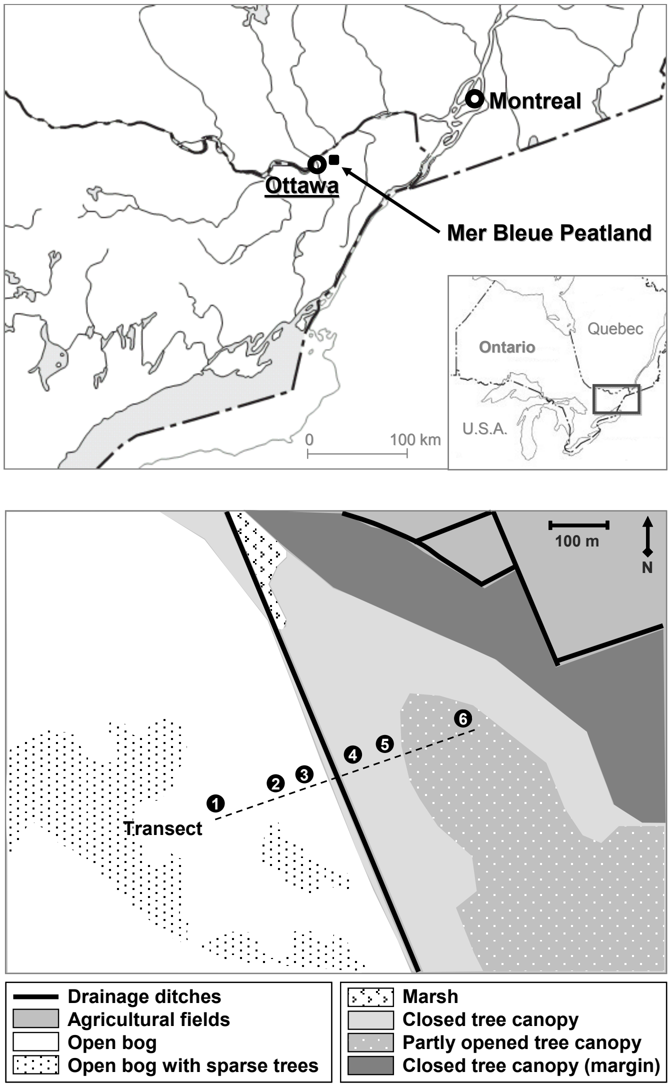

Figure 5.1 – Location of Mer Bleue Peatland, Ontario, Canada (45.41° N, 75.48° W) and location of the 6 sampling sites along the transect, with the main vegetation types and drainage ditches from the eastern portion of the peatland.

Table 5.1 – General description of the sampling sites. Water table depth is the average of growing seasons 2005 and 2006, taken at an intermediate microtopographic location. Electrical conductivity and pH of the peat pore water is the average of seven measurements taken over growing seasons 2005 and 2006. Von Post classes were determined for

Site number	Location relative to ditch[1]	Distance from ditch (m)	Treatment	Water table depth (±SD) (cm)	pH (±SD)	Conductivity (±SD) (mS/m)	Von Post class[2]	Approx. vegetation layer coverage (%)		
								Sphagnum	Shrubs	Trees
1	US	200	Control	12.6 (6.3)	3.7 (0.5)	69.1 (4.3)	3	100	90	10
2	US	60	Drained	25.2 (8.8)	4.0 (0.2)	64.1 (8.8)	3	100	90	0
3	US	30	Drained	31.4 (9.1)	4.1 (0.3)	55.3 (6.6)	5	100	80	10
4	DS	30	Drained	38.6 (17.7)	3.7 (0.1)	155.9 (24.2)	6	50	70	60
5	DS	60	Drained	33.2 (15.0)	4.0 (0.1)	127.7 (13.2)	7	20	60	60
6	DS	200	Drained	28.6 (15.3)	4.1 (0.4)	150.1 (28.1)	7	30	80	50

[1] US = upslope, DS = downslope

[2] Class 3 = very weakly decomposed, class 5 = moderately decomposed, class 6 = strongly decomposed; plant structure somewhat indistinct, class 7 = strongly decomposed; plant structure indistinct.

Sites 4-6 are located downslope from the drainage ditch, where vegetation was clearly affected by persistently lower water tables over the last 85 years (Chapter 3). Paleoecological reconstructions show that the vegetation assemblages from these sites were similar to their close-by neighbors 1-3 before drainage occurred. Site 4 and 5 are located 30 and 60 m away from the ditch, respectively, and both present a closed tree canopy with an underlying shrub layer. Site 4 has been seasonally flooded in recent years due to beaver impoundment of the ditch. Site 6, located 200 m away from the ditch has a partly open tree canopy and a dense and high shrub layer.

5.2.2. CH_4 sampling and flux calculations

Round PVC collars (diameter 25 cm) that support flux measurement chambers were randomly inserted among pre-identified microtope locations for sites 1-3. They were completely randomly installed within sites 4-6 without regards for microtopography it has disappeared from these sites, presumably because of the drainage. More hummocks were sampled in sites 2 and 3 (6 hummock collars each) than in site 1 (3 hummock collars), as a previous study showed that hummock vegetation gets more diverse and that hummocks get higher closer to the ditch (Chapter 3). Measurements were taken at each location approximately once per month from May to September 2005 and May to September 2007, and once every second week from May to November 2006.

The percent coverage of all vegetation species was visually evaluated for each collar in August 2005. To allow for the weighting of the different microforms in the calculation of total fluxes, the percentage cover of the different microforms was calculated based on a microtopography transect, where the surface of peat was measured every 5 cm along a 400 m transect located close to the sampling sites (data not shown).

All CH_4 measurements were made using 18-liters opaque chambers, water-sealed to the PVC collars. Five 10 ml headspace air samples were taken at five minute intervals (time 0, 5, 10, 15 and 20 minutes) at each collar. Headspace gas samples were stored in a cooler for a maximum of 24 hours before being processed in the lab. Water table was measured at the time of CH_4 sampling from a water table tube inserted into the peat next to each collar. Air temperature and peat temperature at a depth of 10 cm were measured.

Gas samples were hand injected into a 1 ml sample loop of a Shimadzu Mini-2 gas chromatograph equipped with a flame ionization detector, using N_2 as a carrier. The column and detector temperatures were 50 and 100 ^{o}C, respectively. The flow rats were 30-40 ml min^{-1} for the N_2 carrier gas, 30 ml min^{-1} for H_2 and 300 ml min^{-1} for air. Fluxes were calculated by linear regression of the concentration change over time. Fluxes with coefficient of determination of less than 0.85 (when the 5 samples were used), of 0.95 (when 4 samples were used) or of 0.99 (when only three samples could be used) were rejected, unless the variation between samples was equal or less than the variation within know gas standards injected before and after each analysis run, in which case the net flux is considered to be equal to zero. Taking these criteria into account, 47 curves were rejected out of 600 (rejection rate of 7.8 %). The CH_4 fluxes are expressed in mg m^{-2} d^{-1}.

5.2.3. CO_2 sampling and flux calculations

Dark chamber ER rates, and/or NEE were measured from the same collars as the ones used for CH_4 sampling, approximately every month from June to November 2005, and twice between May and August 2006 using a clear, climate-controlled chamber water-sealed to the collars and an EGM-4 CO_2 analyzer. All plants were enclosed in the chamber when measuring sites 1-3, allowing the measurement of total ecosystem NEE and respiration. Only respiration was measured for sites 4-6, as the dominant vegetation layers (trees and high shrubs) was too big to fit in the chambers. Shrouds with different mesh sizes were used to reduce the light entering the chamber to approx. 50% and 25% of ambient light when measuring NEE. An opaque chamber was used for measuring ER. On every sampling date, four 3 min sampling runs at different light intensities were conducted for the collars of sites 1-3 on each sampling date, whereas only a 3 min dark chamber run was conducted for sites 4-6. Photosynthetically active radiation (PAR) was measured using a PAR sensor (PP Systems). Water table depth and air and peat temperatures at the beginning and the end of each run were also recorded.

NEE is the difference between gross primary productivity (GPP) and ecosystem respitation (ER). Rectangular hyperbolas were fitted to create light response curves to relate NEE and PAR (the photosynthetically active radiation) (Thornley and Johnson, 1990) using the curve fitting tool in Matlab, as:

$$NEE = \frac{GP_{\max} \times \alpha \times PAR}{\alpha \times PAR + GP_{\max}} + R$$

where NEE is in mg CO_2 m^{-2} s^{-1}, GP_{max} is the maximum photosynthesis rate, α is the apparent quantum yield (or initial slope of the rectangular hyperbola) and R is the dark respiration value (y axis intercept). For the comparison of NEE between the collars, I averaged the values taken in the middle of the growing seasons of 2005 and 2006 (mid-June to mid-August) and when PAR > 1000. To avoid the use of counter-intuitive negative axes, we present NEP (defined as –NEE by Chapin *et al.*, 2006) in the figures.

5.2.4. Biomass carbon content

Above-ground biomass was measured by clipping 33 0.5 x 0.5 m (sites 1-3) and 18 0.75 x 0.75 m quadrats (sites 4-6), located about 20 m away from the collars location (for details, see Chapter 4). Water table was measured prior to clipping using PVC tubes within each quadrat. The samples were oven-dried at 80^{o} C and weighed. The biomass of the trees on the downslope side of the drainage ditch was evaluated using allometric relationships (Ker, 1980; Bond-Lamberty *et al.*, 1992) based on non-destructive measurements within three sampling parcels of a radius of 5 m, randomly located within each site (4, 5, 6). Within each radius, we measured the diameter at breast height of all living trees (breast height is defined as 1.37 m above the forest floor on the uphill side of the tree). We also present estimates of the belowground biomass conducted close to sites 1 and 3 (Murphy, 2009). A less rigorous estimate of root biomass based on one core only conducted close to site 5 is also presented (A. McKinley, pers.com.).

The carbon content of green material from *Ledum groenlandicum* and *Vaccinium myrtilloides* (two species present in all sites) was determined. Three subsamples of each species were randomly selected from the biomass plots material of sites 1, 3, 4 and 6 (24 samples in total) and the %C content of dry weight was determined at the GEOTOP the stable isotope lab (Montréal, Canada). We used the C content values averaged for each species for the upslope plots (1, 3) and the downslope plots (4, 6) to calculate the C content of the biomass by using the coverage of evergreen (*Ledum*) and deciduous (*Vaccinium*) shrubs as a weighting factor for each site.

