**Dissertationes Forestales 67**

# Fen ecosystem carbon gas dynamics in changing hydrological conditions

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Academic dissertation
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Fen ecosystem carbon gas dynamics in changing hydrological conditions

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# ABSTRACT

Northern peatlands are thought to store one third of all soil carbon (C). Besides the C sink function, peatlands are one of the largest natural sources of methane ($CH_4$) to the atmosphere. Climate change may affect the C gas dynamics as well as the labile C pool. Because the peatland C sequestration and $CH_4$ emissions are governed by high water levels, changes in hydrology are seen as the driving factor in peatland ecosystem change.

This study aimed to quantify the carbon dioxide ($CO_2$) and $CH_4$ dynamics of a fen ecosystem at different spatial scales: plant community components scale, plant community scale and ecosystem scale, under hydrologically normal and water level drawdown conditions. C gas exchange was measured in two fens in southern Finland applying static chamber and eddy covariance techniques.

During hydrologically normal conditions, the ecosystem was a $CO_2$ sink and $CH_4$ source to the atmosphere. *Sphagnum* mosses and sedges were the most important contributors to the community photosynthesis. The presence of sedges had a major positive impact on $CH_4$ emissions while dwarf shrubs had a slightly attenuating impact. C fluxes varied considerably between the plant communities. Therefore, their proportions determined the ecosystem scale fluxes.

An experimental water level drawdown markedly reduced the photosynthesis and respiration of sedges and *Sphagnum* mosses and benefited shrubs. Consequently, changes were smaller at the ecosystem scale than at the plant group scale. The decrease in photosynthesis and the increase in respiration, mostly peat respiration, made the fen a smaller $CO_2$ sink. $CH_4$ fluxes were significantly lowered, close to zero. The impact of natural droughts was similar to, although more modest than, the impact of the experimental water level drawdown. The results are applicable to the short term impacts of the water level drawdown and to climatic conditions in which droughts become more frequent.

**Keywords:** peatland, carbon dioxide, methane, water level, climate change, functional groups

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## LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles which are referred to in the text by Roman numerals. The articles are reproduced with the kind permission from Springer Science + Business Media (Paper **I**) and Wiley-Blackwell Publishing Ltd. (Papers **III, IV** and **V**).

**I** **Riutta, T.**, Laine, J. & Tuittila, E.-S. 2007. Sensitivity of $CO_2$ exchange of fen ecosystem components to water level variation. Ecosystems 10: 718-733. doi: 10.1007/s10021-007-9046-7.

**II** **Riutta, T.**, Laine, J. & Tuittila, E.-S. The role of vegetation in methane dynamics in a boreal fen under pristine and water level drawdown conditions. Submitted manuscript.

**III** **Riutta, T.**, Laine, J., Aurela, M., Rinne, J., Vesala, T., Laurila, T., Haapanala, S., Pihlatie, M. & Tuittila, E.-S. 2007. Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem. Tellus 59B: 838-852. doi: 10.1111/j.1600-0889.2007.00302.x

**IV** Aurela, M., **Riutta, T.**, Laurila, T., Tuovinen, J.-P., Vesala, T., Tuittila, E.-S., Rinne, J., Haapanala, S. & Laine, J. 2007. $CO_2$ exchange of a sedge fen in southern Finland — the impact of a drought period. Tellus 59B: 826-837. doi: 10.1111/j.1600-0889.2007.00309.x

**V** Rinne, J., **Riutta, T.**, Pihlatie, M., Aurela, M., Haapanala. S., Tuovinen, J.-P., Tuittila, E.-S. & Vesala, T. 2007. Annual cycle of methane emission from a boreal fen measured by the eddy covariance technique. Tellus 59B: 449-457. doi: 10.1111/j.1600-0889.2007.00261.x

# AUTHOR’S CONTRIBUTION

**I & II** The water level drawdown study was initiated in 2001. The author joined the research team in 2002. She participated in the planning and establishment of the extension of the study to include the ecosystem component aspect. She was responsible for the data collection during the years 2002 to 2004. She analyzed the data and wrote the papers upon which the co-authors commented.

**III** The author participated in the planning and establishment of the research site. She was responsible for the chamber flux and vegetation measurements. She participated in the set up and the maintenance of the eddy covariance flux measurements. She analyzed the chamber flux and vegetation data and wrote the paper upon which the co-authors commented.

**IV & V** The author participated in the planning and establishment of the research site, and in the set up and the maintenance of the eddy covariance flux measurements. She collected and analyzed the chamber flux (**IV**) and vegetation (**IV** and **V**) data. She participated in the interpretation of the results and helped write the papers.

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## SUMMARY OF THE ARTICLES

**I** We studied the contribution of the fen plant community components, namely sedges, dwarf shrubs, *Sphagnum* mosses and the underlying peat, to the $CO_2$ fluxes in prevailing hydrological conditions and in water level drawdown conditions.

**II** We assessed the role of the fen plant community components, namely sedges, dwarf shrubs, *Sphagnum* mosses and the underlying peat in the $CH_4$ fluxes in prevailing hydrological conditions and in water level drawdown conditions.

**III** We described the plant community scale spatial variation in vegetation, and in $CO_2$ and $CH_4$ fluxes in a boreal fen. The spatial variation in the fluxes was determined with chamber measurements and the fluxes were upscaled to the ecosystem scale. The upscaled estimates were compared with the eddy covariance measurements. We assessed the sensitivity of the ecosystem fluxes to the spatial variation at the plant community scale.

**IV** We studied the $CO_2$ fluxes in a boreal fen ecosystem using the eddy covariance technique. We described the annual cycle, seasonal variation, and the response of the $CO_2$ fluxes to environmental, especially hydrometeorological, factors. Some plant community scale (chamber flux) data was included to strengthen the interpretation of the hydrometeorological responses.

**V** In this paper, we report the annual cycle and seasonal variation of $CH_4$ fluxes in a boreal fen, and the factors controlling the fluxes. To our best knowledge, this is the first continuous year-long time series of peatland methane fluxes measured by the eddy covariance technique.

# 1 INTRODUCTION

## 1.1 Background

Peatlands are ecosystems sustained by water table levels close to the surface where organic matter accumulates as peat. Northern peatlands cover approximately 4 million km$^2$, ca. 3% of the Earth's land area (Lappalainen 1996, Charman 2002). Of the total peatland area, the proportion of boreal and subarctic peatlands is approximately 85% (Joosten and Clarke 2002). . In terms of land area, peatlands are a minor feature in the global landscape. However, the accumulated peat, the mass of which about half is carbon, makes them an important carbon reservoir. Up to one third of all terrestrial carbon, 250 to 400 Pg, is stored in northern peatlands (Gorham 1991, Turunen et al. 2002). This equals 30-50% of the carbon pool in the atmosphere (Denman et al. 2007). On the other hand, peatlands among other wetlands are the largest natural source of methane ($CH_4$) to the atmosphere (Matthews and Fung 1987, Mikaloff Fletcher et al. 2004). The high water levels and the consequent anoxic conditions that support carbon sequestration are also suitable for $CH_4$ production.

