

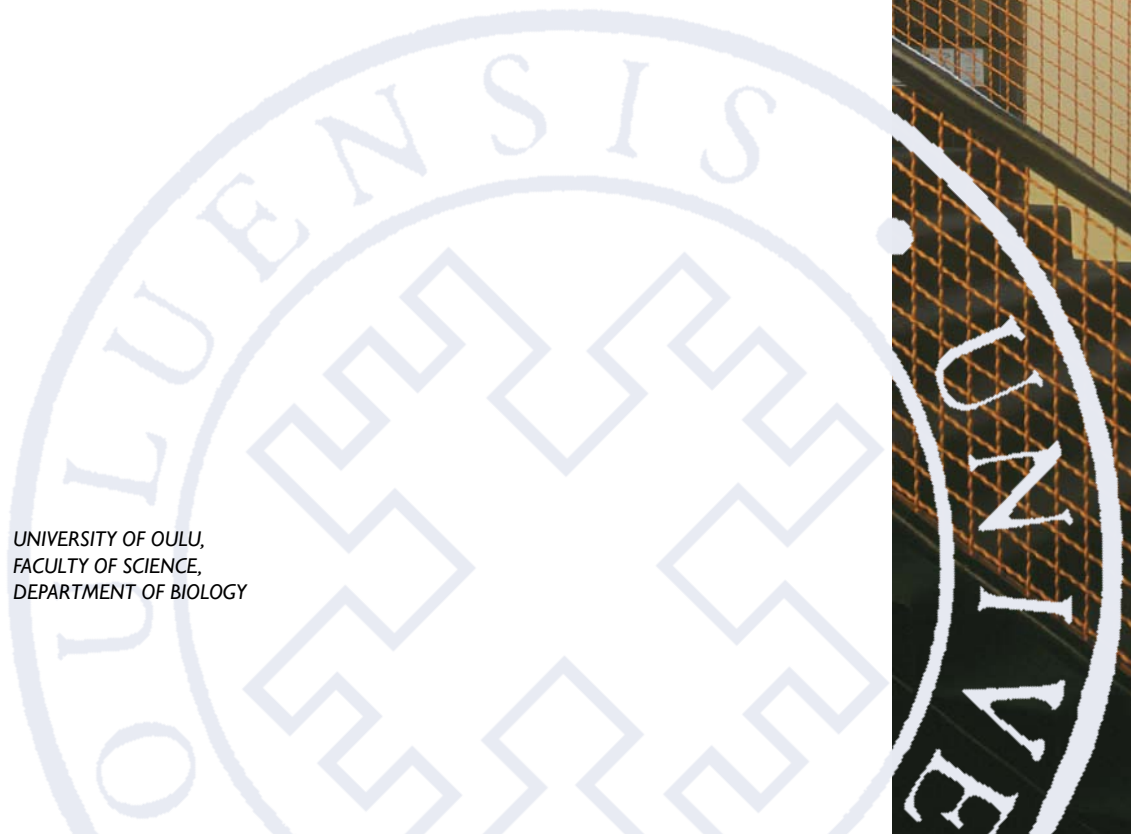
Mirva Leppälä

SUCCESSIONAL CHANGES IN
VEGETATION AND CARBON
DYNAMICS DURING BOREAL
MIRE DEVELOPMENT

UNIVERSITY OF OULU,
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DEPARTMENT OF BIOLOGY

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MIRVA LEPPÄLÄ

**SUCCESSIONAL CHANGES IN
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Abstract

Succession is a compositional change of species and other ecosystem characteristics over time. Mire development, i.e., long-term mire succession is basically driven by an increase in peat layer height, promoting changes in hydrology, vegetation and nutrient status of a particular mire. Due to this, ecosystem processes, such as production and loss of carbon due to decomposition (i.e. carbon gas functions), change with increasing successional mire stage. An adequate method for studying the changes in ecosystem C functions is to measure CO₂ and CH₄ fluxes between the ecosystem and atmosphere.

Succession and carbon dynamics of boreal pristine mires have been much studied. However the link between these phenomena is largely unknown. Further, if and how the C gas functions of mires change during mire succession it is rather poorly understood. The main objective of this thesis was to study how ecosystem functions, measured as CO₂ and CH₄ exchange, change during mire development. The study also aims to explore the drivers of succession in mire development, i.e., mire succession. Successional mire C dynamics were studied along an eight-kilometer-long successional sequence of primary paludified mires located in the land uplift coast of the Bothnian Bay. Due to the short distance between sites, they all have been under the same climatic control for most of their development.

The gradual replacement of plant species with different photosynthetic potential, phenology and assimilating green area resulted in lower-level and temporal variation of CO₂ exchange patterns at the later successional stages. Similar to this, CH₄ also had the lowest interannual variation in the later stages. In general, CH₄ emissions increased with mire age even though this trend did not emerge during the rainy season. Further, this study showed that the wintertime C function pattern was related to the C pattern during the previous summer confirming the important effect of growing season patterns on wintertime C dynamics.

In addition to the fundamental effect of vegetation as a driver of succession which was also confirmed in this study, the role of hydrological conditions appeared to be equally important. More constant hydrological conditions at later successional stages resulted in lower temporal variation in CH₄ and CO₂ fluxes. The present results suggest that the stability of ecosystem C gas functions increases during mire development due to increasing autogenic control.

Keywords: carbon dioxide, carbon dynamics, chronosequence, functional plant group, greenhouse gas, land uplift, methane, mire development, primary paludification, primary succession, succession

Leppälä, Mirva, Kasvillisuuden ja hiilidynamiikan sukkessionaaliset muutokset boreaalisen suon kehityksen aikana.

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Tiivistelmä

Sukcessio on ekosysteemin lajistossa ja sen muissa ominaisuuksissa ajan kuluessa tapahtuva muutos. Suon kehitystä eli pitkäaikaista suosukcessiota vie eteenpäin turpeen paksuuskasvu, joka saa aikaan muutoksia suoekosysteemin hydrologiassa, kasvillisuudessa ja ravinnetilassa. Tästä johtuen myös suoekosysteemin erilaiset prosessit, kuten tuotanto sekä hajoamisen kautta tapahtuva hiilen vapautuminen eli hiilikaasutoiminta muuttuu suon ikääntyessä. Ekosysteemin hiilikaasutoiminnassa tapahtuvia muutoksia voidaan tutkia muun muassa mittaamalla ekosysteemin ja ilmakehän välisiä hiilidioksidin- ja metaanivirtoja.

Boreaalisten luonnontilaisten soiden sukkessiota ja hiilidynamiikkaa on tutkittu runsaasti, mutta niiden välistä yhteyttä ei sen sijaan juuri tunneta. Tämän vuoksi ei tiedetä kuinka soiden hiilikaasutoiminta mahdollisesti muuttuu suon kehityksen aikana eli suosukcession edetessä. Tämän tutkimuksen päätavoitteena oli tutkia kuinka hiilidioksidin ja metaanin vaihdolla mitattu ekosysteemit toiminta muuttuu suon kehityksen aikana. Tutkimus pyrki myös selvittämään suosukcessiota kontrolloivat tekijät. Eri-ikäisten soiden hiilikaasudynamiikkaa tutkittiin mittaamalla hiilikaasuja Perämeren maankohoamisrannikolla kahdeksan kilometrin pituisella sukkessiogradientilla, joka koostuu primaarisoitumisen kautta syntyneistä soista. Soiden lyhyestä keskinäisestä etäisyydestä johtuen ne ovat olleet saman ilmastollisen kontrollin alaisena suurimman osan kehityksestään.

Vaiheittainen kasvilajien muutos sukkessiogradientilla yhdessä kasvilajien erilaisen yhteyttämis-potentiaalin, fenologian ja yhteyttävän lehtipinta-alan kanssa johti hiilidioksidivaihdon alhaisempaan tasoon sekä pienempään ajalliseen vaihteluun vanhemmilla sukkessiovaiheilla. Myös metaanin vaihdolla oli alhaisimmat vuosien väliset vaihtelut vanhemmilla vaiheilla. Yleisesti ottaen metaanipäästöt kasvoivat suon iän myötä, vaikkakaan tätä trendiä ei havaittu sateisena kasvukautena. Lisäksi tutkimus osoitti, että talviaikaiset hiilivirrat (CO₂, CH₄) seurasivat kesäaikaisen hiilidynamiikan vaihtelua.