5.4.5. Peat carbon content

The C content of the upper portion of the peat was measured at sampling site 5 and approximately 25 meters upslope from site 2. Three 10 x 10 x 100 cm long peat cores were extracted from each location using a box corer in September 2004 (cores 2a and 5a) and in August 2005 (cores 2b, 2c, 5b and 5c). Cores were collected from intermediate microtopographic locations at site 2 and the downslope cores were sampled in small clearings. The cores were placed in plastic boxes, transported to the lab within 6 hours and kept at 4°C until further analyses. The cores were sliced every 1 cm, except for the first 5 cm to the surface that comprises loose *Sphagnum* moss or fresh litter. The stratigraphy of the cores was described every 5 cm (or less, in case of transition zones) following the Troels-Smith (1955) nomenclature. Subsamples of 4 cm^3 (upper part of the core) or 2 cm^3 (lower part of the core) were taken from the center of every slice down to a depth of 90 cm, were oven-dried at 80° C and weighed. They were subsequently burned at 600° C (loss-on-ignition) and weighed. Seven additional subsamples were taken from each core (one every 10 cm starting 5 cm from the top) for peat carbon content determination (at the GEOTOP the stable isotope lab, Montréal, Canada), to derive an LOI vs. C content curve.

A chronology for the upper portions of cores 2a and 5a was established using ^{210}Pb and palynostratigraphic markers (Chapter 3). This chronology, in combination with obvious patterns in peat density and the presence of a charcoal layer from a known event, the Carleton County fire (or Green's Creek fire), in 1870, were used to synchronize the chronology of all cores.

5.2.6. Statistical analyses

Regression analyses were conducted between flux averages per date, per collar or per site with environmental descriptors (water table depth and variability, peat temperature, vegetation percent coverage of *Sphagnum* and shrubs). The significance of the different relationships were tested with ANOVAs, the level of significance was fixed at $\alpha = 0.05$. When averaging fluxes both spatially and temporally, the basic principles of error propagation were applied to calculate the standard deviation. Groups of data were compared using t-tests or, when more than two groups were compared, using post-hoc multiple comparisons (Tukey's method with a Bonferroni correction), after making sure that an omnibus ANOVA test indicates that some groups are different. The statistical significance of all test used $\alpha = 0.05$. All statistical analyses were performed using SAS.

5.3. Results

5.3.1. CH_4 fluxes

The CH_4 fluxes follow a typical seasonal pattern, with lower fluxes in the spring and fall, and higher values reached mid-summer. Although the fluxes from most collars are in the same range in all three years of measurements, some collars reached very high values in 2006, where the water table was on average higher (Figure 5.2). However, the relationship between the average CH_4 fluxes of all collars and water table average, standard deviation or peat temperature are not significant (Table 2B).

The CH_4 fluxes from each individual collar averaged over the three years were not significantly correlated with any of the vegetation descriptors (Table 5.2A). The three most notable hotspots are hummocks from site 1, emitting much more CH_4 on any sampling date than the hollows from the same site, although the hollows had consistently shallower water tables. When these hotspots, which are highly variable in time, are excluded from the analyses, the CH_4 fluxes are significantly related to average water table depth (Figure 5.3). However, there is no relationship between instantaneous water table depth at the time of CH_4 sampling and the fluxes for any of the collars.

When spatially averaging the values from the individual collars by site, site 1 stands out as the site with the highest variations in fluxes and, as a result, the highest average (Figure 5.4). The average water table from collars from sites 4 to 6, located in treed areas, is not significantly different from the average water table of the collars located in the low shrub-covered "high hummocks" microforms in sites 2 and 3 ($p = 0.6522$). Similarly, the average CH_4 fluxes from both groups of collars are also not significantly different from each other ($p = 0.2794$).

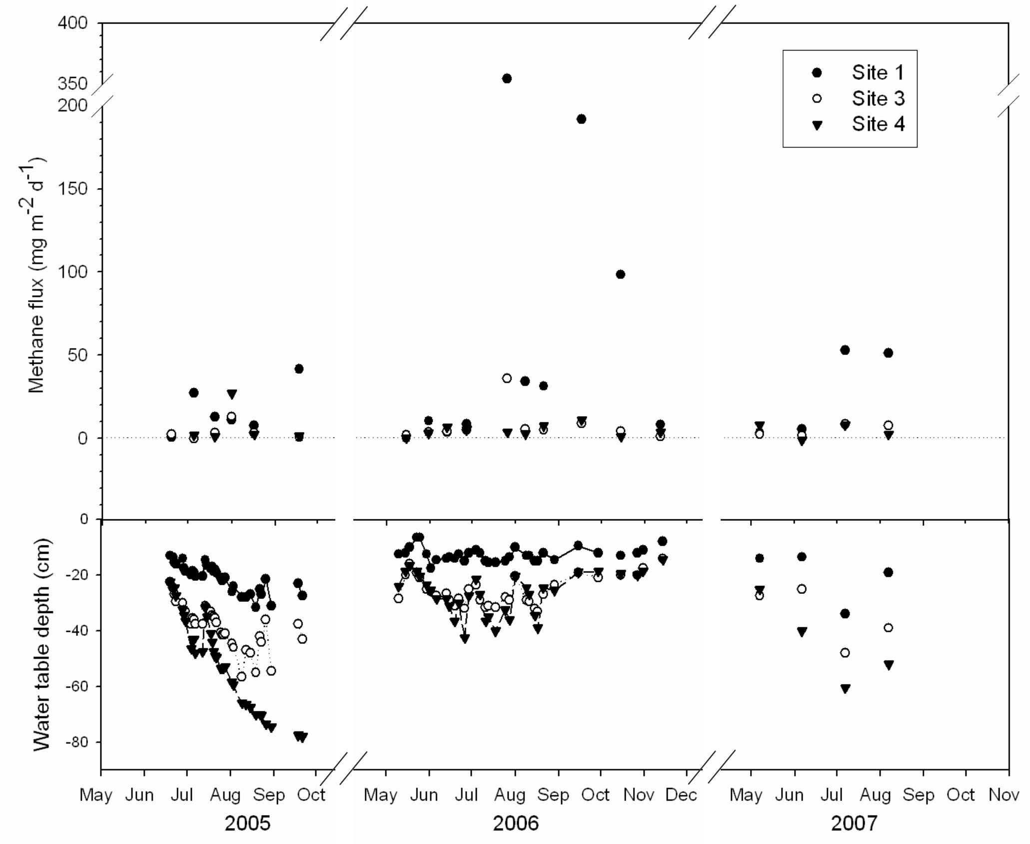

Figure 5.2 – Variations in the spatially weighted CH_4 emissions and the water table for sites 1, 3 and 4. The water table measurements are from a PVC tube located in the middle of the sites, taken twice weekly for 2005 and 2006, and at the time of methane sampling in 2007.

Table 5.2 – Regression analyses between measured fluxes and environmental descriptors. The values averaged per collar are the average of the three (CH_4) or two (CO_2) years of measurements for each collar (CH_4 relationships excluding the three outliers as shown on Figure 4). The values averaged per date are the average of all collars for a given date. When p-values are followed by an asterisk, the relationships are statistically significant. Only the equations of the statistically significant relationships are presented.

Flux	Environmental variable	P value	Equation	r^2
A CH_4 (per collar)	Water table average	< 0.0001*	$y = 0.2789x + 17.8496$	0.52
	Water table SD	0.0076*	$y = -0.7291x + 13.1460$	0.25
	Peat temperature	0.0310*	$y = -0.3498x + 8.9465$	0.17
	Sphagnum coverage	0.1354	n/a	n/a
	Shrub coverage	0.1832	n/a	n/a
B CH_4 (per date)	Water table average	0.9696	n/a	n/a
	Water table SD	0.5935	n/a	n/a
	Peat temperature	0.2465	n/a	n/a
C ER (per collar)	Water table average	0.0031*	$y = 0.0540x + 1.1507$	0.27
	Water table SD	0.0138*	$y = 0.1895x + 1.9955$	0.20
	Peat temperature	0.0696	n/a	n/a
	Sphagnum coverage	0.1704	n/a	n/a
	Shrub coverage	0.0161*	$y = 0.0151x + 2.5234$	0.19
D ER (per collar, sites 1-3 only)	Water table average	0.0044*	$y = 0.0373x + 1.4860$	0.35
	Water table SD	0.0212*	$y = 0.1473x + 1.9428$	0.25
	Peat temperature	0.4739	n/a	n/a
	Sphagnum coverage	0.2317	n/a	n/a
	Shrub coverage	0.1061	n/a	n/a
E ER (per date)	Water table average	0.6521	n/a	n/a
	Water table SD	0.5567	n/a	n/a
	Peat temperature	0.0003*	$y = 0.2065x + 0.0797$	0.82
F GPmax (per collar, sites 1-3 only)	Water table average	<0.0001*	$y = 0.2632x – 1.7085$	0.63
	Water table SD	0.0214*	$y = 0.7775x + 3.2941$	0.25
	Peat temperature	0.7291	n/a	n/a
	Sphagnum coverage	0.0096*	$y = -0.0950x + 16.9812$	0.30
	Shrub coverage	<0.0001*	$y = 0.0892x + 4.0358$	0.68
G NEE (per collar, sites 1-3 only)	Water table average	<0.0001*	$y = 0.2009x – 4.4149$	0.61
	Water table SD	0.0456*	$y = 0.5331x – 0.1853$	0.19
	Peat temperature	0.9255	n/a	n/a
	Sphagnum coverage	0.0159	$y = -0.0694x + 9.5759$	0.30
	Shrub coverage	<0.0001*	$y = 0.0764x – 0.4495$	0.83

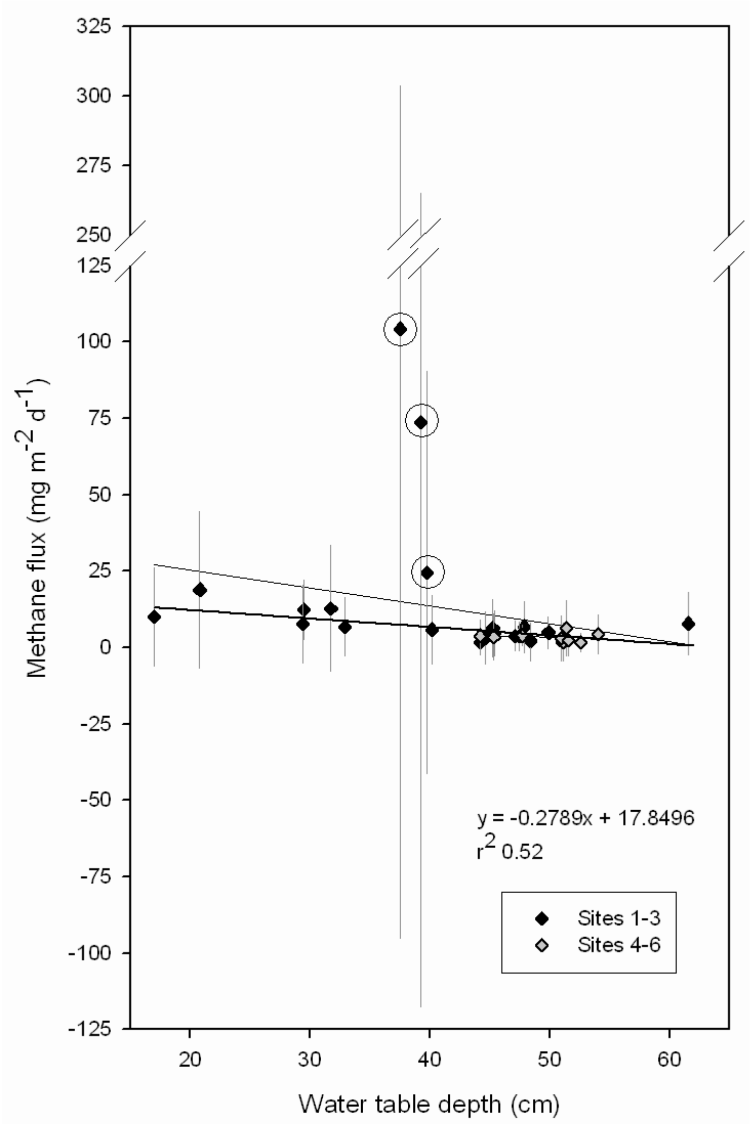

Figure 5.3 – Relationship between CH_4 fluxes, averaged (± one standard deviation) over the three years of measurements for each collar, and water table depth. The regression excludes the three collars that are circled.

