PATRICK FAUBERT

THE EFFECT OF LONG-TERM WATER LEVEL DRAWDOWN ON THE VEGETATION COMPOSITION AND CO_2 FLUXES OF A BOREAL PEATLAND IN CENTRAL FINLAND.

Mémoire
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Résumé

Cette étude a permis d’acquérir une meilleure compréhension des implications potentielles du réchauffement climatique sur les tourbières dominées par les sphaignes. Le drainage d’une partie de la tourbière a débuté il y a 55 ans. La composition végétale des parties naturelle et drainée a été comparée à l’aide de six transects et analysée par des techniques d’ordination. Les flux de CO_2 ont été mesurés durant la saison de croissance sur un transect de la partie drainée et modélisés. En réponse au drainage, la composition végétale a changé et ce n’était pas relié au gradient naturel centre-bordure. Dans la partie humide du transect (éloigné du canal de drainage), la photosynthèse et la respiration totale ont diminué. La captation du CO_2 y était légèrement moins élevée que dans la partie sèche. Cette étude suggère que les effets des changements climatiques seraient atténués par un changement des communautés végétales.

Abstract

This study is providing a better understanding of the potential implications of the global climatic warming on *Sphagnum* dominated peatlands. The drainage of a part of the peatland began 55 years ago. Vegetation composition of the drained and natural areas was compared along six transects and analysed by ordination techniques. CO_2 fluxes were measured during the growing season on one transect of the drained area and inferred by modelling. In response to drainage, vegetation composition changed and it was not related to a natural mire margin-mire expanse gradient. In the wetter part of the transect (far from the drainage ditch), gross photosynthesis and total respiration decreased. There was also slightly less CO_2 sequestration than in the drier part. This study suggests for *Sphagnum* dominated peatlands that the effect of climate change might be reduced by a change of vegetation communities.

Avant-Propos

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1.0 Introduction

In Europe and North America, peatlands are used for many purposes, for instance horticulture, agriculture, energy and forestry (Vasander 1996; Payette and Rochefort 2001; Joosten and Clarke 2002). Among the goods and services produced by natural peatland ecosystems such as filtration, wildlife habitat, regional landscape diversity, etc., much attention is paid these days to their role in global carbon cycling. Boreal and subarctic peatlands act as a carbon sink (Gorham 1991), which implies an important role in mitigating the effects of the global climatic warming (Laine *et al.* 1996). From this perspective, knowledge of peatlands in a changing climate is important when estimating their role as carbon sinks.

The present study concentrates on one type of peatlands perturbation: drainage that created a water level drawdown. The general objective is to estimate the effects of water level drawdown of a boreal peatland on vegetation composition and carbon dioxide fluxes taking the water level drawdown as one potential scenario of global climatic warming. To have a better overview of the effects of water level drawdown on peatlands and its implications to understand the effects of global climatic warming, I will define in the following introductory sections, the boreal peatlands, the problematic of the global climatic warming and its potential effects on peatlands. I will also present the methods used to estimate the effects of water level drawdown and global climatic warming on the carbon cycle of a peatland.

1.1 Peatland ecology

The structure, the development and the ecosystemic functions of peatlands will be relevant for interpreting the results of the present study. In the following sections, these aspects will be explained by seeing the peatland definition, the peatland types, the peatland formation, the gradients of peatland vegetation and the carbon cycle of peatlands.

1.1.1 Peatland definition

A natural peatland ecosystem is characterized by an accumulation of an organic deposit with time caused by a decomposition rate of the organic matter which is lower than the production rate. Water table level is near the soil surface, which creates anaerobic conditions slowing the microbial activity. Peatlands are distinguished from marshes and swamps by the decomposition/production ratio. In marshes and swamps, decomposition and production are both high, which means that there are no accumulation of organic matter.

1.1.2 Peatland types

There are two main peatland types: minerotrophic and ombrotrophic. Minerotrophic peatlands are also called fen (from Swedish). Water supplies come from both precipitations and runoff of surface water or the underground sources of mineral water. Water table is under the influence of the surrounding topography. Fens have a trophic status varying between oligotrophic (poor) and eutrophic (rich), depending of the concentrations of basic cations Ca, Mg and Na. Cation concentrations depend in turn of mineral inputs from water runoff percolating into peat. Water and substrate of poor fens have a pH ranging between 3.8-6.5 whereas for rich fens it is higher than 5.8 and can reach 8.4 (Sjörs 1950a). Dominant vegetation of poor fens are *Sphagnum* mosses while on rich fens, herbaceous species from the Cyperaceae family and brown mosses from the Amblystegiaceae family are dominant. Dwarf shrubs and trees are also present on both poor and rich fens.

Ombrotrophic peatlands are also called bog (from Irish). Water supplies come exclusively from precipitations. Trophic status is poor, mainly because no nutrients come from the surrounding area by water supplies, nutrients come only from precipitations. Water and substrate of bogs have a pH below 4.2 (Sjörs 1950a). Dominant vegetation of bogs is *Sphagnum* mosses. Ericaceous shrubs and some species of the Cyperaceae family are also widely present. Bogs often succeeds a fen, because with time peat accumulation isolates the peatland from the mineral soil by forming a perched water table, thus lessening the influences of water runoff. Consequently the peatland becomes poorer. The conditions are then suitable for *Sphagnum* growth, which will further induce its own growth conditions by its capacity to acidify the soil. Indeed, because of their high ion exchange capacity (Clymo 1963) and the release of organic acids through its own decomposition (Hemond 1980), *Sphagnum* species can lower the pH of their environment. Bog conditions are reached and this process is called ombrotrophication. Bogs have a diplotelmic soil structure: the catotelm and the acrotelm (Ingram 1978). Catotelm is the deeper layer saturated in water, with a low hydraulic conductivity and anaerobic conditions. Acrotelm is the surface layer comprising the oscillating water table, high hydraulic conductivity and aerobic conditions. The catotelm is usually the thicker layer that accumulates peat whereas the acrotelm is the production layer.

1.1.3 Peatland formation

Peatlands are initiated via two processes: terrestrialization and paludification. Their further development is driven by allogenic and autogenic factors. I will explain these concepts in the next sections. On a long-term basis, these concepts can interact with the water level drawdown studied in this study. Indeed, we will see that water level influences the peatland formation and development.

1.1.3.1 Terrestrialization and paludification

Terrestrialization occurs when a peatland is initiated from a lake or a water body whereas paludification is a process where *Sphagnum* mosses invade and begin to accumulate peat on uplands. In North America, paludification is more common than terrestrialization (Gorham *et al.* 2003), but in temperate regions, it has been observed that terrestrialization was the primary mechanism of the initiation of peatlands followed by paludification (Anderson *et al.* 2003).

1.1.3.2 Allogenic and autogenic factors

Peatlands are formed and developed with the influence of allogenic and autogenic factors. Allogenic factors are related with the external influences on the ecosystem, for instance climatic conditions as atmospheric humidity and temperature. Autogenic factors are related with the internal influences on the ecosystem, for instance succession of peatland vegetation, topography, substrate and hydrology.

For the initiation of peatlands by paludification, allogenic factors are rather specific (Payette 2001). A positive hydric regime (water input higher than water output) is needed.

Low temperatures and high precipitations favour this condition. For instance, in southern Québec, temperatures are rather high for peatland formation but precipitations are over 800 mm per year. In northern Québec: precipitations are between 600 and 900 mm per year but temperatures are colder, mean annual temperature is between -6 and 2 °C. For the initiation of peatlands by terrestrialization, allogenic factors can be in a wider range because the water table is already at the soil surface (Payette 2001). Indeed, even in drought periods, the initiation of peatlands by terrestrialization is possible because of the water table near the soil surface that keeps the ground constantly humid.

When reading the literature on peatland formation, one finds two main schools of thought to understand if peatlands are predominantly influenced by allogenic or autogenic factors in their development. As often, a mixture of both factor types exists between these schools. Here will follow an overview of these two schools of thought.

In the promotion of allogenic factors as the main factors responsible for the formation of a peatland, Damman (1979) had a great influence. According to his studies, climatic conditions mainly drive peatland development. Firstly, the amount of precipitations determines peat accumulation by maintaining the water level high and thus, slowing the decomposition rate. High precipitations during the vegetative season increase the elevation of a bog surface. The magnitude of the moisture surplus also increases the proportion of bogs compared to fens. Indeed, by increasing the moisture surplus, bogs have the tendency to expend by slowing the peat decomposition. At the opposite, it is not the case for fens because with an increasing moisture surplus, water becomes more important in the landscape and consequently fens become more fertile. Thus, the decomposition rate increases compared to the production rate. Finally, other climatic factors as the length of the vegetative season, the distribution of the moisture surplus over the vegetative season and winter period, and the snow accumulation have a great influence on the ratio bog/fen in a landscape. Damman (1979) was able to define west-east and north-south transects for peatland distribution in North America. The west-east transect represents the differences between the continental to the maritime climate whereas the north-south transect determines the temperature and the length of the day gradient.

Other peatland ecologists, as Foster and Wright (1990), promoted the autogenic factors as the main drivers for the formation of peatlands. Glaser (1992) gives an explanation of how autogenic factors can influence the development of peatlands. Firstly, the diplotelmic structure of bogs affects the water flow, which at the same time control the mineral uptake and thus the alkalinity in a peatland. The mineral uptake and the alkalinity are for instance some of the factors that controls fen and bog distribution in a peatland complex. Autogenic factors are also responsible for chemical transformations in peatland water where there is a decline in pH and calcium concentration from the margin to the centre of the peatland. *Sphagnum* mosses for instance play a great role in decreasing pH with their high ion exchange capacity. Peat formers can also have a great impact on the peatland hydrology. Sedge peat has a higher porosity than *Sphagnum* peat. This different porosity between both peat types affects the water flow within a peatland. On a regional scale, autogenic factors were also promoted by Anderson *et al.* (2003) who showed that they were important drivers for the development of three peatlands in New England.

Finally one can find advocates to state that both allogenic and autogenic factors are responsible in certain steps of peatland formation as Frenzel (1983). According to Glaser and Janssens (1986), peat hydraulic properties, an autogenic factor, was as important as climate, an allogenic factor, in the development of raised bogs on a regional scale in eastern North America. Janssens *et al.* (1992) demonstrated the influence of both allogenic and autogenic factors in the development of the bog complex of Red Lake peatland in Minnesota. Kuhry *et al.* (1993) showed that some peatlands are first initiated by allogenic factors but following evolution is often dominated by autogenic factors. Payette (2001) also stated that allogenic factors are dominant in peatland evolution but autogenic factors are responsible of peatland ombrotrophication. In oceanic British Columbia, Turunen and Turunen (2003) showed that allogenic and local autogenic factors were responsible of the development of a sloping bog system.

1.1.4 Gradients of peatland vegetation

Peatlands present vegetation gradients. Sjörs (1950b) describes three vegetation gradients. Malmer (1986) adds a fourth one. These vegetation gradients are the *i*) microtopography of the peatland surface, *ii*) the mire margin-mire expanse, *iii*) rich to poor in fen indicator species between fens and bogs and *iv*) for bogs, the distance from the sea represented by climate.

1.1.4.1 Microtopographic gradient

The clear repartition of mosses, *Sphagna* and vascular plants along the microtopography of hummocks and hollows (Fig. 1) in peatlands makes this gradient to be easily recognized (Gauthier 1980; Hayward and Clymo 1982). In starting from the upper part of the gradient, there are the hummock, lawn and hollow habitats. Hummocks are drier and hollows are wetter. In fens and bogs, each habitat has typical mosses, *Sphagna* and vascular plants species. The scale of the microtopographic gradient is in the order of metres in length and 40 to 80 cm in height (Campbell and Rochefort 2001). The small "human" scale of this gradient is probably another reason why this gradient was one of the first to be recognized by peatland ecologists. Several explanations have been put forward to understand this gradation of vegetation along the microtopography: hydrology, pH, nutrient content and production/decomposition ratio. More details about each of them can be found in Campbell and Rochefort (2001).

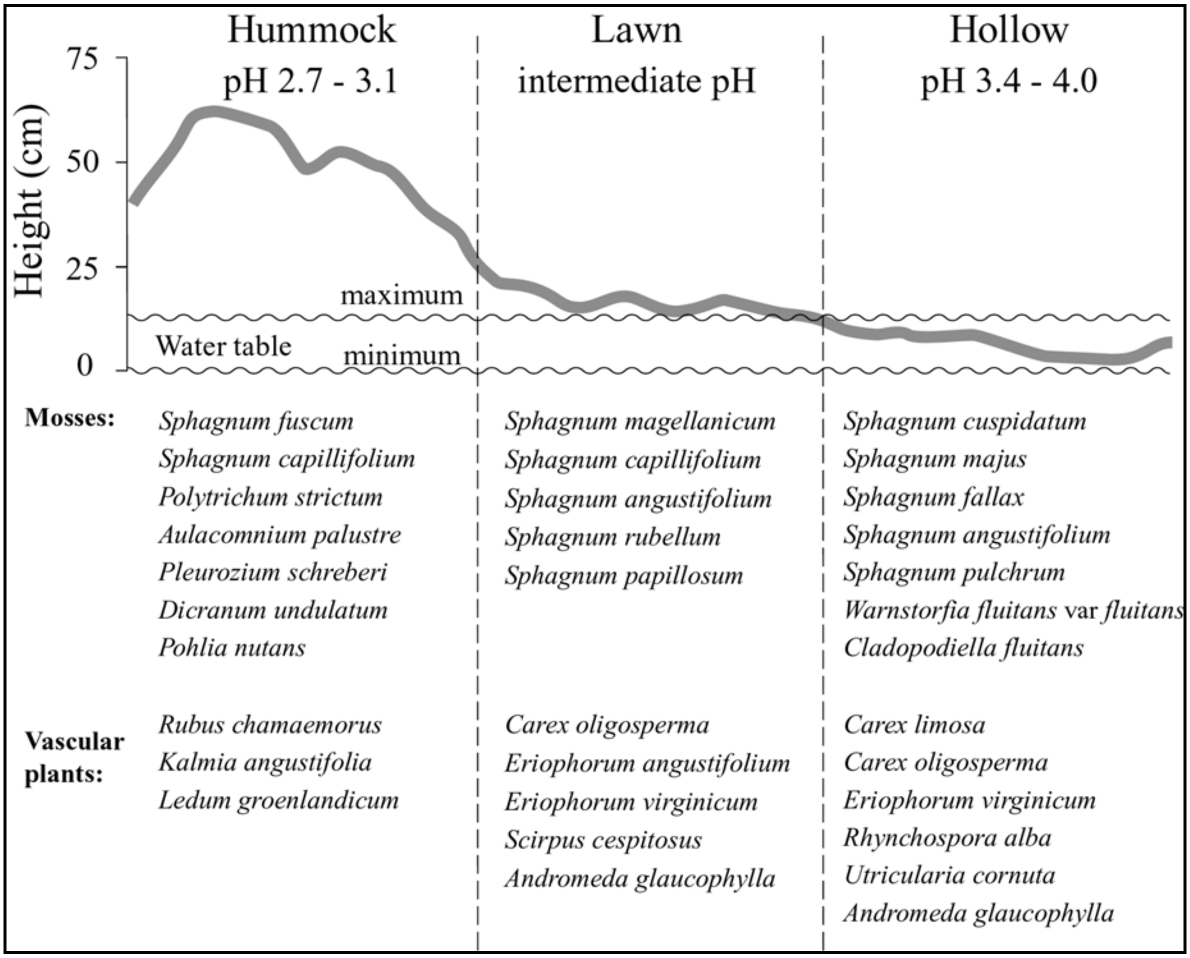


Figure 1. Microtopographic gradient for the bog species of eastern Canada showing the average pH for each topographical community. Species are ordered according to their typical occurrence. Figure modified from Campbell and Rochefort (2001).

1.1.4.2 Mire margin-mire expanse gradient

The scale of the mire margin-mire expanse gradient lies between the centre and the margin of a peatland. This gradient is mostly defined by the repartition of trees. At the margin there are more trees and shrubs than in the centre. Water table is higher and stable in the centre compared to the margin where it is deeper and fluctuating (Damman and Dowhan 1981; Bubier 1991). Nutrient status is richer at the margin than in the centre because minerals come from the water flow of the centre to the margin (Ingram 1967; Damman and Dowhan 1981). The repartition of *Sphagnum* species between the margin and the centre will also differ as it is controlled by shading effect of trees (Gignac 1992), nutrient status and water table (Damman and Dowhan 1981).

1.1.4.3 Gradient of fen indicator species

The scale of the gradient in fen indicator species is regional or within a complex of peatlands. This gradient is defined by the amount of indicator species for a specific trophic level of fen (Sjörs 1950a). There are eutrophic, mesotrophic and oligotrophic fens and there are indicators species for each trophic level (Laine and Vasander 1996). The trophic status of a fen is thus determined by the amount of indicator species of a specific trophic level. Finnish classification of peatlands also uses this concept (Laine and Vasander 1980). Sjörs (1950a) and Gorham (1953) found that within this vegetation gradient, there is a chemical gradient expressed by pH, corrected electric conductivity and alkalinity. Species repartition is strongly influenced by this chemical gradient.

1.1.4.4 Gradient of the distance from the sea

The scale of the gradient of the distance from the sea is continental and expressed only in bogs. This gradient is expressed from west to east and north to south or from maritime to inland climate. The distribution of bog species differs according to the geographical location (Malmer 1986). For instance, oceanic climate allows a high and constant water level for bogs (Sparling 1967), which is not the case inland where summer drought periods are more frequent. In that case, species distribution follows this humidity gradient among bogs. Bogs in an oceanic climate receive also more salinity from sea spray, which for instance is an important phenomenon in New Brunswick or on the coast of Maine in the United States.

1.1.5 The carbon cycle of peatlands

We have seen the structure and development of peatlands, these aspects will be of great importance for interpreting the results of the present study. Another aspect which is also important is the ecosystemic functions of peatlands mainly by their role in the carbon cycle. In the following sections, I will present the global carbon pool contained in peatlands and three important cycles in a peatland: the carbon dioxide, the methane and the dissolved organic carbon cycles.