Human activities, such as fossil fuel burning and land use, have significantly increased the radiation absorbing gases in the atmosphere, most importantly carbon dioxide ($CO_2$), $CH_4$ and nitrous oxide ($N_2O$), leading to an enhanced greenhouse effect. Based on ice records, the current atmospheric $CO_2$ concentration (approximately 380 ppm) exceeds by far the natural range (180-300 ppm) during the last 650 000 years. The estimated total temperature increase from 1850–1899 to 2001–2005 is in the range of 0.6-1°C and the warming has been most rapid during the last 50 years. The warmth of the last half century is unusual in at least the previous 1,300 years. Most of the observed increase in global average temperatures since the mid-20th century is very likely due to the observed increase in anthropogenic greenhouse gas concentrations. Further warming and larger changes in the global climate system will occur if the greenhouse gas emissions continue at or above the current rates. (IPCC 2007)

Carbon accumulation in peatlands reduces the $CO_2$ burden of the atmosphere. Because of the $CH_4$ emissions, however, the impact of peatlands on the climate system is dual. In a time horizon of 100 years, a pulse emission of $CH_4$ has a 23 times larger radiative forcing impact than a pulse emission of the same mass of $CO_2$ (Ramaswamy et al. 2001). Therefore, if the annual $CH_4$ emissions and $CO_2$ sequestration of a peatland are considered as pulse events, the greenhouse warming potential (GWP) balance in many northern peatlands over a 100 year time scale is positive, i.e. the warming impact of the $CH_4$ emissions exceeds the cooling impact due to $CO_2$ sequestration (Whiting and Chanton 2001). However, peatlands have persistent, rather than pulse, $CO_2$ sequestration and $CH_4$ emission. If the radiative forcing impact is calculated for the entire Holocene, taking into account that $CO_2$ has a longer atmospheric lifetime than $CH_4$, the existence of peatlands have had a net cooling impact on the global climate, dominated by the persistent $CO_2$ sink function (Frolking and Roulet 2007).

Growing concern about global climate change has made the carbon cycle and carbon accumulation in peatlands a research priority. Biotic feedbacks from ecosystems on the climate system and the lability of carbon stocks in peatlands have been identified as some of the key uncertainties and research priorities by the Intergovernmental Panel on Climate Change (Fischlin et al. 2007). Northern peatlands have been resilient ecosystems, persisting through Holocene climatic variation during which the mean annual temperature in the boreal and arctic regions has varied approximately 3ºC above and 4ºC below the current value (Andreev and Klimanov 2000, Antonsson and Seppä 2007). However, because climate change is projected to be most severe at the latitudes where northern peatlands are situated (Christensen et al. 2007), changes may be too rapid or too extreme for peatlands to maintain their stability.

## 1.2 Carbon cycle in peatlands

Phototrophic primary producers fix atmospheric $CO_2$ into organic compounds using radiative energy. Photosynthesis rates depend on photosynthetically active radiation (PAR), $CO_2$ concentration, water supply, temperature, and photosynthesizing plant biomass. Photosynthates (products of photosynthesis) are allocated to growth, respiration and storage, leached as root exudates or used by mychorrhizae. Compared to other terrestrial ecosystems, such as grasslands and forests, photosynthesis rates in peatlands are low (Frolking et al. 1998) Some 40 to 70% of the carbon fixed in photosynthesis is used in plant respiration (Gifford 2003, Litton et al. 2007). Consideration of plant respiration often includes the respiration of the rhizosphere microbes and mycorrhiza because their respiration rates are difficult to separate from other root functions (Chapin et al. 2006). The term ‘plant-derived respiration’ accounts for both the plant respiration and the heterotrophic rhizosphere respiration.

Dead plant litter and other soil organic matter, such as dissolved organic carbon, is decomposed by heterotrophic soil organisms (microbes and soil fauna), primarily under aerobic conditions. This process is called soil respiration or heterotrophic respiration. Soil respiration rates depend upon temperature, moisture and oxygen ($O_2$) availability, decomposer community, nutrient availability, and substrate availability and quality (Laiho 2006). Water level divides the peat layer into the oxic zone above and the anoxic water saturated zone below the water level. $O_2$ diffusion to the water saturated zone is very slow because the diffusion of gases is approximately $10^4$ times slower in water than in air. The aerobic decomposition of the organic matter to $CO_2$ in the oxic zone is fast compared to the anaerobic decomposition of organic matter to $CH_4$ in the anoxic zone.

If there is an imbalance between the photosynthesis and the plant and soil respiration the incompletely decomposed organic matter will accumulate as peat. The slow decomposition rate is the main reason for the carbon accumulation in peatlands (Clymo 1983). The decomposition of organic matter in peatlands is slow because of the small volume of the oxic layer, low soil temperatures during large part of the year and the poor decomposability of the plant material, particularly *Sphagnum* moss tissue. Over millennial time scales, the persistent carbon sink function has created substantial carbon reservoirs as peatlands have expanded and grown in height. However, most of the assimilated $CO_2$ is released back into the atmosphere via autotrophic or heterotrophic respiration and only a small fraction of the gross primary production, up to 15% annually (Clymo 1984, Gorham 1991, Francez and Vasander 1995), is sequestered in the peat. Therefore, even small changes in the $CO_2$ uptake or release can cause considerable variation in the annual $CO_2$ balances, which can be small, variable, and dependent on the weather conditions (e.g. Lafleur et al. 2003, Aurela et al. 2004, Roulet et al. 2007). As a result, a peatland may readily switch from a $CO_2$ sink to a $CO_2$ source between cold and wet and hot and dry years (Alm et al. 1999b).

Because of the high water levels and relatively high rates of carbon supply, conditions in peat are often anoxic. Anoxic conditions and the availability of suitable carbon sources are prerequisites for $CH_4$ production. $CH_4$ is a metabolic end product of strictly anaerobic microbes that belong to the domain Archeae. In peatlands, $CH_4$ is formed either from acetate dissimilation (acetate pathway) or bicarbonate reduction (hydrogen pathway) (Zinder 1993) after a complex organic matter decomposition chain. The acetate pathway dominates in vegetated sites where fresh organic matter is available, while the hydrogen pathway dominates or co-dominates in unvegetated sites, outside of the growing season or in bogs (Bellisario et al. 1999, Popp et al. 1999, Chasar et al. 2000, Keller and Bridgham 2007). Methanogenesis may be suppressed if the concentrations of alternative electron acceptors such as nitrate ($NO_3^-$), sulfate ($SO_4^{-2}$), ferric iron (Fe(III)), manganese (Mn(II)) or humic acids are high (Lovley and Klung 1986, Lovley et al. 1996).