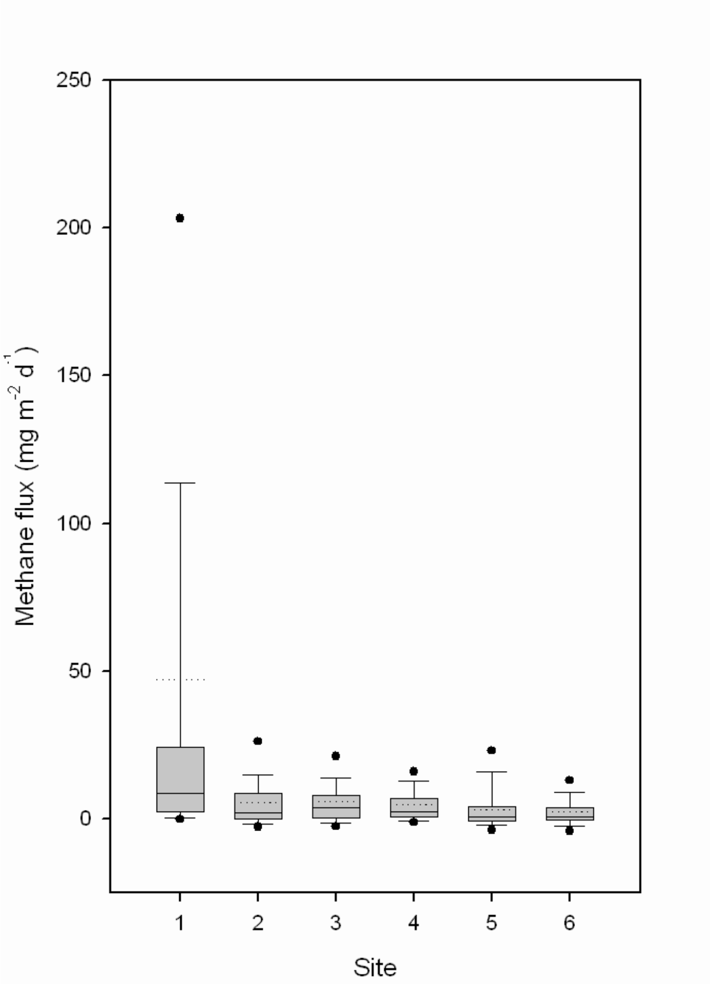

Figure 5.4 – Box plots of all data of each collar from each site for the three growing seasons. Each individual measurement was weighted according to the spatial importance of its microform (sites 1 to 3) to allow for the average to be representative for the sites. The boundaries of the box indicate the 25th and the 75th percentiles, the error bars indicate the 10th and 90th percentiles, and the black dots indicate the 5th and 95th percentiles. The black bar inside the box represents the median and the dotted line represents the average.

5.3.2. CO_2 fluxes

Collar average ER follows an expected seasonal pattern, reaching its highest values in the warmest summer months (Figure 5.5). Hence, it is closely related to peat temperature (Table 5.2E). However, differences in peat temperature do not explain the differences in ER between the different collars. They are rather partly explained by differences in water table depth and variability, especially when taking sites 1-3 only, where no trees are present (Table 5.2C, D; Figure 5.6). When averaged for all sampling dates, upslope sites have a significantly higher ER than downslope sites ($p < 0.001$), with averages of 3.0 (± 2.06) and 4.4 (± 2.37) mg CO_2 m^{-2} s^{-1}, respectively.

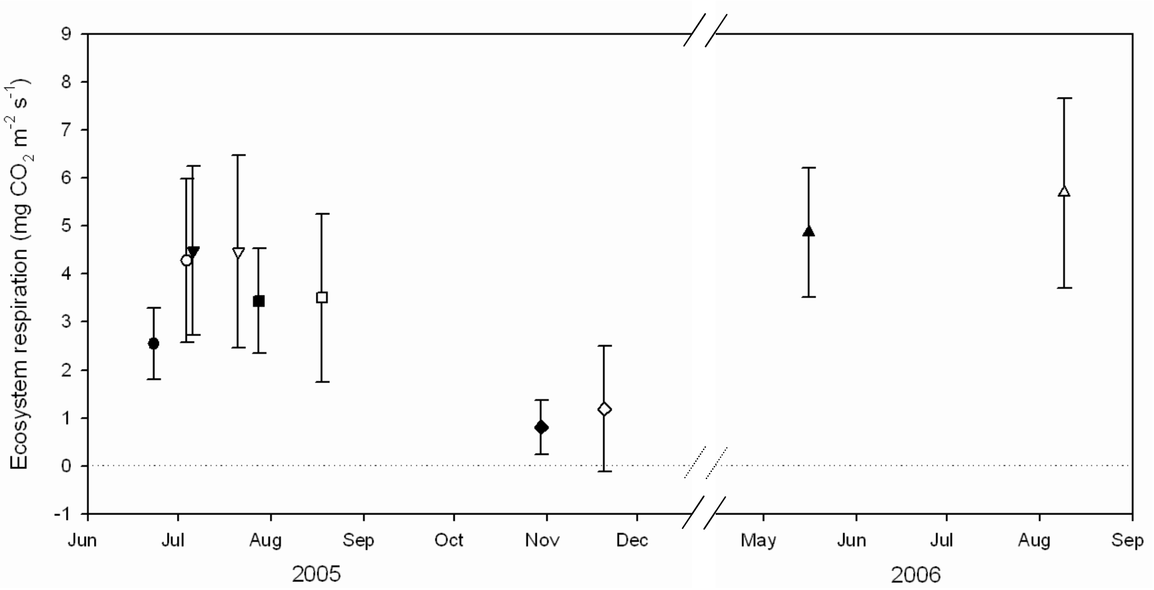

Figure 5.5 – Ecosystem respiration for 2005 and 2006 averaged for all collars (± one standard deviation).

The magnitude and seasonal patterns of NEP vary with vegetation assemblages of the collars (Figure 5.7). The hummock collars follow the same general trends, with high values in mid-summer and lower values early in the season and in the fall. However, the high hummock collars, dominated by deciduous shrubs, have a generally higher NEP than the low hummocks, dominated by evergreen shrubs, although the NEP of deciduous shrubs gets very close to that from evergreen shrubs in the fall. *Sphagnum*-dominated hollow collars follow the opposite pattern, with higher NEP early and late in the season, when the temperatures (and hence, evapotranspiration) are lower.

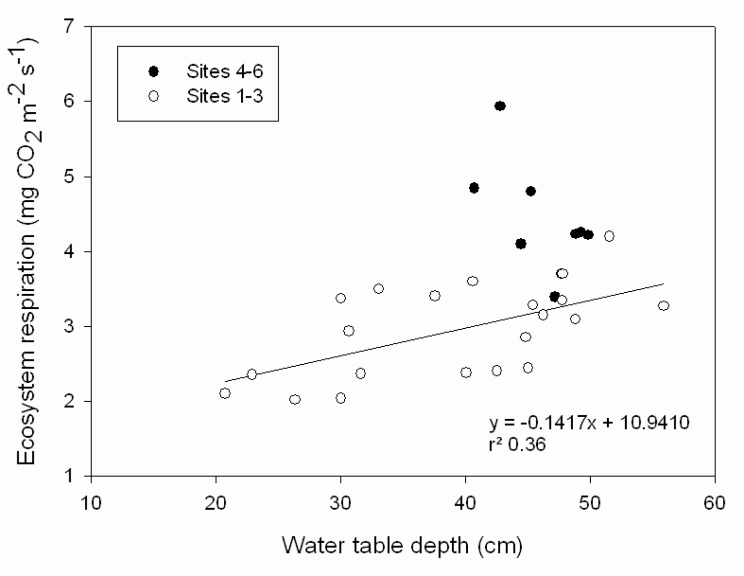

Figure 5.6 – Relationship between ER and water table depth. Each point represents the average of all measurements at a collar. The regression line excludes the collars from the downslope plots (4-6).

NEP, when averaged per collar (for high light, measured in mid-summer), is also closely related to water table depth but even more so to the shrub coverage (NEP not measured for sites 4-6) (Table 5.2G). The maximum photosynthesis rates (GPmax) are mainly related to shrub coverage and water table depth, although the associations are not as strong (Table 5.2F). The light curves of the collars presented by microforms illustrates the differences between the different vegetation types (Figure 5.8).

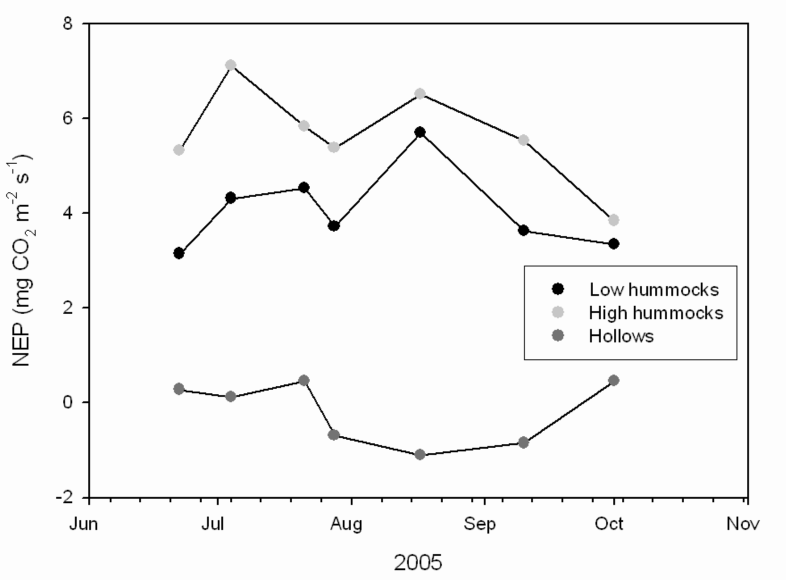

Figure 5.7 – Average NEP over the 2005 growing season by microform. The NEE values are averaged from the PAR values > 1000 µmol m^{-2} s^{-1}. Standard deviation not shown for clarity reasons.