1.1.5.1 Peatlands and its contribution to the carbon pool of the world

Because of the slow decomposition rate, peatlands are characterized by an accumulation of the atmospheric carbon in peat deposits. Peatlands occupy an area of 346 million hectares in the boreal and subarctic zones (Gorham 1991). About one third of the total carbon in soil is stored in boreal and subarctic peatlands (Post *et al.* 1982), which represents 270 to 370 Pg (1 Pg = 10^{15}g) (Turunen *et al.* 2002). The long-term (apparent) rate of carbon accumulation (LORCA) for boreal and subarctic peatlands is 66 Tg yr^{-1} (1 Tg = 10^{12}g) (Turunen *et al.* 2002). Overall, the most important controls of carbon cycle of peatlands are plant community, temperature, hydrology and chemistry of plant tissues and peat (Moore *et al.* 1998).

1.1.5.2 The cycle of carbon dioxide in peatlands

Peatlands exchange carbon dioxide (CO_2) with the atmosphere (Fig. 2). CO_2 is sequestered by vegetation via photosynthesis. Carbon is then accumulated as a peat deposit in anaerobic conditions, in the catotelm (Clymo *et al.* 1998). CO_2 is released in the atmosphere by the respiration of the plants and the soil; the two components together are referred to as “total respiration”. Plants through the photorespiration process release CO_2. Soil also emits CO_2 following the aerobic decomposition of the organic matter (Clymo *et al.* 1998) and methane (CH_4) oxidation (methanotrophy) by bacteria (Sundh *et al.* 1995), two processes that occur in the acrotelm.

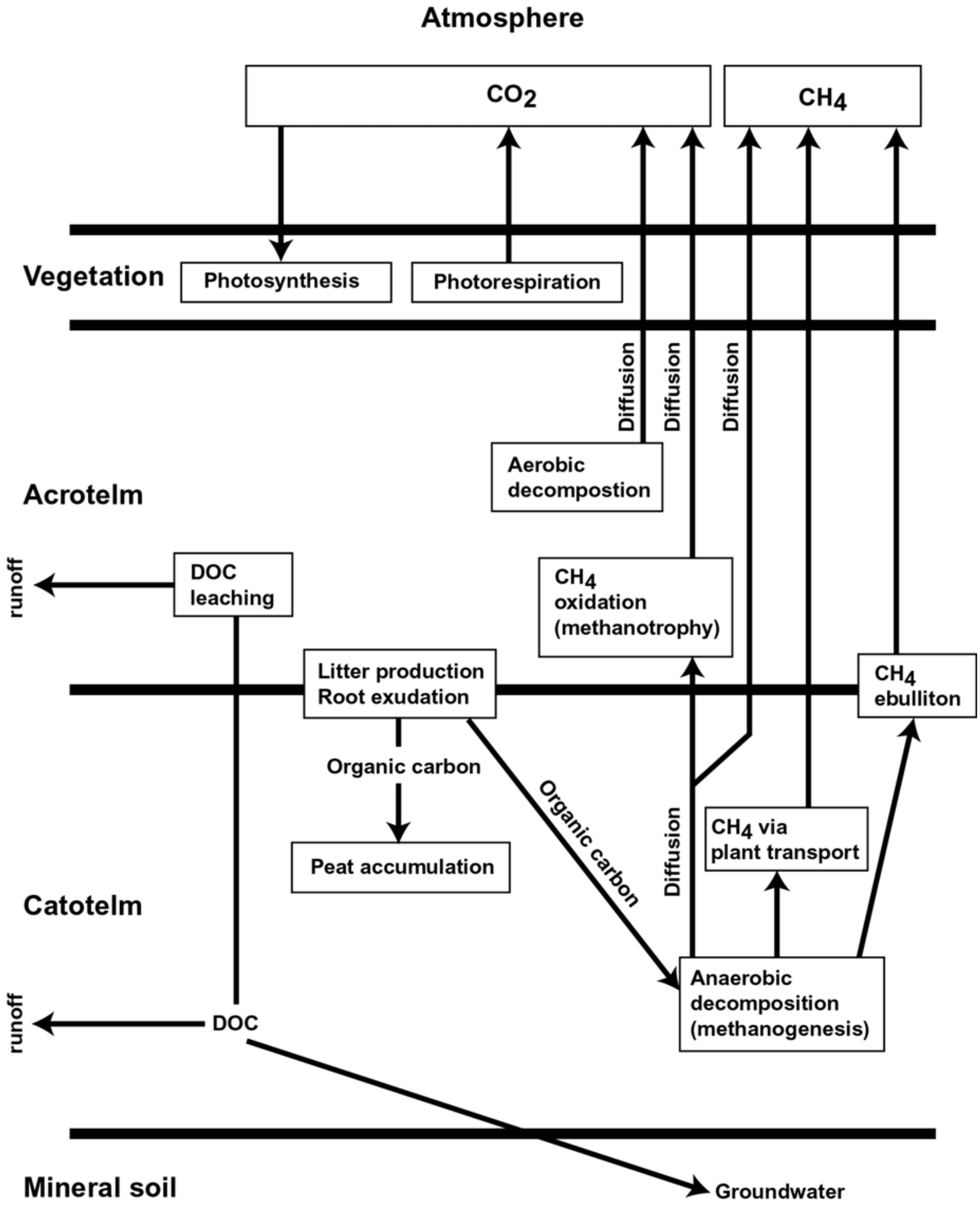


Figure 2. Carbon cycle in a natural peatland.

1.1.5.3 The cycle of methane in peatlands

In the catotelm, CH_4 is produced by anaerobic decomposition of the organic matter (Cao *et al.* 1996), the process is called methanogenesis. Plants stimulate methanogenesis by releasing “young” organic material as root exudates in the catotelm (Schütz *et al.* 1991). This fresh carbon is then easily decomposable by methanogenic bacteria. CH_4 is released in the atmosphere via three processes: diffusion, ebullition and plant transport (Fig. 2). Diffusion of CH_4 occurs through the peat column when it is not oxidized by methanotrophic bacteria. Ebullition of CH_4 is via bubbles that are released from water saturated peat to the atmosphere (Rosenberry *et al.* 2003). Vascular plants release CH_4 via the aerenchymatic tissues from the roots that are in the catotelm to the atmosphere (Schimel 1995; Thomas *et al.* 1996). Controls of CH_4 cycle are temperature (Dunfield *et al.* 1993), water table position (Svensson and Roswall 1984; Moore and Dalva 1993), peat chemistry (Svensson and Sundh 1992) and plant community (Bubier 1995); for instance bryophyte distribution (Bubier *et al.* 1995).

1.1.5.4 The cycle of dissolved organic carbon in peatlands

Organic material is also released from the peatland as dissolved organic carbon (DOC) (Fig. 2). DOC gives the brown colour to peatland water. DOC is released by leaching and enters into downstream aquatic ecosystems as streams, rivers, lakes and ocean (Mulholland and Kuenzler 1979; Urban *et al.* 1989; Dalva and Moore 1991). DOC exports from temperate and boreal peatlands ranges between 4 and 20 g DOC m^{-2} yr^{-1} (Moore 2001).

1.2 The problematic of the global climatic warming

Before examining the effects of the global climatic warming on the structure and function of peatlands, the main aim of this study, I will briefly introduce the concept, define the greenhouse gases and present some scenarios of climatic warming.

1.2.1 Concept and definition

Globally, the climate system of Earth is in balance and controlled by solar energy. To keep a balance and constant temperatures, energy entering in the climate system must leave at the same rate. Energy enters the climate system as solar rays and leaves as infrared radiations. Some atmospheric gases that reflect, absorb and re-emit both incoming solar rays and outgoing infrared radiations control energy fluxes of the climate system. If climate balance is disturbed, Earth temperature will decrease or increase (depending in which way balance is modified) and reach a new balance. This change in energy balance, which forces the climate system to reach a new balance, is called radiative forcing and any factor that can modify this system balance is called a radiative forcing agent (IPCC 1990). Positive radiative forcing values indicate a warming effect whereas negative values a cooling effect (the units are in $W\ m^{-2}$).

With the issue of the global climatic warming, the balance of the climate system of Earth is disturbed in a way that mean temperatures will be higher because the rate of the outgoing energy is lower than the incoming. It is mainly caused by an increase of some atmospheric gases that decrease the outgoing rate of infrared radiations, these gases are called greenhouse gases.

1.2.2 Greenhouse gases

Greenhouses gases are CO_2, CH_4, nitrous oxide (N_2O), ozone (O_3) and halocarbons. Molecule for molecule, CO_2 is the least effective greenhouse gas. Most other greenhouse gases have a stronger effect. On a basis of 100 years time horizon, CH_4 is 21 times more effective than CO_2 in absorbing heat energy, N_2O is 310 and halocarbons are between 4 and 23 900 times more effective (IPCC 1996). However, the net contribution of each gas on the greenhouse effect depends on three factors: the amount of each gas released in the atmosphere per year, the length of time that each gas stays in the atmosphere before being destroyed and the indirect effect that each gas has on atmospheric chemistry and concentration of other greenhouse gases. In taking into account all these factors, the net contribution of CO_2 on greenhouse effect is two to three times higher than CH_4 and about

15 times the one of N_2O (Hengeveld 1995). Data for halocarbons and O_3 effects remain uncertain.

1.2.3 Scenarios of climatic warming

Since preindustrial time (i.e. since about 1750), CO_2 concentration has increased from 280 to 367 parts per million (ppm), most likely due to human activities, fossil fuel use, land use change and agriculture (IPCC 1996; IPCC 2001b). By 2100, CO_2 atmospheric concentration is expected to increase in a range of 478 to 1099 ppm (IPCC 2001b). Other concentrations of greenhouse gases are also expected to increase (IPCC 2000). Consequently, the increase of the atmospheric concentration of greenhouse gases will have an impact on climate. By 2100, extreme climate events will be more frequent and intense, temperatures are expected to increase in a range of 1.4 to 5.8 °C, sea level should rise between 9 and 88 cm and globally, water vapour, evaporation and precipitations will also increase (IPCC 2001a).

1.3 The effects of the global climatic warming on peatlands

Now that we are more familiar with the issue of the global climatic warming, I will explain its effects on the structure and function of peatlands. In the following sections, I will first present the role of peatlands in the global climatic warming. Then I will explain the predicted effects of global climatic warming on the vegetation and the carbon cycle of peatlands.

1.3.1 The role of peatlands in the global climatic warming

In the global climatic warming context, peatlands have an important role because they act as a sink of atmospheric carbon. Peatlands have a negative radiative forcing effect in storing carbon. In that case, it becomes interesting to study the effects of global climatic warming on peatlands and their releases of greenhouse gases, as a feedback exists between both components. An interesting question arises then: how will peatlands react to global climatic warming: would they become a carbon source or would they stay a carbon sink or even become a bigger carbon sink? It is possible to give partial answers to this question by simulating a drought effect (a scenario of global warming) by effectively draining a peatland to lower the water table. In response to global warming, one expects that water table of a peatland to be lower because of increased evapotranspiration and evaporation from the ecosystem. An ideal experimental design would be to simulate global warming by a gradual water level drawdown of low drainage intensity as we do know that climate change is not a spontaneous event. No experimental study has been done in that sense. Nevertheless, studies have been realised on the effects of water level drawdown on carbon dynamic of peatlands used for forestry. In these studies, the intensity of water level drawdown was strong and uniform because forestry drainage was done spontaneously. However, these studies can be quite useful to investigate the end effect of a potential scenario of global warming.

1.3.2 The effects of global climatic warming on the vegetation of peatlands

Drainage practices of *Sphagnum* dominated peatlands for forestry uses modify the vegetation composition by increasing arboreal and shrub vegetation (Laine *et al.* 1995), tree stand volume (Vasander 1982) and by replacing *Sphagna* by forest moss species (Minkkinen *et al.* 1999). In that sense, global climatic warming will modify some vegetation gradients, such as the microtopographic and mire margin-mire expanse gradients, because the water table will be affected.

1.3.3 The effects of global climatic warming on the carbon cycle of peatlands

The effects of global warming on the carbon cycle of peatlands will be explained on the three main cycles already seen earlier: carbon dioxide, methane and dissolved organic carbon cycles. The last section will debate on peatlands as a carbon source or a carbon sink in a global warming context.

1.3.3.1 Carbon dioxide

By increasing the depth of acrotelm, water level drawdown leads to an increase of CO_2 emissions (Kim and Verma 1992; Silvola *et al.* 1996), caused by an overall increased of the range of peat temperature (Prévost *et al.* 1997), aerobic decomposition (Lieffers

1988) and consequently total soil respiration (Waddington *et al.* 2002). After water level drawdown, soil respiration also increases by enhanced root respiration (Silvola *et al.* 1992).

1.3.3.2 Methane

The activity of methanotrophic bacteria increases as aeration depth of acrotelm is enhanced after water level drawdown. This affects CH_4 emissions, which are lower as CH_4 consumption is higher (Moore and Knowles 1989; Svensson and Sundh 1992). In some sites, a net consumption of CH_4 has been found (Martikainen *et al.* 1995). This situation may happen for peatlands of temperate regions, but for peatlands of the boreal and subarctic regions, it may be different. Peatlands of boreal and subarctic regions include floating mats, degrading pools and permafrost (palsa and plateau). With the higher temperatures caused by global warming, these peatland types are expected to release more CH_4 because methanogenic bacteria will be favoured by the melting of the permafrost. In that sense, CH_4 emission rates will be different according to the geographical location of peatlands (Moore *et al.* 1998). Peatlands of temperate regions may release less CH_4 but it may be the opposite for peatlands of boreal and subarctic regions.

1.3.3.3 Dissolved organic carbon

The loss of carbon from peatlands in the form of DOC increases slightly by leaching after water level drawdown (Laine *et al.* 1996). However, in a perspective of climatic warming, DOC discharges are expected to decrease from peatlands because water runoff will decrease. Nevertheless, DOC concentration will increase in the peat matrix, this carbon will be then available for CO_2 and CH_4 emissions (Pastor *et al.* 2003). There might be a carbon transfer from DOC to CO_2 and CH_4 emissions.

1.3.3.4 Peatlands as a source or sink of carbon in a context of climatic warming?

Many aspects and interactions of the carbon cycle have to be taken into account in predicting the effects of climatic warming on peatlands. Researchers who are working on the effects of water level drawdown of peatlands for forestry uses are bringing interesting clues. Even though water level drawdown realised in forestry is not the most representative to simulate global climatic warming, partial answers can be brought about the role of carbon storage of peatlands in a perspective of climatic warming. After drainage of a peatland to improve forest growth, net primary productivity is enhanced (Paavilainen and Päivänen 1995; Prévost *et al.* 2001). Indeed, more carbon is bound in the higher tree stand (Cannell *et al.* 1993) and growth conditions of roots are improved (Kramer 1987), thus peatland drainage increases the above and below ground biomass (Laiho and Finér 1996; Laiho *et al.* 2003). Does it mean that drained peatlands can be more efficient as carbon sink than pristine peatlands? Even though peat carbon losses have been reported (Brække and Finér 1991; Sakovets and Germanova 1992), the increased tree stand plays an important role in storing new carbon (Minkkinen and Laine 1998) and suggests that a few decades after drying, drained peatlands would stay a carbon sink. Results from Hargreaves *et al.* (2003) showed that afforested peatlands after drainage act as a higher carbon sink for 9 to 19 decades but after that time the ecosystem would act as a carbon source. Consequently, to recover the sink role, afforested peatlands should be returned in its former form (Cannell *et al.* 1993). Finally, Gorham (1991) and Moore *et al.* (1998) analysed the prediction on the effects of global climatic warming on northern peatlands and concluded that many uncertainties exist and it is impossible to give an accurate answer whether peatlands would become a carbon sink or source.

1.4 Estimating the effects of global climatic warming on the carbon cycle of peatlands

Practically, the assessments of the effects of water level drawdown or global climatic warming on the carbon cycle of peatlands must be measured and estimated in the field. Carbon budget has to be partly measured by carbon fluxes and many techniques exist to measure it on peatlands. The main ones are the chamber and the tower methods, a description and a comparison of both methods will be made in the next sections.

1.4.1 Chamber methods

Briefly, the chamber methods consist of measuring carbon fluxes with a chamber placed onto a collar inserted into the peat soil. There is two chamber methods used to measure gases on different ecosystems: static and dynamic. The static method, which has now been in use for 75 years (Lundergårdh 1927), measures carbon fluxes indirectly, i.e.

not *in situ*. Gases are absorbed in an alkali solution (Lundergårdh 1927) or in soda lime (Edwards 1982) in order to be detected. Gas can also be sampled in the field in syringes for a short time period (up to 24 hours) before being analysed with a gas chromatograph in laboratory (Alm *et al.* 1999b; Tuittila *et al.* 2000). More recently, dynamic methods have been developed to measure CO_2 fluxes *in situ* with the aid of infrared gas analysers (for instance see Kim and Verma 1992). Two types of dynamic systems exist: open and closed. In dynamic open systems, fresh air of known CO_2 concentration enters into the chamber while an equal volume of air is withdrawn and analysed. CO_2 exchanges are calculated using the flow rate and the difference in CO_2 concentration between the air entering and leaving the chamber. In dynamic closed systems, air circulates from the chamber to the analyser and returns to the chamber. CO_2 exchanges are calculated using the rate of increase of CO_2 concentration in the chamber (Rochette *et al.* 1992).

1.4.2 Tower method

The main tower method to measure carbon fluxes is called the eddy covariance method. Theoretical framework of eddy covariance was established by Reynolds (1895). Baldocchi (2003) gives an accurate definition of the eddy covariance technique: *it ascertains the exchange rate of* CO_2 *across the interface between the atmosphere and a plant canopy by measuring the covariance between fluctuations in vertical wind velocity and* CO_2 *mixing ratio*. The optimal conditions to use the technique are when the field is flat, the environmental conditions are steady and the underlying vegetation is homogeneous for an extended distance upwind.

1.4.3 Chamber methods *vs.* tower method

The main difference between chamber and eddy covariance methods is the scale over which both can be used. Chamber methods are used on a microtopographic scale whereas eddy covariance is used at the ecosystem scale. Chamber methods are more accurate if we are seeking differences within an ecosystem or working on processes of the ecosystem whereas for comparisons between ecosystems, eddy covariance is more appropriate.