$CH_4$ is released from the anaerobic peat layers to the atmosphere via diffusion through the peat matrix, passage through plants or ebullition. Diffusion through the peat matrix, especially through the water saturated layer is slow because of the slow diffusion of gases in the liquid phase. Compared to the diffusion through peat matrix, passage through the plant tissue is fast. $CH_4$ molecules move through the vascular plant tissue by passive diffusion along the concentration gradient (Schimel 1995, Shannon et al. 1996) or by an active gas transport system, such as pressure induced convection (Dacey and Klug 1979, Brix et al. 1992). Plant-mediated transport dominates in the presence of vascular plants (Sebacher et al. 1985, Whiting and Chanton 1992, Schimel 1995) while ebullition dominates in the absence of vascular plants (van der Nat et al. 1998). Bubbles may be formed if gases become supersaturated in the pore water. The mass of stored $CH_4$ as gas bubbles can be are much as three times the mass of dissolved $CH_4$, depending on the time of year (Fechner-Levy and Hemond 1996). Changes in air pressure and fluctuations in water level may trigger a degassing of the bubble pool, resulting in large episodic fluxes that may contribute significantly to the annual or seasonal fluxes also in vegetated sites (Moore et al. 1990, Glaser et al. 2004, Tokida et al. 2005).

A considerable part, up to 100% (Le Mer and Roger 2001, Pearce and Clymo 2001, Whalen 2005), of the $CH_4$ diffusing through the upper, aerobic peat layer can be oxidized to $CO_2$ by methanotrophic and methylotrophic bacteria before reaching the atmosphere. The net $CH_4$ flux is the balance between the $CH_4$ production, $CH_4$ consumption, transport rate and storage.

Peatland $CH_4$ fluxes are regulated by temperature, water level, substrate availability and quality, and variations in weather conditions. Water level regulates the volume ratio between the aerobic and anaerobic zones and, consequently, the extent of the $CH_4$ production and oxidation zones. Therefore, in most cases there is a positive correlation between the water level and $CH_4$ fluxes (Clymo and Reddaway 1971, Moore and Roulet 1993, Laine et al. 2007b). The activity of methanogenic and methanotrophic microbes is temperature dependent. $CH_4$ production has a stronger temperature response than $CH_4$ oxidation (Dunfield et al. 1993). Therefore, $CH_4$ fluxes generally increase with increasing temperature (Moore and Dalva 1993, Daulat and Clymo 1998, Bellisario et al. 1999, Christensen et al. 2003) but the response can also be negative (MacDonald et al. 1998). New, recently fixed carbon is a more easily decomposable substrate for the anaerobic decomposition chain compared to the old, recalcitrant peat. Therefore, $CH_4$ fluxes should correlate positively with net ecosystem $CO_2$ exchange (NEE) (Whiting and Chanton 1993, Bellisario et al. 1999, Christensen et al. 2000). However, the controlling factors of the $CH_4$ flux are not independent but there are complex interactions. For example, the temperature effect can also be enhanced or constrained by substrate availability (Whiting and Chanton 1993, Bergman et al. 1998) and substrate type (Svensson 1984), and the importance of the plant-mediated $CH_4$ flux depends on the water table level (Waddington et al. 1996): the deeper the water level, the fewer roots and photosynthates reach the anaerobic layer of the peat. Owing to these interactions and the individual responses of $CH_4$ production, oxidation and transport to the controlling factors, identifying the responses of the net flux is difficult and different studies show different results, depending on the climatic conditions and site characteristics.

In comparison to $CO_2$ uptake and efflux, $CH_4$ fluxes are small. However, they can be an important component of the peatland carbon balance (Table 1). Another important component is dissolved organic carbon. Loss of carbon in that form can be up to 23 to 37% of the annual carbon balance (Waddington and Roulet 2000, Roulet et al. 2007). The estimates for the long term average carbon accumulation rates in northern peatlands range from 17 to 29 g C $m^{-2}$ in different parts of the boreal region (Clymo et al. 1998, Gorham 1991, Korhola et al. 1995, Laine et al. 1996, Turunen et al. 2002). However, these rates may not reflect current or future situations. Recent studies on pristine peatlands have shown that annual $CO_2$ balances and $CH_4$ efflux rates are highly variable, both in space (within and between sites) and in time (Table 1).

## 1.3 Role of vegetation in peatland carbon cycle

Peatlands can be divided into fens that receive water and nutrient inputs from the surrounding mineral soils and bogs that receive water and nutrients solely from the atmospheric inputs. The hydrological dynamics of the system and the amount of incoming nutrients are the main factors controlling species occurrence in peatlands (Wheeler and Proctor 2000, Økland et al. 2001). The anoxic rooting environment impedes the growth of plants which have not adapted to such conditions, including most tree species (Jeglum 1974, Macdonald and Yin 1999). Plant communities in Eurasian fens typically consist of sedges, dwarf shrubs and *Sphagnum* mosses (Botch and Masing 1983, Ruuhijärvi 1983, Sjörs 1983). Dividing the species into functional plant groups has provided a useful simplification when studying ecosystem change because group members are likely to have similar responses to environmental factors (Aguiar et al. 1996, Chapin et al. 1996).

Peatland plants differ in their photosynthetic capacity (Bubier et al. 2003b), respiration (Bubier et al. 2003b), quality of produced litter (Szumigalski and Bayley 1996), and role in $CH_4$ dynamics (Shannon et al. 1996, Joabsson et al. 1999). Therefore, the plant composition of a peatland ecosystem influences the autotrophic $CO_2$ exchange rates as well as the soil processes. Because plant groups respond differently to environmental factors, a change in environmental conditions alters the contribution of the different species to the community $CO_2$ and $CH_4$ exchange (Karlsson 1989, Lovelock and Feller 2003, Strack et al. 2006b) or to the community biomass accumulation and allocation (Parsons et al. 1994, Wijesinghe et al. 2005). Eventually internal (ecological succession) and external (weather and hydrological conditions) forcings modify not only the carbon dynamics but also the autotrophic and heterotrophic communities, which in turn feeds back on the carbon cycle.