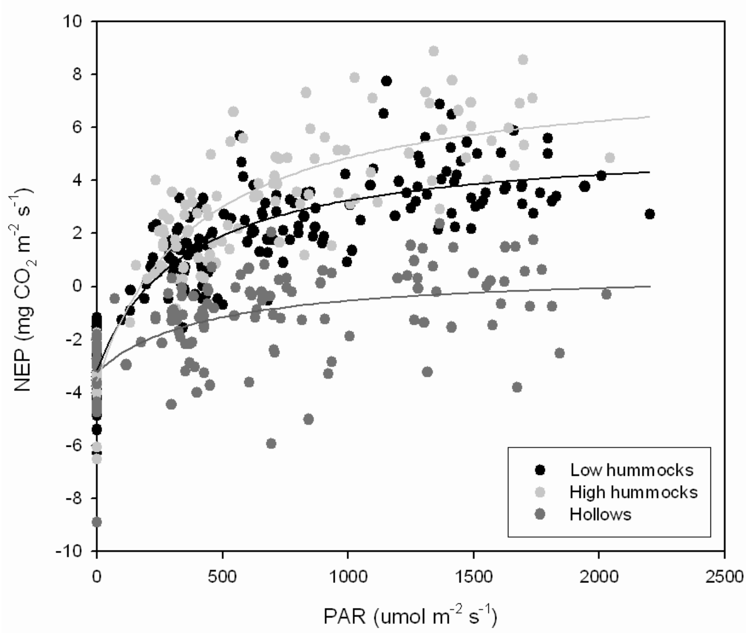

Figure 5.8 – Relationship between NEP and PAR of all collars of sites 1 to 3, for all sampling dates, presented by microform with the corresponding rectangular hyperbole relationship.

5.3.3. Biomass carbon content

The C content differs significantly ($p < 0.0001$) between *Ledum* and *Vaccinium* leaves, when averaging for all sites, with values (± standard deviation) of 52.62 ±1.42 and 49.35 ±0.56 % of dry weight, respectively. The values also vary among sites for *Ledum*, whereas the C content of *Vaccinium* does not change along the transect (Figure 5.9).

The total C content of biomass is significantly higher on the downslope side than the upslope side of the ditch ($p < 0.0001$), mostly due to the presence of a dense tree layer on the downslope side (Figure 5.10). There is also an increase in belowground biomass, but to a lesser extent. The number of belowground samples does not allow for the assessment of the statistical significance of the increase.

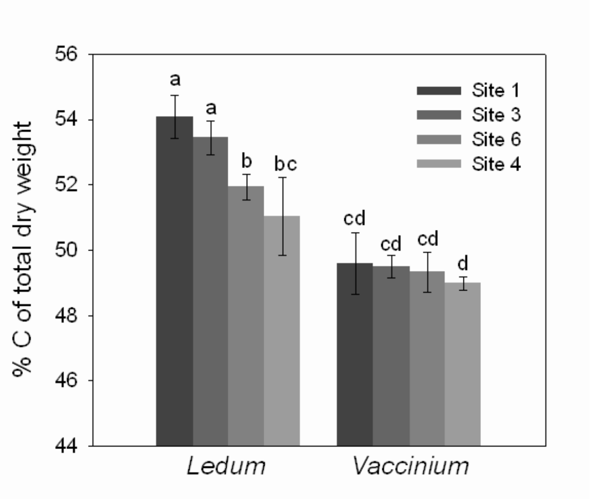

Figure 5.9 - Carbon content of leaves from *Ledum groenlandicum* and *Vaccinium myrtilloides* shrubs, taken at four sites along the transect. The bars with the same letters are not significantly different from each other.

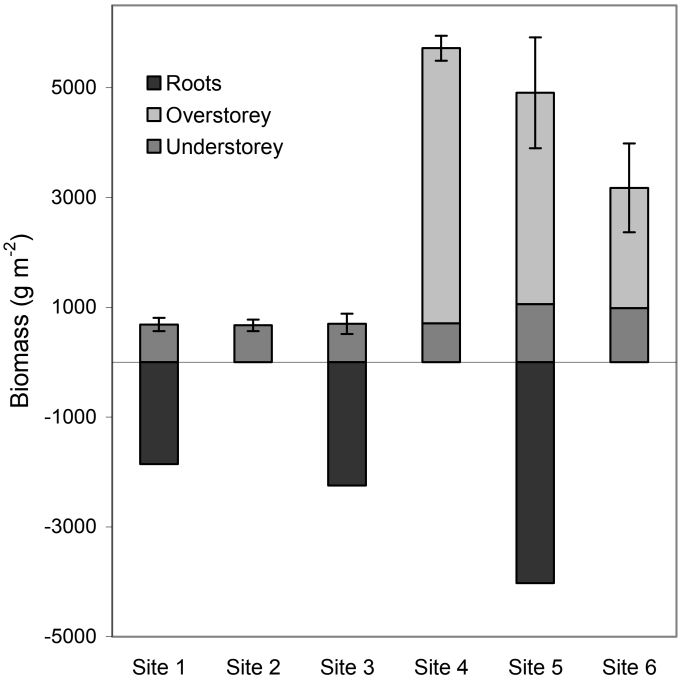

Figure 5.10 - Carbon content of biomass. Understorey represents shrubs, mosses, herbs and tree seedlings; overstorey is trees. The error bars represent ± one standard deviation of the total aboveground biomass components only (not enough samples to calculate belowground standard deviation).

5.3.4. Peat carbon content

The C content analyses showed that the downslope cores generally have a higher carbon content than the upslope cores for a given depth (Figure 5.11). The fluctuations in the carbon content of the downslope cores correspond well to fluctuations observed deeper in the upslope cores, showing a combination of peat compaction and oxidization of the peat (Figure 5.12). When adding peat carbon above the synchronized portions showed in Figure 5.12, the downslope and upslope cores have significantly different carbon content ($p = 0.0387$), with values of 1.4 (± 0.1) and 2.2 (± 0.4) g C cm^{-2}, respectively.

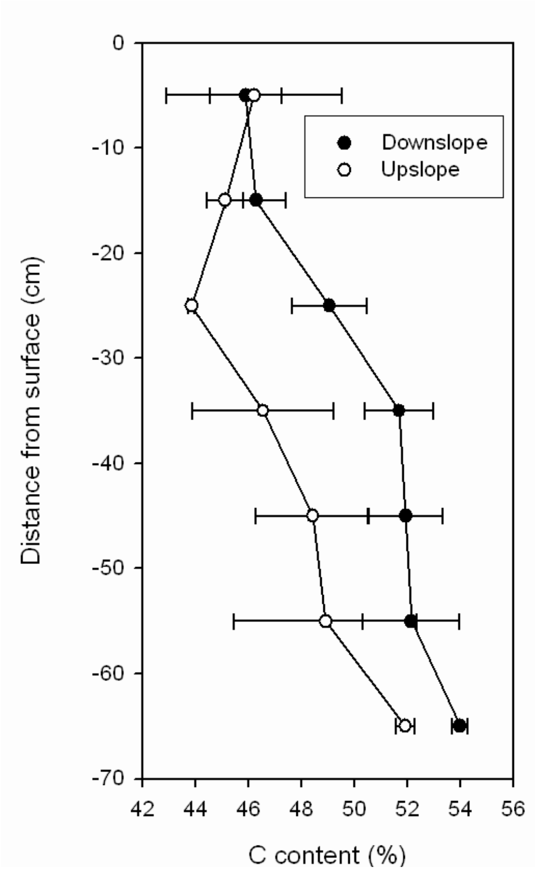

Figure 5.11 – Average peat carbon content (% of dry weight) of cores from site 2 (upslope) and 5 (upslope).

5.4. Discussion

Although this study could not compare all the components of the carbon balance of the peatland among all sites because of methodological limitations, this long-term drainage study enabled me to establish links between the vegetation structure and the function of the ecosystem, an aspect that has largely been ignored in the past, with the exception of a few recent studies (Belyea and Malmer, 2004; Bauer 2004; Eppinga *et al.*, 2008). Moore *et al.* (1998), building on the pioneering work of Gorham (1991, 1995), speculated on a number of changes that might occur to the components of the carbon balance of peatlands with climate change. Our study provides some qualitative assessments of some of the Moore *et al.* (1998) conjectures (Table 5.3).

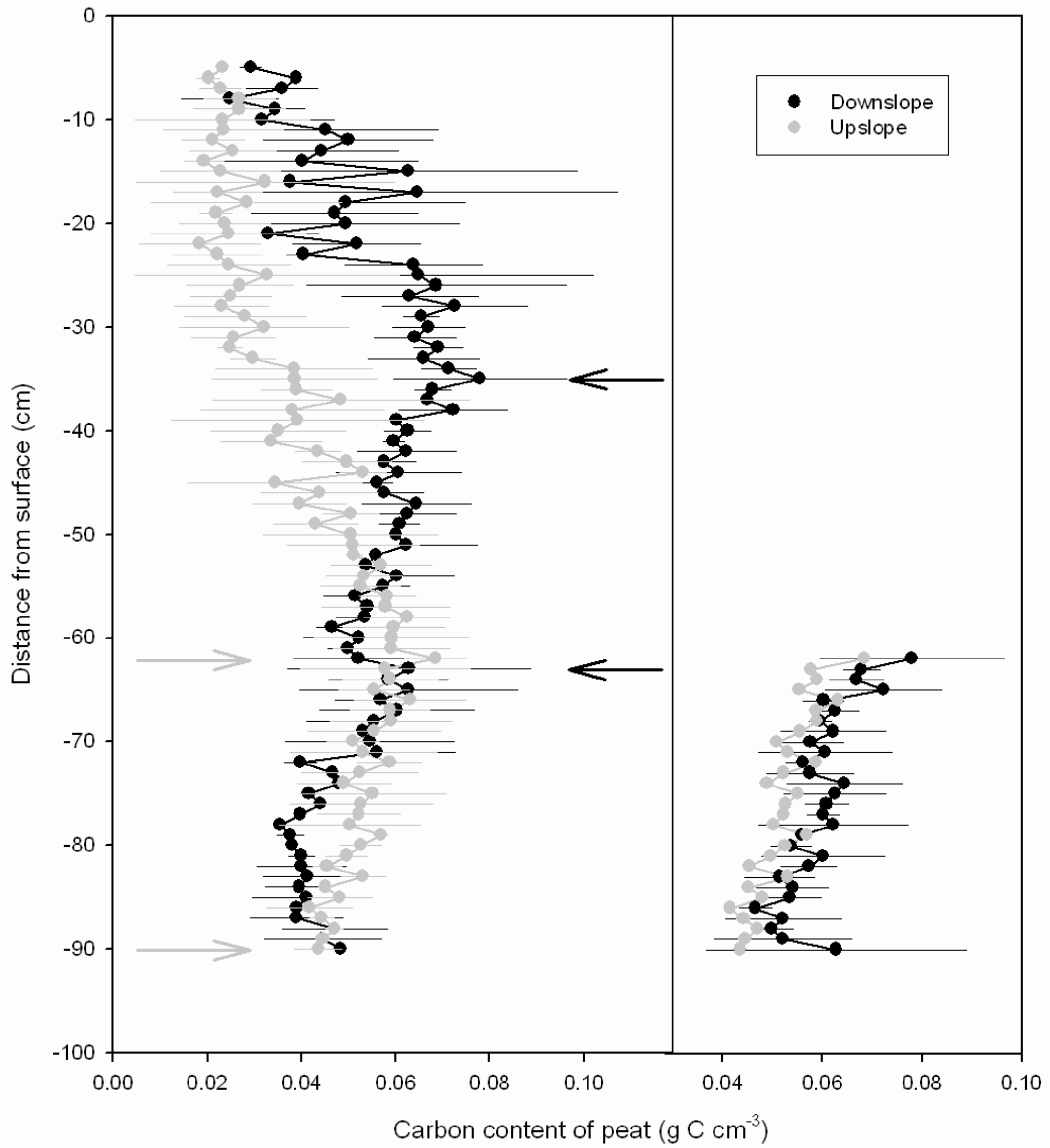

Figure 5.12 – Average carbon content of cores (± standard deviation) from site 2 and 5 from LOI and peat carbon content value. The right side of the figure shows the portions of the curves identified by the arrows on the right, synchronized.