1.5 Objectives of the study

Drainage of peatland sites for forestry production could be useful sampling sites to study the effect of global warming as it would simulate the drawdown effect on the water table that could be induced by greater evapotranspiration rates. Several studies have been done on the effects of water level drawdown practiced on peatlands drained for few years (often 40 or less) for forestry uses (Vasander 1982; Vasander 1984; Laine and Vanha-Majamaa 1992; Martikainen *et al.* 1995; Laine *et al.* 1996; Silvola *et al.* 1996; Minkkinen *et al.* 1999). Because forestry practices command a regularly space grid drainage, the intensity of water level drawdown was strong and uniform in those studies and not compatible with global scenarios for peatland responses (Roulet *et al.* 1992). Thus a site was sought to evaluate the effect of water level drawdown on peatlands, where the drainage intensity is low and where a moisture gradient existed. In that regards, we found a 55 years old drained site in Finland of low intensity because it was not drained for forestry production and with time the drainage was not maintained. We considered this site to be a good simulation for a scenario of global climatic warming which predicts a water level drawdown in summer over the regions of the high latitudes (Manabe and Wetherald 1986). Moreover, the realised water level drawdown reached 10 cm (Fig. 6) which corresponds approximately to the 14 cm water level drawdown predicted to happen in a scenario of twice the elevation of CO_2 air concentration (2 X CO_2) (Roulet *et al.* 1992).

In this context, hypotheses were drawn for the vegetation and CO_2 aspects. On the vegetation aspect along the moisture gradient, it is expected that the species changes would follow the moisture gradient. Also for the aspect of CO_2 fluxes a hydric stress would be applied near the drainage influences. It is expected that in going away from the drainage influences, CO_2 emissions would decrease by an increase of photosynthetic potential of the vegetation and by a decrease of total respiration.

The objectives of this study are to quantify the effect of long-term water level drawdown, as caused by drainage done 55 years ago, on (1) vegetation composition and (2) CO_2 fluxes of a boreal peatland in central Finland, (3) in order to gain better understanding of the potential implications of the global climatic warming on *Sphagnum* dominated peatlands. Drainage of a part of the peatland area caused a moisture gradient from the edge of a ditch towards the middle of the peatland.

2.0 Material and Methods

2.1 Study site

The measurements were realised between May and November 2002 on Hanhisuo peatland (61º 47’ N; 24º 18’ E) in Central Finland. It is located on the southern boreal coniferous forest zone (Ahti *et al.* 1968) and the eccentric raised bog region (Ruuhijärvi 1982), 150 m above sea level. The mean annual temperature in the region is +3 °C; the mean temperature of the warmest month, July, is +16 °C. The mean annual temperature sum (accumulated mean daily temperatures ≥ +5°C) varies between 1150 and 1250 degree-days. The annual precipitation is 650 mm, of which 240 mm falls as snow. In the summer of the year 2002, when the field measurements were taken, the weather conditions were particularly hotter and drier than the long-term reference period, 1971-2001 (Fig. 3; data from the Finnish Meteorological Institute 2003). Indeed, mean temperatures were higher than the reference period from May to August 2002 (Fig. 3). The mean precipitations were higher than the reference period for June and July 2002, but extremely lower for August and September 2002 (Fig. 3).

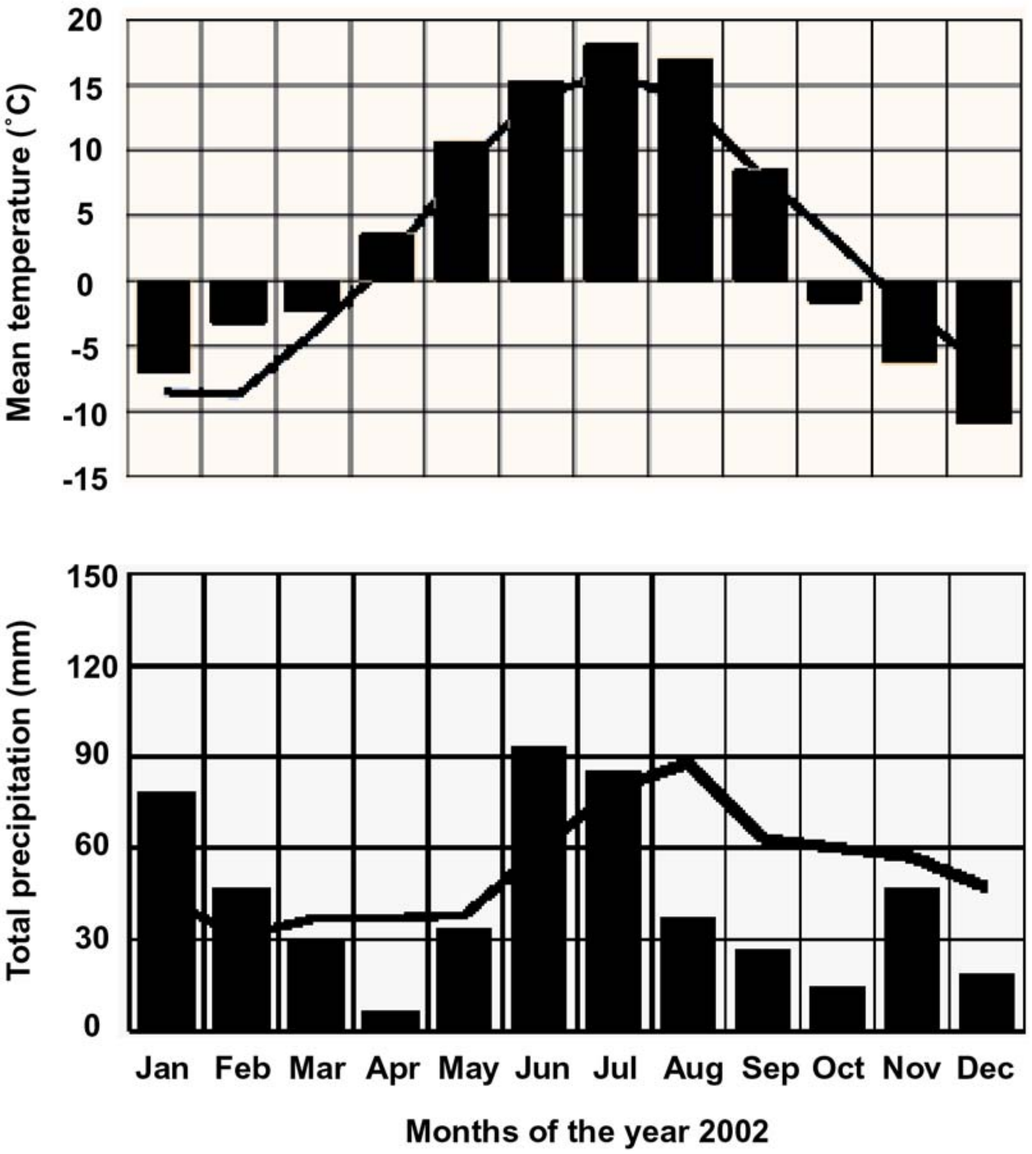


Figure 3. Mean temperatures and total precipitations for the months of the year 2002. Data come from the Jyväskylä meteorological station, approximately 100 km from the study site. The columns represent the mean temperatures or the total precipitations for each month. The line represents the reference period of 1971-2001 of the mean temperatures or the mean precipitations. Figure modified from the Finnish Meteorological Institute (2003).

The peatland site ranges between ombrotrophy and oligotrophy in nature. According to the Finnish classification (Laine and Vasander 1980), the peatland type is classified between a low-sedge *Sphagnum papillosum* pine fen (LkR) and a low-sedge *Sphagnum papillosum* fen (LkKaN). For one non familiar with the Finnish classification of peatland types, it should be noted that it defines a site type according to its indicator species. The low-sedge *Sphagnum papillosum* pine fen type has the following indicator species: *Sphagnum papillosum, Trichophorum cespitosum, Eriophorum vaginatum, Carex pauciflora, Carex lasiocarpa, Carex rostrata* and *Pinus sylvestris*. The indicator species of the low-sedge *Sphagnum papillosum* fen are *Sphagnum papillosum* (with *Sphagnum compactum* in northern Finland), *Carex pauciflora, Eriophorum vaginatum, Trichophorum cespitosum* with some minerotrophic species such as *Eriophorum angustifolium, Carex magellanica, Carex rostrata* and *Carex lasiocarpa*. The study area of Hanhisuo peatland has most of the indicator species of the low-sedge *Sphagnum papillosum* pine fen and the low-sedge *Sphagnum papillosum* fen peatland types and the ground layer is dominated by *Sphagnum papillosum, Sphagnum fuscum* and *Sphagnum rubellum*. A part of Hanhisuo peatland was drained 55 years ago by farmers who harvested the peat for bedding. Drainage age was determined by an aerial photography of the National Land Survey of Finland (1946). The drainage created a moisture gradient from the edge towards the middle of the peatland.

2.2 Sampling

In order to evaluate the effects of water level drawdown on vegetation composition and CO_2 fluxes, six transects of 100 m were established on the peatland. Three transects were established on the drained area of the peatland and three other, on the natural (undisturbed) area (Fig. 4 and 5). Transects were positioned on the same peatland type defined earlier. Transects had six measuring points placed systematically at 20 m of distance from each other. Each point had three sample plots (56 cm X 56 cm). A well for water table measurements was installed at each point. Transects started at about 10 m from the drainage ditch or the natural edge, except for transects 2 and 3 of the drained area that started at about three metres from the ditch, in order to fix the first measuring point (the one near the ditch) on the same site type as transect 1. On the natural area, the edge was defined at the point where the mineral soil began and the peat deposit ended. On the drained area, transects 1, 2 and 3 were at 30 m from each other. No such uniform separations were possible on the natural area because of the presence in patches of the site type. Transect 4 was bent to remain on the same peatland site type. The area abandoned after peat harvesting was near the end of transect 4 (about 15 m) but did not have an effect on it (Vasander, pers. comm.).

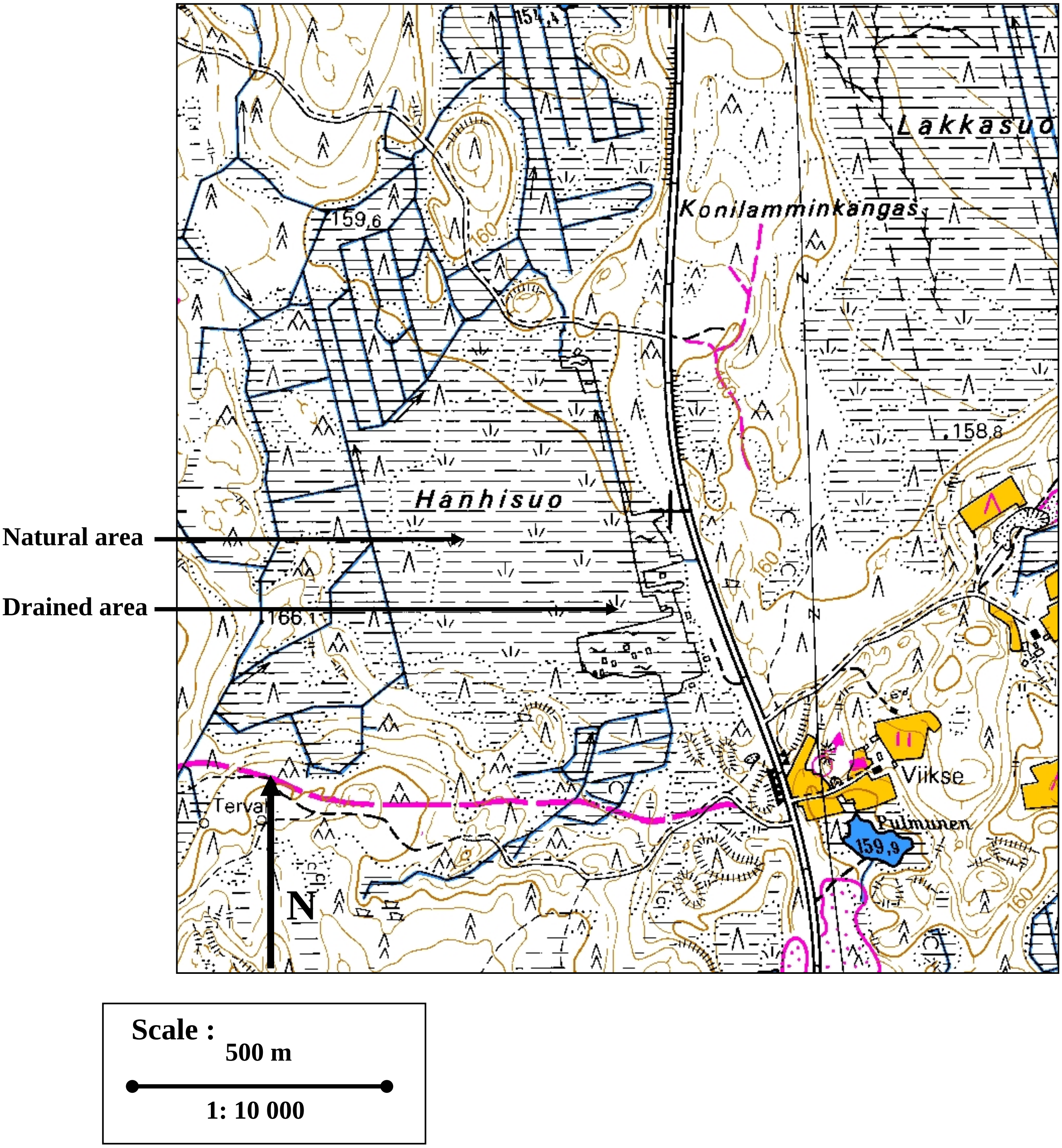


Figure 4. Map of Hanhisuo peatland, the study site. The sampling design is on the figure 5.

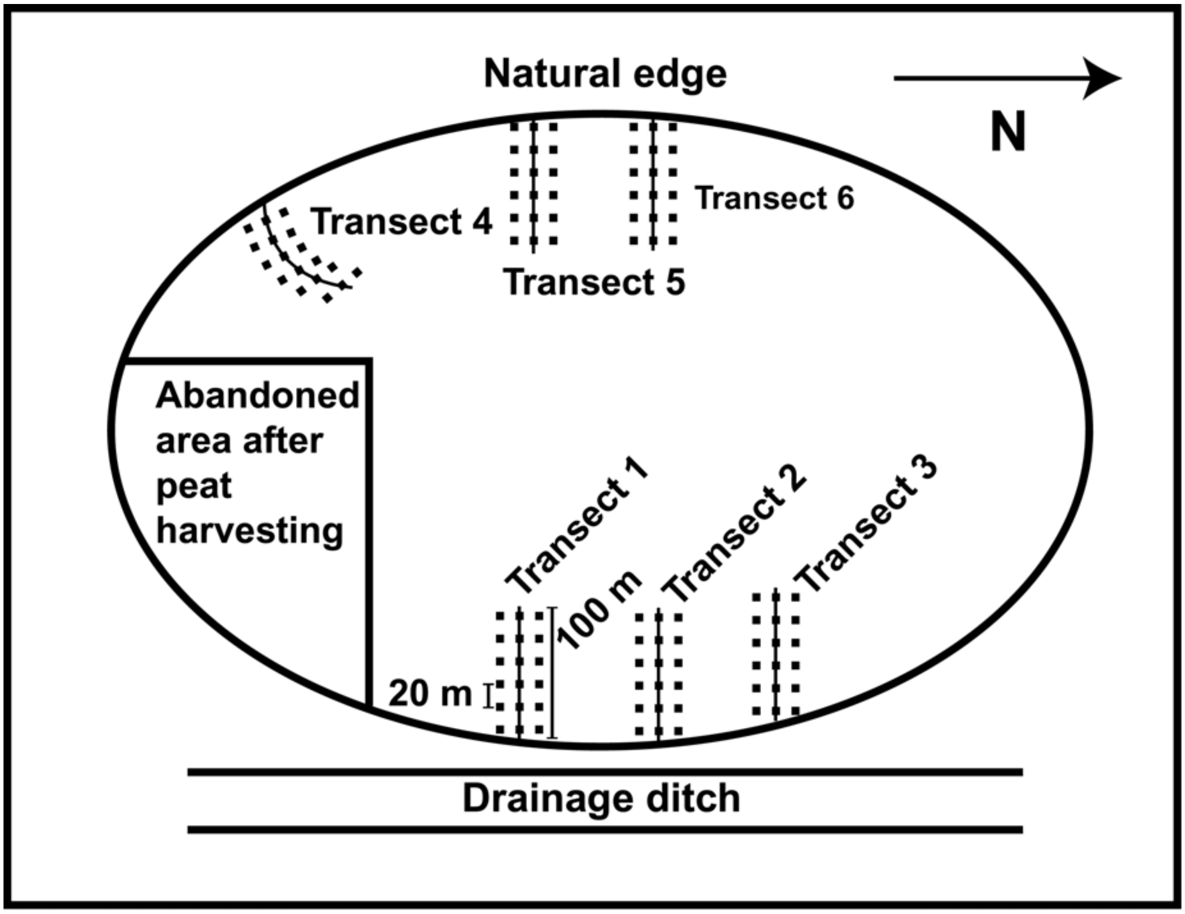


Figure 5. Position of transects on the study site.

2.2.1 Monitoring of vegetation

In order to evaluate if the water level drawdown affected the vegetation composition along the moisture gradient, vegetation surveys were done by the cover estimation of the species in the sample plots at the end of July and early August, when the biomass is highest in the season. Cover was estimated to the closest 1 % under covers of 25 % and to the nearest 5 % for above. In order to compare the hydroseral gradients sustaining the plant communities of each transect, water table level measurements were done every two weeks between July 11 and August 23, 2002 and once in September 2002. The nomenclature in this study follows that of Hämet-Ahti *et al.* (1998) for vascular plants and Koponen *et al.* (1977) for bryophytes.

2.2.2 Measurements of CO_2 fluxes

In order to evaluate if water level drawdown had an impact on the CO_2 fluxes along the moisture gradient, CO_2 measurements were monitored. The CO_2 measurements were done only on the sample plots of the transect 1 of the drained area (Fig. 5). CO_2 measurements were done at 10, 30, 50, 70, 90 and 110 metres from the drainage ditch. As mentioned earlier, there is a moisture gradient from the drainage ditch towards the middle of the peatland. Indeed, the moisture gradient is approximately 10 cm along the transect 1, i.e. the water table at 10 metres from the drainage ditch is 10 cm lower than at 110 metres (Fig. 6). The moisture gradient of 10 cm corresponds approximately to a water level drawdown of 14 cm predicted in a scenario of global warming in which the elevation of the CO_2 air concentration is twice (Roulet *et al.* 1992).