**Table 1.** Observed carbon fluxes in some undrained sedge-dominated fens, measured using eddy covariance (EC) or chamber method. Unit of the fluxes is g C m$^{-2}$, and the range of the fluxes is shown. “Spatial” is the range of fluxes between vegetation types within one study year and “Temporal” is the range of spatially averaged fluxes between study years. The number of vegetation types / study years is given in parenthesis. Positive NEE indicates a CO$_2$ sink and negative NEE a CO$_2$ source to the atmosphere.

| | | Latitude; Longitude | MAT[a] | Annual NEE | |
|---|---|---|---|---|---|
| Site | Method | N; E | °C | Spatial | Temporal |
| Zackenberg, Greenland | EC | 74; 20 | -19.5 | | 64 (1) |
| Barrow, Alaska, USA | Chambers | 70; 156 | -12.6 | | |
| Churchill, Manitoba, Canada | EC | 58; 94 | -7.2 | | |
| Schefferville, Québec, Canada | Chambers | 54; 66 | -4.9 | | |
| Lek Vorkuta,Komi Republic, Russia | Chambers | 67; 63 | -6.0 | -3.0 - 43 (5) | |
| James Bay Coast, Québec, Canada | Chambers | 54; 78 | -3.1 | | |
| Kaamanen, Finland | EC | 69; 27 | -1.1 | | 4.1 - 53 (6) |
| Degerö, Sweden | EC | 61; 19 | 1.2 | | 48 - 61 (3) |
| Salmisuo, Finland | Chambers | 62; 30 | 1.9 | 53 - 105 (4) | |
| Lakkasuo, Finland | Chambers | 61; 24 | 3.4 | | |
| Siikaneva, Finland | Chambers, EC | 61; 24 | 3.4 | | 51 - 60 (2) |
| Sallie’s Fen, New Hampshire, USA | Chambers | 43; 71 | 8.1 | | |
| Big Cassandra, Michigan, USA (BC4) | Chambers | 42; 84 | 8.3 | | |

[a] Mean annual temperature

[b] Range of individual sample plots instead of vegetation types

| Growing season NEE | | Annual $CH_4$ emission | | Growing season $CH_4$ emission | | |
|---|---|---|---|---|---|---|
| Spatial | Temporal | Spatial | Temporal | Spatial | Temporal | Reference |
| | 96 (1) | | | | | Soegaard and Nordstroem (1999) |
| -14 - 4 (5) | | | | | | Oechel et al. (1995) |
| | -76 - 235 (5) | | | | | Griffis et al. (2001) |
| | | 0.98 - 7.4 (5) | | | | Moore and Knowles (1990) |
| 1.0 - 49 (5) | | 1.2 - 12 (5) | | 0.1 - 8.2 (5) | | Heikkinen et al. (2002) |
| | | | | 0.47 - 13 (5) | | Pelletier et al. (2007) |
| | | | 5.5 (1) | | | Aurela et al. (2004); Hargreaves et al. (2001) |
| | | | | | | Sagerfors et al. (2008) |
| 108 - 160 (4) | | 13 - 36 (4) | | 11 - 30 (4) | | Alm et al. (1997) |
| | 32 - 130 (4) | | | | 2.6 - 6.8 (4) | Papers **I** and **II** |
| 21-193 (5) | | | 9.4 (1) | 5.4 -18 (5) | | Papers **III**, **IV** and **V** |
| | | | | 16 - 62 $(11)^b$ | 17 - 39 (5) | Treat et al. (2007) |
| | | | 3.1 - 36 (3) | | | Shannon and White (1994) |

Sedges, family *Cyperaceae* (e.g. genera *Carex*, *Eriophorum,* and *Trichophorum*), are perennial grasses that reproduce mainly vegetatively (Bernard 1976, Bedford et al. 1988). Sedges produce new shoots throughout the growing season while old shoots die (Bernard 1976, Bedford et al. 1988). The shoots produced in late autumn overwinter (Bernard et al. 1988), which ensures high photosynthetic capacity during the entire growing season. Sedges are deep-rooting and allocate approximately 90% of their total biomass to the roots (Sjörs 1991, Saarinen 1996). The root biomass is mainly located in the top 25 to 30 cm layer (Sjörs 1991, Saarinen 1996), but some *Carex rostrata* Stokes roots have been found as deep as 230 cm (Saarinen 1996). Because of the deep roots, new organic matter is simultaneously injected at different depths of the peat profile in sedge-dominated sites, not just on the surface layer. Sedges have aerenchymatous tissue, an adaptation to wet conditions, for transporting molecular $O_2$ from the above ground parts to the roots (Fagerstedt 1992, Moog and Bruggemann 1998, Visser et al. 2000). Consequently, sedges can tolerate anaerobic, water-logged conditions and are strong competitors in such habitats. Sedges are most abundant in minerotrophic peatlands where the water level is close to the surface (Laine and Vanha-Majamaa 1992).

Sedges are particularly important in peatland $CH_4$ dynamics; the deep roots produce fresh substrate, with relatively little structural carbohydrates compared to woody species, for the methanogenic consortia in the anoxic peat layer and the aerenchymatous tissue serves as a conduit for $CH_4$ molecules from the soil to the atmosphere, bypassing the oxic surface layer. Plant mediated transport accounts for a major fraction (75-97%) of the total $CH_4$ emissions in sedge dominated sites (Whiting and Chanton 1992, Schimel 1995, Kelker and Chanton 1997). On the other hand, $O_2$ transport through the aerenchyma to the rhizosphere inhibits $CH_4$ production (Whalen and Reeburgh 2000) and stimulates $CH_4$ oxidation (King 1994, Popp et al. 2000). All in all, the net effect of the presence of aerenchymatous species is to increase $CH_4$ fluxes in most cases (Waddington et al. 1996, Frenzel and Rudolph 1998, King et al. 1998, Bellisario et al. 1999, Greenup et al. 2000, Rinnan et al. 2003).

Dwarf shrubs are a diverse group consisting of both deciduous and evergreen species. Shrub photosynthesis is less sensitive to environmental conditions (Bubier et al. 2003a) and the shoot growth depends more on the age of the individual ramet (stems that had emerged above the moss layer which might not be genetic individuals) than on climatic variables (Shevtsova et al. 1995). The fundamental difference between these woody plants and herbaceous sedges is that the above ground growth of shrubs is cumulative whereas sedges have to rebuild their aboveground parts each growing season. Some $CH_4$ can be emitted through woody species though at considerably lower rates than through aerenchymatous species (Shannon et al. 1996, Garnet et al. 2005). Recently, it was suggested that terrestrial plants would produce and emit significant amounts of $CH_4$ (Keppler et al. 2006). The findings were then questioned (Dueck et al. 2006), but later an independent data set demonstrated $CH_4$ emissions from shrubs (Wang et al. 2008). A probable source of $CH_4$ is methoxyl groups of pectin split by UV radiation (Keppler et al. 2008).

*Sphagnum* mosses are the dominant moss genus in boreal peatlands. *Sphagna* can tolerate very wet, acidic and nutrient poor conditions (Clymo and Hayward 1982) and photosynthesize efficiently at low temperatures (Harley et al. 1989), as long as the moss surface is not frozen (Malmer et al. 2003). Like other bryophytes, they are poikilohydric plants that lack internal water conducting structures, which makes their physiological processes highly sensitive to water availability. *Sphagnum* mosses have a species specific optimal water content for photosynthesis and a narrow tolerance to water content variation

(Silvola and Aaltonen 1984, Rydin and McDonald 1985b, Gaberscik and Martincic 1987, Schipperges and Rydin 1998).