Kasvillisuuden keskeinen rooli ekosysteemin sukkessiossa havaittiin myös tässä tutkimuksessa. Kasvillisuuden ohella merkittäväksi suosukcessiota sääteleväksi tekijäksi osoittautui hydrologisten olojen vaikutus. Tasaisemmat hydrologiset olot vanhemmilla sukkessiovaiheilla johtivat vähäisempään ajalliseen vaihteluun metaani- ja hiilidioksidivirroissa. Tutkimuksen tulokset viittaavat siihen, että ekosysteemin hiilidynamiikka stabilisoituu suon kehityksen aikana lisääntyvän autogeenisen kontrollin kautta.

Asiasanat: hiilidioksidi, hiilidynamiikka, kasvihuonekaasu, maankohoaminen, metaani, primäärisoituminen, primäärisoituminen, primäärisukcessio, sukkessio, suon kehitys, toiminnallinen kasviryhmä

”Se, mitä on takanamme tai edessämme, on pientä verrattuna siihen, mitä on sisällämme.” – R. Emerson

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At the time I started measuring the gases at the study mires I probably would not have guessed that I was actually gathering data for my doctoral thesis. However, after the idea and the chance for that came to me, ever since I have felt privileged to work with such a fascinating topic. I want to express my gratitude to people who made this possible through coming up with such an interesting idea for research and making it possible for me to study: Jukka Laine, Kari Kukko-oja and my supervisor Eeva-Stiina Tuittila. Further, I owe my sincere thanks to Eeva-Stiina (University of Helsinki) for all the scientific guidance and help throughout the project. I warmly thank also my other supervisor Jari Oksanen (University of Oulu) for all his advice and support, especially in the hectic last stages of this thesis. Even though I physically worked rather far away from my supervisors, I never felt alone as the communion worked just excellently and I always felt welcomed with my several questions and wonderings. Especially the visits to Helsinki to work intensively with the manuscripts were always fruitful and also gave me the possibility to meet new people, such as Mirkka Kotiaho, whom I thank for intriguing discussions along the way. I thank all the co-authors for their contribution to the papers, especially Kari Kukko-oja for the inspiring discussions and Anna Laine for her valuable help. I am grateful to Satu Huttunen, Anne Tolvanen, Marja-Leena Päätaalo, Oili Tarvainen and Anu Hilli for the valuable comments on this thesis and all the support. I thank Prof. Line Rochefort and Dr. Edgar Karofeld for reviewing this thesis.

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Muhos, May 2011

Mirva Leppälä

The list of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Leppälä M, Kukko-oja K, Laine J & Tuittila E-S (2008) Seasonal dynamics of CO₂ exchange during primary succession of boreal mires as controlled by phenology of plants. *Écoscience* 15: 460–471.
- II Leppälä M, Oksanen J & Tuittila E-S (2011) Methane flux dynamics during mire succession. *Oecologia* 165: 489–499.
- III Leppälä M, Seväkivi M-L, Laine AM & Tuittila E-S (2011) Differences in CO₂ dynamics between successional mire plant communities during wet and dry summers. *Journal of Vegetation Science* 22: 357–366.
- IV Leppälä M, Laine A & Tuittila E-S (2011) Winter carbon losses from a boreal mire succession sequence follow summertime patterns in carbon dynamics. In press.

Author's contribution: M. Leppälä (ML) participated in establishing the experiments and was responsible for all the field work including the gas measurements, vegetation analyses and environmental data. ML was responsible for data handling of all the gathered data. (I–IV). She did the statistical analyses of all the papers, guided by E-S. Tuittila and A. Laine, except for the modeling and PCA ordination of paper II, which were done by J. Oksanen. ML prepared all the figures for the papers and wrote the English versions of the manuscripts.

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1 Introduction

Change is an inevitable and natural component of ecosystems and it may occur as a result of changes in climate, soil conditions or in the interactions between the members of a living community, such as vegetation and microbes. If the change starts after a disturbance (fire, landslide, land uplift) and is followed by ecosystem development, it is called ecological succession.

Mire development, i.e. mire succession, generally begins from a minerotrophic fen stage and proceeds towards an ombrotrophic bog stage (Klinger *et al.* 1990, Hughes & Dumayne-Peaty 2002). The increasing peat layer thickness during mire development is accompanied by changes in vegetation, hydrology and nutrient status (Rydin & Jeglum 2006). Eventually this will be reflected in ecosystem function, such as carbon (C) fluxes. The processes that control both the binding and loss of carbon in ecosystems highly determine the sink and source carbon effects of a particular ecosystem. Processes controlling C functions include both autogenic and allogenic factors, and they can be seen as a major driving force in ecological succession.

In this thesis, the influence of both autogenic and allogenic factors on the control of C dynamics is studied in five mires forming an eight-kilometer-long successional sequence from the coast to inland areas. The short distance between the mires assures that they are under the same climatic control during most of the time of their development. Therefore, the differences in species composition and ecosystem C functioning between the mires results mainly from autogenic succession, in other words, the succession is driven by ecosystem internal forces.

1.1 Ecological succession

Succession is a change of species composition and other community characteristics. Succession involves the colonization and establishment of species and, eventually, their replacement with new species. Traditionally, vegetation succession is seen to include changes both in the floristic and community structures (Odum 1969, Miles 1987). It has also been extended to affect the functions and processes of the ecosystem (Whittaker 1975, Lawton 1994, Chapin *et al.* 1994), such as biogeochemical cycles, colonization and species interactions.

Ecological succession is one of the fundamental topics of ecology. The conceptual framework for successional studies was given by Clements (1928) with an idea of a deterministic and directional change during ecosystem

succession. In his idea, succession led towards a stable endpoint, i.e. a climax, where biotic communities at a certain site reach a stability and equilibrium with their environment (Glenn-Lewin *et al.* 1992, Walker & del Moral 2003). Ever since, successional theories concentrating mainly on changes in vegetation have undergone debate and refinement, (Gleason 1927, Tansley 1935, Whittaker 1953, Odum 1969, Connell & Slatyer 1977) but remain rather controversial (McCook 1994, Johnson & Miyanishi 2008). However, some general common conceptions seem to exist. In general, successional theory has changed towards a more dynamistic view of community change; with several endpoints instead of a single equilibrium (Connell & Sousa 1983). This is partly due to the recognition that late successional vegetation may be different under similar environments (McCune & Allen 1985) and that retrogressive succession, i.e., succession away from the climax state, does exist (Wardle *et al.* 2004).

Succession can be initiated from two different conditions: primary and secondary. Primary succession starts in environments that lack organic matter due to a complete removal or burial of the substrate (Walker & del Moral 2003). This may be due to natural causes such as landslides, volcanoes, dune formation, glaciers and land uplift and due to man-made reasons, such as mining (Jones & Henry 2003, Walker & del Moral 2003, Yuping *et al.* 2008). Secondary succession starts after disturbances, which do not completely destroy the organic substrate. Examples are forest fires and clear-cuts, after which succession can initiate from the remaining vegetation, soil and seed bank. Peet (1992) notes, however, that many cases of successions are intermediate, and he therefore proposes new definitions for the primary and secondary succession terms. In his idea, primary succession refers to successions with dominant mechanisms, such as soil development, controlling the environmental change. Instead, secondary succession would be controlled by population processes.

The mechanism that largely determines succession, is called the driving force. In general, there are two main categories for these mechanisms: autogenic and allogenic succession initiated by either autogenic or allogenic mechanisms. Autogenic succession is usually generated by plant-induced environmental changes (Clements 1928, Tansley 1935). For example, the establishment of new species is determined by the modification of soil properties by resident organisms. Allogenic succession occurs when external abiotic forces cause changes in the physical environment. For example wind, fire and flood may initiate the immigration of new species to an area (Tansley 1935). However, biogenic succession has also been categorized as an independent type of succession

(Kimmins 2004). It occurs when a sudden interference, such as herbivore pressure, becomes the major driving force for succession.

Both autogenic and allogenic forces play a major role in primary and secondary successions (Miles 1987, Matthews 1992). However, primary succession is usually seen to be initiated by allogenic processes, and after that the internal, autogenic mechanisms become more important (Matthews 1992). Nevertheless, it is rather complicated to make general conclusions regarding what the trajectories in succession are within different substrates and initiation conditions (Horn 1974, McIntosh 1999, Walker & del Moral 2003).