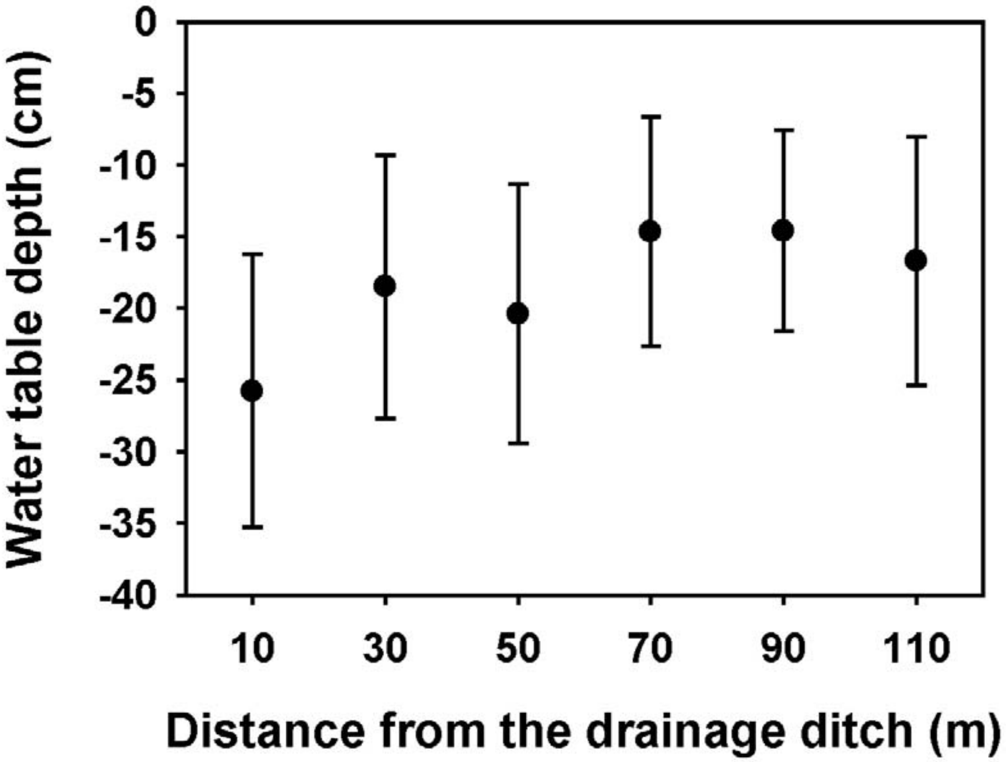


Figure 6. Water table depths along the transect 1. The means (± standard deviation) are the water table depths for 24 days of measurements taken at regular intervals between May 22 and November 4, 2002.

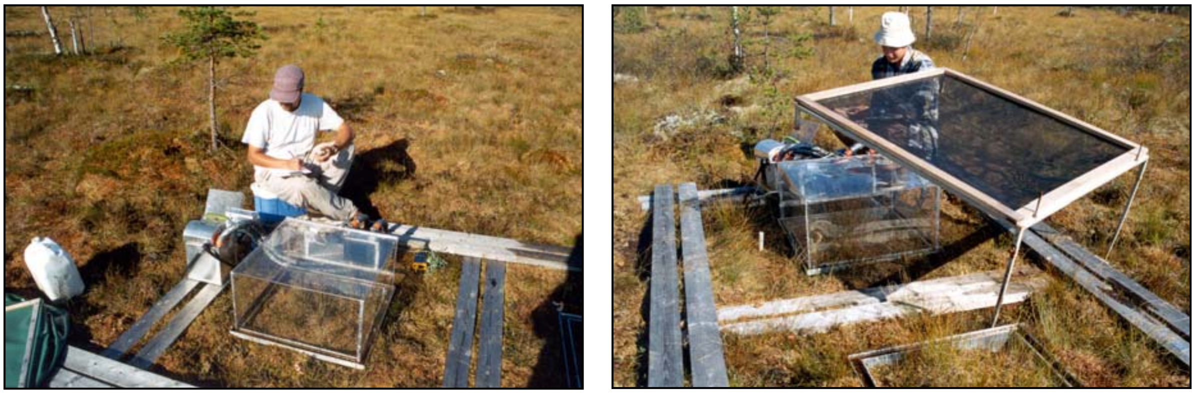
Boardwalks were built along the transect and around the sample plots to avoid disturbance during measurements. Sample plots were surrounded by aluminium collars of 0.31 m^2 (56 cm X 56 cm), which were inserted to a depth of 30 cm into the peat. The collars were equipped with grooves that were filled with water before CO_2 flux measurements to provide an airtight seal between the chamber and the collar. One might think that the collars alter the water flow within the sample plot, but that is not the case. Even though no measurements were taken on the field, it has been clearly observed that the water table was the same inside and outside the collars under both wet and dry conditions (Vasander, pers. comm.). This observation confirmed that the collars do not affect the water flow within the sample plot. Collars were inserted in late June 2001 and CO_2 measurements were monitored between late May 2002 and late September 2002. Measurements were done at a two weeks interval from May to August and once in September. A total of nine measuring days were sampled throughout the growing season.

The measurements of CO_2 exchange were done with the dynamic chamber method in a closed system. Measurements were taken within a vented and air-conditioned transparent plastic chamber (0.115 m^3) similar to the one used by Tuittila and Komulainen (1995) and Alm *et al.* (1997, 1999b). The chamber was placed onto the collar in a hermetic way. The CO_2 concentration in the chamber was measured with a portable infrared gas analyser (PP Systems, model EGM-2 and EGM-3) equipped with a vacuum pump (suction from the headspace 150-180 ml air min-1). Analyser readings were in parts per million (ppm). The net CO_2 exchange (P_N) was one of the variables measured on the field. P_N is the difference between the gross CO_2 assimilation in photosynthesis (P_G) and the total respiration (R_{TOT}):

$$P_N = P_G - R_{TOT}$$

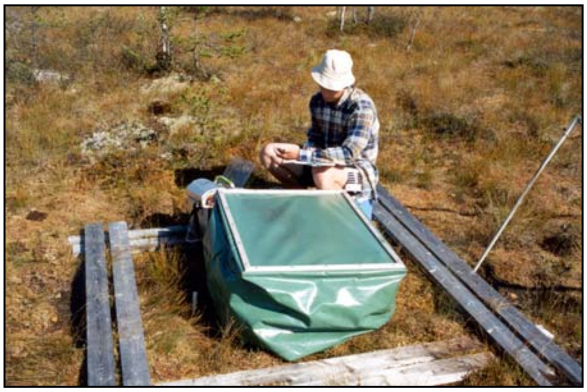
In the present study, P_N has a positive value when CO_2 is sequestrated in the peatland, i.e. P_G is higher than R_{TOT}. P_N has a negative value when CO_2 is released from the peatland, i.e. R_{TOT} is higher than P_G. P_G and R_{TOT} always have positive values. The P_N was measured with the chamber uncovered and exposed to ambient illumination for 60 to135 s at intervals of 15 s (Fig. 7a). P_N values were also measured under lower irradiation levels, achieved by shading, in order to better establish the relationship between photosynthesis and irradiation

(Fig. 7b). After each measurement period, the chamber was removed for a while to allow stabilisation of the gas concentration in the plot. After P_N measurements, total respiration rate (R_{TOT}) was measured with the same chamber covered with an opaque plastic lid, under temperature and moisture conditions similar to those for P_N measurements (Fig. 7c).



a) P_N measured with the chamber uncovered and exposed to ambient illumination.

b) P_N measured under a lower irradiation level, achieved by shading.



c) R_{TOT} measured with the chamber covered with an opaque plastic lid.

Figure 7. Method for the measurements of P_N and R_{TOT} on the field.

Simultaneously with each measurement of CO_2 fluxes, air temperature inside the chamber, water table level and soil temperature at peat profiles (at 5, 10 and 20 cm below the peat surface) were measured in order to relate the CO_2 fluxes to prevailing environmental conditions. During P_N measurements, photosynthetic active radiation (PAR) was measured every 15 s with a quantum sensor (phototransistor BPW 21 R, range of voltage metre of 0-200mV, calibration trimmer-potentiometre of 5 kohm). CO_2 measurements were related to the leaf area index of the vegetation throughout the growing season. Leaf area index is an index of the leafiness of plants in a sample plot. It is calculated by the ratio between the total leaf area of plants and the total ground area upon which it stands, the values are positive pure numbers and represent the leaf area per unit ground area (Hunt 1990). In this study, only the vascular plants were included in the leaf area index. Indeed, the index is calculated by the ratio between vascular plants (m^2) and the surface of ground area of the collar sample plot (m^2). In the field, the leaf area index was measured with the following sampling strategy. In each sample plot, five sub-plots (8 cm X 8 cm) were established systematically, i.e. one placed in the middle and four placed in the corners of the collar sample plot. In each sub-plot, the number of leaves of each vascular species was counted monthly. At each transect point, leaf area of the representative species of the collar sample plots was measured on individuals randomly taken outside of the collar sample plots. Leaf area was measured at every two weeks from May to August and once in September and November. On days of the growing season where the leaf area was not measured on the field, leaf area index was interpolated from days it was measured. For the other less representative species, the average value of the leaf area was measured once in the season (late July) on plants taken outside of the collar sample plots. For few less representative species, the theoretical value (Hämet-Ahti *et al.* 1998) of the leaf area had to be taken because it was present seldom in the field during the sampling period. This sampling strategy estimated leaf area of different species within sampling plots without disturbing the plants. Leaf area index was interpolated from May 20 to November 4, 2002.

Rates of CO_2 fluxes were calculated by regression from the linear change of CO_2 concentration in the chamber headspace as a function of time, base area, chamber volume, and the molar volume of CO_2 at chamber air temperature.

2.3 Data analysis

In the following sections, I will explain the methods used to analyse the vegetation and the CO_2 fluxes data. For vegetation aspect, the method will determine the effects of water level drawdown on species composition along the moisture gradient. The method will compare if there are differences in the species composition between the natural and the drained areas of the peatland. In comparing both areas, the method will examine whether the species composition of the drained area is really due to water level drawdown or a natural mire margin-mire expanse gradient of vegetation. For the aspect of CO_2 fluxes, models relating environmental conditions to P_G and R_{TOT} will be built. These models will explain whether water level drawdown created differences for P_G, R_{TOT} and P_N values along the transect of the drained area.

2.3.1 Analysis of vegetation data

An ordination approach was used to examine if sample plots (drained and natural) distribution was related to the moisture gradient created by the ditching. Separate analyses were done for all plots as well for drained and natural plots to examine clearly the differences between both peatland areas. The data sets were ordinated by a Canonical Correspondence Analysis (CCA) run with four environmental variables: 1) water table depth (average of the season measurements), 2) distance to the drainage ditch or the natural edge, 3) percentage of shade created by vascular plants and 4) litter covers on the ground layer (ter Braak 1987). The distance to the drainage ditch or the natural edge was included in the analysis in order to examine if the differences in the vegetation composition of both areas were caused by the moisture gradient on the drained part or only a natural mire margin-mire expanse gradient. The percentage of shade and the litter covers were estimated in the same way than the cover estimation of the species in the sample plots (see section 2.2.1). These environmental variables were included in the analysis in order to examine if it could explain additional variations in the species composition.

The results from the CCA were also compared with those of a Detrended Correspondence Analysis (DCA). This allowed to evaluate what part of the variation explained by theoretical variables (with DCA) could not be explained by the four environmental variables (with CCA) enumerated earlier. Ordinations were run with the percentage cover of all species present in more than one sample plot. The axes 1 and 2 of the DCA explained about two times more variation that did the CCA (24.8 % vs. 13.3 % for all plots; 25.8 % vs. 15.1 % for drained plots; 28.3 % vs. 16.2 % for natural plots). This can be explained by a lack of environmental variables measured on the field. Nevertheless, the patterns of plot types were about the same between the DCA and CCA analyses. CCA results are thus only presented.

The significance of the environmental variables used in the CCA was tested by using Monte Carlo simulations with 999 restricted permutations adapted for the sampling method (ter Braak 1987). Permutations were restricted in a way that they were done only within a transect and the 18 sample plots of a transect were permuted using cyclic shifts with shifts from the mirror image disabled. Ordinations and Monte Carlo permutation procedures were conducted with the program CANOCO, version 4.5 (ter Braak and Šmilauer 2002).

Cluster analyses were also used to reveal the different plant communities and serve as a complementary information given by the ordinations (van Tongeren 1987; Thomas *et al.* 2002). A two-way indicator species analysis (TWINSPAN) with a divisive method (Hill *et al.* 1975; Hill 1979) was done on the same data sets as for the ordinations with the program PC-ORD, version 4 (McCune and Mefford 1999).

2.3.2 Analysis of CO_2 fluxes data

In the two following sections, I will first explain the method used for modelling CO_2 fluxes. Then I will show how the models were built for CO_2 fluxes.

2.3.2.1 Explanation of the modelling method

Models for CO_2 fluxes of P_G and R_{TOT} were selected using the method of the Akaike's information criterion (AIC) (Burnham and Anderson 1998). A brief explanation of the method must first be shown. For model selection, AIC uses the principle of parsimony and enforces the trade-off between bias and variance as the number of parameters is increased (Anderson *et al.* 2000). AIC method comes from the theory of Kullback-Leibler information (Kullback and Leibler 1951).

In a group of *a priori* candidate models carefully defined, the model with the lowest AIC value is selected as the best model. AIC value is calculated with the following formula:

$$(1) \qquad \text{AIC} = -2\ (\text{maximized log-likelihood}) + 2\ K$$

where *K* is the number of parameters. In this study, the maximized log-likelihood value was obtained with the GENMOD procedure of the SAS software (SAS Institute Inc. 2000). The 2 *K* term represents a “penalty” for added parameters while minimizing AIC, which enforces the principle of parsimony. In this study, a second-order AIC (AIC_c) (Hurvich and Tsai 1989, 1995; Burnham and Anderson 1998) had to be used to take into account the small sample size. AIC_c is calculated in adding to the equation (1) the following correction term:

$$(2) \qquad \frac{2\ K\ (K + 1)}{(n - K - 1)}$$

where *n* is the sample size. Although the best model can be selected with the lowest AIC value, it can be very useful to rank the models to know if another model is also plausible among the *a priori* group of models. In that case, the models have first to be rescaled in giving the value 0 to the model with the lowest AIC (or AIC_c) value. The models are then ranked using the Δ_i, which is calculated with this formula:

$$(3) \qquad \Delta_i = \text{AIC}_i - \min \text{AIC}$$

Δ_i can easily be interpreted following this scale (Burnham and Anderson 2001): models having $\Delta_i \leq 2$ are strongly plausible, those where $4 \leq \Delta_i \leq 7$ are considerably less plausible whereas models having $\Delta_i \geq 10$ are improbable. It can be also convenient to normalize the Δ_i values such that they sum to 1 in calculating the w_i, called Akaike weight:

$$(4) \qquad w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^{R} \exp(-\Delta_i/2)}$$

The Akaike weight allows to know the probability that a model is the best among the others. If more than one model are strongly plausible in the set of *a priori* models, model averaging must be applied. In this case, inferences are based on the entire set of *a priori* models. In the final model resulting from the method of model averaging, parameter values are calculated according to the Akaike weight of the models where they are present. For a parameter, a model-averaged estimator has often better precision and reduces bias compared to the estimator coming only from the best selected model (Burnham and Anderson 2001). In this study, model averaging method was applied when more than one model in the set of *a priori* models had a $\Delta_i \leq 4$. A more detailed explanation of the model averaging method is shown in Burnham and Anderson (1998).

2.3.2.2 Modelling CO_2 fluxes

CO_2 fluxes for P_G and R_{TOT} were inferred for all the samples plots at each hour from May 22 to September 22, 2002. Here are the set of *a priori* models defined for P_G:

(5)

General model: $\ln P_G = DAY + DAY^2 + DIST + PAR + LAI + WT + WT^2 + T_{-5} + T_{AIR}$
Model 1: $\ln P_G = DAY + DAY^2 + DIST + PAR + LAI + T_{-5}$
Model 2: $\ln P_G = DAY + DAY^2 + DIST + PAR + LAI + WT + WT^2 + T_{-5}$
Model 3: $\ln P_G = DAY + DAY^2 + DIST + PAR + LAI + WT + WT^2 + T_{AIR}$
Model 4: $\ln P_G = DAY + DAY^2 + DIST + PAR + LAI + WT + WT^2$
Model 5: $\ln P_G = DAY + DAY^2 + DIST + PAR + LAI$
Model 6: $\ln P_G = DAY + DAY^2 + DIST + PAR$

where DAY is the day of the growing season (e.g. DAY 1 = May 22), DIST is the distance of the sample plot from the drainage ditch, PAR is the photosynthetic active radiation, LAI is the leaf area index, WT is the water table level, T_{-5} is the soil temperature at five centimetres under the surface and T_{AIR} is the air temperature. PAR, T_{-5} and T_{AIR} were measured every hour at the meteorological station of Lakkasuo peatland, five kilometres from the study site. LAI was interpolated as already mentioned in section 2.2.2. WT was measured weekly and values for the days where it was not measured were interpolated from the measured values. P_G was log transformed to respect the condition of the homogeneity of variances. Models to be selected for P_G were built according to the literature and the knowledge of the system. Tuittila *et al.* (1999) and Alm *et al.* (1997) inspired models 1 and 2, respectively. From model 2 to 6, the effects of air and soil temperature, water table and leaf area index were taken out sequentially to test whether or not it explains P_G. DAY, DAY^2 and DIST are included in all the models to take into account the season and the distance from the ditch, which are really important in the objectives of this study. DAY^2 is included for the quadratic effect of the season on P_G, which is shown in Tuittila *et al.* (1999). PAR is also included in all the models because it is strongly recognized to have an important effect on photosynthesis.