Different litter materials may have markedly different decomposition rates which influences the peatland carbon accumulation rates (Laiho 2006). Of the three functional groups described above, the litter produced by *Sphagna* is the most decomposition resistant, the litter produced by sedges is the least decomposition resistant and the litter produced by shrubs is intermediate (Szumigalski and Bayley 1996).

Typically, a fen ecosystem comprises a continuum of microforms along the water level gradient, from dry hummocks through lawns to wet hollows. The microforms have distinct plant community composition. The relative abundance of sedges and shrubs changes from the sedge dominance in the hollows to the shrub dominance in the hummocks. *Sphagnum* mosses are present throughout the continuum but the species composition varies. *Sphagnum* mosses hold species-specific niches in the hummock-hollow gradient (Vitt and Slack 1984, Rydin 1985) having morphological adaptation to different moisture condition (Clymo and Hayward 1982). Spatial variation in C gas fluxes between communities is very high (Table 1, Svensson and Rosswall 1984, Moore and Knowles 1990, Waddington and Roulet 2000, Laine et al. 2007a, Laine et al. 2007b). In patterned ecosystems, the proportions of the communities determine the ecosystem fluxes (Laine et al. 2006).

## 1.4 Climate change impact on peatland ecosystems

Although most climate models predict an increase in global temperatures and precipitation, the changes are not evenly distributed among the different regions of the globe (Christensen et al. 2007). There is higher uncertainty in the regional projected changes in precipitation than in temperature. Some climate models predict a water level drawdown in northern peatlands. Using the scenario of a doubled $CO_2$ concentration, leading to a 3°C increase in the June, July and August monthly mean temperatures and a 1 mm increase in daily precipitation (Mitchell 1989) Roulet et al. (1992) estimated a water level drawdown of 14 to 22 cm in northern peatlands, due to the increased evapotranspiration which more than compensates the effect of the increased precipitation. Water level drawdown, the indirect effect of the global warming, is the most important effect of the climate change on peatlands, overshadowing the direct temperature effect, the effect of the elevated atmospheric $CO_2$ concentration, and the effect of the prolonged growing season (Gorham 1991, Gitay et al. 2001, Moore 2002). The water level effect dominates, because water level regulates the plant community composition and the volume ratio of the oxic and anoxic zones and therefore, the relative rates of aerobic and anaerobic decomposition.

Studies on the short term impact of water level drawdown, caused either by natural variability in weather conditions or by treatment, have demonstrated decrease in photosynthesis (Alm et al. 1999b, Bubier et al. 2003a), increase in respiration (Alm et al. 1999b, Bubier et al. 2003a, Strack et al. 2006a), decreased $CO_2$ sink function (Alm et al. 1999b, Bubier et al. 2003a, Lafleur et al. 2003), and decrease in $CH_4$ emissions (Strack and Waddington 2007). However, the responses are not unidirectional but depend on the initial water level conditions and on the vegetation composition (Bubier et al. 2003a, Bubier et al. 2003b, Strack et al. 2004, Strack et al. 2006a).

Over the long term, permanently drier conditions will lead to a vegetation change in northern peatlands. A moderate water level drawdown makes them suitable to a larger number of species (Visser et al. 2000, Weltzin et al. 2003) and the plants that are adapted to high water levels lose their competitive advantage. Studies on the impact of forestry drainage have shown that following the water level drawdown of 20-50 cm, a sedge and *Sphagnum* dominated community will turn into a pine and forest moss dominated community in a few decades (Laine et al. 1995, Laiho et al. 2003).

## 1.5 Aims of the study

The general aim of the study was to quantify the $CO_2$ and $CH_4$ dynamics of fen plant community components (sedges, dwarf shrubs, *Sphagnum* mosses and the underlying peat), a continuum of fen plant communities, and the fen ecosystem as a whole, under hydrologically normal and water level drawdown conditions. More specifically:

The aim of the plant community component scale studies (Papers **I** and **II**) was to assess the contribution of the plant community components to the $CO_2$ and $CH_4$ fluxes in different water level conditions and the sensitivity and response of the components to water level variation.

The aim of the plant community scale study (Paper **III**) was to define the plant communities of the fen, to quantify the $CO_2$ and $CH_4$ exchange of the communities and to examine how the spatial variation at the plant community scale is reflected in the carbon gas dynamics at the ecosystem scale.

The aim of the ecosystem scale studies (Papers **IV** and **V**) was to quantify the annual $CO_2$ and $CH_4$ exchange of the fen, temporal variation in the C gas exchange, and the response to environmental, especially hydrometeorological, factors.

# 2 MATERIALS AND METHODS

## 2.1 Study sites

### *2.1.1 Study region*

The study was carried out at two sites in southern Finland, 60 km from the city of Tampere. The sites are situated approximately 6 km from the Hyytiälä Forestry Field station and 8 km from one another. Annual precipitation in the region totals 710 mm, of which about a third falls as snow. The average temperatures for January and July are - 8.9 and 15.3 C, respectively, and the average cumulative temperature sum (≥+5°C) is 1160 degree days (Juupajoki-Hyytiälä weather station, Drebs et al. 2002). The region lies in southern boreal vegetation zone, close to the border of the middle boreal zone (Ahti et al. 1968).

### *2.1.2 Lakkasuo study site*

Lakkasuo is an eccentric raised bog complex with extensive minerotrophic margins. This study was carried out at an oligotrophic, treeless fen site (61 47’ N; 24 18’ E). In the field layer, sedges (*Carex lasiocarpa* Ehrh., *Eriophorum vaginatum* L.) are the dominant plant group. In addition, dwarf shrubs (*Betula nana* L., *Andromeda polifolia* L. and *Vaccinium oxycoccos* L.) make up a considerable proportion of the field layer. The moss layer is a continuous peat moss carpet dominated by *Sphagnum papillosum* Lindb., *S. fallax* (Klinggr.) Klinggr. and *S. flexuosum* Dozy & Molk.

In Lakkasuo, we studied the C gas exchange at the plant community component scale (Papers **I** and **II**) in prevailing and water level drawdown conditions, using a closed chamber method. The study site was divided into two subsites, namely the control and the water level drawdown subsites. The water level drawdown subsite was surrounded with a shallow ditch that lowered the water level by 10 to 25 cm. The measurements were carried out during four growing seasons, 2001 to 2004. The first year was a calibration season when both subsites were measured prior to the water level drawdown treatment. Water level treatment was implemented in April 2002.