Succession happens on a broad range of scales of area and time; from microscopic to continental and from minutes to millennia (McCook 1994, Wardle *et al.* 2004). For example, the last stage of primary succession can be exceeded in millennia or already as fast as in a century (Lawrence 1958, Tishkov 1986). The rate of the succession depends largely on the substrate, initial conditions and climate (Peet 1992). Due to the generally rather slow rate of succession processes, experimental manipulations are usually needed in order to determine the mechanisms behind succession such as manipulation of nutrients and hydrological conditions or plant species removals (Walker & del Moral 2003). Succession can also be studied by exploring oral histories (Arce-Nazario 2007), aerial photos and satellite images (Shanmugam & Barnsley 2008, McDonald *et al.* 2009), and changes in the geological and paleoecological evidence using pollen cores or macro fossils (Hughes *et al.* 2000, Kalis *et al.* 2006, Väliiranta 2006). Also tree cores, lake-bottom deposits (Grudd *et al.* 2002, Korhola *et al.* 2002), permanent study plots and chronosequence studies with a space-for-time approach are used in order to clarify the successional change in ecosystems (Pickett 1989, Glenn-Lewin *et al.* 1992, Walker & del Moral 2003). Chronosequence studies, like the present study, suppose that the initial conditions are the same across the different successional stages under the similar environment (Pickett 1989) and they are especially useful for comparisons of ecosystem functions (Walker & del Moral 2003) such as C gas functions. Finally, the modeling approach offers an especially good tool for studying the drivers of succession (Frolking *et al.* 2010).

1.2 Boreal mires and succession

In northern mires, mire development is usually seen as a shift from younger groundwater-fed (minerotrophic) fen stages to older solely rainwater-fed

(ombrotrophic) bog stages (Klinger *et al.* 1990, Hughes & Dumayne-Peaty 2002, Bauer *et al.* 2003). Ombrotrophic mires characterized by a thicker peat layer have lost contact with the mineral soil and are therefore fed only by precipitation. Contrary to this, younger minerotrophic mires still receive nutrients and water through groundwater. Mires are characterized by water-saturated conditions owing to anaerobic conditions and low decomposability of the plant material. This results in incomplete decomposition of the organic matter, which is accumulated as peat during mire development (Clymo 1984). During mire development peat layer thickness increases and promotes changes in the state of above- and below-ground processes and conditions and it results in height growth of the mire. This ombrotrophication in turn leads to diminishing capillary contact, and eventually to total isolation from groundwater, which results in decreasing nutrient levels, i.e., of mineral base cations and more acid conditions as succession proceeds (Eurola *et al.* 1984, Glaser & Janssens 1986, Belland & Vitt 1995, Laine & Vasander 1996, Rydin & Jeglum 2006). Increasing peat depth results in a less fluctuating water table level as peat has high water-retention capacity. Therefore, during mire development accompanied with peat depth increase, the fluctuation of water table level decreases and the older mire stages, such as bogs, are commonly characterized by a rather stable water table level (Laitinen *et al.* 2008). The stabilizing hydrology due to increasing peat depth is usually connected to the diplotelmic structure of mires, that is, there are two peat layers: aerated actotelm and constantly anaerobic catotelm. Of these, the catotelm constrains water providing higher water-retention capacity. However, opinions on whether all mires develop towards diplotelmic structure or not, varies (Rydin & Jeglum 2006).

The most visible change in mire development is the change in vegetation as a result of changes both in abundance and composition of plants (Matthews 1992). Herbs and sedges, typical for the earlier successional stages of mire succession, are gradually replaced by dwarf shrubs towards the older mire stages, while the *Sphagnum* cover simultaneously increases (Klinger & Short 1996). Compositional change is accompanied by a concurrent change in microtopography, from low spatial variation in younger mires towards high spatial variation in later successional mire stages, where the amount of hummocks is usually higher (Tallis 1994).

Mire development takes time, estimates vary from 3000 years to nearly 10 000 years (Walker 1970, Korhola & Tolonen 1996, Jauhiainen 2003). The rate of mire development depends mostly on the climate, initiation type and basin

characteristics (Tallis 1973, Hughes *et al.* 2000). Mire initiation, i.e., the beginning of mire development, can be divided into three types: paludification of mineral soils usually carrying a forest (due to a rise in water table, for example due to beaver activity or a clear cut), infilling of water bodies, and primary paludification (Huikari 1956). Peat formation on soils with little or no organic substances, is called primary peat formation, i.e. primary paludification, analogous to primary succession (Kujala 1924, Huikari 1956, Rydin & Jeglum 2006). Primary paludification, which mostly starts on land exposed under sea due to land uplift, starts rather quickly due to the moister climate and rather long growing season in coastal regions (Mäkilä 2007). Of the different mire initiation types, primary paludification most commonly occurs also nowadays; around 1 000 ha of mire formation is annually initiated through primary paludification (Virtanen 2008). However, mire initiation is not strictly limited to just one type, as also all the initiation types may be found from one particular mire ecosystem (Korhola 1992a).

1.3 Mire functions

In general, compared to other ecosystems, mires have low rates of plant production and decomposition as a result of nutrient-poor conditions, cold and waterlogged soils and the presence of decay-resistance *Sphagnum* (Clymo 1984, Johnson & Damman 1993, Frohling *et al.* 1998, Blodau *et al.* 2004). Thus, mires are challenging environment for plants and decomposers. During mire succession, vegetation, hydrology and nutrient status change. In addition, the responses to environmental factors such as temperature and moisture conditions also differ between different successional mire stages (Weltzin *et al.* 2000). Eventually, this leads to an accompanied change in C gas cycles. During mire development, changes in above- and below-ground properties lead to changes in the ratio between production and decomposition, which is seen in the exchange of C gases between the mire and atmosphere, particularly carbon dioxide (CO₂) and methane (CH₄) (Fig. 1).

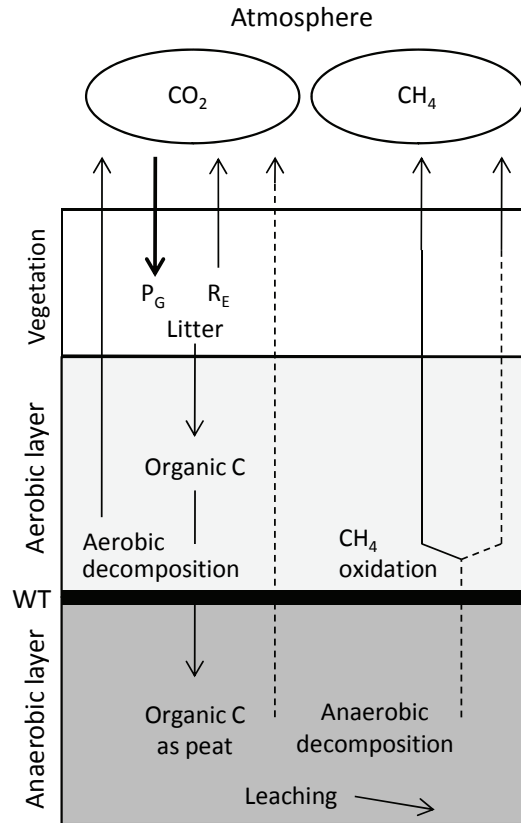


Fig. 1. Simplified presentation of the gaseous carbon (CO₂, CH₄) cycle typical of pristine boreal mires. P_G denotes gross photosynthesis, R_E respiration and WT water table level.

In general, pristine boreal mires are sources of methane (Crill *et al.* 1988, Bubier *et al.* 1995, Nykänen *et al.* 1998, Granberg *et al.* 2001) and also a large fraction of the assimilated CO₂ is released back into atmosphere (Gorham 1991). Despite this, boreal mires are regarded as important carbon storage ecosystems. This is due to incomplete decomposition that results in the accumulation of organic matter as peat (Clymo 1984, Gorham 1991). However, boreal mires may act either as a source or a sink of carbon, depending on their developmental stage and prevailing environmental conditions, especially during growing seasons (Warner *et al.* 1993, Alm *et al.* 1999b). There may also be a large spatial variation in the C functions within a particular mire ecosystem (Bubier *et al.* 2003, Laine *et al.* 2006).

The exchange of C fluxes between the atmosphere and the mire surface is defined by the ratio between production and decomposition. First, vegetation provides input of carbon (CO₂) through photosynthesis (Fig. 1). The level and amount of photosynthesis is controlled by many factors, of which light, temperature and hydrological conditions are most important. In addition to these factors, different plant species have different potentials for photosynthesis, i.e., for carbon binding. (Larcher 2003.) Part of the carbon bound in photosynthesis is stored as peat due the incomplete decomposition of organic matter in mires (Clymo 1984). However, most of the bound C is released back to the atmosphere as gaseous CO₂ and CH₄ (Crill *et al.* 1988, Clymo *et al.* 1998). The release of CO₂ results from both respiration conducted by plants (autotrophic respiration) and soil fauna in aerobic and anaerobic layers of the peat (heterotrophic respiration). In addition, a part of respiration in anaerobic layers that is conducted by methanogenic archaea results in CH₄ production and CH₄ is released from the peat. Part of the methane produced can thereafter become oxidized to CO₂ in upper aerobic layers by methanotrophic bacteria while diffusing towards the atmosphere (Whalen 2005). (Fig.1).