Here are the set of *a priori* models defined for R_{TOT}:

(6)

General model: $\ln R_{TOT} = \text{DAY} + \text{DAY}^2 + \text{DIST} + \text{T}_{-5} + \text{WT} + \text{WT}^2 + \text{LAI} + \text{T}_{AIR}$
Model 1: $\ln R_{TOT} = \text{DAY} + \text{DAY}^2 + \text{DIST} + \text{T}_{-5} + \text{WT} + \text{LAI}$
Model 2: $\ln R_{TOT} = \text{DAY} + \text{DAY}^2 + \text{DIST} + \text{T}_{-5} + \text{WT}$
Model 3: $\ln R_{TOT} = \text{DAY} + \text{DAY}^2 + \text{DIST} + \text{T}_{-5} + \text{WT} + \text{WT}^2 + \text{T}_{AIR}$
Model 4: $\ln R_{TOT} = \text{DAY} + \text{DAY}^2 + \text{DIST} + \text{T}_{-5} + \text{WT} + \text{WT}^2 + \text{LAI}$
Model 5: $\ln R_{TOT} = \text{DAY} + \text{DAY}^2 + \text{DIST} + \text{T}_{-5} + \text{WT} + \text{WT}^2$
Model 6 : $\ln R_{TOT} = \text{DAY} + \text{DAY}^2 + \text{DIST} + \text{T}_{-5}$

R_{TOT} was log transformed to respect the condition of the homogeneity of variances. Tuittila *et al.* (1999), Alm *et al.* (1997) and Chimner and Cooper (2003) inspired models 1, 2 and 3, respectively. From model 4 to 6, air temperature, leaf area index and water table effects were taken out sequentially to test whether or not it explains R_{TOT}. DAY, DAY^2 and DIST are included in all the models for the same reasons mentioned for P_G. T_{-5} is included in all the models because it is recognized to have an important effect on R_{TOT} (Alm *et al.* 1997;

Alm *et al.* 1999b; Tuittila *et al.* 1999; Chimner and Cooper 2003). P_N was not inferred by modelling, the values were calculated from the differences between P_G and R_{TOT} inferences.

3.0 Results

3.1 Vegetation

In this section, I will show how water level drawdown had effects on the vegetation composition of the peatland along the moisture gradient created by the drainage ditch. The CCA analyses were used to show whether the drainage ditch had a real effect, i.e. not comparable to a natural mire margin-mire expanse gradient. Then a cluster analysis was done to reveal the vegetation communities of the study area.

The CCA biplot revealed a relatively clear segregation between sample plots from the drained and natural areas of the peatland (Fig. 8). Surprisingly though, the natural plots were found in the driest part of the peatland as they are distributed in the opposite direction of the water table vector (Fig. 8). Indeed, the water table was higher and showed a gradient in the drained area whereas in the natural area, the water table was slightly deeper and constant along the transects (Fig. 9). Natural plots were also more shaded, because they are arranged in the same direction than the shade vector (Fig. 8). However, the drained plots seem to have a stronger gradient on the second CCA axis than the natural plots. This is shown by the wider dispersion of the drained plots and the narrow dispersion of natural plots along the second CCA axis. This gradient represents mainly the distance to the drainage ditch and the abundance of litter. In that respect, a separate analysis on drained plots only confirmed that there was indeed a clear gradient from the ditch, following the water table depth (Fig. 10). Drained plots of the same distance from the drainage ditch are regrouped together and these groups are mainly led by the water table vector. The groups of plots near the drainage ditch are in the driest part of the gradient whereas the ones far from the ditch are found in the wetter part of the gradient. This gradient seems to be a consequence of the drainage and not only a natural mire margin-mire expanse gradient because no clear patterns of that sort were found for the natural plots (Fig. 10). The total percentage of variance explained by all the axes for the CCA biplot of all plots, drained plots and natural plots were respectively of 16.8 %, 19.5 % and 19.8 %. Finally, even though the percentages of variance explained by the two first axes are rather low in the

CCA analyses (see section 2.3.1), sample plots were significantly related to the environmental variables (Monte Carlo permutation test, $P = 0.001$).

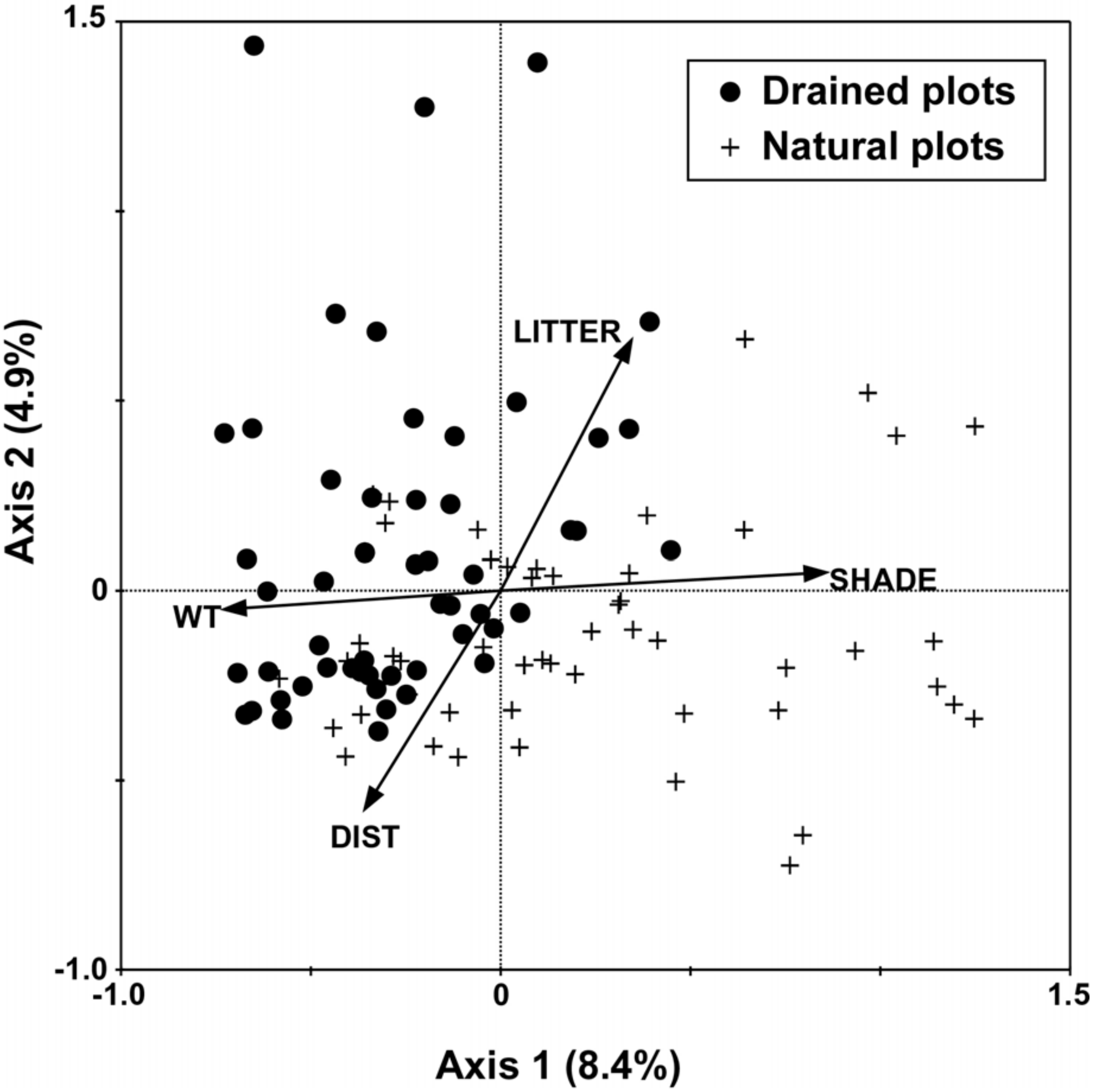


Figure 8. CCA biplot showing the distribution of all samples and the influence of environmental variables. The environmental variables are: WT = water table depth (cm); DIST = distance from the ditch or the natural edge of the peatland (m); SHADE = shade cover on the ground layer (%); LITTER = litter cover on the ground layer (%).

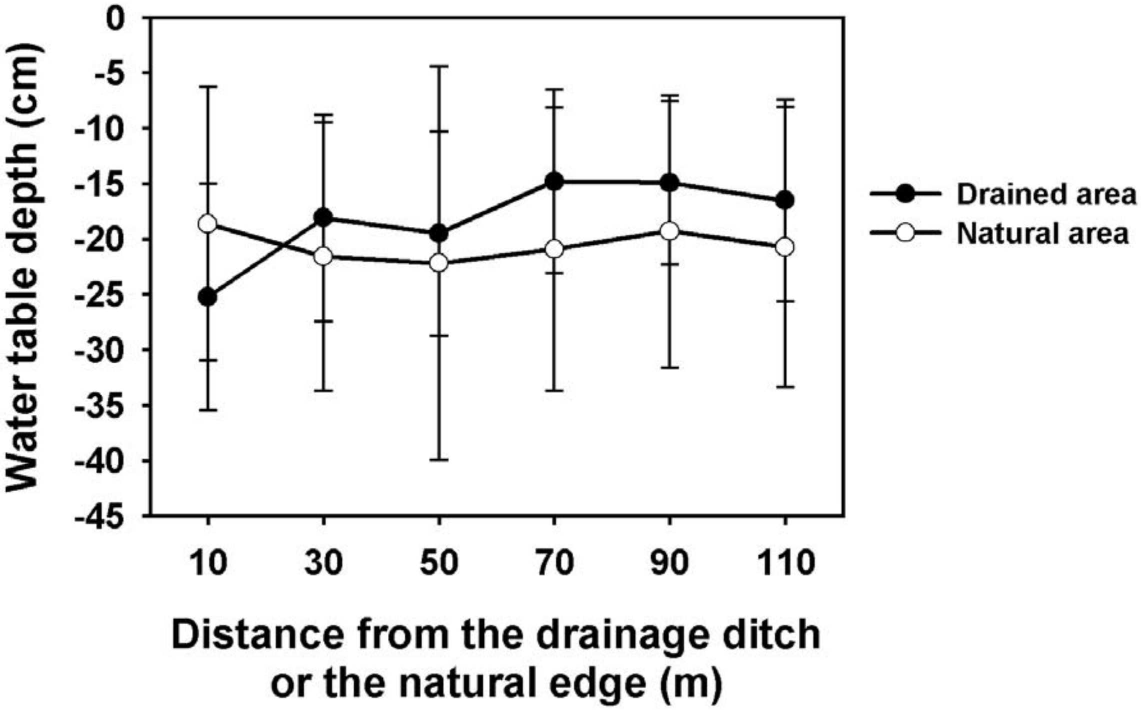


Figure 9. Water table depths along the transects of the drained and the natural areas. For each distance from the drainage ditch or the natural edge, the means (± standard deviation) are the water table depths of the transects 1, 2 and 3 for the drained area and the transects 4, 5 and 6 for the natural area. For the transect 1, measurements were taken for 24 days at regular intervals between May 22 and November 4, 2002. For the transects 2 to 6, measurements were taken for 5 days at regular intervals between July 11 and September 23, 2002.

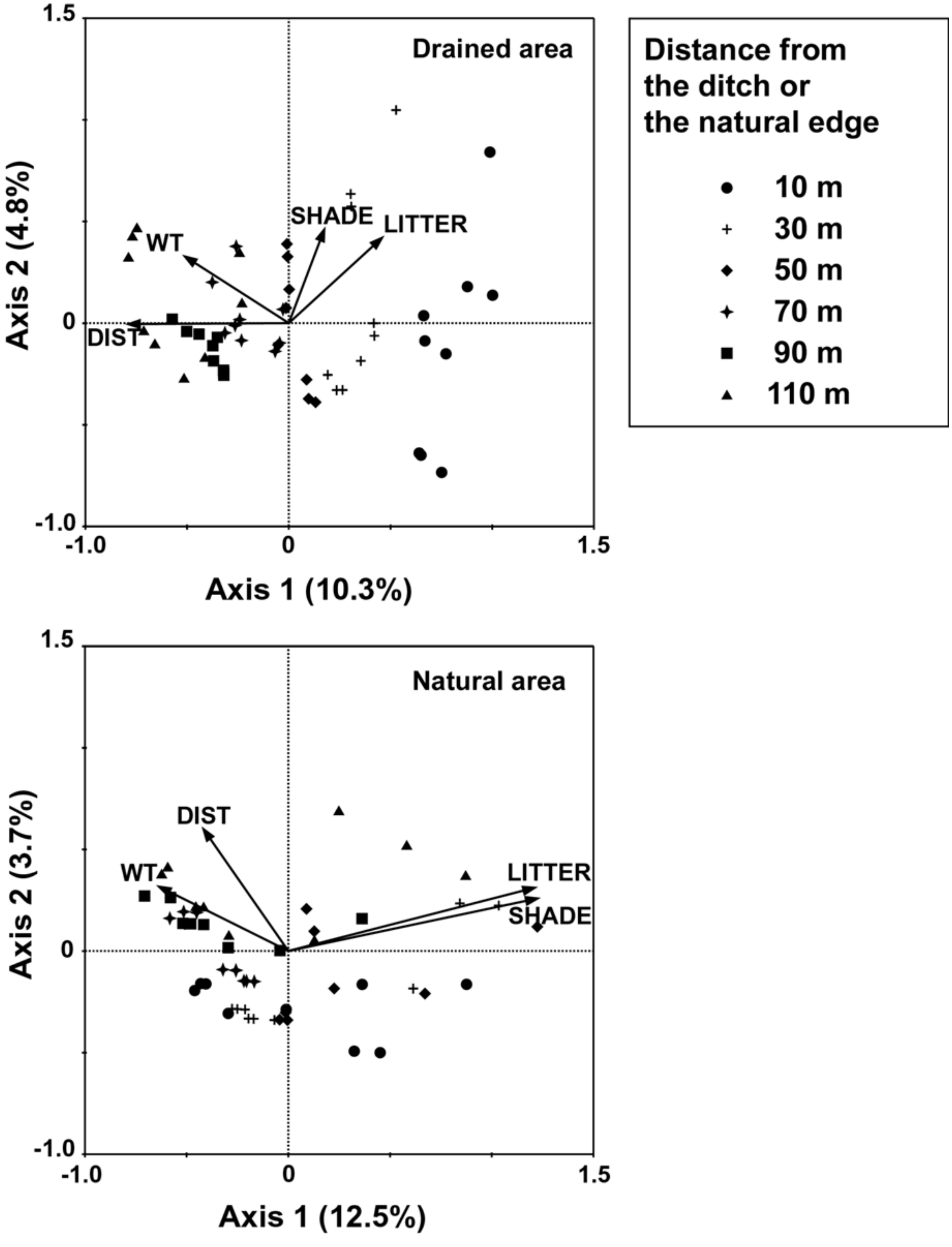


Figure 10. CCA biplot showing the distribution of samples and the influence of environmental variables for the drained and the natural areas of the peatland. Environmental variables as in Fig. 8.

The TWINSPAN analysis conducted with all samples plots revealed six communities (Fig. 11). In the field, each community could be recognized as briefly described below and by the more specific taxon listed in Appendix 1. *Pleurozium schreberi – Cladina* spp. community showed high abundances of *Polytrichum strictum* and high occurrences of *Andromeda polifolia*. *Sphagnum* species were sparse and rare. *Betula pubescens – Polytrichum strictum* community was characterized by rather high abundances of *Vaccinium uliginosum* and *Sphagnum papillosum* and high occurrences of *Pinus sylvestris*, *Betula pubescens*, *Eriophorum vaginatum*, *Rhynchospora alba* and *Mylia anomala*. *Trichophorum cespitosum* community showed high abundances and occurrences of *Sphagnum magellanicum* and *Sphagnum rubellum*. *Betula pubescens – Polytrichum strictum* and *Trichophorum cespitosum* communities shared rather high abundances of *Sphagnum balticum*, *Gymnocolea inflata* and *Cladopodiella fluitans* and high occurrences of *Andromeda polifolia* and *Vaccinium oxycoccos*. Therefore, on the drained area, *Pleurozium schreberi – Cladina* spp. community had species more adapted to drier conditions in a peatland habitat whereas *Betula pubescens – Polytrichum strictum* community is a transition zone between the drainage influences and the *Trichophorum cespitosum* community, where *Sphagnum* species had higher abundances and occurrences. *Sphagnum angustifolium – Sphagnum magellanicum* community was not characterized by species that had particularly high abundances or occurrences. Only the constant occurrence and abundance of the indicators species, *Sphagnum angustifolium* and *Sphagnum magellanicum*, characterized this community. *Empetrum nigrum – Sphagnum angustifolium* community showed high abundances and occurrences of *Pinus sylvestris* and *Sphagnum fuscum*. *Sphagnum papillosum* community was characterized by high abundances and occurrences of *Sphagnum rubellum*. Among *Sphagnum angustifolium – Sphagnum magellanicum, Empetrum nigrum – Sphagnum angustifolium* and *Sphagnum papillosum* communities, several species were common, such as *Betula nana, Andromeda polifolia, Vaccinium oxycoccos, Eriophorum vaginatum* and *Sphagnum angustifolium*. Between the drained and the natural areas, it is noteworthy that some species were exclusively present on one of the area. Indeed, *Gymnocolea inflata* and *Cladopodiella fluitans* occurred only on the drained area, whereas *Sphagnum angustifolium* was exclusively present on the natural area. For more details on the species composition of the study site, the list of each species with its percent cover in each sample plot is shown in the Appendix 1.

TWINSPAN analysis first separated communities between the drained and the natural areas. Sample plots of the *Pleurozium schreberi – Cladina* spp., *Betula pubescens – Polytrichum strictum* and *Trichophorum cespitosum* communities were exclusively located in the drained area along a moisture gradient whereas *Sphagnum angustifolium – Sphagnum magellanicum*, *Empetrum nigrum – Sphagnum angustifolium* and *Sphagnum papillosum* communities were revealed only among the sample plots of the natural area (Fig. 11). Most of the sample plots of a specific distance from the drainage ditch were classified in a specific community (Fig. 11). *Pleurozium schreberi – Cladina* spp. community was located within 10 metres of the drainage ditch and was characterized by the presence of species indicating a drier habitat near the ditch (Appendix 1). *Betula pubescens – Polytrichum strictum* community was located between 30 and 50 metres from the drainage ditch. The relatively greater abundance of *Pinus sylvestris* within this community is indicative of drier conditions than the natural area. *Trichophorum cespitosum* community was located between 70 and 110 metres from the ditch and was characterized by a higher abundance of *Sphagnum* species indicating a wetter habitat. On the natural area, the communities did not reveal a moisture gradient, because the sample plots located at different distances from the edge were rather evenly distributed among *Sphagnum angustifolium – Sphagnum magellanicum*, *Empetrum nigrum – Sphagnum angustifolium* and *Sphagnum papillosum* communities (Fig. 11). In the *Sphagnum angustifolium – Sphagnum magellanicum* community, even though seven sample plots out of nine were at the 10 m distance from the edge, it did not show a moisture gradient because *Sphagnum angustifolium* and *Sphagnum magellanicum* are not typical of either dry or wet habitats (Gignac 1992). Finally, because no distribution patterns of the sample plots were found on the natural area, it emphasises the fact that the moisture gradient of the drained area may originate from the ditch and do not represent a natural mire margin-mire expanse gradient.