The contribution of the plant community components was studied by means of vegetation removal treatments. In both control and water level drawdown subsites, there were four types of permanent gas exchange sample plots consisting of:

peat, *Sphagnum* mosses, sedges, and shrubs (intact vegetation)
peat, *Sphagnum* mosses, and sedges (shrubs removed)
peat and *Sphagnum* mosses (shrubs and sedges removed)
peat (all vegetation removed).

The contribution of each plant community component to the $CO_2$ and $CH_4$ fluxes was assessed by comparing the fluxes in the different plot types. In 2001, only the plots with intact vegetation were established. The removal treatment plots were added in 2002. Above-ground parts of the vascular plants, and the top two cm of the moss layer was removed. Emerging re-growth was clipped off once a week, if necessary. Progressively less clipping was needed over the course of the study, hardly any during the third removal treatment year (2004). After clipping, soil respiration can decrease significantly and reach a new steady state as fast as in two days (Bremer and et al. 1998, Wan and Luo 2003). Therefore, $CO_2$ flux data from all removal treatment years could be used in the analyses (Paper **I**). The $CH_4$ flux data, on the other hand, showed a highly irregular pattern, indicating considerable disturbance, during the first two years of the treatment (Paper **II**). Therefore, only the data from the growing season 2004 was used.

### *2.1.3 Siikaneva study site*

Siikaneva is the second largest undrained peatland complex in the southern part of the country. It is comprised of raised bogs, southern aapa fens and upland forest patches. Peatlands make up 80% of the total area. The study site (61 49’ N, 24 11’E) is situated in an open oligotrophic fen part of the complex. We studied the C gas exchange at the ecosystem scale using an eddy covariance (EC) technique (Papers **IV** and **V**) and at the plant community scale using a chamber technique (Paper **III**). The site was suitable for an ecosystem scale study, as it offers a large, open and relatively homogeneous fetch, and for the plant community scale study because it comprises a continuum of communities. Although the microforms in Siikaneva site are not very pronounced, the site has a gradient from dry hummock to intermediate lawns and wet hollows. Lawns are the dominant microform, covering some 75% of the site and can be further classified into different types based on their species composition.

Dominant vascular plant species are sedges *Eriophorum vaginatum*, *Carex rostrata* Stokes, and *C. limosa* L., the shrubs *Andromeda polifolia* L. *Betula nana* L., and the herb *Rubus chamaemorus* L. *Sphagnum* mosses form a continuous carpet. Dominant species are

*Sphagnum balticum* (Russow) Russow ex C.E.O. Jensen and *S. papillosum* in lawns, *S. magellanicum* Brid. in hummocks, and *S. majus* (Russow) C.E.O. Jensen in hollows.

In Siikaneva, we established 24 permanent gas exchange sample plots that covered the variation in vegetation and water level. Vegetation was removed from six plots to examine the contribution of the soil processes to the fluxes. Infrastructure was built and the sample plots were established in the autumn 2003. Measurements were started in the spring 2004. During 2004, we measured $CO_2$ and $CH_4$ fluxes at the plant community scale and $CO_2$ fluxes at the ecosystem scale. In February 2005, we began to measure also $CH_4$ fluxes at the ecosystem scale.

## 2.2 Measurement methods

### *2.2.1 Fluxes measured using closed chamber and snowpack diffusion methods*

Closed chambers are containers that, when placed on the measurement spot, isolate a piece of the ecosystem from the surrounding atmosphere. The measurement of the net flux is obtained as the rate of change in gas concentration during a known period of time. The source area of the flux is quite well defined, especially if permanent measurement collars are inserted into the soil. The chamber method allows the quantification of spatial variation in the fluxes, the quantification of the properties of the source area, and the examination of the relationship of the fluxes with those properties. In addition, experimental manipulations are relatively easy to carry out. $CO_2$ fluxes can be partitioned into gross photosynthesis and respiration by conducting successive measurements in light and dark. A serious limitation of the chamber method is the disturbance of the measurement collar and the chamber to the system. Manual chamber measurements are labor intensive and thus lead to poor temporal resolution. Therefore, episodic fluxes are unlikely to be captured reliably.

In this study, plant community and plant community component scale fluxes were measured by the manual chamber technique (Papers **I, II** and **III**). Permanent rectangular (56×56 cm) measurement collars were inserted to a depth of 30 cm into each gas exchange sample plot to isolate the majority of the roots. On the top of the collar there was water groove that allowed chamber placement and air-tight sealing of the measurement system. Chamber measurements were carried out at weekly or biweekly intervals during the snow-free season.

Instantaneous $CO_2$ flux was measured with a temperature controlled transparent plastic chamber of 60×60×30 cm (NSNF-1 in Pumpanen et al. 2004, Alm et al. 2007). $CO_2$ concentration in the chamber was monitored with a portable infrared $CO_2$ analyzer (EGM-2, EGM-3, EGM-4, PP Systems, UK) for 90 to 180 seconds. $CO_2$ concentration, PAR, and temperature inside the chamber were recorded at 15 second intervals. To determine the dependence of the $CO_2$ exchange rate on PAR, a series of measurements were performed at each plot, first in full light, then under shades of varying thickness and lastly in the dark. The chamber was lifted from the collar between the measurements to restore the ambient conditions.

An opaque aluminum chamber of 60×60×30 cm was used in the $CH_4$ flux measurements, (Crill et al. 1988). A 40 ml air sample was drawn to a polypropylene syringe at 5, 15, 25 and 35 minutes after closure. The samples were analyzed with a gas chromatograph (HP-5710A and HP-5890A) equipped with a flame ionization detector (GC-FID) within 36 hours. The performance of the instrument was evaluated by analyzing calibration gas samples ($CH_4$ concentrations of 1.84 and 10.6 ppm). The precision of the analysis was 0.16%, determined as coefficient of variation of replicate calibration gas samples.

The emphasis of the plant community and plant community component scale studies was on the growing season fluxes. At the Siikaneva site, the spatial variation in the fluxes during the snow-covered season was assessed by occasional winter measurements. Chambers were used when the snow depth was < 20 cm, otherwise a snowpack diffusion method (Alm et al. 1999a) was applied. The chamber method was the same as the $CH_4$ measurement method during the snow-free season. In the snowpack diffusion method, gas samples from the top of the snow pack and from the moss surface were drawn into syringes using a metal pipe of 1-mm diameter. At each sampling point, the porosity of the snow was determined by weighting a volumetric snow sample throughout the depth of the snow layer and calculated using the density of pure ice (0.92 g $cm^{-3}$). $CH_4$ concentrations in the samples were analyzed with the GC-FID and $CO_2$ concentrations with EGM-4 in the laboratory.