Soil respiration is largely controlled by water table level, determining the end product but also controlling the rate of gas diffusion from the peat to the atmosphere. In addition, temperature plays a major role in respiration as soil fauna and microbes are known to function better in warmer conditions (Bubier *et al.* 1995, McDonald *et al.* 1998, Updegraff 2001). In addition, vegetation determines the supply and quality of substrate for the soil fauna. In CH₄ release, vegetation also acts as a direct pathway for methane to the atmosphere as plants with aerenchymatic tissues offer a direct route for CH₄ transport to the atmosphere (Schimel 1995). Both production and diffusion of stored gaseous CO₂ and CH₄ continue during winter and wintertime C losses have an important impact on annual C gas exchange budget (Alm *et al.* 1999a, Lafleur *et al.* 2003).

1.4 Aims of the study

In general, the research field of succession has become a central and timely issue in ecology. A detailed knowledge of ecosystem structure and functions is essential to be able to make more accurate predictions, especially in changing climate conditions and climatic warming. Mire carbon dynamics largely influence atmospheric CO₂ and CH₄ concentrations and therefore the future changes in peatland carbon storage have the potential to influence climate change.

Most of the previous studies related to primary succession, are mainly concentrated on the vegetation development on different substrates such as volcanic deposits, dunes and floodplains mires (Sjörs 1980, Walker & Chapin 1986). Furthermore, the seashore meadows and mires along the coast of the Bothnian Bay formed by land uplift have been studied in the context of vegetation change during primary succession (Siira 1970, Elveland 1976, Ericson 1980, Cramer & Hytteborn 1987, Ecke & Rydin 2000). However, the time span of the studied chronosequences, except paleoecological studies, is seldom more than tens or hundreds of years. Further, studies that report the impact of successional change in ecosystem functions and more precisely in mire development, i.e., long-term mire succession are lacking. Although both C functions of boreal mires (e.g. Bubier *et al.* 1995, Waddington & Roulet 1996, Laine *et al.* 2006) and mire development have been studied (Cajander 1913, Auer 1930, Walker 1970, Korhola 1990, Bauer *et al.* 2003), the link between them is largely unknown.

Ecosystem functions can be studied with several methods such as measuring C gas cycles, which is the method used in this study. This thesis aims to explore factors controlling functional change, measured as C gas fluxes (CO₂, CH₄), during primary succession of boreal mires. The experimental design forms an eight-kilometer-long successional sequence of primary paludified mires located in the land uplift coast of the Bothnian Bay. All the mires are located in the same middle boreal vegetation zone (Hämet-Ahti 1981) and due to the short distance between them, they have been under the same climatic control most of their existence. Thus, the study sequence enables exploring the influence of autogenic factors in the control of C dynamics during mire development. The main objectives of this study can be divided into the following themes:

1. to study the effect of vegetation and its compositional change on C functions during mire development, (I–III),
2. to explore what factors other than vegetation drive successional change in C functions (II–IV),
3. to study whether there is an abrupt change in ecosystem C functions, either in the levels of C gas fluxes or in the overall ecosystem function, during mire development, (I–IV).

2 Material and methods

2.1 Study sequence and experimental design

The study was carried out in Siikajoki, on the Finnish coast of the Bothnian Bay (64°45'N, 24°42'E) (Fig. 1). The area was covered by ice during the last Ice Age. The weight of the ice depressed the land and after the glaciers retreated, land slowly started to rise. This land uplift is ongoing, and in the study area the annual land uplift rate is 7.5 mm/yr (Ekman 1996). Thus, new land is continuously becoming exposed due to this and some of it has developed into mire ecosystems through primary paludification, which is a unique phenomenon also on a global scale. The annual long-term average precipitation sum in the area is 521 mm and the mean annual temperature +2.3 degrees (Drebs *et al.* 2002).

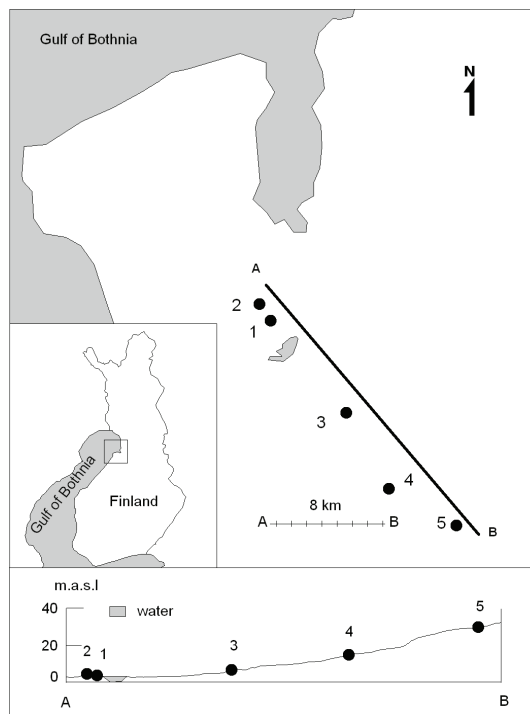


Fig. 2. Location of the study mire sites (1–5) and general features of the study area also showing the cross-section profile (below) with the altitude of the sites. m.a.s.l. = Meters above sea level.

Five small undisturbed mire basins were selected with different ages (from 178 to 2520 ± 50 years) and peat depths (from a few cm to 1.8 meters) to form a mire chronosequence from the first stages of paludification towards the ombrotrophic bog stage along an eight-kilometer-long gradient from the coast inland (Table 1). All the mires are born via primary paludification after emerging from under the sea (Merilä *et al.* 2006) and are formed in depressions between sand dune formations with similar underlying soil. The bottom ages of the peat layers in sites 4 and 5 were ^{14}C dated. The ages of the three youngest sites (1, 2 and 3 in Fig. 1) were estimated based on the elevation above sea level and the land uplift rate using the equation described in Ekman (2001).

The two youngest sites, with estimated ages of 178 and 205 years, are wet meadows dominated by sedges and grasses (*Carex nigra*, *Agrostis canina*) with a sparse moss layer. The sites 1 and 2 are likely younger than the estimated terrestrial age imply, as seawater flooded the nearby road in the 1920s (Kärenlampi *et al.* 2002). The vegetation cover of site 1 is not yet fully closed. The organic soil layer in site 1 is still patchy and in both sites its thickness is only 10 centimeters at most. These two sites (sites 1 and 2, referred as meadows) lie 1.5 to 2.0 meters above sea level (Table 1).

Two intermediate sites (sites 3 and 4, referred as mesotrophic and oligotrophic fen) are dominated by sedges (*Carex chordorrhiza*, *C. rostrata*, *C. canescens*) (Table 1, Fig. 1). The moss layer of both sites is rather dense and hummocks with a dense *Sphagnum* carpet can already be found. Sites 3 and 4 are approximately 700 and 1070 ± 70 years old, their peat depths 50 and 75 cm, and height above sea level 7 and 12 meters, respectively. (Table 1).

The oldest site (site 5, referred as fen-bog transition) is 2520 ± 50 years of age (Fig. 1). The drier hummock surfaces are clearly ombrotrophic (referred as bog stage) and their field layer consists mainly of dwarf shrubs (*Rubus chamaemorus*, *Empetrum nigrum*), but also *Eriophorum vaginatum* is abundant. Wet surfaces (referred as fen stage) are dominated by *Scheuchzeria palustris* and *Carex limosa* (Table 1). The moss carpet is well developed with a high coverage of *Sphagnum* and the peat layer is 1.8 meters thick. The site is located 25 meters above sea level. (Table 1.) In papers III and IV the sites 1–5 are referred as SJ1-SJ5.

For the vegetation and C flux measurements, 0.56×0.56 m sample plots with collars were established at each mire site in order to isolate the sampling area (roots of the vegetation) during measurement. There were five sample plots at sites 1 and 2 and six at sites 3, 4 and 5. The sampling covered the characteristics

variation in vegetation, moisture and spatial variation at all the mires. The variation in microtopography increased along the sequence, therefore the number of sample plots was higher at sites 3, 4 and 5. The sample plots were surrounded by boardwalks in order to minimize disturbance during the measurements.

Table 1. The site-specific characteristics in peat thickness, average water table level (WT) \pm SD during years 2003–2005, altitude (m.a.s.l. = meters above sea level), vascular plant and moss species (covers 3% or more). Age estimation described in methods part. C = *Carex*, Sph = *Sphagnum*.