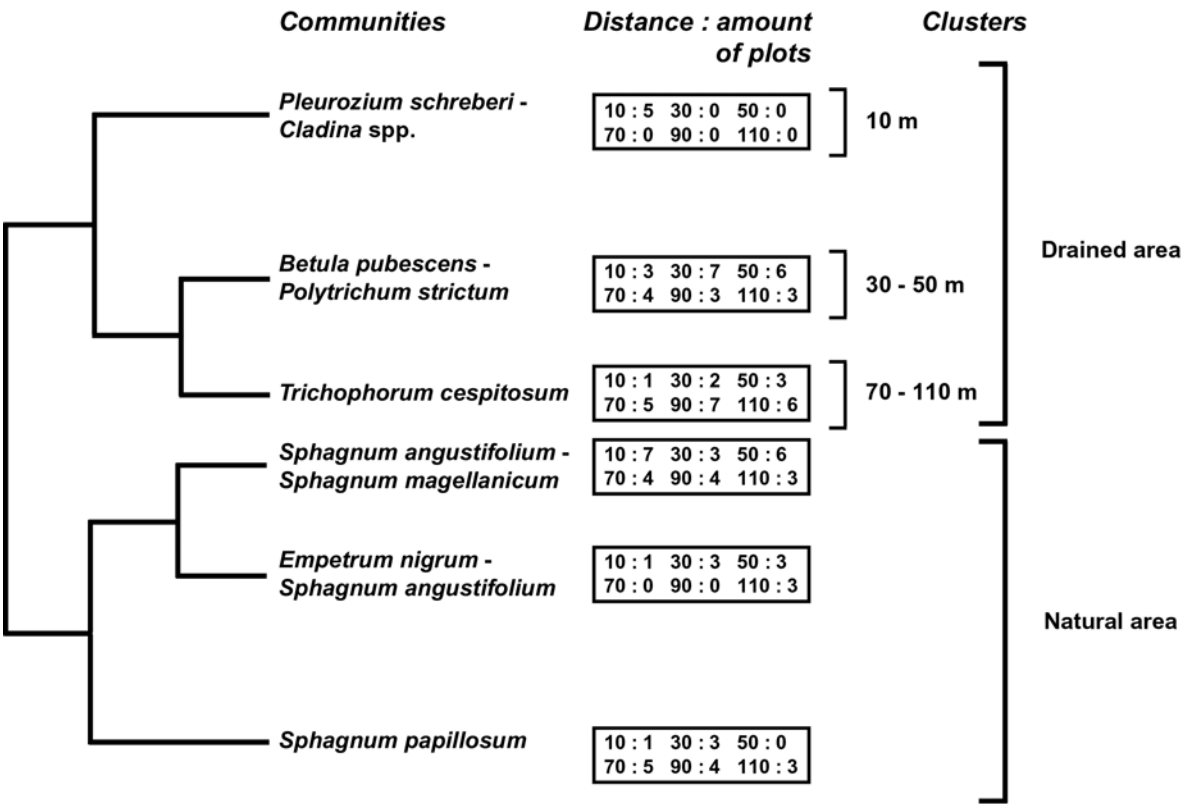


Figure 11. Cluster analysis of all sample plots. Communities are named by the indicator species given by the TWINSPAN analysis. Numbers in the boxes represent the amount of plots present at a distance from the drainage ditch or the natural edge (for instance, 10 : 5 means that there are 5 sample plots at 10 metres from the drainage ditch or the natural edge).

3.2 CO_2 fluxes

CO_2 fluxes were measured along the moisture gradient to evaluate the impacts of the water level drawdown. At the same time, some environmental conditions were monitored to help in the interpretation of CO_2 fluxes. I will first present the results for the gross photosynthesis (P_G), then for the total respiration (R_{TOT}) and finally for the net CO_2 exchange (P_N).

According to the method of AIC for model selection (see section 2.3.2), the best model to infer P_G fluxes was the general model because the AIC_c value was the lowest

(Table 1). The other *a priori* candidate models were not plausible because all Δ_i were higher than 10.

Table 1. Statistics of the model selection for P_G adjusted for small sample size (AIC_c). Models are described in the section 2.3.2.2.

Model	Maximized Log-likelihood	n	K	AIC_c	Δ_i	w_i
General	-154.01	382	10	328.61	0	0.999
1	-173.50	382	7	361.30	32.69	$7.954 \cdot 10^{-8}$
2	-171.32	382	9	361.12	32.51	$8.715 \cdot 10^{-8}$
3	-162.46	382	9	343.41	14.80	$6.115 \cdot 10^{-4}$
4	-171.32	382	8	359.02	30.42	$2.484 \cdot 10^{-7}$
5	-173.66	382	6	359.55	30.94	$1.907 \cdot 10^{-7}$
6	-175.23	382	5	360.61	32.01	$1.121 \cdot 10^{-7}$

The best selected model explained 60.5 % of the variance in P_G (Table 2). LAI did not have a significant effect on P_G (value 0 included in the Wald confidence limits, Table 2), however it was kept in the best selected model to respect the *a priori* principle of model selection. DAY had a positive estimate and DAY^2 had a negative one, which means that the effect of the season is positively unimodal. PAR and T_{AIR} had a positive estimate in the model: the higher is the irradiance and the air temperature, the higher is P_G. WT and WT^2 had also a positive estimate in the model: the effect of water table is negatively unimodal on P_G. T_{-5} and DIST had a negative estimate in the model: the lower is temperature under five centimetres and the further it is from the ditch, the lower is P_G. The effect of the distance from the ditch is also clearly demonstrated on the figure 12. There is a clear gradient for P_G in going towards the middle of the peatland (r^2 = 98.3 %, P = 0.0001).

Table 2. Estimated parameter values for the model used to reconstruct hourly gross photosynthesis (P_G).

Gross photosynthesis ($\ln P_G = b0 + b1 \cdot DAY + b2 \cdot DAY^2 + b3 \cdot DIST + b4 \cdot PAR + b5 \cdot LAI + b6 \cdot WT + b7 \cdot WT^2 + b8 \cdot T_{-5} + b9 \cdot T_{AIR}$)

Variable	**Parameter**	**Estimate**	**Standard error**	**Wald confidence limits, 95 %**	
				Lower	**Upper**
Intercept	*b*0	5.094	0.153	4.793	5.394
DAY	*b*1	$3.110 \cdot 10^{-2}$	$3.688 \cdot 10^{-3}$	$2.387 \cdot 10^{-2}$	$3.833 \cdot 10^{-2}$
DAY^2	*b*2	$-2.779 \cdot 10^{-4}$	$3.255 \cdot 10^{-5}$	$-3.417 \cdot 10^{-4}$	$-2.141 \cdot 10^{-4}$
DIST	*b*3	$-3.163 \cdot 10^{-3}$	$7.449 \cdot 10^{-4}$	$-4.623 \cdot 10^{-3}$	$-1.703 \cdot 10^{-3}$
PAR	*b*4	$7.190 \cdot 10^{-4}$	$5.233 \cdot 10^{-5}$	$6.164 \cdot 10^{-4}$	$8.216 \cdot 10^{-4}$
LAI	*b*5	$5.585 \cdot 10^{-2}$	$4.384 \cdot 10^{-2}$	$-3.007 \cdot 10^{-2}$	0.142
WT	*b*6	$2.757 \cdot 10^{-2}$	$8.069 \cdot 10^{-3}$	$1.175 \cdot 10^{-2}$	$4.338 \cdot 10^{-2}$
WT^2	*b*7	$7.818 \cdot 10^{-4}$	$2.445 \cdot 10^{-4}$	$3.025 \cdot 10^{-4}$	$1.261 \cdot 10^{-3}$
T_{-5}	*b*8	$-4.994 \cdot 10^{-2}$	$1.201 \cdot 10^{-2}$	$-7.348 \cdot 10^{-2}$	$-2.640 \cdot 10^{-2}$
T_{AIR}	*b*9	$4.839 \cdot 10^{-2}$	$8.038 \cdot 10^{-3}$	$3.263 \cdot 10^{-2}$	$6.414 \cdot 10^{-2}$
r^2 (%)	60.5				

To infer R_{TOT} fluxes, the method of AIC for model selection showed that two *a priori* candidate models were strongly plausible because Δ_i were lower than 2 (Table 3). In that case, model averaging had to be done because more than one model had a Δ_i lower than 4.

Table 3. Statistics of the model selection for R_{TOT} adjusted for small sample size (AIC_c). Models are described in the section 2.3.2.2.

Model	**Maximized Log-likelihood**	***n***	***K***	**AIC_c**	**Δ_i**	**w_i**
General	11.79	162	9	-4.39	1.73	0.296
1	-29.39	162	7	73.51	79.63	$3.595 \cdot 10^{-18}$
2	-30.30	162	6	73.14	79.26	$4.326 \cdot 10^{-18}$
3	11.53	162	8	-6.12	0	0.704
4	-25.25	162	8	67.45	73.57	$7.431 \cdot 10^{-17}$
5	-26.04	162	7	66.81	72.93	$1.024 \cdot 10^{-16}$
6	-32.75	162	5	75.89	82.02	$1.090 \cdot 10^{-18}$

The model resulting from the calculations of model averaging explained 81.1 % of the variance in R_{TOT} (Table 4). DAY, DAY^2, T_{-5} and LAI did not have a significant effect on R_{TOT} (value 0 included in the confidence interval, Table 4), however these variables could not be taken off from the model to respect the *a priori* principle of model selection. $\mathrm{T}_{\mathrm{AIR}}$ had a positive estimate in the model whereas WT and WT^2 had a negative one. DIST had also a negative estimate in the model: the further it is from the ditch, the higher is R_{TOT}. The distance effect is also evident on the figure 12. There is a clear gradient for R_{TOT} in going towards the middle of the peatland ($r^2 = 99.7$ %, $P < 0.0001$).

Table 4. Estimated parameter values for the model used to reconstruct hourly total respiration (R_{TOT}). Parameters are estimated according to model averaging.

Total respiration ($\ln R_{\mathrm{TOT}} = b0 + b1\cdot\mathrm{DAY} + b2\cdot\mathrm{DAY}^2 + b3\cdot\mathrm{DIST} + b4\cdot\mathrm{LAI} + b5\cdot\mathrm{WT} + b6\cdot\mathrm{WT}^2 + b7\cdot\mathrm{T}_{-5} + b8\cdot\mathrm{T}_{\mathrm{AIR}}$)

Variable	**Parameter**	**Estimate**	**Unconditional standard error**	**Confidence intervals, 95 %**	
				Lower	**Upper**
Intercept	*b*0	4.041	0.139	3.768	4.314
DAY	*b*1	$5.208\cdot10^{-3}$	$3.302\cdot10^{-3}$	$-1.265\cdot10^{-3}$	$1.168\cdot10^{-2}$
DAY^2	*b*2	$-5.327\cdot10^{-5}$	$2.906\cdot10^{-5}$	$-1.102\cdot10^{-4}$	$3.681\cdot10^{-6}$
DIST	*b*3	$-3.240\cdot10^{-3}$	$6.857\cdot10^{-4}$	$-4.584\cdot10^{-3}$	$-1.897\cdot10^{-3}$
T_{-5}	*b*4	$2.674\cdot10^{-4}$	$1.184\cdot10^{-2}$	$-2.294\cdot10^{-2}$	$2.347\cdot10^{-2}$
WT	*b*5	$-2.671\cdot10^{-2}$	$7.336\cdot10^{-3}$	$-4.109\cdot10^{-2}$	$-1.233\cdot10^{-2}$
WT^2	*b*6	$-5.988\cdot10^{-4}$	$2.134\cdot10^{-4}$	$-1.017\cdot10^{-3}$	$-1.805\cdot10^{-4}$
LAI	*b*7	$3.037\cdot10^{-2}$	$4.253\cdot10^{-2}$	$-5.298\cdot10^{-2}$	0.114
$\mathrm{T}_{\mathrm{AIR}}$	*b*8	$7.805\cdot10^{-2}$	$8.006\cdot10^{-3}$	$6.235\cdot10^{-2}$	$9.374\cdot10^{-2}$
r^2 (%)	81.1				

Reconstruction of P_{N} fluxes from P_{G} and R_{TOT} inferences showed only a slight gradient along the transect ($r^2 = 65.0$ %, $P = 0.0526$; Fig. 12). P_{G} and R_{TOT} both decreased with increasing distance from the drainage ditch showing higher rates in dry conditions (Fig. 12). This trend was reflected in P_{N}. However, it is noteworthy that all the transect points were net CO_2 sinks over the growing season regardless of the distance from the drainage ditch.

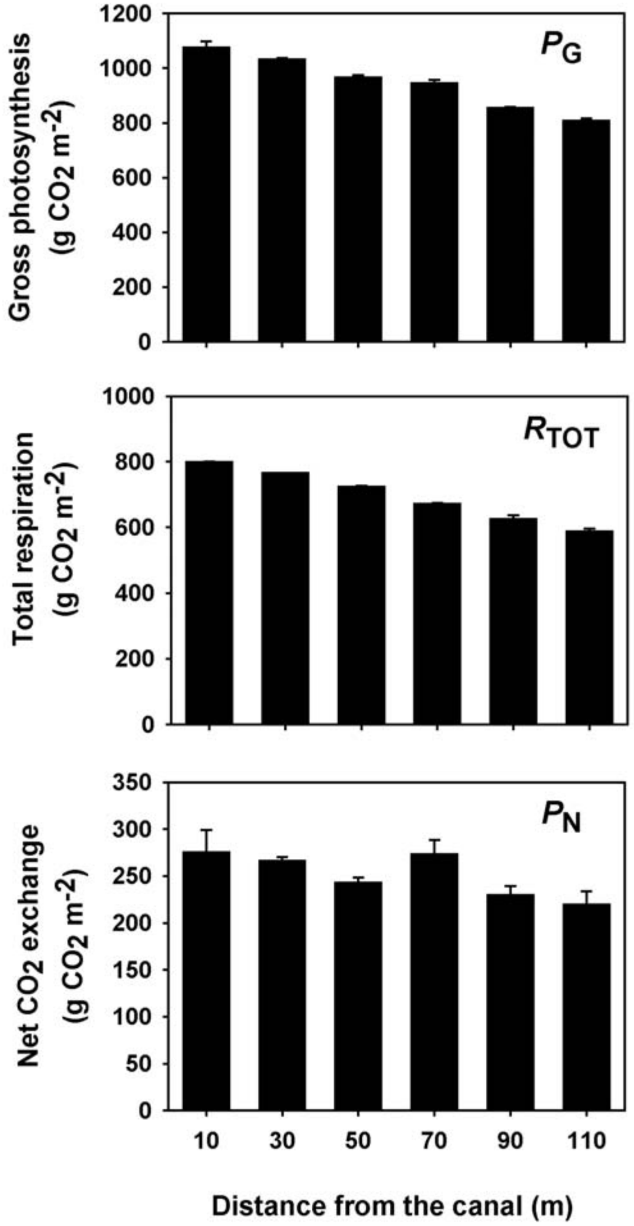


Figure 12. Reconstructed seasonal budget for the gross photosynthesis (P_G), the total respiration (R_{TOT}) and the net CO_2 exchange ($P_N = P_G - R_{TOT}$) from May 22 to September 22, 2002. Values for each distance from the drainage ditch are the mean of the fluxes of the three sample plot. Seasonal flux for each sample plot is the sum of the hourly fluxes. Error bars represent the standard error.

4.0 Discussion

4.1 Vegetation community

The effect of 55 years of water level drawdown had a long-lasting effect on peatland vegetation, which responded to the moisture gradient. Moisture gradient created a gradient in the vegetation composition, even though the ditch has not been cleaned in the later years (10 to 20 years) and it is becoming less effective in draining the site (Fig. 9). Drainage ditch did not have the effects of a natural mire margin-mire expanse gradient (Fig. 8, 10 and 11). Abundance of species typical to drier peatland habitats, such as *Betula pubescens*, *Polytrichum strictum* and *Pinus sylvestris*, increased with the intensity of drainage (Appendix 1). Indeed, *Polytrichum strictum* is more typical of drier peatland habitats (Campbell and Rochefort 2001), whereas the amount of the natural establishment of *Betula pubescens* and *Pinus sylvestris* is recognized to increase with ditching, especially up to a distance of 10 metres (Sundström and Hånell 1999). On the natural area, most of the sample plots at 10 metres from the edge occurred in the *Sphagnum angustifolium* – *Sphagnum magellanicum* community (Fig. 11). The indicators species, *Sphagnum angustifolium* and *Sphagnum magellanicum*, do not represent a moisture gradient because these species are known to have a large spectrum of hydrological preferences (Gignac 1992; Gauthier 2001; Laine *et al.* 2002). Moreover, *Sphagnum angustifolium* and *Sphagnum magellanicum* have relatively wide breadths on other gradients, as pH, water corrected conductivity, height relative to the water table and overstory cover (Gignac 1992). Therefore, *Sphagnum angustifolium* – *Sphagnum magellanicum* community did not indicate a specific peatland habitat. The fact that vegetation communities are changing along the distance perpendicular to the drainage ditch, but not in the natural area from margin to mire expanse, indicates that the mire margin-mire expanse gradient is not particularly strong for this peatland site type. Therefore, it emphasises the influence of the ditch in the drained area.

4.2 CO_2 fluxes

In the following sections, I will explain the biological meanings underlying the results of the modelling for the gross photosynthesis, the total respiration and the net CO_2 exchange.