Flux rates in the chamber measurements were calculated as the linear rate of change in $CO_2$ or $CH_4$ concentration inside the chamber headspace. $CO_2$ flux measurements in the dark represented total (plant-derived and soil) respiration (R). An estimate for photosynthesis ($P_G$) was calculated by subtracting the $CO_2$ exchange rate in the light conditions from the exchange rate in the subsequent dark measurement. The flux in the snowpack diffusion method was calculated from the concentration difference between the top and the bottom layer as a function of the layer depth, snow porosity and snow temperature by applying Fick's first law of diffusion through porous media and using the diffusion coefficients of 0.139 $cm^{-2}$ $s^{-1}$ and 0.22 $cm^{-2}$ $s^{-1}$ for $CO_2$ and $CH_4$, respectively (Sommerfeld et al. 1993). The snow pack at each sampling point was assumed homogeneous, that is, density changes or ice lenses were not monitored.

### *2.2.2 Fluxes measured using eddy covariance*

The ecosystem scale measurements were conducted with an eddy covariance (EC) method in Siikaneva site (Papers **IV** and **V**). The EC technique is a continuous micrometeorological flux measurement method. The flux is determined as the covariance of the correlation between the vertical wind velocity and the scalar of interest, such as temperature, water vapor, $CO_2$, or $CH_4$ concentration. Both the vertical wind velocity and the scalar are measured at similar rates with fast-response sensors typically at the rate of 10 Hz. The flux is obtained using the following general formula (cf. Baldocchi 2003):

$$F = \overline{\rho_a}\,\overline{w'c'} \tag{1}$$

In the Equation 1, $F$ is the flux, $\rho_a$ is the air density, $w$ is the vertical wind velocity and $c$ is the mixing ratio of the scalar (e.g. $CO_2$). Overbars denote the mean of discrete time averaging and primes denote the residuals from the mean ($w' = w - \overline{w}$ and $c' = c - \overline{c}$). The fluxes in our studies are averaged over 30-minute periods.

Measurements are conducted above the vegetation canopy and the measured fluxes represent an average exchange rate from an area upwind from the measurement point. Therefore the flux estimates reflect the processes at the ecosystem scale. The source area, or the flux footprint, varies continuously with atmospheric stability and wind strength and direction. The change in the footprint does not affect the flux estimates if the spatial variation in the ecosystems is small relative to the footprint. If the horizontal length scale of the heterogeneities is small enough the heterogeneities are smeared by turbulence below the measurement height. In heterogeneous ecosystems, however, the analysis of the source area and knowledge of the degree of spatial variation are necessary for the interpretation of the results (Schmid 2002, Laine et al. 2006)

EC has many advantages: it offers good temporal resolution and the gas exchange estimates can be calculated for different time scales, from half hours to years. The technique is a direct measurement of the flux at the ecosystem scale and the measurement system does not cause disturbance to the ecosystem. The limitations of the method include the assumption of the composition of the source area and often a poor night time data coverage due to the lack of turbulence.

The EC instrumentation in this study included a USA-1 (METEK, Germany) three-axis sonic anemometer/thermometer, a LI-7000 (Li-Cor Inc., USA) closed path analyzer for $CO_2$/$H_2O$ and a tunable diode laser absorption spectrometer (TDL, TGA-100, Campbell Scientific Inc., USA) for $CH_4$. The measurement frequency was 10 Hz. The flux tower (measurement height 3.0 m) was located in a position where the open peatland area extends 200–400 m in all directions (see aerial photograph in Paper **III**).The chosen measurement height was low enough to keep the flux footprint within the open peatland under most conditions and high enough to spatially average the fluxes originating from individual elements composing the surface.

### *2.2.3 Auxiliary measurements: meteorology and vegetation monitoring*

In order to relate the C gas fluxes to prevailing environmental conditions, meteorological parameters (air and peat temperatures, photosynthetically active radiation, precipitation, relative humidity, and water level) were measured continuously at weather stations in both study sites. In addition, water level, and air and peat temperatures in each sample plot were measured simultaneously with the chamber flux measurements.

The amount of vegetation, the species composition and the relative abundance of the species varies both spatially, between locations, and temporally; interannually and over the course of the growing season. Because vegetation is a fundamental controller of the C gas exchange it was important to monitor this variation.

In the permanent gas exchange sample plots, vegetation was monitored monthly during the snow-free period. We employed the method by Wilson et al. (2007) to obtain the vascular green leaf area in each sample plot. In short, the number of the green leaves of each species was calculated in every plot. The average size of the leaves was determined based on the leaf samples outside the plots. To these monthly observations, we fitted a unimodal curve to estimate the continuous development of the species-specific green area in each sample plot. The green area of mosses was determined as a percent cover of moss capitula once during each growing season.

In Siikaneva site, where the ecosystem scale fluxes were of interest, we also conducted a vegetation inventory (Paper **III**). This was a systematic inventory in a 30 m grid that extended to 200 m radius from the EC measurement mast. The inventory data allowed for the identification of the vegetation communities and the quantification of the proportions and average green areas of the communities in different parts of the site.

## 2.3 Data analysis

### 2.3.1 $CO_2$ fluxes measured using chamber method

The main method for analyzing the $CO_2$ flux data measured by chambers (Papers **I** and **III**) was the use of nonlinear regression models. The models served two purposes: 1) the reconstruction of the continuous time series of the $CO_2$ fluxes, and 2) the analysis of the response of the $CO_2$ dynamics to different biotic and abiotic factors.

Because photosynthesis reacts almost immediately to the amount of incoming light, which changes on a time scale of seconds, the rate of photosynthesis can vary very rapidly. Respiration varies over hourly time scales, responding to the variation in temperature and, with a time lag, photosynthesis (Kuzyakov and Cheng 2001, Tang et al. 2005). Therefore, the chamber flux measurements in the field, where environmental conditions cannot be standardized, reflect only a momentary $CO_2$ exchange rate. In this study, the measurements were conducted only weekly or biweekly and cannot be used directly to draw conclusions on the seasonal $CO_2$ exchange or on the differences between the sample plots. This problem can be overcome by modeling the response of the $CO_2$ flux using the environmental conditions during the measurements. With the models and continuous time series of the explanatory variables, it is possible to calculate a $CO_2$ flux rate in any given time. The models also reveal the potential differences in the responses among sample plots, vegetation communities or plant groups.