Site	1	2	3	4	5
Age (yrs)	178	205	700	1070 \pm 70	2520 \pm 50
Peat (cm)	< 10	< 10	44	87	1.8
WT (cm)	-3 \pm 11.0	-7 \pm 16	-9 \pm 19	-1 \pm 6	-6 \pm 2
Altitude (m.a.s.l.)	1.5	2.0	7	12	25
Vascular plants	<i>Carex nigra</i> <i>C. canescens</i> <i>Potentilla palustris</i> <i>Agrostis canina</i>	<i>C. nigra</i> <i>Agrostis canina</i> <i>Potentilla palustris</i> <i>Eriophorum angustifolium</i>	<i>C. chordorrhiza</i> <i>C. canescens</i> <i>C. rostrata</i> <i>C. limosa</i> <i>Vaccinium oxycoccus</i> <i>Potentilla palustris</i> <i>Eriophorum vaginatum</i> <i>Peucedanum palustris</i>	<i>C. chordorrhiza</i> <i>C. livida</i> <i>C. rostrata</i> <i>C. magellanicum</i> <i>Vaccinium oxycoccus</i> <i>Andromeda polifolia</i> <i>Equisetum fluviatile</i> <i>Menyanthes trifoliata</i>	<i>C. limosa</i> <i>C. rostrata</i> <i>Rubus chamaemorus</i> <i>Vaccinium</i> <i>oxycoccus</i> <i>Eriophorum vaginatum</i> <i>Scheuchzeria palustris</i> <i>Empetrum nigrum</i> <i>Betula nana</i> <i>Drosera rotundifolia</i> <i>Empetrum nigrum</i> <i>Betula nana</i> <i>Drosera rotundifolia</i> <i>Scheuchzeria palustris</i>
Mosses	<i>Warnstorfia exannulata</i>	<i>Warnstorfia exannulata</i> <i>Warnstorfia fluitans</i> <i>Sph. papillosum</i>	<i>Sph. fimbriatum</i> <i>Sph. obtusum</i> <i>Sph. squarrosom</i>	<i>Sph. papillosum</i>	<i>Sph. balticum</i> <i>Sph. majus</i> <i>Sph. angustifolium</i> <i>Sph. papillosum</i> <i>Sph. magellanicum</i> <i>Sph. mage</i> <i>Polytrichum strictum</i> <i>Warnstorfia fluitans</i>

2.2 Measurements and data analysis

2.2.1 Monitoring and data analysis of vegetation

Vegetation is known to play a major role in C gas exchange. In order to relate CO₂ and CH₄ fluxes to vegetation, the seasonal development of vegetation was recorded during the growing season in the sample plots (I–III). The green area of each vascular species was calculated as by multiplying the average leaf size by the number of leaves. The leaf sizes of different species were measured biweekly from marked individuals outside the sample plots and the number of living leaves of each vascular plant species in the sample plots was calculated monthly. The green area of mosses was estimated as a percent cover (m² m⁻²) once during each growing season. Together with the seasonal vegetation analysis, the vascular and moss species composition was surveyed from the sample plot on a percentage scale in the middle of the growing season in 2003.

The vegetation data was grouped into functional groups based on the phenological behavior and growth form of the plant species: herbs/forbs, graminoids, sedges, deciduous and evergreen dwarf shrubs, and *Sphagnum* and bryales mosses (I). The grouping of the functional plant groups was done in order to study the effect of different functional plant groups on both CO₂ (I, III) and CH₄ (II) exchange along the sequence. The seasonal development of green area of each group was achieved by fitting a log-linear relationship between the leaf area and the number of days since the beginning of year.

In order to define plant communities along the sequence (III), Two Way Indicator Species Analysis (TWINSPAN) was used with the vascular cover data gathered in 2003 (Hill & Šmilauer 2005). The analysis divided the sample plots based on their vegetation data into six plant communities. To further examine the variation in vegetation and its relationship to CH₄ functions (II), a principal component analysis (PCA) of standardized data was conducted using seasonal green area data in the different functional plant groups and coverage of mosses collected during three growing seasons. Finally, ANOVA for repeated measurements was used to test for differences in vascular green area between the growing seasons (III).

2.2.2 C gas measurements and environmental parameters

In order to measure CO₂ exchange during growing seasons, a chamber method was used (I, III). The instantaneous CO₂ flux was measured with the chamber exposed to different levels of light in order to obtain CO₂ exchange rates under a wide range. CO₂ concentration in ppm, chamber headspace temperature and photosynthetic photon flux density (PPFD) were recorded for 120–140 seconds at 15-second intervals after closing the chamber. Finally, CO₂ exchange was measured with the chamber covered with an opaque hood in order to get an estimate of the instantaneous ecosystem respiration rate (R_E). Water table level (WT) and peat temperature profiles at each sample plot were measured simultaneously with the CO₂ measurements. The CO₂ measurements were conducted biweekly during growing seasons from June 2002 to July 2005.

The CH₄ flux measurements during growing seasons were conducted using the closed chamber method (II). Air samples of 30 ml were drawn into syringes after 5, 15, 25 and 35 minutes closing the chamber. The methane concentration of the samples was determined within 24 hours in the laboratory. The gas samples for CH₄ determination were collected biweekly during the growing seasons from July 2003 to June 2005.

Both CO₂ and CH₄ were measured once a month during winters 2003–2004 and 2004–2005 (IV). A chamber method similar to that for methane measurement during growing seasons was used when snow cover was less than 20 cm. In times with a snow layer thicker than 20 cm, a snowpack diffusion method was applied. Samples were taken into syringes from the top and bottom of the snow pack by using a metal pipe of 1mm diameter. Simultaneously the snow temperature and depth, and the porosity of the snow were determined by weighting a volumetric snow sample and relating that to the density of pure ice. The CO₂ concentrations of the samples were analyzed within 24 hours in the laboratory and CH₄ concentrations were analyzed in a way similar to that of samples from the growing season. The wintertime sampling was conducted monthly from October 2003 to the end of March 2005 (altogether 13 different times per site) during this time the snow pack diffusion method was used from January to March in 2004 and from February to March in 2005.

In order to simulate CO₂ exchange, continuous air temperature, precipitation and photosynthetic photon flux density (PPFD) were measured at the weather station nearby (64°41'N, 25°05'E). Hobo data loggers (H08-008-04, Onset

Computer Corporation, USA) were used to obtain continuous soil temperature data at the depths of 5 and 30 cm at each site.

2.2.3 Data analysis of C gas data

In the chamber method, the CO₂ and CH₄ flux rates were calculated from the linear change in chamber headspace concentration in relation to time, area, volume and temperature. Net ecosystem exchange (NEE) over time was calculated from the linear change in gas concentration in the chamber with respect to chamber volume and temperature. NEE was calculated as a sum of P_G (positive) and R_E (negative). In the snowpack diffusion method, the CO₂ and CH₄ flux rates were calculated from the difference in gas concentrations between the bottom and top samples with respect to snow depth, porosity and snow temperature.

The CO₂ data gathered from the transparent chamber was used in modeling to 1) quantify the role of different functional plant groups to CO₂ exchange during mire development, i.e., long-term mire succession (I), and 2) to examine the effect of different successional plant communities on CO₂ fluxes (III). Seasonal estimates of NEE and its components (R_E, P_G) were achieved through using reconstructions of the non-linear regression models and continuous weather and green area data (I, III).

To diminish the effect of varying weather conditions and to focus on differences between the successional stages (I), data from only one year was used and P_G and R_E were modeled separately. In parameterizing the model, the seasonal and spatial variation in P_G in all the successional stages was combined by using the entire data set from 2004 (I). In the paper III the parameterization of the models was done by using community-specific environmental variables and the simulated cumulative fluxes of P_G, R_E and NEE were compared between the different plant communities with paired t-test between the growing seasons 2003 and 2004 (III). A linear interpolation between the wintertime CO₂ fluxes (both snow-free and snow-covered seasons), was used to reconstruct the fluxes over the winters and the difference in CO₂ fluxes between the winters and sites was tested by using ANOVA for repeated measurements (IV).

The measured CH₄ fluxes were linearly interpolated between the measurement days to cover the study period 2003–2005, during the growing seasons (II) and in the winters (IV). ANOVA for repeated measurements was used to test the differences in CH₄ fluxes between the two winters and sites. In order to study the effect of successional drivers on methane fluxes, linear mixed effects

models were used (II). The models were used to examine the controlling effect of vegetation, temperature, site and water table level on the measured methane. ANOVA for repeated measurements was used to test for differences in the WT between the growing seasons (III) and for difference in snow pack between winters and sites (IV). More detailed descriptions for the modeling of C data and data analysis in general can be found in the corresponding original papers.