The CH_4 fluxes measured along the water table transect are highly variable both spatially and temporally. Although there is a general relationship between CH_4 fluxes and water table depth (averaged over a long period of time), there are "hotspots" of CH_4 emissions that do not correspond to high water tables. These hotspots could be the result of different factors, including the rooting system architecture or variations in the peat characteristics. CH_4 emissions have been related to vegetation composition in the past, either directly because of the presence of sedges (Strack *et al.*, 2006; Pelletier *et al.*, 2007) or using vegetation as an indicator of water table depth (Bubier, 1995). However, our study sites did not include any areas that were covered by more than 1% of the surface by sedges. The fluxes measured in the hotspots are too high for the possible gas diffusion rates of the peat, which indicates that they are probably due to a sustained bubbling.

CH_4 emissions do not show a relationship with daily variations in water table depth, and this could be due to a lag time between the production and emission of CH_4 (Strack and Waddington, 2008). Some upslope collars (mostly high hummocks) have a similar water table depth as the downslope collars (located in an area that was invaded by trees after drainage). However, these two sets of collars have similar CH_4 emission magnitudes. Hence, it is a clear indication that CH_4 emissions are more related to water table depth than vegetation composition, at least when sedges are not present (Table 5.3).

While ER is temporally explained by peat temperature (similar to Lafleur *et al.*, 2005), we found the spatial variability in ER to be explained by water table. Contrary to CH_4 emissions, when comparing collars with similar water tables, the downslope sites respire more CO_2 than the upslope ones, indicating that ER is also related to vegetation composition (Table 5.3). Therefore, the combined effect of a lower water table and a change in vegetation (or subsequent changes in the peat characteristics) are more important than the individual effects. Although we could not measure NEE on the downslope portion of the ditch, our results indicate that a higher proportion of deciduous species increase the primary production.

As a result of the changes in the carbon fluxes following drainage, the carbon stores changed significantly. The biomass carbon content changed substantially, as is usually the case after drainage (Laiho and Laine, 1997; Laine *et al.*, 1995; Silvola *et al.*, 1996; Minkkinen *et al.*, 1999; Macdonald and Yin, 1999; Strack *et al.*, 2006). However, the drainage also affected the peat carbon content, because of a combination of a lower accumulation since drainage and the oxidisation of old peat layers, as the effect of drainage on peat C content goes deeper than the depth of drainage (Chapter 3).

Table 5.3 - Synthesis of the possible interacting and individual effects of water table and vegetation changes on flux components. The arrows indicate the direction of changes. The double ended arrow indicates that there is no change.

Carbon cycle component		Water table lowering	Vegetation changes	Combined water table / vegetation
		Wet → Dry	Pristine → Trees	Open bog → Forest type
CH_4 emission		↓	-	↓
NEE	NEE	?	?	?
	GPP	?	↑	↑
	ER	↑	↑	↑
Biomass C[1]		↑	↑	↑
Peat C		?	?	↓
NECB (short-term)		↑	↑	↑
NECB (long-term)		↓	↓	↓

1 – See chapter 3

5.5. Conclusion

A water table lowering and the consequent vegetation changes in an open bog following an 85-years old drainage affected the components of the carbon balance of the system in different ways. The combination of a decrease in CH_4 emissions and an increase in GPP and ER resulted into a higher amount of C stored in the living biomass and a lower amount of C stored in the peat, resulting in a higher overall C storage in the short-term, but a potentially lower C storage in the long-term. The implications of a change in the carbon functioning of peatlands in a changing climate are especially important as a release of C from peatlands would have the potential to contribute to the C carbon burden of the atmosphere.

Chapter 6 – Modelling the long-term influence of hydrology on peatland vegetation dynamics and carbon storage

Context within the thesis and overview

This last research chapter builds on the empirical knowledge acquired in the preceding three chapters to evaluate the use of a preliminary version of the Holocene Peatland Model (HPM) to simulate the effect of a water table drawdown on long-term peatland carbon dynamics.

The results of the simulations show that HPM generally reproduces well the direction of the carbon dynamics changes that occur with a water table lowering, although the magnitudes of the carbon loss is higher than the empirical evidences presented in Chapter 5. The high carbon losses might be due to an overestimation of the respiration increase following the water table drawdown. The vegetation response of the model was also evaluated and was found to be more abrupt that what happens in reality, where vegetation needs a certain period of time to establish and colonize a new site. Because of the instantaneous nature of the vegetation response, the highly responsive respiration and perhaps other factors not studied here, the model is more resilient than what is observed in reality.

6.1. Introduction

The functional importance of peatlands in the global carbon cycle varies temporally from sink to source of atmospheric carbon depending on the climatic conditions, although the net carbon uptake of peatlands is positive in the long term (Roulet *et al.*, 2007). Northern peatlands have therefore been a slight but continuous sink for atmospheric carbon dioxide (CO_2) since their development after the last deglaciation, now storing between 250 and 370 Pg C in total (Gorham, 1995; Clymo *et al.*, 1998; Turunen *et al.*, 2002, 2004). The net uptake of carbon by peatlands is the result of a persistent water saturation that prevents rapid decomposition of the litter (especially in fens), in combination with dominant plant assemblages that are resistant to decomposition (especially in bogs, Figure 6.1). Hence, in the absence of a major external driver such as fire or anthropogenic disturbance, the role of a peatland as a source or sink of carbon depends on the dynamic interaction between the wetness (often simplified to the water table depth) and the vegetation communities.

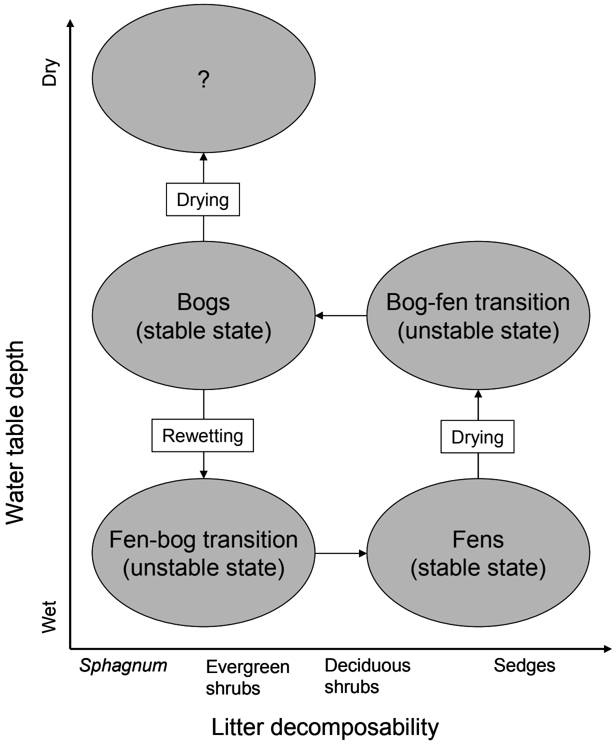

Figure 6.1 – Conceptual representation of equilibrium and non-equilibrium states corresponding to different hydrological conditions and plant assemblages in peatlands.

Climate might now be changing at a faster rate than most climate simulation models predicted (C. Field, oral presentation at the America Association for the Advancement of Science Chicago symposium, February 14, 2009). Although peatlands are considered to be generally resilient to changes in climate or local hydrological conditions (Belyea and Clymo, 2001; Gunnarsson *et al.*, 2002), rapid changes in the structure and carbon function of peatlands have been observed in the past (Pellerin and Lavoie, 2003; Belyea and Baird, 2006). These changes are sometimes referred to as "catastrophic shifts", although they are often the result of gradual changes in the boundary conditions that maintain peatlands in a long-term state of equilibrium (e.g. Scheffer *et al.*, 2001, Eppinga *et al.*, 2009). Because of the important role of peatlands in the global carbon cycle, it is crucial to identify at what rates and/or magnitude of change will peatlands be pushed beyond the bounds of the feedback mechanisms (shown in Figure 6.1) maintaining their role as carbon sinks.

The paleoecological studies that have identified past catastrophic shifts in peatland ecosystems are not designed to isolate and identify the drivers of the changes, or are limited by the temporal resolution or the accuracy of paleo-environment indicators. The use of natural proxies or experimental manipulations as analogs to climate change can provide valuable insights into the mechanisms involved in short-term vegetation and carbon dynamics responses to disturbances, but their extent is often too short to measure any significant changes in the functioning of the system studied. Also, even when the time scale of a study is long enough, the number of interactions operating in complex ecosystems makes the interpretation of the results of field-based studies a very complex (and often impossible) task (Chapter 5). Restrained manipulative studies are easier to interpret, but they are unrealistic because they prevent many feedbacks that would exist in the natural ecosystems from happening. The simulation of long-term (decadal to centurial) carbon accumulation processes and its biophysical drivers via process-oriented models is a way to overcome the limitations of field- and lab-based studies and mechanistically address questions about the fate of peatland ecosystems with climatic changes. If models are to be used for future prediction purposes, they should be able to reproduce the past dynamics reasonably well. This, in turn, requires that the measurements on which models are evaluated are appropriate, accurate and representative of the variety of conditions being simulated. Models should also find the right balance between the necessary simplification of complex processes to render the model computationally efficient and making the results easy to interpret, and an over-simplification that would make the model too dependent on empirical relationships that are usually site-specific.