4.2.1 Gross photosynthesis

Modelling of the gross photosynthesis gave important clues about the influences of biotic and abiotic factors along the moisture gradient. Surprisingly, the leaf area index did not have a significant effect on the gross photosynthesis (Table 2). On the biological aspect, this result is contrary to the common theory, other studies included the vegetation in the model of gross photosynthesis (Alm *et al.* 1997; Alm *et al.* 1999b; Tuittila *et al.* 1999). This result means that the best selected model had a weakness in representing the reality. However, all the other parameters had a significant effect on the gross photosynthesis. The selected model showed that the gross photosynthesis is unimodal throughout the growing season. The photosynthesis rate was lower at the beginning and the end of the season whereas in the middle it reaches a peak, as usually noted (Alm *et al.* 1997; Tuittila *et al.* 1999; Frolking *et al.* 2002). This trend follows also the air temperature and precipitations throughout the growing season (Fig. 3). The selected model also showed that an increase of irradiance increases photosynthesis, which coincides with what is already well recognized (Alm *et al.* 1997; Alm *et al.* 1999b; Tuittila *et al.* 1999; McNeil and Waddington 2003). The model showed that an increase of air and soil temperatures increases the enzymatic activity of photosynthesis. Finally, the effect of water table was negatively unimodal on the photosynthesis. Indeed, according to the selected model, photosynthesis is higher if the water table is at low or high levels. This relation might be unexpected, but in fact there are no clear trends observed when the relation between the gross photosynthesis and the water table is taken alone.

Along the moisture gradient, higher rates of photosynthesis were noticed in drier conditions, i.e. near the drainage ditch (Fig. 12). This clear result goes against the former hypothesis of the present study, which was that in going away from the drainage influences, photosynthetic potential of the vegetation would increase. Nevertheless, it can be explained by the weather conditions of the growing season. Summer 2002 was exceptionally hot and dry in Finland (Fig. 3). In that respect, the drier part of the moisture gradient had a vegetation composition with a capacity to support these kinds of conditions, such as a higher cover of *Polytrichum strictum* near the ditch (Appendix 1) and thus, showed a higher photosynthesis rate compared to the wetter part. *Polytrichum strictum* is recognized to have wide ecological and climatic ecotopes (Nicholson and Gignac 1995; Bragazza 1999). *Polytrichum strictum* can also successfully grow in environments with harsh conditions (Groeneveld 2002). Moreover, it is known that mosses of the Polytrichaceae are able to continue to photosynthesize in hot and dry conditions (Callaghan *et al.* 1978) which is quite the opposite with *Sphagnum* species that can hardly photosynthesize if a long period of desiccation happens (Gerdol *et al.* 1996; Schipperges and Rydin 1998). The hot and dry conditions of summer 2002 were suitable for long periods of desiccation and may have decreased the photosynthesis rate of *Sphagnum* species. Thus, the highest photosynthesis rate near the drainage influences can be explained in part by the ability of *Polytrichum strictum* to photosynthesize in drier conditions.

4.2.2 Total respiration

Model averaging for the total respiration showed that some biotic and abiotic factors did not have a significant effect (Table 4). This was the case for the time of the season, the soil temperature and the leaf area index. Here again, this result might represent a weakness of using this approach in modelling because these factors have already been proven to be significant parameters to infer total respiration in other studies (Alm *et al.* 1997; Alm *et al.* 1999b; Tuittila *et al.* 1999; Chimner and Cooper 2003). Nevertheless, the other abiotic factors had a significant effect on total respiration. Model averaging showed that an increase of air temperature increased total respiration, which can be explained by an increase of the bacterial activity of the soil with air temperature. Indeed, as air temperature, total respiration rate increases towards the mid-season and decreases at the end of the season (Tuittila *et al.* 1999). This follows the bacterial biomass that is higher towards the mid-season and decreases at the end of the season (Clarholm and Roswall 1980). The effect of the water table was positively unimodal on the total respiration rate, which means that the total respiration rate is higher when the water table reaches a certain level. This unimodal effect is surprising, because it is recognized to be linear (Silvola *et al.* 1996). Water table controls the deepness of the acrotelm. Indeed, when the acrotelm is thick, there is more oxygen that increases the bacterial activity and in turn the total respiration rate. This effect of the water table was also observed in other studies (Lieffers 1988; Kim and Verma 1992; Waddington *et al.* 2002). In the modelling method presented in this study, the quadratic effect of the water table on the total respiration (WT^2) was included *a priori* according to Chimner and Cooper (2003). In fact, no clear trends were observed in the relation between the water table and the total respiration taken alone, even though the estimate of WT^2 has a significant effect (Table 4). Thus, according to the literature and the results presented in this study, the quadratic effect of the water table should not be included in future models. Finally, along the moisture gradient, the rate of total respiration was higher in the drier part (Fig. 12). This agreed with the former hypothesis of the present study, which was that in going away from the drainage influences, total respiration would decrease.

4.2.3 Net CO_2 exchange

Gross photosynthesis and total respiration both decreased with increasing distance from the drainage ditch (Fig. 12) showing higher rates in dry conditions. This trend was reflected in net CO_2 exchange (Fig. 12). However, all the transect points were net CO_2 sinks over the growing season, regardless of the distance from the drainage ditch. This result is contrary to the former hypothesis of the present study, where it was expected that in going towards the wetter part of the moisture gradient, CO_2 emissions would decrease by a greater rate of photosynthesis and a decreasing total respiration. In fact, there were no CO_2 emissions but only sequestration and this sequestration was higher in the drier part of the moisture gradient. As for the gross photosynthesis, the vegetation of the dry part of the moisture gradient was more capable to support the drier and hotter conditions of the growing season 2002. As already explained earlier, the high abundance of *Polytrichum strictum* was responsible for this ability. In that respect, CO_2 sequestration, one of the fundamental functions of a peatland, was maintained. The drainage of this peatland began 55 years ago; along this long-term period a natural regeneration must have acted as a process that recovered partly the natural functions of the peatland ecosystem. The vegetation communities of the peatland changed but the ecological functions remained.

The values of the CO_2 sequestration were surprisingly high, the scale was between 200 and 300 g CO_2-C m^{-2} for the growing season (Fig. 12). The long-term apparent rate of carbon accumulation for Finnish peatlands is between 21 and 26 g C m^{-2} yr^{-1} (Tolonen and Turunen 1996; Clymo *et al.* 1998) and the CO_2 sequestration to maintain this accumulation rate must be at least between 64-76 g CO_2-C m^{-2} during the active season (Alm *et al.* 1999b), which is far lower than the values obtained in this study. For modelling CO_2 fluxes, the data were taken only on day time during the growing season. Night measurements were thus not included for inferring fluxes. For the gross photosynthesis and total respiration, modelling had also some weaknesses already pointed out earlier. For the model of the gross photosynthesis it was not possible to constrain the model in a way that photosynthesis would have been nil when the irradiance was also nil. It explains why the values of the net CO_2 exchange were relatively high. Moreover, the models for the gross photosynthesis and the total respiration did not include a "*Sphagnum* or bryophyte index". In *a priori*, only the leaf area index was considered important to include because this index is used in the models to describe the seasonal variation in the amount of vascular plant, whereas the *Sphagnum* or the bryophyte cover is the same over the season. Thus, a *Sphagnum* or bryophytes index was not expected to bring additional information to the models (Tuittila, pers. comm.). Future models should include a *Sphagnum* or bryophyte index in order to realize an annual calculation of CO_2 balance for this peatland and to represent more accurately the reality. Nevertheless, the absence of such an index does not prevent to conclude about the effect of a long-term water level drawdown on a *Sphagnum* dominated peatland. The water level drawdown of a peatland affects other elements than *Sphagnum*, for instance the change of the vegetation communities, these elements were considered in the present study. Moreover, future models should be built with CO_2 fluxes taken during day and night times and also during the four seasons of the year. Alm *et al.* (1999a) pointed out that winter CO_2-C release cannot be ignored in annual calculations of the carbon balance for peatlands. In conclusion, the modelling method should be reviewed although the percentages explained by models were relatively high (Tables 2 and 4). A process based approach was used to infer the CO_2 fluxes, according to the weaknesses showed by this approach in this study, a physiologically based approach would be more appropriate. Nevertheless, results brought important clues about the CO_2 balance of the growing season for *Sphagnum* dominated peatlands where there has been a long-term water level drawdown.

4.3 Understanding the global climatic warming

In the context of this study, the water level drawdown simulated the effect of a potential scenario of global warming. Similar to the water level drawdown in this study, climatic warming would lower the water table by increasing evapotranspiration in the peatland ecosystem. Results showed that by lowering the water table, global warming will modify the vegetation of *Sphagnum* dominated peatlands. Fifty five years of drainage resulted in a change of plant communities more typical of drier conditions. In the exceptionally dry growing season of 2002, *Pleurozium schreberi – Cladina* spp., and in a lower scale *Betula pubescens – Polytrichum strictum* communities, were advantaged over the *Trichophorum cespitosum* community adapted to wetter conditions. This indicates that the effect of climate change on *Sphagnum* dominated peatlands might be reduced by a shift of the peatland communities towards communities more typical of drier conditions. In the context of global warming, vegetation succession, peat substrate and hydrology might adapt to maintain the ecological functions of a pristine peatland, especially the role of CO_2 sequestration. This agrees with the studies of Minkkinen and Laine (1998) and Hargreaves *et al.* (2003) where it was suggested that peatlands stay a carbon sink for some decades after being drained. The study of Minkkinen and Laine (1998), realized on the carbon store of peatlands drained for forestry, suggested that tree stand development plays an important role in the post-drainage carbon balance of peat soils. The present study added a new understanding by studying a type of drainage different from the forestry drainage. Other plant types may play an important role in the carbon store of drained peatlands. The present study suggests that plant communities with a high abundance of *Polytrichum strictum* may also be important in the carbon store of drained peatlands because of its ability to photosynthesize in hot and dry conditions, which are more frequent in drained peatlands (Prévost *et al.* 1997).

Conclusion

The present study brought additional knowledge about the effects of a long-term water level drawdown on *Sphagnum* dominated peatlands which created a moisture gradient. This moisture gradient allowed to quantify the impacts on the vegetation community and the CO_2 fluxes. The moisture gradient finally add new knowledge in simulating a potential scenario of global climatic warming on *Sphagnum* dominated peatlands.

The long-term water level drawdown caused effective changes of the plant communities. Even after 55 years of drainage, vegetation communities still register the effects from the water level drawdown. These effects are different from the natural mire margin-mire expanse gradient of a pristine peatland. The long-term water level drawdown has had also impacts on CO_2 fluxes showing that the plant community became more typical of drier peatland habitats to maintain CO_2 sequestration, one of the important ecological functions of a peatland ecosystem. This study was realized over one growing season, which is a short term of monitoring to assess the effect of global climatic warming on *Sphagnum* dominated peatlands. Nevertheless, it showed that carbon sequestration can be possible for *Sphagnum* dominated peatlands during a hot and dry growing season, which are likely to happen in the perspective of the predicted global warming. Thus, for *Sphagnum* dominated peatlands, this study suggests that in the context of global warming, growing seasons where carbon is sequestrated can be possible. The effect of global warming on *Sphagnum* dominated peatlands might be reduced by the change of their vegetation communities that will continue to sequestrate carbon.

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Appendix 1

Species data for each sample plots. Data are the percent cover of the species in a sample plot of 56 cm X 56 cm. Transect 1, 2 and 3 are on the drained area whereas 4, 5 and 6 are on the natural area. The number for each sample plot represents its replicate number (1, 2 and 3). Community numbers are coded (*Pleurozium schreberi – Cladina* spp. community: 1; *Betula pubescens – Polytrichum strictum* community: 2; *Trichophorum cespitosum* community: 3; *Sphagnum angustifolium* + *Sphagnum magellanicum* community: 4; *Empetrum nigrum – Sphagnum angustifolium* community: 5; *Sphagnum papillosum* community: 6).

Transect	Distance from drainage ditch or natural edge (m)	Sample plots	Community number	*Andromeda polifolia*	*Betula nana*	*Betula pubescens*	*Carex echinata*	*Carex lasiocarpa*	*Carex pauciflora*	*Dactylorhiza maculata*	*Drosera rotundifolia*	*Empetrum nigrum*	*Eriophorum vaginatum*	*Pinus sylvestris*	*Rhynchospora alba*	*Rubus chamaemorus*	*Trichophorum cespitosum*	*Vaccinium microcarpum*	*Vaccinium oxycoccos*	*Vaccinium uliginosum*	*Pleurozium schreberi*	*Pohlia nutans*	*Polytrichum strictum*	*Warnstorfia fluitans*	*Sphagnum angustifolium*	*Sphagnum balticum*	*Sphagnum capillifolium*	*Sphagnum fuscum*	*Sphagnum magellanicum*	*Sphagnum papillosum*	*Sphagnum rubellum*	*Sphagnum tenellum*	*Cladina arbuscula*	*Cladina rangiferina*	*Cladina sp.*	*Mylia anomala*	*Other liverworts*	*Gymnocolea inflata* and *Cladopodiella fluitans*
Drained area																																						
1	10	1	1	5	0	0,5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	75	0	0	0	0	0	0	0	0	0	6	2	7,5	0	0	0,5
1	10	2	1	0	0	2	0	0	0	0	0	0	0,5	1	0	0	0	0	0	0	0	0	60	0	0	0	0	4	0	0	0	0	3	2	8,5	0	0	0
1	10	3	2	2	0	0,5	0	0	0	0	0	0,5	0,5	0,5	0	0	0,5	0	0,5	1	0	0	55	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
1	30	1	2	1	0	0	0	0	0	0	0	0,5	0,5	0,5	1	0	0,5	0	4	10	0,5	0	3	0	0	25	0	8	20	20	12	0	0	0	0	0	0	10
1	30	2	2	0,5	0	0,5	0	0	0,5	0	0	0,5	1	0,5	3	0	1	0,5	1	10	0	0	1	0	0	8	0	1	0	10	15	0	0,5	0	0	0	0	0,5
1	30	3	2	1	0	0,5	0	0	0	0	0,5	0,5	0,5	0,5	0,5	0	0,5	0	2	7	0,5	0	0,5	0	0	60	0	10	3	7	0	0	0	3	0	10	0	10
1	50	1	2	2	0,5	0,5	0	0	0	0	0	0	3	0	0,5	0	0,5	0	1	3	0	0	1	0	0	10	0	0	20	1	25	0	3	0	0,5	2	3	7
1	50	2	2	2	0	0	0	0	0,5	0	0,5	0	0,5	0	1	0	1	0,5	0,5	9	0	0	0,5	0	0	30	0	0	0	3	17	0	0,5	0	0,5	0,5	4	0
1	50	3	2	0,5	0	0,5	0	0	0,5	0	0	0	1	0,5	3	0	0,5	0,5	2	12	0	0	12	0	0	6	0	0	25	0	4	0	0	0	0	0,5	0	20
1	70	1	2	0,5	0	0,5	0	0	0,5	0	0,5	0	0	0,5	2	0	0,5	1	1	3	0	0	0,5	0	0	20	0	10	5	15	0	0	0	0,5	0	1	10	20
1	70	2	2	0,5	0	0,5	0	0	0,5	0	0,5	1	0	0,5	15	0	0,5	0,5	0,5	2	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	10	0,5
1	70	3	2	0,5	0	0,5	0	0	0	0	1	2	2	0	7	0	0,5	0,5	1	6	0	0	0,5	0	0	15	0	0	0	35	0	0	0	0	0	0,5	0	40
1	90	1	2	0,5	0	0,5	0	0	0,5	0	0,5	0,5	0,5	0,5	0	0	2	0	1	5	0	0	0	0	0	70	0	0	20	5	1	0	0	0	0	0	5	0,5
1	90	2	2	2	0,5	0	0	0	0,5	0	3	0	0,5	0	0	0	2	0	1	0,5	0	0	0	0	0	15	0	0	40	40	0	0	0	0	0	0	15	3
1	90	3	2	0,5	0	0,5	0	0	0,5	0	0	0	0,5	0,5	0	0	2	0	1	6	0	0	0	0	0	10	0	0	0	50	0,5	0	0	0	0	0	1	0,5