3 Results

3.1 Change in environmental parameters

The 2004 growing season was clearly wetter (415 mm) than the previous growing season in 2003 (204 mm) and the long-term average (250–280 mm). Further, the wet season in 2004 was also cooler (13.8 °C) than the dry season (14.8 °C). The soil temperature did not differ greatly between the years or between the sites (I–III).

The variation in precipitation was reflected in water table positions with lower variation in the older end of the sequence. During the dry season in 2003, the WT remained within 10 cm of the soil surface at site 5, but fell below 30 cm depth at the youngest sites (1–3), site 4 being the intermediate of these. During the following moister years in 2004 and 2005, the WT remained within the range of 10 cm of the soil surface at all of the sites. The site-specific spatial variation in WT levels increased along the sequence. (II–III.)

3.2 Change in vegetation

There was a gradual replacement of sedges and herbs with dwarf shrubs and *Sphagnum* along the sequence, which also resulted in a gradual decrease in the abundance of plants with efficient photosynthesis and efficient green area production along the sequence (I–III). The seasonal variation in plant phenology decreased along the sequence so that in the later stages the dominant vegetation had a less pronounced seasonal development of green area. The plant heterogeneity increased along the sequence as the number of dominant plant species along the sequence increased (Table 1).

The TWINSpan analysis resulted in six different successional plant communities, where the first division was made between an ombrotrophic bog and minerotrophic vegetation (III). Furthermore, the minerotrophic vegetation was further divided into mesotrophic and oligotrophic fens and meadows. The bog vegetation was divided into two groups, of which the lawn community represented the transition stage between the fen and bog communities and was the first community with full coverage of *Sphagnum*. The oldest successional stage along the sequence was the hummock community with hummock and bog-like vegetation. The true mire plants appeared from the second successional plant

community (site 2) onwards, while the first community (site 1) was dominated mainly by wetland species (species classification based on Eurola *et al.* 1995).

The vascular green area (VGA) of the early-successional plant communities, meadow communities, was significantly higher during the wet growing season in 2004 than in 2003. Differences in the VGA of the other communities between the two years were not detected (III).

3.3 Patterns in C gas dynamics

3.3.1 CO₂ dynamics

In general, there was a decrease in the level of photosynthesis along the mire sequence (I, III). This was linked strongly to the compositional change in vegetation: a gradual decrease in the abundance of plants with efficient photosynthesis and green area production (I). In general, the level of ecosystem respiration varied less than P_G along the sequence (I, III). However, the source of respiration differed between the successional stages. At the earlier stages, most of the respiration was plant derived as the organic layer at these sites was very thin. The most stable and lowest R_E was detected in the oligotrophic community with a high and stable WT (III). Further, the wintertime R_E strictly followed the pattern of growing season CO₂ dynamics (IV) so that only minor variations in CO₂ emissions were noticed between the successional mire stages.

CO₂ dynamics were more stable at the later successional stages, as the temporal variation in dynamics of P_G and R_E decreased along the mire sequence (I, III). Similar to the level of photosynthesis, most of the seasonal dynamics of CO₂ were determined by plants groups with high photosynthetic effectiveness and strong phenological variation in their green area, namely sedges and grasses (I).

CO₂ dynamics of different successional plant communities reacted differently to changing weather conditions (III) as the net uptake of CO₂ of the earlier successional communities decreased during the dry growing season due to a decrease in photosynthesizing leaf area. Contrary to this, CO₂ uptake of the later successional communities slightly increased or did not change (III). Further, also the R_E of the two meadow communities was significantly lower during the dry season (III). Thus, CO₂ dynamics in the earlier stages of mire succession were indirectly controlled by the WT as it changed the green area of vegetation.

There seemed to be a direct link between P_G and NEE rather than between NEE and R_E (I, III). The youngest sites were the most effective at fixing carbon due to their high rate of photosynthesis and relatively low respiration level (I, III). The complexity in production was detected as models describing P_G of the later successional plant communities needed to have more factors included to explain the variation in P_G : light, vascular green area, air temperature, water table level and moss coverage.

Most of the total annual C release was contributed by CO_2 . Wintertime CO_2 loss was 14–62% of the growing season NEE and 8–14% of the annual CO_2 loss (IV). According to the first study (I), there was a general decreasing trend in NEE along the successional sequence. If the average annual CO_2 -C and CH_4 -C loss estimated in study IV was taken into account, all the sites were acting as C sinks. The two youngest sites had the largest sink effect (112.1 and 160 C g m⁻² yr⁻¹) and the two fen sites in the middle of the sequence had the lowest effect (27.0 and 18.1 C g m⁻² yr⁻¹). The oldest site, site 5, had intermediate values compared to the other two groups (48.7 C g m⁻² yr⁻¹).

3.3.2 CH_4 dynamics

The cumulative CH_4 emissions increased with mire age. However, the increase in CH_4 emissions along the mire sequence was due to the negligible emissions at the younger successional stages during the dry season (II). Therefore, the difference in CH_4 emissions between sites seemed to narrow towards the end of the 2-year study period due to the negligible emissions at the younger successional stages during the dry season.

Temporal variation in CH_4 emissions decreased along the mire sequence as the later stages acted in a more stable way due to more constant hydrological conditions. There seemed to be a delay in methanogenesis after drying out as CH_4 emissions increased for over a year after the dry season with the negligible emissions. Similarly to CO_2 , there was a stronger spatial variation in CH_4 dynamics at the later successional mire stages (II, III).

The water table level was the major controlling factor for CH_4 dynamics along the mire sequence. The three youngest sites had negligible emissions during the prevailing dry conditions with a lower WT due to lower precipitation. Further, under moister conditions with a higher WT, the emissions clearly increased at these same sites (II). The same pattern, negligible emissions during a dry season and increasing in moist conditions, was also observed during the winters

following the dry and wet summers (IV). Together with the WT, both vegetation and temperature also controlled CH₄ emissions. However, their control in CH₄ emissions started only when the water table was sufficiently high. The water table range that was favorable for CH₄ emissions, increased along the successional sequence. Sites 1 and 2 at the younger end of the mire sequence emitted CH₄ only when the WT remained within the range of 10 cm from the soil surface. At site 3 emissions occurred at the water table within 20–30 cm above or below the surface and at sites 4 and 5 the emissions occurred when the WT remained within 40 cm of the surface (II).

The seasonal variation in CH₄ emissions was controlled by temperature only at the oldest study site, which had the lowest variation in the WT. Within-season variation in emissions that was related to plant phenology was highest at the fen stage (site 3), which was dominated by aerenchymatous plants with a strong seasonal pattern, namely sedges and forbs (II).

4 Discussion

4.1 Drivers of mire succession

The variation in carbon dynamics along the mire sequence was mainly related to changes in vegetation and hydrological conditions. The change in vegetation composition, consistent with earlier findings in mire vegetation succession, was followed by changes in the phenology and photosynthesis potential of the dominant vegetation. This in part resulted in lower temporal variation of C gas exchange in the later stages, respectively. In addition, the effect of stable hydrological conditions on mire C functions and further on mire succession was crucial. These results imply that both vegetation and hydrology acted as major controllers of the change in carbon dynamics (CO₂, CH₄) along the successional mire gradient, that is, they act as the main drivers of mire succession.

4.1.1 Successional change in vegetation

The change in vegetation along the successional mire sequence was seen as gradual replacement of sedges and herbs with dwarf shrubs and *Sphagnum* along the mire sequence (I, III). Similar to this, primary succession usually includes a shift in dominant plant species from species that are herbaceous, short-lived and have a high reproductive output to those species that are woody and long-lived (Elveland 1976, Grime 1987). Further, the change in mire vegetation during mire development leads to a plant community composition change, such as different functional plant groups in different successional stages (Elveland 1976, Ecke & Rydin 2000).

Even though vegetation in later successional stages under similar environments can diverge from each other (McCune & Allen 1985), the later mire successional stages are dominated by *Sphagnum* (see Korhola 1990 and references therein). In the present study, the abundance of *Sphagnum* increased along the mire sequence from site 3 onwards. *Sphagnum* plays a major role in overall mire development and an increase in *Sphagnum* usually implies an important step in succession (Walker 1970, Rydin *et al.* 2006, Granath *et al.* 2010). For example, only a very significant allogenic effect can hinder the transition from lake to mire after the establishment of *Sphagnum* (Korhola 1992b). The important role of *Sphagnum* in mire development and further in C functions

of boreal mires, arises from its ability to absorb and retain moisture and nutrients from the air and from its hindering effects on vascular plant growth and peat decomposition (Clymo & Hayward 1982, van Breemen 1995, Verhoeven & Liefveld 1997). In addition, a link between *Sphagnum* and methanotrophic bacteria has been recorded (Larmola *et al.* 2010).