Several different ecosystem modelling approaches have been developed for and/or applied to peatlands for the simulation of different aspects of the peatland environment at different time scales (see review by Frolking *et al.* (in press)). The conceptual peatland development models of Clymo (1978, 1984) and Ingram (1982) provided the basis of many later peat accumulation models. Some models simulate the long-term development of peatlands as controlled by water table dynamics (Hilbert *et al.*, 2000; Belyea and Malmer, 2004) and decomposition rates of different vegetation types (Frolking *et al.*, 2001; Bauer, 2004). The microtopography of peatlands has been modelled based on the hydrology and vegetation dynamics (Nungesser, 2003) or on plant competition mechanisms (Eppinga *et al.*, 2009). Other models concentrate on the simulation ground-water flow in and around peatlands (Reeve *et al.*, 2000). Net primary production and decay rates have been empirically modeled based on dated peat cores (Wieder, 2001). Detailed process-oriented models have also been applied to simulate the contemporary daily to weekly fluxes of carbon of peatlands (Frolking *et al.*, 2002; Sonnentag *et al.*, 2008; St-Hilaire *et al.*, in press), or the spatially-distributed coupled water and carbon cycling for the entire Holocene (Borren and Bleuten, 2006). The latter type of process-oriented models applied to peatlands generally lack the explicit representation of the dynamic relationship between peatland hydrology and vegetation composition.

The latest climate simulations predict that the boreal and subarctic ecozones will be subject to temperature increases and precipitation fluctuations that will result in changes in regional hydrology (IPCC, 2007). These changes might lead to drier conditions during the growing season as a result of a change in the timing of precipitation, a lower snowmelt water input and/or higher evapotranspiration. The implications of a water table drawdown and consequent vegetation changes for peatland carbon storage are explored in this chapter, using the Holocene Peatland Model, HPM (Frolking *et al.*, in prep.). HPM has recently been developed based on the simple coupled peat accumulation – water table dynamics model of Hilbert *et al.* (2000) and the peat decomposition model of Frolking *et al.* (2001), to simulate peat accumulation as influenced by the hydrology and vegetation dynamics, over a time scale that is relevant to vegetation succession. My goal is to improve the simulation of long-term hydrologically-triggered vegetation succession in peatlands and the combined and separate impacts of vegetation changes and hydrological changes on peat accumulation. Our objectives are to (1) evaluate how HPM's vegetation assemblages and carbon accumulation respond to different types of hydrological disturbances and (2) compare the model results to the measured data presented in the preceding three chapters of this thesis.

6.2. Model background and description

The annual peat accumulation model of Hilbert *et al.* (2000) is based on the coupled dynamics of water table depth and peat accumulation using two equations:

$$\frac{dh_{PD}}{dt} = G - (k_a - k_c)z_{wt} - k_c h_{PD}$$

$$\frac{dz_{wt}}{dt} = \frac{dh_{PD}}{dt} - \left(\frac{1}{\theta_{\max}}\right)\frac{dW}{dt}$$

where h_{PD} is the total peat height, G is the annual plant litter input (all vegetation types aggregated together), k_a and k_c are the annual fractional mass loss rates due to decomposition in the acrotelm and catotelm, z_{WT} is the water table depth, $\theta_{\max}$ is the water content at peat saturation, and dW/dt is the annual water balance. All vegetation types are pooled together in the G term. Hence, the major feedback explored in the simple model is the water table – peat accumulation, ignoring the dynamic linkages between water table and vegetation composition. The peat decomposition model of Frolking *et al.* (2001) provides the basis for the inclusion of the effect of different litter types to peat accumulation rates via differential decomposition of peat cohorts depending on the litter origin (vascular vs. non-vascular) and their depth in the peat profile:

$$\frac{dm(t)}{dt} = -k_0 \frac{m(t)^2}{m_0} \times f(T) \times f(W)$$

where $dm(t)/dt$ is the annual decomposition of a given peat layer of a mass m at time t, k_0 is the initial mass loss rate for the particular layer (based on litterbag decomposition studies for various peatland plant tissues), m_0 is the initial mass of the peat (litter) layer and where $f(T)$ and $f(W)$ are soil climate modifiers for temperature and water table depth, respectively. About 90% of the initial mass of an annual litter input is lost during the decades when the layer was part of the acrotelm, the upper portion of the peat located above the long-term mean growing season water table depth (Ingram, 1978).

The Holocene Peatland Model (HPM) combines the basic principles of those two models, making the interaction between water table, vegetation and peat accumulation dynamic, although some feedbacks are still under development. It simulates vegetation production, decomposition and peat accumulation (peat carbon content) vertically (i.e. non spatially-distributed) as a result of peat properties, water table depth and peat water content, and vegetation composition, at an annual time step (Figure 6.2). The vegetation component of the model is based on the relationship between the productivity of different plant functional types (PFT) with water table depth and the trophic level of the peatland, approximated by the peat depth (Figure 6.3). The version of the model used in this study is a preliminary version, hence some of the feedbacks intended for the final version are not implemented yet, and some functions are in the process of being refined (Figure 6.2). Also, the number of plant functional types of the final version will be increased to 12.

The influence of water table disturbances and vegetation dynamics on peat accumulation was assessed by conducting a series of simulations with various magnitudes of water table lowering (from 5 to 30 cm) and durations of persistence (5 and 80 years). The precipitation scenario used is based on the approximate precipitation patterns from Mer Bleue as derived from paleoecological reconstructions (Muller *et al.*, 2003). The water table lowering was simulated by adding a drainage (D) term to the water balance. A run mimicking the approximate range of post-drainage water table conditions based on the testate amoeba reconstructions of Chapter 3 was also conducted. The model was run over 8000 years before the disturbance was introduced, to allow for a peat mat similar to what is found at Mer Bleue to build up. The modelling results were qualitatively compared with measurements derived from chapters 3, 4 and 5 from this thesis.

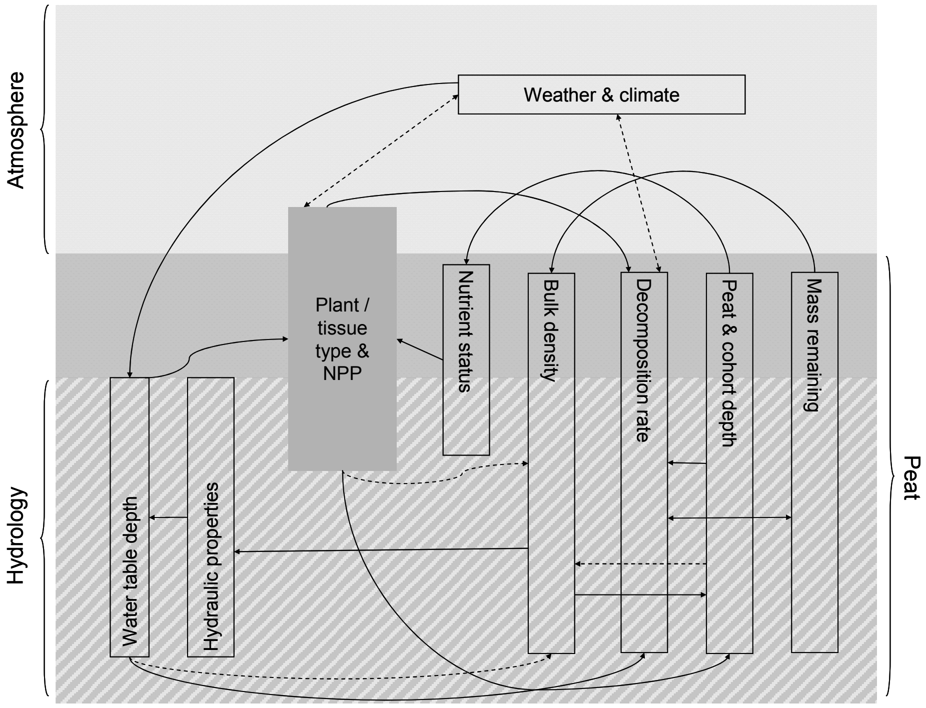

Figure 6.2 – Feedbacks (or planned feedbacks, dashes arrows) linking peat properties, peat accumulation, hydrology, vegetation dynamics and climate in HPM. Figure adapted from a presentation given at the American Association of Geographers in 2008 by S. Frolking (with the permission of the author).

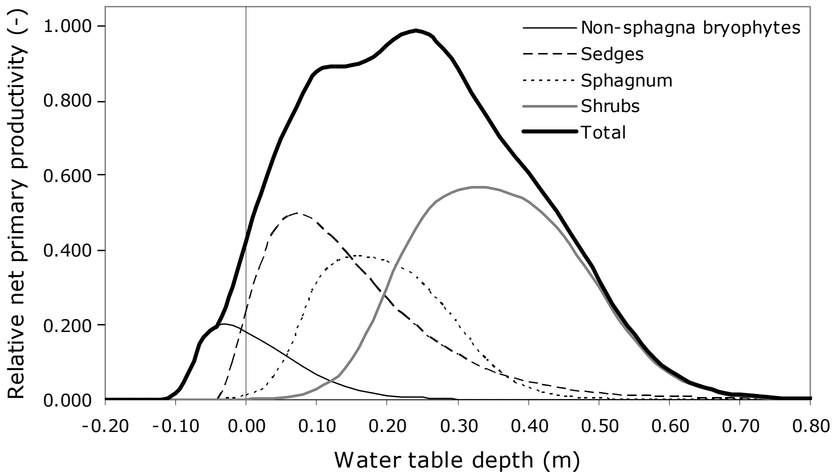

Figure 6.3 – Relative net primary productivity of the 4 plant functional types of HPM related to water table and peat depths. Figure adapted from a presentation given at the American Association of Geographers in 2008 by S. Frolking (with the permission of the author).

6.3. Results and Discussion

The simulated peat accumulation is very responsive to changes in simulated water table depths. When HPM is run for the baseline simulation over 9000 years, the responsiveness of the peat accumulation to water table variations due to precipitation variations is obvious, with the peatland loosing considerable amounts of peat whenever the water table gets deeper than approx. 18 cm (Figure 6.4). As a result, HPM simulates well the depth and characteristics of the peat for a bog such as Mer Bleue.

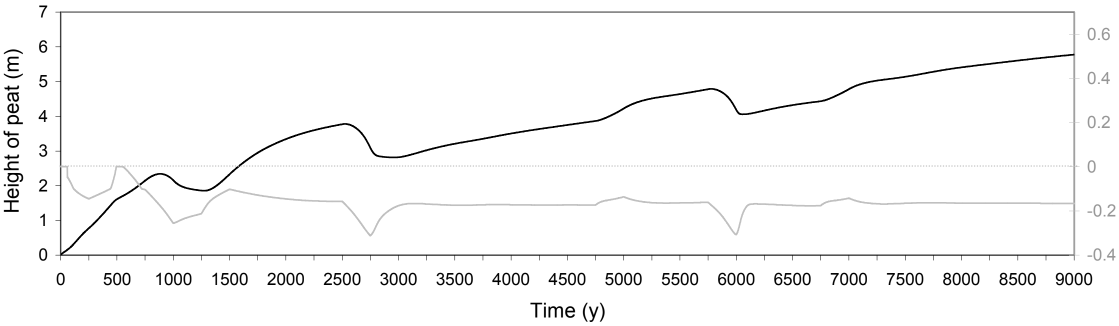

Figure 6.4 – Simulated peat accumulation (left axis) and water table depth (right axis) over 9000 years.