Transect	Distance from drainage ditch or natural edge (m)	Sample plots	Community number	*Andromeda polifolia*	*Betula nana*	*Betula pubescens*	*Carex echinata*	*Carex lasiocarpa*	*Carex pauciflora*	*Dactylorhiza maculata*	*Drosera rotundifolia*	*Empetrum nigrum*	*Eriophorum vaginatum*	*Pinus sylvestris*	*Rhynchospora alba*	*Rubus chamaemorus*	*Trichophorum cespitosum*	*Vaccinium microcarpum*	*Vaccinium oxycoccos*	*Vaccinium uliginosum*	*Pleurozium schreberi*	*Pohlia nutans*	*Polytrichum strictum*	*Warnstorfia fluitans*	*Sphagnum angustifolium*	*Sphagnum balticum*	*Sphagnum capillifolium*	*Sphagnum fuscum*	*Sphagnum magellanicum*	*Sphagnum papillosum*	*Sphagnum rubellum*	*Sphagnum tenellum*	*Cladina arbuscula*	*Cladina rangiferina*	*Cladina sp.*	*Mylia anomala*	Other liverworts	*Gymnocolea inflata* and *Cladopodiella fluitans*
1	110	1	2	0,5	0	0,5	0	0	0	0	3	0	0,5	0,5	0	0	0,5	1	1	10	0	0	0,5	0	0	60	0	25	5	0	10	0	0	0	0	10	10	0
1	110	2	2	0,5	0	0	0	0	0	0	0,5	0	1	0,5	0	0	1	0	2	2	0	0	0	0	0	45	0	0	0	0	0	0	0	0	0	0,5	12	40
1	110	3	2	0,5	0	0,5	0	0	0,5	0	2	3	1	0,5	0	0	1	0,5	1	0	0	0	0,5	0	0	50	0	1	1	18	0	0	0	0	0,5	0	4	11
2	10	1	2	1	0	0	0	0	0	0	0,5	4	0	5	2	0	4	0	1	10	0	0	0,5	0,5	0	15	0	15	0	25	30	0	5	0	0	0	0	0
2	10	2	2	0,5	0	0	0	0	0	0	0	1	0	3	0,5	0	12	0	1	10	0	0	2	30	0	1	0	0	0	4	5	0	0	0	0	0	0	0
2	10	3	1	0,5	0	0	0	0	0	0	0	4	0	0	0,5	0	2	0	1	10	30	0	0	5	0	0	0	0	0	25	0	0	20	0	0	0	0	0
2	30	1	3	0,5	0	0	0	0	0	0	0,5	1	0	2	0	0	7	0	1	5	0	0	0	0	0	5	0	0	60	10	10	0	0,5	0	0	0,5	0	1
2	30	2	2	1	0	0,5	0	0	0	0	0,5	0	0,5	0,5	7	0	3	0	1	3	0	0	0	0	0	10	0	0	0	1	0	0	0	0	0	0	0	50
2	30	3	2	0	0	0	0	0	0	0	6	3	0	0,5	3	0	1	1	0,5	7	0	0	0	0	0	20	0	0	0	0	5	0	0	0	0	2	0	40
2	50	1	3	1	0	0	0	0	0	0	2	1	0	0	1	0	6	0	1	0	0	0	0	0	0	25	0	0	65	0	3	0	0	0	0	0	0	5
2	50	2	3	1	0	0	0	0	0	0	1	0	0	0	10	0	5	0	1	0	0	0	0	0	0	5	0	0	40	0	0	0	0	0	0	0	0	15
2	50	3	2	1	0	0,5	0	0	0	0	1	0,5	0	0	7	0	4	0	1	5	0	0	0	0	0	35	25	0	5	0	25	0	0	0	0	0	0	5
2	70	1	3	0,5	0	0	0	0	0	0	1	6	0	0	0	0	30	0	0,5	0	0	0	0	0	0	3	0	80	1	7	3	0	0	0	0	0	0	1
2	70	2	2	1	0	0	0	0	0	0	1	0	0	0	0	0	5	0	3	0	0	0	2	0	0	15	50	5	15	5	0	0	0	0	0	0,5	0	2
2	70	3	3	0,5	0	0	0	0	0	0	1	3	1	0	0	0	7	0	1	0	0	0	0	0	0	40	0	15	0	5	10	0	0	0	0	0	0	20
2	90	1	3	0,5	0	0	0	0	0	0	1	2	0	0	0	0	10	0	1	0,5	0	0	0	0	0	40	0	1	45	1	2	0	0	0	0	0	0	10
2	90	2	3	2	0	0	0	0	0	0	0	1	0	0	0	1	5	0	1	7	0	0	0	0	0	55	0	0	15	0	25	0	0	0	0	0	0	0,5
2	90	3	3	1	0	0	0	0	0	0	0,5	0	0	0	0	0,5	5	0	1	0	0	0	0	0	0	0	0	0	75	20	5	0	0	0	0	0	0	1
2	110	1	3	1	0	0	0	0	0	0	0	1	0,5	0	0	0	20	0	1	0	0	0	0	0	0	35	0	0	25	0	35	0	0	0	0	0	0	1
2	110	2	3	1	0	0	0	0	0	0	0	2	0,5	0	0	1	20	0	0,5	0	0	0	0	0	0	15	0	0	45	0	40	0	0	0	0	0	0	1
2	110	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	18	0	1	0	0	0	0	0	0	30	0	0	60	0	10	0	0	0	0	0	0	1
3	10	1	1	0,5	0	0	0	0	0	0	0,5	7	1	0	0,5	0	0	0	0	20	15	1	0	0	0	0	20	0	0	0	0	20	0	20	0,5	0	0	0
3	10	2	1	0,5	1	0	0	0	0	0	0,5	5	0	0	0	0	5	0	0	10	15	0	0	0	0	0	5	0	65	0	0	0	7	5	0	0	0	0,5
3	10	3	3	1	1	0	0	0	0	0	1	1	0	0	3	0	2	0	0	5	0	0	0	1	0	0	0	0	70	0	5	20	5	0	0	0	0	0
3	30	1	2	0	0	1	0	0	0	0	0	0,5	0,5	0	25	0	0	0	0,5	1	0	0	0	0,5	0	0	0	0	0	2	0	0	2	0	0	0	0	20
3	30	2	3	0	0	0	0	0	0	0	0,5	0	0	0,5	15	0	10	0	1	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	10
3	30	3	2	0,5	0	0,5	0	0	0	0	0	1	7	0	15	0	3	0	0,5	7	0	0	0	0	0	5	0	0	25	0	0	0	3	5	0	0	0	0
3	50	1	3	1	0	0	0	0	0	0	0,5	0,5	0	0	0	0	10	0	1	15	0	0	0	0	0	40	0	0	5	0	10	0	0	0	0	0	0	5
3	50	2	2	1	0	0,5	0	0	0	0	0,5	4	1	0,5	0	0	10	0	1	5	0	0	10	0	0	0	25	40	5	0	0	0	0	0	0	0,5	0	0,5
3	50	3	2	1	0	0,5	0	0	0	0	2	0	1	0	1	0	4	0	1	2	0	0	0	0	0	0	0	0	2	0	1	75	7	0	0	0	0	3
3	70	1	3	1	0	0	0	0	0	0	0,5	0	0	0,5	0	0	0	0	1	0,5	0	0	0	0	0	15	0	0	45	0	40	0	0	0	0	0	0	1
3	70	2	3	1	0	0	0	0	0	0	0	0	2	0	0	0	25	0	1	0	0	0	0	0	0	60	0	0	20	0	20	0	0	0	0	0	0	2
3	70	3	3	3	0	0	0	0	0	0	0	1	3	0	0	0	12	0	2	0	0	0	0	0	0	0	0	20	45	0	25	0	0	0	0	0	0	1

Transect	Distance from drainage ditch or natural edge (m)	Sample plots	Community number	*Andromeda polifolia*	*Betula nana*	*Betula pubescens*	*Carex echinata*	*Carex lasiocarpa*	*Carex pauciflora*	*Dactylorhiza maculata*	*Drosera rotundifolia*	*Empetrum nigrum*	*Eriophorum vaginatum*	*Pinus sylvestris*	*Rhynchospora alba*	*Rubus chamaemorus*	*Trichophorum cespitosum*	*Vaccinium microcarpum*	*Vaccinium oxycoccos*	*Vaccinium uliginosum*	*Pleurozium schreberi*	*Pohlia nutans*	*Polytrichum strictum*	*Warnstorfia fluitans*	*Sphagnum angustifolium*	*Sphagnum balticum*	*Sphagnum capillifolium*	*Sphagnum fuscum*	*Sphagnum magellanicum*	*Sphagnum papillosum*	*Sphagnum rubellum*	*Sphagnum tenellum*	*Cladina arbuscula*	*Cladina rangiferina*	*Cladina sp.*	*Mylia anomala*	*Other liverworts*	*Gymnocolea inflata* and *Cladopodiella fluitans*
3	90	1	3	1	0	0	0	0	0	0	0	0	0	0,5	0	0	5	0	1	0	0	0	0	0	0	20	0	0	65	0	15	0	0	0	0	0	0	5
3	90	2	3	0,5	0	0	0	0	0	0	0,5	0	0	0	0	0	0	0	0,5	7	0	0	0	0	0	5	0	0	20	0	1	0	0	0	0	0	0	20
3	90	3	3	1	0	0	0	0	0	0	0,5	0	0	0	0	0	5	0	1	0	0	0	0	0	0	33	0	0	33	0	33	0	0	0	0	0	0	1
3	110	1	3	1	0	0	0	0	0	0	0	0	1	0	0	0	25	0	0	0	0	0	0	1	0	30	0	0	7	0	45	0	0	0	0	0	0	7
3	110	2	3	2	0	0,5	0	0	0	0	0	0	0,5	0	0	0	10	0	2	0	0	0	0	0	0	60	0	0	1	0	40	0	0	0	0	0	0	0,5
3	110	3	3	2	0	0	0	0	0	0	0	1	0,5	0	0	0	0	0	2	0	0	0	1	0	0	20	0	0	5	0	60	0	0	0	0	0	0	5
Natural area																																						
4	10	1	4	0	5	0	0	0	0	0	0	0,5	7	0	0	0	0	0	1	0	0	0	0	0	85	0	0	0	15	0	0	0	0	0	0	0	0	0
4	10	2	4	1	5	0	0	0	3	1	0	0	0	0	0	0	0	0	0,5	0	0	0	0	0	98	0	0	0	1	0	0	0	0	0	0	0	0	0
4	10	3	4	2	3	0	0	0	0	0	0	0,5	6	0	0	0	0	0	2	1	0	0	0	0	90	0	0	0	10	0	0	0	0	0	0	0	0	0
4	30	1	5	0	4	0	0	0	0	0	0	10	6	10	0	15	0	0	3	15	3	0	0	0	80	0	0	5	0	0	0	0	0	0	0	0	0	0
4	30	2	5	0	5	0	0	0	0	0	0	20	10	10	0	15	0	0	2	15	10	0	0	0	40	0	0	20	0	0	0	0	0	1	0	0	0	0
4	30	3	5	0	0	0	0	0	0	0	0	3	5	0	0	15	0	0	1	8	25	0	0	0	60	0	0	5	0	0	0	0	0	0	0	0	0	0
4	50	1	4	0	5	0	0	0	5	0	0,5	0,5	15	0	0	0	0	0	1	0	0	0	0	0	90	0	0	1	1	0	5	0	0	0	0	0	0	0
4	50	2	4	4	5	0	0	0	25	0	0	5	35	0	0	0	5	0	1	0	0	0	0	0	60	0	0	10	3	0	2	0	0	0	0	0	0	0
4	50	3	5	3	4	0	0	1	0	0	0	10	40	0	0	0	0	0	5	0	0	0	0	0	45	0	5	45	3	0	0	0	0	0	0	0	0	0
4	70	1	6	2	3	0	0	0	0	0	0,5	0	10	0	0	0	5	0	2	0	0	0	0	0	40	0	0	0	10	0	45	0	0	0	0	0	0	0
4	70	2	6	1	0	0	0	0,5	0	0,5	0,5	0	3	0	0	0	5	0	1	1	0	0	0	0	15	0	0	0	50	20	10	0	0	0	0	0	0	0
4	70	3	6	1	1	0	0	0,5	0	0	0	0	6	0	0	0	12	0	1	0	0	0	0	0	15	0	35	0	5	0	40	0	0	0	0	0	0	0
4	90	1	6	2	1	0	0	0	0	0	0,5	0	5	0	0	0	8	0	1	0	0	0	0	0	15	0	0	10	0	60	10	0	0	0	0	0	0	0
4	90	2	6	1	3	0	0	0	0	0	1	0	1	0	0	0	2	0	0	0	0	0	0	0	10	0	0	0	0	85	5	0	0	0	0	0	0	0
4	90	3	6	1	1	0	0	0	1	0	1	0	1	0	0	0	12	0	0,5	0	0	0	0	0,5	5	0	0	0	0	70	20	0	0	0	0	0	0	0
4	110	1	6	4	4	0	0	0	0	0	0,5	0,5	4	1	0	0	7	0	1	0	0	0	0	0	20	0	0	0	35	0	40	0	0	0	0	0	0	0
4	110	2	6	5	1	0	0	0	0	0	0	10	7	0	0	0	40	0	0	0	0	0	0	0	20	0	0	0	25	0	25	0	0	0	0	0	0	0
4	110	3	6	2	1	0	0	0	0	0	0	0	0	0	0	0	10	0	3	0	0	0	0	0	90	0	0	0	5	0	1	0	0	0	0	0	0	0
5	10	1	4	10	7	0	2	0	10	0	0	1	10	0	0	0	0	0	0	5	0	0	0	0	85	0	0	5	5	0	0	0	0	0	0	0	0	0
5	10	2	4	5	0,5	0	0	0	0	0	0	15	0	0	0	1	0	0	0,5	15	0	0	0	0	90	0	0	0	5	0	2	0	0	0	0	0	0	0
5	10	3	5	10	20	0	0,5	0	0	0	0	20	1	0	0	0	0	0	1	5	5	0	0	0	40	0	0	15	10	0	0	0	0	0	0	0	0	0
5	30	1	6	5	1	0	0	0	1	1	0,5	2	2	0	0	0	2	0	1	0	0	0	0	0	15	0	0	70	5	0	5	0	0	0	0	0	0	0
5	30	2	4	1	1	0	0	0	1	1	1	1	1	0	0	0	5	0	1	0	0	0	0	0	70	0	0	20	10	0	3	0	0	0	0	0	0	0
5	30	3	6	1	0,5	0	0	0	0	0	2	0	0,5	1	0	0	4	0	1	0	0	0	0	0	15	0	0	0	0	70	10	0	0	0	0	0	0	0
5	50	1	5	1	3	0	0	0	0	0	0	5	50	10	0	0	0	0	0	0	1	0	0	0	30	0	0	0	5	0	0	0	0	15	0	0	0	0

Transect	Distance from drainage ditch or natural edge (m)	Sample plots	Community number	*Andromeda polifolia*	*Betula nana*	*Betula pubescens*	*Carex echinata*	*Carex lasiocarpa*	*Carex pauciflora*	*Dactylorhiza maculata*	*Drosera rotundifolia*	*Empetrum nigrum*	*Eriophorum vaginatum*	*Pinus sylvestris*	*Rhynchospora alba*	*Rubus chamaemorus*	*Trichophorum cespitosum*	*Vaccinium microcarpum*	*Vaccinium oxycoccos*	*Vaccinium uliginosum*	*Pleurozium schreberi*	*Pohlia nutans*	*Polytrichum strictum*	*Warnstorfia fluitans*	*Sphagnum angustifolium*	*Sphagnum balticum*	*Sphagnum capillifolium*	*Sphagnum fuscum*	*Sphagnum magellanicum*	*Sphagnum papillosum*	*Sphagnum rubellum*	*Sphagnum tenellum*	*Cladina arbuscula*	*Cladina rangiferina*	*Cladina sp.*	*Mylia anomala*	*Other liverworts*	*Gymnocolea inflata* and *Cladopodiella fluitans*
5	50	2	4	5	5	0	0	0	1	0	0	0	30	10	0	0	0	0	0	2	1	0	0	0	90	0	0	0	1	0	0	0	0	0	0	0	0	0
5	50	3	5	4	1	0	0	0	0,5	0	0	10	5	0	0	0	0	0	2	5	0	0	0	0	30	0	0	60	0	0	0	0	0	0	0	0	0	0
5	70	1	4	4	1	0	0	0	0	0	1	0,5	7	0	0	0	0	0	0	1	0	0	0	0	90	2	0	0	5	0	0	0	0	0	0	0	0	0
5	70	2	4	4	1	0	0	0	1	0	0,5	2	4	0	0	0	0	0	1	4	0	0	0	0	95	0	0	0	5	0	0	0	0	0	0	0	0	0
5	70	3	6	2	1	0	0	0	3	0	0	0	1	0	0	0,5	0	0	0,5	0	0	0	0	0	5	0	0	0	5	90	0	0	0	0	0	0	0	0
5	90	1	3	0	1	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	0	0	0	0	0	85	0	0	5	0	0	0	0	0	0	0	0	0
5	90	2	6	1	2	0	0	0	4	0	0,5	1	5	0	0	0	4	0	2	1	0	0	0	0	15	0	0	0	3	80	0	0	0	0	0	0	0	0
5	90	3	4	0	2	0	0	0	1	0	0	0	7	0	0	0	0	0	1	0	0	0	0	0	80	0	0	0	15	0	5	0	0	0	0	0	0	0
5	110	1	5	3	4	0	0	0	0	0	0	3	0	5	0	0	0	0	2	0	0	0	0	0	20	0	20	60	0	0	0	0	0	0	0	0	0	0
5	110	2	5	5	7	0	0	0	0	0	0	25	15	0	0	0	0	0	3	0	0	0	0	0	0	0	60	30	0	0	0	0	0	0	0	0	0	0
5	110	3	4	2	1	0	0	0	0	0	0	0	8	0	0	0	0	0	1	0	0	0	0	0	80	0	0	0	20	0	0	0	0	0	0	0	0	0
6	10	1	6	0	2	0	4	1	0	0	0	10	5	0	0	4	0	0	1	0	0	0	0	0	10	0	0	0	25	60	0	0	0	0	0	0	0	0
6	10	2	4	3	3	0	3	0	2	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	40	0	0	5	45	0	5	0	0	0	0	0	0	0
6	10	3	4	2	3	0	0	0	0	0	0	3	40	0	0	5	0	0	1	0	0	0,5	0	0	40	0	0	35	20	0	0	0	0	0	0	0	0	0
6	30	1	4	1	1	0	0	0	0	0	1	1	1	1	0	0	5	0	0	0	0	0	0	0	25	0	0	65	7	0	0	0	0	0	0	0	0	0
6	30	2	6	3	0	0	0	0,5	2	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	8	0	0	0	7	85	0	0	0	0	0	0	0	0
6	30	3	4	2	1	0	0	0	0	0	0	5	1	0	0	0	7	0	2	0	0	0,5	0	0	98	0	0	0	1	0	0	0	0	0	0	0	0	0
6	50	1	4	1	1	0	0	0	1	0	0	0	6	0	0	0	0	0	0	2	0	0	0	0	20	1	0	0	80	0	1	0	0	0	0	0	0	0
6	50	2	4	2	2	0	0	0	2	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	90	0	0	0	10	0	0	0	0	0	0	0	0	0
6	50	3	4	0,5	1	0	0	0	1	0	0	0	6	0	0	0	0	0	1	0	0	0	0	0	90	0	0	0	10	0	0	0	0	0	0	0	0	0
6	70	1	4	6	0,5	0	0	0	1	0	0	0	5	0,5	0	0	0	0	1	0	0	0	0	0	95	0	0	0	5	0	0	0	0	0	0	0	0	0
6	70	2	6	2	1	0	0	0	4	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	50	0	0	0	5	40	0	0	0	0	0	0	0	0
6	70	3	4	3	0,5	0	0	0	2	0	1	1	2	0	0	0	0	0	1	0	0	0	0	0	45	0	0	30	20	0	0	0	0	0	0	0	0	0
6	90	1	4	0	5	0	0	0	0	0	1	0	45	0	0	0	0	0	1	0	0	0	0	0	80	0	0	0	15	0	0	0	0	0	0	0	0	0
6	90	2	4	0	6	0	0	0	0	0	0	0	0	0	7	0	0	0	1	0	0	0	0	0	93	0	0	0	7	0	0	0	0	0	0	0	0	0
6	90	3	4	7	0	0	0	0	0	0	0	1	20	0	0	7	0	0	1	0	0	0	0	0	75	0	0	20	5	0	0	0	0	0	0	0	0	0
6	110	1	4	1	3	0	0	0	0	0	0	2	30	0	0	0	0	0	3	2	0	0	0	0	50	0	25	5	15	0	0	0	0	0	0	0	0	0
6	110	2	4	2	1	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	0	0	0	0	30	0	0	0	70	0	0	0	0	0	0	0	0	0
6	110	3	5	0	4	0	0	0	0	0	0	20	25	15	0	0	0	0	4	10	10	0	0	0	80	0	0	0	0	0	0	0	0	0	0	0	0	0