Besides the change in functional plant groups along the successional mire sequence, there was also a change in successional mire plant communities. TWINSpan analysis resulted in six different successional plant communities, where the first division was made between ombrotrophic bog-like and minerotrophic fen-like vegetation. This division between minerotrophic fen and ombrotrophic bog, is the main natural division in boreal mire development (Klinger *et al.* 1990, Hughes & Dumayne-Peaty 2002). Furthermore, the minerotrophic vegetation was further divided into mesotrophic and oligotrophic fens and meadows and bog vegetation was divided into lawn and hummock communities (III). This successional sequence from wet meadows towards bog-like vegetation during mire succession is in accordance with earlier findings in paleoecological studies (Tallis 1973, Muller *et al.* 2003, Bhiry & Robert 2006, Tuittila *et al.* 2007).

4.1.2 Effect of vegetation succession on C functions

The results of the present study about the successional change in vegetation during mire development corresponded well to the results of previous studies, as discussed in the previous chapter. Successional change in vegetation inevitably also leads to changes in ecosystem functions as differences in plant community composition have strong effects on microbial activity (Stroo & Jencks 1982) and on overall ecosystem processes, such as carbon cycles (Peet 1981, Riutta *et al.* 2007b). The results of the present study confirm this as the change in functional plant groups was accompanied by different plant phenology and potential for photosynthesis between the successional stages resulting in lower temporal variation in C dynamics, especially that of CO₂.

Even though the control of vegetation on CH₄ emissions was evident only when the water table level was sufficiently high (II), the phenology of plants did control the seasonality of emissions and it had a strong effect on the seasonality of CH₄ emissions in the fen stage (site 3) (II). The particular site is dominated by aerenchymatous plants and by plants with strong seasonal patterns in their leaf area, such as sedges and forbs. Plants with aerenchymatous roots have an

important effect on CH₄ emissions as they offer a pathway for CH₄ diffusion to the atmosphere (Schimel 1995). Further, forbs are large-leaved and thus may have an important impact on the carbon dynamics via their high rate of photosynthesis, which assures more substrate for anaerobic and aerobic decomposition processes.

The different response of successional plant communities to changing weather conditions was related to dissimilar responses to dry and moist conditions (III). Measured as vascular green area and gross photosynthesis, the earlier successional plant communities, dominated by sedge and graminoids, had lower production during the dry season (III). On the contrary, the later successional plant communities had higher production during dry seasons, or at least about the same as in wet season (III). This different response of vegetation is linked to differences in sensitivity to drought. The production of fen plants that dominate early stages of mire succession, especially that of sedges and graminoids, is sensitive to soil moisture changes (Bubier *et al.* 2003, Weltzin *et al.* 2000). Contrary to this, hummock plant communities (III), characteristic of later successional mire stages are known to be almost continuously moist (Rydin 1985) and the later successional species, shrubs, actually prefer dry conditions (Weltzin *et al.* 2000).

Vegetation plays an important role in ecosystem C functions during succession. It is not only the effect of plant phenology controlling the seasonal dynamics of C functions, nor only the different plant community responses to changing weather conditions, but also the effect of litter on ecosystem functions during succession that may be important. In general, ecological succession includes the replacement of early successional plant species with decreasing litter quality and decomposition rates (Grime 1987, Wardle *et al.* 1997). In the present study, the emergence of shrubs and *Sphagnum* in the late successional mire stages also means a change towards poorer litter quality as these plant groups are known to produce a poor quality of substrate as they decompose (Johnson & Damman 1993, Moore *et al.* 2002). Further, the plant heterogeneity increased along the successional mire sequence as the number of dominant plant species increased along the sequence, which will inevitably result in higher litter heterogeneity in the later stages. Litter directly hampers germination and establishment of plant species, which is accompanied by effects on soil biota (Wardle *et al.* 1999, Jensen & Gutkunst 2003). Therefore, the changes in litter dynamics inevitably lead to a comprehensive change in both production and respiration dynamics of a particular ecosystem, yielding a change in ecosystem functions. Straková *et al.* (2010) noticed that changes in litter type, composition and its chemical quality as a result

of changes in hydrological conditions and vegetation, will strongly affect both soil properties and the C cycle of peatlands. In the present study, the highest green area was observed in the middle of the mire sequence (I), which will assure more substrate through higher litter production for decomposition processes. This was seen as higher wintertime C fluxes at the particular site (IV).

4.1.3 Hydrology and soil temperature

As discussed in the previous chapter, the overall change in vegetation did control both the CO₂ and CH₄ dynamics during mire development. Together with plant-induced changes, i.e., autogenic controls of ecosystem processes, the allogenic mechanisms, such as climate, drive ecosystem succession (e.g. Charman 2002). In general, weather conditions are known to control C dynamics in boreal mires and already small changes in weather conditions, especially precipitation, may cause variation in C fluxes in boreal mires (Bubier *et al.* 2005, Aurela *et al.* 2007, Laine *et al.* 2007, Riutta *et al.*, 2007a, Maanavilja *et al.* 2010).

The control of climate-driven, allogenic factors was seen in the present study mainly through variation in precipitation, which caused variation in water table level at the early stages. In general, peatlands experience rather small water fluctuations because a rather stable water regime is needed for peat growth (Rydin & Jeglum 2006). Therefore, especially the low water tables, i.e., dry conditions, may have a crucial effect on the ecosystem function of boreal mires. A lower WT may harm mire plants as they are usually better adapted to wet conditions and a low WT may slow down the exchange of gases through both hindering methanogenesis and by speeding up oxidation (Roulet *et al.* 1993, Dise *et al.* 1993, Sundh *et al.* 1994, Strack *et al.* 2006), while a high WT has the opposite effect: it speeds up methanogenesis and decreases oxidation. However, the variation in C functions related to a fluctuating WT due to changing precipitation conditions, is not just a perturbation but a natural part of dynamics typical of mires (Laitinen *et al.* 2008). Further, the early successional stages started to emit methane after a delay, that is, only after a certain WT was achieved. This delay gives support to the result of the study by Kotiaho *et al.* (2010), which revealed the adaptation of methanogens to fluctuating WT levels. Therefore, in mires with low peat thickness, i.e., the earlier successional mire stages of this study, the methane producing processes can occur in mineral soil with different geochemical properties than peat. Mineral soil is usually richer in nutrients than peat, which

may partly explain the high methane emissions during favorable conditions as during the wet season of this study.

Hydrology had a major role in controlling CH₄ emissions along the successional mire sequence. More constant hydrological conditions at later successional stages, as a consequence of the thicker peat layer, appeared to result in lower temporal variation of both CH₄ and CO₂ fluxes. As greater peat height is known to result in more stable hydrological conditions through the high water retention capacity of peat (Walczak *et al.* 2002), it is logical that the self-sustaining hydrological conditions increase during mire succession with an increase in peat depth. Thus, the important effect of hydrology on mire development noticed earlier in many stratigraphical studies (e.g. Singer *et al.* 1996, Belyea & Baird 2006), was confirmed by the present results. Further, the important effect of a rather stable WT on mire development has been authenticated by van Diggelen *et al.* (1996) who noted that if stable water conditions are restored, it may take only a couple centuries for the peatland to develop from an open water stage to a stage with more or less bog characteristics.

In addition to the effects of the WT and vegetation, soil temperatures also had an effect on C dynamics. The seasonal variation in C dynamics is connected to temperature directly (Klinger *et al.* 1994, Bergman *et al.* 2000) but also indirectly through temperature-controlled plant phenology and consequently substrate availability (Karlsson & Nordell 1996, Bjerketvedt *et al.* 2003). The direct effect of temperature on CO₂ was evident in this study but for CH₄ emissions temperature control was seen only after a certain WT level was achieved.

4.2 C functions during mire development

4.2.1 Long-term mire succession

There was a change from meadow communities representing the early-successional mire plant communities, towards ombrotrophic bog-like vegetation in the hummock community, representing the oldest successional stage along the successional mire sequence. The final stages of long-term mire succession are regarded to be ombrotrophic conditions preceding the bog stage (Ruuhijärvi 1982, Van Breemen 1995, Klinger & Short 1996, Rydin *et al.* 1999) even though peat core studies have shown that also reverting succession from a bog to a fen does happen, mostly as a result of flooding (Rydin & Jeglum 2006). However, a recent

study shows that the final stages diverge between mires originating from primary and forest paludification (Rehell & Heikkilä 2009). Mires initiated from primary paludification seem to develop towards flark fens and those initiated from paludifying forests more likely towards bogs. On the other hand, for example the Hudson Bay area in Canada, it is actually the bog stage that represents the final stage for both, primary and forest paludification (Klinger & Short 1996).