The short-term (5 years) lowering of the water table over a range of different depths (from 5 to 30 cm) creates a hiatus in the peat accumulation but does not change the long-term functioning of the system (Figure 6.5). The response of vegetation to water table lowering is instantaneous, and the system looses peat up to a point where the water table gets higher than the pre-drainage conditions, but eventually re-equilibrates to a depth similar to what is was before the disturbance. For all but the most extreme simulations (25, 35 cm), this re-equilibration begins in less than 50 years. When the water table is lowered by the same magnitudes, but maintained for 80 years, the model behaves similarly and, after loosing peat for the entire time the water table is lowered, it moves back to its equilibrium state over 50 to 300 years, depending on the depth of the water table drop (Figure 6.6).

The simulation representing the approximate range of post-drainage water table conditions shows that HPM simulates well the direction of the response of the system (Figure 6.7A, 6.7C), although the magnitude of the simulated carbon loss is higher than the measured losses (Chapter 3). The bulk density of the peat layers accumulated after drainage is much higher (Chapter 4), whereas the simulated bulk density of the post-drainage layers doesn’t differ from the pre-drainage layers. However, the decomposition – bulk density is a planned feedback that should be added to the model shortly. A steep jump in respiration and a small decline in NPP are responsible for the post-drainage carbon simulated loss. A derived respiration vs. time after drainage relationship (from the water table vs. time reconstruction based on testate amoeba data from Chapter 3, and the respiration vs. water table depth relationship presented in Chapter 5) does not respond to water table changes to the same extent (Figure 6.7B). However, once the model takes into account the impact of decomposition on peat bulk density, an increased respiration will increase the bulk density of the peat, which will increase the hydraulic retention of the peat and therefore reduce the respiration by diminishing the oxic space in the upper peat layers. This feedback is therefore expected to reduce the magnitude of the respiration response to a water table drawdown.

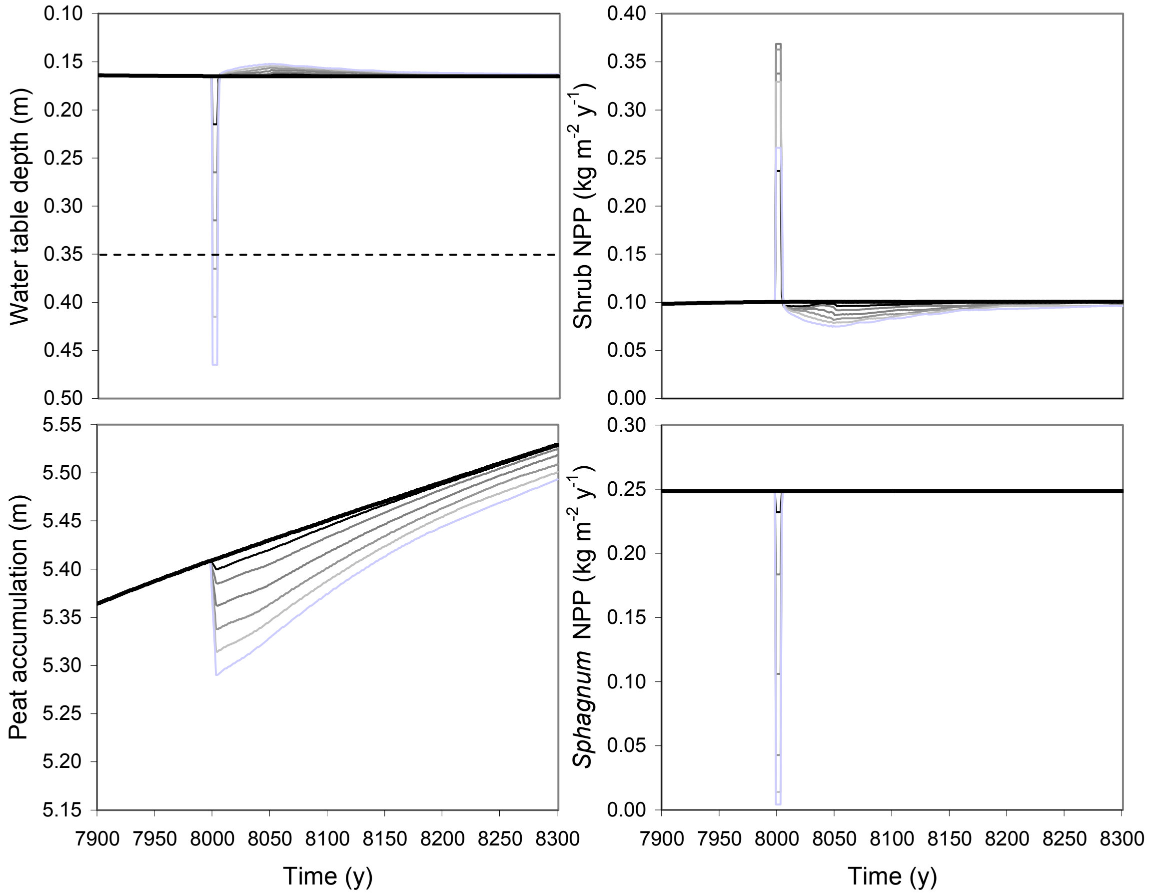

Figure 6.5 – Peat depth, water table depth and shrub and *Sphagnum* NPP derived from a set of simulations introducing a range of water table lowering at year 8000. The bold line represents the baseline simulation. The shades of grey get paler as the disturbance introduced gets more important (lowering of the water table from 5 cm to 30 cm, in 5 cm increments). The lowering is maintained for 5 years, and then the water table is allowed to equilibrate. The dashed line represents the maximum post-drainage water table drop (Chapter 3).

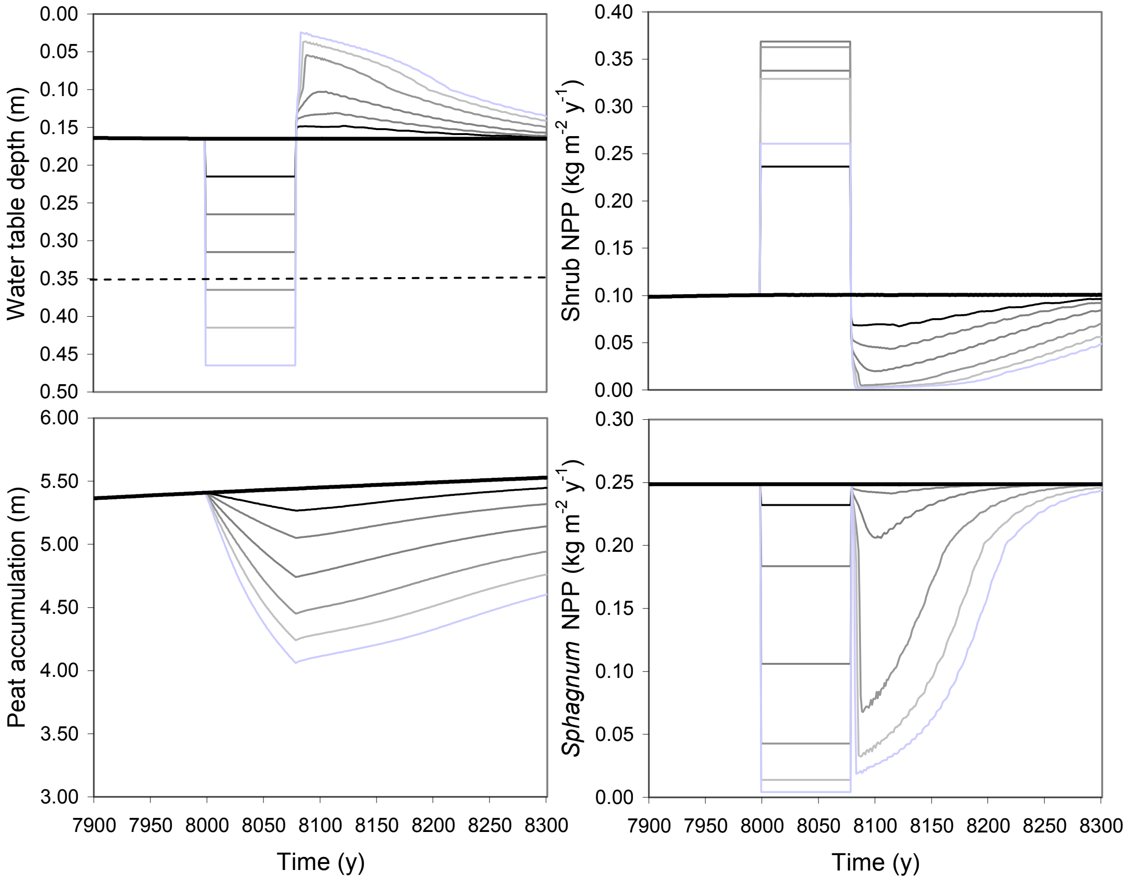

Figure 6.6 – Peat depth, water table depth and shrub and *Sphagnum* NPP derived from a set of simulations introducing a range of water table lowering at year 8000. The bold line represents the baseline simulation. The shades of grey get paler as the disturbance introduced gets more important (lowering of the water table from 5 cm to 30 cm, in 5 cm increments). The lowering is maintained for 80 years, and then the water table is allowed to equilibrate. The dashed line represents the maximum post-drainage water table drop (Chapter 3).

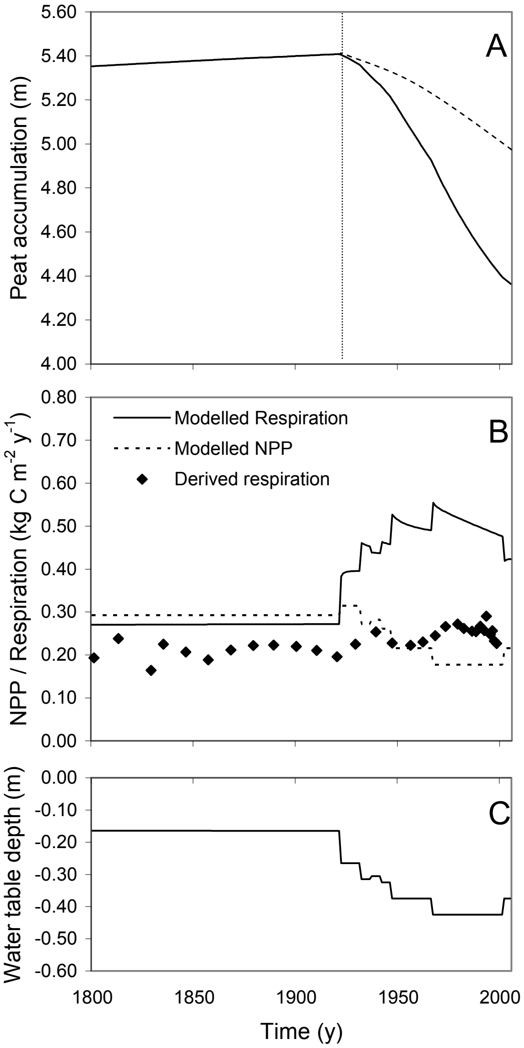

Figure 6.7 – Results from simulation conducted using post-drainage water table reconstructions based on testate amoeba assemblages. (A) Comparison of simulated peat accumulation (solid line) with peat accumulation derived from contemporary peat level measurements and paleoecological reconstructions (dashed line), with the vertical line representing the year of drainage; (B) Simulated respiration and NPP and derived respiration over time and (C) water table forced for post-drainage conditions.