Despite the uncertainty of whether the last stage of mire succession is the ombrotrophic bog stage or not, it can be assumed the C functions described in the present study are valid in late successional stages in general for many reasons. First, mire development certainly includes an increase in peat depth, in which the results of the present study largely lean on. Thus, regardless of what is the successional trajectory of pristine mires, the lost contact to the mineral soil due to an increase in peat thickness during mire development inevitably leads to different ecosystem C functions between the earlier stages with low peat thickness and later stages with deep peat layer. Second, a nearly complete ecosystem function often occurs before the structure is fully developed, that is before the definite final stage (Lockwood & Pimm 1999, del Moral *et al.* 2007). Finally, a study about a change in microbial community composition along a successional chronosequence in Sweden in the area of isostatic rebound and under rather similar climatic conditions (Wallander *et al.* 2009), showed that the successional change in microbial communities was most rapid during the first 2 000 years. Therefore, as the mire sequence in this study covers more than this, it seems conceivable that the sequence is long enough for obtaining valid results from the plant- and microbe-driven processes, that is, ecosystem C functions.

4.3 Links to ecological succession theory

The lower temporal variation in C gas functions, both CO₂ and CH₄, at the later end of the mire sequence implies an increasing stability of ecosystem C functions during mire succession. Stability has been linked to ecosystem functions already a long time ago (e.g. O'Neill 1976) and this is often referred to as the persistence of plant species and increasing diversity (Tilman 1996, Bai *et al.* 2004) even though it can be defined in several ways (Connell & Slatyer 1977, Woods 2007). Partly due to the different definitions of the term stability in general, it has been rather difficult to make judgments about whether stability increases (Odum 1969, Titlyanova 1982, Bai *et al.* 2004) or decreases during ecological succession (Bengtsson 1998).

Stability can be also connected to predictability and ecosystem resistance that is resilience to perturbation (O'Neill 1976, Pimm 1984), which in this study is also determined as a radical change or difference in weather conditions controlling ecosystem functions. The quicker an ecosystem recovers from the perturbation, the higher is its resilience and the more predictable it is. Odum (1969) noted that early successional stages usually maximize productivity and on the contrary, the late successional ecosystems maximize protection against variation in environmental conditions. The resistance to environmental perturbation, radical changes in precipitation in this case, seems to increase during mire development as a result of increasing water retention capacity at the later stages due to a thicker peat layer and *Sphagnum* moss abundance. In addition, the increasing resistance can be linked also to a change in vegetation. In the present study, the plants with lower seasonal dynamics and less effective photosynthesis dominate the later stages of succession. It is common that plant communities develop towards a greater stability during succession as they become dominated by evergreen species and species with stable phenology (Walker & del Moral 2003). However, if the old mires were able to avoid the perturbation resulting from dry weather conditions, the young mires were able to recover their function after being exposed to the large variation in the water table due to strongly differing precipitation conditions between the seasons.

Based on this study, the stability and ecosystem resilience together with the predictability of ecosystem C functions increase during succession. This change can be also linked to changes in both complexity and site-heterogeneity, which both increased along the study sequence (Table 2).

Table 2. The summary of conclusions made in papers about the directional change during succession. + refers to an increasing effect during mire succession; '-' decreasing and (0) no effect. An empty field indicates that the particular function has not been studied or discussed in the results of the given paper.

Paper	I	II	III	IV
Production (CO ₂)	-		-	
Loss (CO ₂ , CH ₄)	0 (CO ₂)	0 (CH ₄)	0 (CO ₂)	0 (CO ₂)
C balance	-		-	-
Spatial variation	+	+	+	
Stability	+	+	+	+
Complexity			+	
Environmental resistance	+	+	+	
Predictability	+	+	+	

Increasing complexity was seen so that both the heterogeneity of vegetation and the number of factors needed for explaining the variation in P_G increased along the mire sequence. The increase in site-heterogeneity during mire succession was linked to an increase in spatial variation in WT, vegetation and C dynamics (CO_2 , CH_4) along the mire sequence. Changes in these characteristics result from a higher number of species with different demands for photosynthesis at the later stages, i.e., increasing spatiality. It is known that the hummock surfaces become more dominant in the bog stages, leading to a higher variation in microtopography, WT, vegetation composition and further C fluxes in bogs and bog-like communities (Tallis 1994, Waddington & Roulet 1996, Belyea & Clymo 1998, Kutzbach *et al.* 2004), that is, in the later mire successional stages. Site heterogeneity improves the number and variety of safe-sites, and niche-differentiated plant species populations are known to be needed for more stable community functions (Whittaker 1975).

Despite the rather evident increasing trend of stability in ecosystem C functions, the relationship between C gas functions and successional mire stages seemed to be rather complex (II, III). Succession itself is a complex interaction of different factors and further, the effect of these interactions on peat accumulation are even more complex (Walker & Chapin 1986, Bauer 2004, Tuittila *et al.* 2007). In a broader context, an understanding of succession is one of the most challenging subjects in ecology (Prach 2003, Walker *et al.* 2007). As the community dynamics are complex processes and usually take a long time to complete, it creates challenges for successional studies. Together with this, the generalization of successional changes in ecosystem functions are complicated as succession itself differs so much among different successional types, environments and furthermore between primary and secondary succession (McIntosh 1999, Walker & del Moral 2003).

However, the main part of successional studies are mostly done with sequences covering a rather short time scale, rarely exceeding more than tens or hundreds of years. Contrary to this, the successional mire sequence represented here covers more than 2 000 years. This difference in the time span may explain part of the controversial results in successional studies in general. In addition, most of these theoretical considerations of succession have addressed secondary succession.

Especially in vegetation succession, some of the previous results of chronosequence studies have later been noticed to be determined by the ecological conditions rather than the actual age of particular sites (Johnson &

Miyanishi 2008 and the references therein). The limitation of the chronosequence approach commonly includes the absence of replicates, which also impedes extensive conclusions based on the results in this study. In addition, the estimated C balance of the present study may produce different results if long-term studies covering different weather conditions were conducted. Therefore, more various sequences of ecological succession are needed in order to make more specific generalizations about the functional change during mire development, i.e. long-term mire succession and further, in ecological succession general.

5 Conclusions

Despite the inability to make strong inferences about the trend in the level of C fluxes during long-term mire succession, especially of CH₄, it seems clear that the stability of ecosystem C functions increases with mire age. This was linked to higher autogenic control of the physical environment at the older stages, which resulted from the thicker peat layer assuring more stable hydrological conditions. This was seen as a more steady C function, both CO₂ and CH₄, at the older successional mire stages, implying higher predictability due to higher resistance to changing weather conditions but also revealing the important effect of hydrology on mire succession.

The increasing stability and predictability in C gas functions with increasing mire age is an important result as mires are known to be a major player in global methane emissions (Gorham 1991). Therefore, estimating the probable impact of climatic change on the C storage of boreal mires, this higher stability in the later successional mire stages should be taken into account. Further, the study showed that the C function patterns detected during growing seasons also continued during the following winters. Summers with high summertime CH₄ emissions were followed by winters with similar high emissions, and after a summer with negligible emissions, the wintertime emissions were also minor. Further, the steady pattern in summertime CO₂ emissions between years and between sites was followed with the same steady pattern in wintertime emissions. This confirms the important effect of growing season patterns on wintertime C dynamics and reminds us that the wintertime C loss estimates cannot be ignored in C balance calculations. This study showed the important effect of hydrology on mire succession. If the predicted climate warming would lead to drier conditions, its impact on mire succession through lower WT could be crucial.

Successional studies offer important knowledge about the global need for restoring different substrates. Understanding of ecosystem succession is essential in restoration, as restoration is fundamentally manipulation and management of ecological succession (Luken 1990, Hobbs *et al.* 2007). The results of succession studies may be used in restoration studies in order to help overcome bottlenecks (Walker *et al.* 2007) and directly as a reference system for restoration studies (Aronson & van Andel 2006, Yuping *et al.* 2008). For example, the first stages of primary paludified pristine mires correspond well with the structure of cut-away peatlands with low peat thickness. Thus, based on the results of this study, after

peat extraction, a sufficiently thick layer of peat is inevitably needed to ensure moist conditions for ecosystem C functions and further, for successful restoration.

Successional studies have lot to offer, especially for restoration and climate change studies. However, in the future more studies are needed in order to make generalizations about whether the trend of increasing stability is a common phenomenon in mire succession and in ecological succession in general. Especially the effect of litter as a successional driver on mire succession should be quantified in future studies.

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- IV Leppälä M, Laine A & Tuittila E-S (2011) Winter carbon losses from a boreal mire succession sequence follow summertime patterns in carbon dynamics. In press.

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