The vegetation response of the model to water table changes is expressed by the evolution of the NPP of shrubs with time (Figure 6.8) that increases by more than 4 times the year the drainage is introduced in the simulation. Because of the way the NPP of the different plant functional types is modeled (Figure 6.3), the vegetation response to water table disturbances is instantaneous, not taking into account the time it takes for a new vegetation community to establish and the buffering effect of vegetation on its growing environment (Scheffer *et al.*, 2001). The pollen influx increase of *Betula*, used as an indicator of the timing of establishment and growth of the tree population, shows that the the process was gradual, taking at least 20 years before the *Betula* trees that invaded the peatland following drainage produced pollen. As trees generally start producing pollen when they reach about 10 years of age, it can be deducted that the establishment buffer time is approximately 10 years.

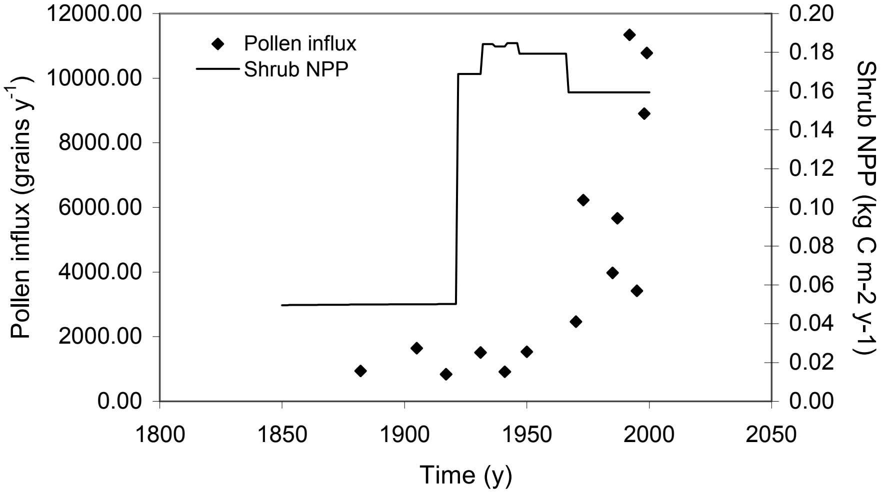

Figure 6.8 – Comparison of the NPP of the modeled species that is the closest to trees (shrubs) and of the pollen influx of *Betula* trees.

As a result of all the fast responses of respiration and NPP, the modeled peatland is unstable in the short term, but very stable in the long term. This stability has been observed frequently in the past and peatlands are considered to be very resilient systems. Bog phases of peatlands have been shown to last up to several thousands of years (Rydin and Barber, 2001; McMullen *et al.*, 2004; Hughes and Barber, 2004; Kuhry and Turunen, 2006). This stability is mostly due to a fast and strong feedback of the respiration, which makes the system loose peat even when the water table is lowered by only 5 cm. Because the peat mat gets shallower, the water table bounces back quickly, and eventually gets back to its equilibrium state, around 16 cm deep. These results indicate that the way HPM is parameterized at the moment does not allow to push the simulated peatland to an alternative stable state such as the one described in the previous chapters – a system dominated by productive woody species, where the respiration is higher but where the system still accumulates carbon or looses carbon at a lower rate.

6.4. Conclusion

The direction of the response of peat accumulation to water table dynamics is well represented by the HPM simulations. The abrupt peat accumulation response to water table variations simulated by HPM is dominated by the relationship between ecosystem respiration and water table depth, and the model's vegetation response to disturbance is characterized by its steepness. Neither behavior is supported by field evidence, which indicates that the system overall does not loose as much carbon as HPM tends to show.

To improve the simulation of water table disturbances and their effect on the vegetation and carbon dynamics of peatlands, I suggest several improvements. Firstly, the establishment of vegetation should be a gradual process, needing at least a few years (10 years or so for trees) of disturbance before species replacement take place. Secondly, respiration should be less responsive to water table variations, as the sensitivity of respiration to water table creates an unrealistic hiatus in the peat accumulation patterns, even when the water table just varies by a few cm. Lastly, I suggest that the NPP should be allowed to evolve outside of the typical "peatland NPP" boundaries after an important lowering of the water table is maintained for more than a few years. As showed by the results presented in Chapter 4, the long-term equilibrium of peatlands might change once the system's boundaries are pushed enough. The way in which HPM limits the production of vegetation in dry conditions prevents it from reaching a new equilibrium. The appropriate simulation of post-disturbance vegetation and carbon dynamics is a necessary step to be able to include peatlands in General Climate Models.

Chapter 7 - Summary, contributions and conclusion

The relationship between peatland wetness, carbon cycling and vegetation communities has been explored in various types of studies in the past. However, the relationship between long-term vegetation changes and the biogeochemistry of peatlands is still poorly understood, mainly because of the time frame at which vegetation succession operates. This limits the use of conventional techniques to study the peatland vegetation structure vs. carbon functioning link. My main research question was therefore: what is the impact of a long-term (decadal) water table drawdown on vegetation succession and, in turn, how does vegetation succession alter the carbon dynamics of peatlands? To answer this question, my Ph.D. research focused on the description of vegetation changes and water table changes and the quantification of biomass, peat carbon content and carbon flux changes around a portion of a peatland that was drained 85 years ago, and the use of these results to improve the simulation of post-disturbance carbon accumulation in peatlands.

The first objective of my thesis was to examine how a peatland vegetation community changes in response to long-term water table drawdown. My results reveal that the present-day average difference between the area that is the most affected by drainage and a reference site is ~18 cm. The main effects of the persistent water table drawdown on vegetation is an increase in tree cover, especially *Betula populifolia* and *Larix laricina*, leading to a 10-fold increase in the amount of aboveground biomass (mostly woody) in the areas that are the most affected by drainage. I observed a decrease in *Sphagnum* cover, accounting for close to 20% of all aboveground biomass at the reference site, and decreasing to less than 1% of aboveground biomass as the drainage effect increases, although it is still present at all sites. A shift in the species composition of dominant shrubs, from evergreen ericaceous shrubs (*Chamaedaphne calyculata*, *Ledum groenlandicum*) to deciduous ericaceous shrubs (*Vaccinium myrtilloides*) was also an important effect of drainage. Present-day vegetation patterns along the hydrosequence are mostly related to variability in seasonal water table depth and, secondarily, to average water table depth. These patterns are similar to those observed in the pollen-based paleoecological reconstructions from the same sites. Water table reconstructions based on the testate amoeba assemblages reveal that in an area where the present-day vegetation has been impacted by drainage, a persistent water-table lowering occurred in response to drainage. However, in an area where the water table was affected but the vegetation assemblages remain typical of an open bog, a transient drop in water-table depth occurred at the time of drainage. Hence, the temporal and spatial patterns revealed by my study show that the bog response to drainage was spatially and temporally heterogeneous, and probably mediated by feedbacks among vegetation, peat structure, and hydrology. The observed changes in vegetation structure and composition suggest that there might be two alternative stable states following drainage.

My second objective was to assess how the changes in water table depth and vegetation community structure changes the carbon functioning of the system. The changes in vegetation coverage led to changes in the leaf area of the vegetation. This has important implications for the productivity of the ecosystem. Mid-day net ecosystem production is closely related to the vegetation type, with deciduous shrubs > evergreen shrubs > *Sphagnum* mosses, but the impact of the water table lowering alone is hard to assess as vegetation assemblages and water table depth are correlated. Methane emissions decrease with a lower water table but are not affected by vegetation changes, whereas ecosystem respiration increases as a result of both water table lowering and vegetation changes.

My third objective was to assess if vegetation changes alter the amount of C accumulated in peatlands, both as peat and as living biomass. Following the changes in vegetation, the amount of carbon stored in the living biomass increases by an order of magnitude, although the carbon content of the vegetation tissues differs between species and along the transect. The amount of carbon stored in the peat decreased because of the drainage, as a result of a combination of a lower rate of accumulation since drainage and an oxidation of the deeper layers of peat following drainage. The amount of carbon in the peat is therefore 36% less in the upper portion of the peat that has been affected by drainage compared to the core that has not (or slightly) been affected by drainage.

Overall, my results emphasize that (1) peatlands, although they are known as resilient systems, might experience profound changes in their vegetation structure because of a long-term water table drop; (2) the vegetation changes or the persistence of the changes might depend more on the variability of the water table depth than on the average water table depth; (3) a water table drop and subsequent vegetation changes influence, in combination and individually, the carbon functioning of a peatland and (4) the combined effects of a water table drawdown and vegetation changes result in the displacement of the carbon stored in the system from the long-term carbon pool (peat) to the short-term carbon pool (biomass).

Taken together, these results indicate that drier conditions might lead to a decreased role of peatlands as a long-term carbon pool. However, drained peatlands are by no means a perfect 'model' for studying the influence of climate change on the water table and peatland environment. Although the drainage effect on water table is more gradual than direct manipulations, it is still far more abrupt than what would be expected from climate change, thus not leaving the time for the system to adjust to its new conditions. Also, many other feedbacks besides vegetation changes have an influence on the carbon functioning of the drained portion of the peatland. Most of these feedbacks were not taken into account in this study or were considered as included in the general "vegetation feedback". These feedbacks could include: enhanced nutrient turnover, change in diffusion rate of gases due to changes in the peat properties, changes in the microbial communities and biomass, changes in the peat surface microclimate and its possible effects on evapotranspiration, etc.

My results clearly indicate that vegetation dynamics should not be ignored when trying to predict the long-term fate of the carbon pools of peatlands. They also indicate that a system with a completely different vegetation structure might evolve from open bogs, if the boundary conditions are pushed enough. My study is one example of such a transformation of a peatland towards a new stable condition. Whether the hypothesis that drier surface conditions will happen because of climate change holds true or not does not diminish the importance of my findings, as my thesis provides evidence that the understanding and modelling of long-term carbon cycling of peatlands cannot ignore the dynamic nature of its vegetation. This finding demonstrates that if peatlands are to be included global models and climate-carbon coupling, the dynamics of vegetation and not just the ecosystem carbon function needs to be characterized.

Several research orientations should be pursued to better understand the role of long-term changes in peatlands on their carbon function and to further their inclusion in global climate models. Long-term studies are needed to establish the amount of change already experienced by peatlands due to contemporary climate change. These studies could be field-based (revisiting old sampling sites for example) or based on satellite or airborne imagery. Also, controlled experiments are needed to have a better mechanistic understanding of the vegetation – carbon cycling interactions. Finally, efforts should be continued to model changes in peatlands at time scales that are relevant for the current climate change issues, with the inclusion of feedbacks that consider the important role vegetation is playing in the long-term carbon balance of peatlands.

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