A semi-empirical modeling approach was adapted from Tuittila et al. (2004). The forms of the response functions have theoretical premises. The parameter values were derived empirically from the data using non-linear regression, but before a model was accepted, we checked that the parameter values were ecologically reasonable. We used PAR, the amount of green area, temperature, and water level as explanatory variable in photosynthesis models and the amount of green area, temperature, and water level as explanatory variables in respiration models. The default versions of the models are given in Eq. 2 ($P_G$) and Eq. 3 (R). However, not all responses could be identified in every case.

$$
\begin{aligned}
\mathrm{P_G} = P_{max}\underbrace{\frac{\mathrm{PAR}}{k+\mathrm{PAR}}}_{I}\underbrace{\exp\left[-0.5\left(\frac{\mathrm{T}-T_{opt}}{T_{tol}}\right)^2\right]}_{II}\underbrace{\exp\left[-0.5\left(\frac{\mathrm{WL}-WL_{opt}}{WL_{tol}}\right)^2\right]}_{III} \\
\times\underbrace{\left[1-\exp\left(-a\mathrm{GA}\right)\right]}_{IV}
\end{aligned}
\tag{2}
$$

The Eq. (2) has the following explanatory variables:

| | |
|---|---|
| PAR | photosynthetically active radiation (µmol m$^2$ s$^{-1}$) |
| T | air temperature inside the measurement chamber ( C) |
| WL | water level relative to the moss surface (cm) |
| GA | green area (m$^2$ m$^{-2}$) |

And the following parameters:

| | |
|---|---|
| $P_{max}$ | potential maximum rate of gross photosynthesis when all factors (PAR, T, WL, GA) are non-limiting |
| $k$ | level of PAR at which $P_G$ reaches 50% of the potential maximum rate |
| $T_{opt}$ | optimum temperature for photosynthesis |
| $T_{tol}$ | temperature tolerance, i.e. deviation from the optimum T at which $P_G$ is 61% of its maximum, if other factors are non-limiting. |
| $WL_{opt}$ | optimum water level for photosynthesis |
| $WL_{tol}$ | water level tolerance, analogous to parameter $T_{tol}$ |
| $a$ | initial slope of the saturating GA response function |

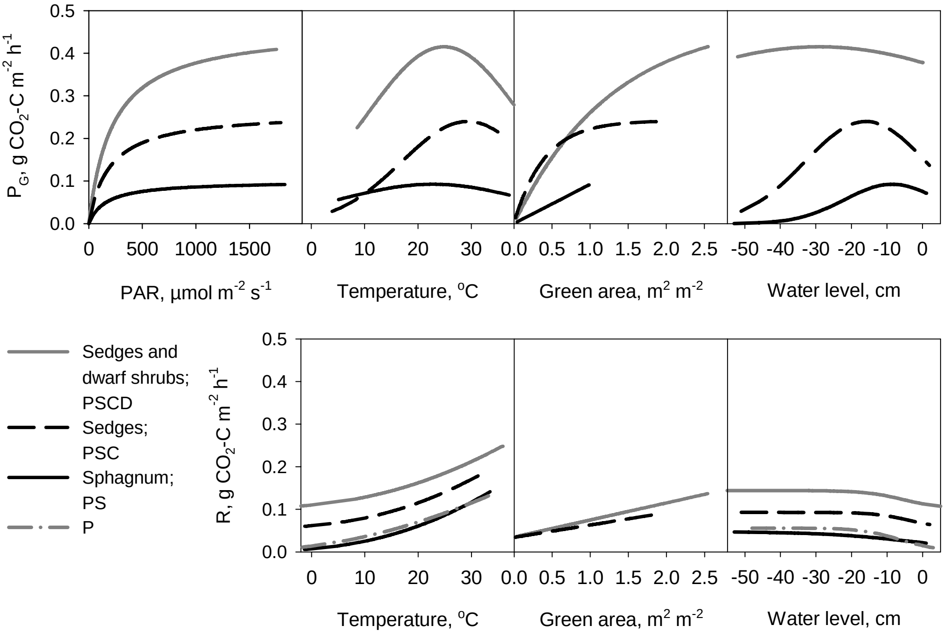

**Figure 1.** Modeled (Eqs. 2 and 3) response of gross photosynthesis ($P_G$) and respiration (R) to photosynthetically active radiation (PAR), air temperature, the amount of green area and water level. Water level is negative when it is below the moss/peat surface. The photosynthetic responses (upper panels) are shown for three plant groups: *Sphagnum* mosses, sedges, and mixed sedge and dwarf shrub vegetation. The respiratory responses (lower panels) are shown for different sample plot types: plots consisting of peat (P); peat and *Sphagnum* mosses (PS); peat, *Sphagnum* mosses and sedges (PSC); and peat, *Sphagnum* mosses, sedges and dwarf shrubs (PSCD). To illustrate the form of the responses, only one variable is allowed to change at the time while other are held constant. Data from Lakkasuo site, Paper **I**.

The photosynthetic response to PAR was described with a saturating function (term I) and the response to T and WL with unimodal (Gaussian) functions (terms II and III). In most cases, the response of photosynthesis to green area was saturating, described either with an exponential rise to maximum function (term IV, Paper **I**) or with a hyperbolic saturating function, similar to the response to PAR (Paper **III**). In case of *Sphagnum* mosses (Paper **I**) or plant communities where the green areas were quite low (Paper **III**), no self-shading could be observed and the response to GA was described as linear. In those cases, the $P_{max}$ term has a slightly different interpretation: it denotes the potential maximum rate of gross photosynthesis when PAR, T and WL are non-limiting and GA (or the term s+GA, Paper **III**) equals 1. The form of the responses is illustrated in Fig. 1. In the plant community scale study (Paper **III**), the water level response (term III) could not be detected in two of the five communities.

$$\mathrm{R} = \underbrace{R_{10}\exp\left[b_1\left(\frac{1}{T_{ref}-T_0}-\frac{1}{\mathrm{T}-T_0}\right)\right]}_{I}\frac{1}{\underbrace{1+\exp\left(-\frac{\mathrm{WL}-b_2}{b_3}\right)}_{II}}+\underbrace{b_4\mathrm{VGA}}_{III} \tag{3}$$

The Eq. (3) has the following explanatory variables:

| | |
|---|---|
| T | air temperature inside the measurement chamber (K) |
| WL | water level relative to the moss or peat surface (cm) |
| VGA | green area of vascular plants ($m^2$ $m^{-2}$) |

And the following parameters:

| | |
|---|---|
| $R_{10}$ | respiration rate at 10 C, when WL is non-limiting and VGA is zero |
| $b_1$ | activation energy divided by the gas constant |
| $T_{ref}$ | reference temperature, set at 283.15 K |
| $T_0$ | temperature minimum at which respiration reaches zero, set at 227.13 K (Lloyd and Taylor 1994) |
| $b_3$ | slope determining the speed and direction of change in R along the WL range |
| $b_2$ | WL at the centre of the fastest change along the WL range |
| $b_4$ | change in respiration per VGA unit |

The response of R to T was exponential and described with a function from Lloyd & Taylor (1994) (term I). Air temperature inside the measurement chamber and soil temperatures in different depths were tested for the model; air temperature explained the variation in respiration best. The response to water level was described with a sigmoidal function (term II), except in the model for *Carex lasiocarpa* lawns (Paper **III**) where the water level gradient was not long enough for that parameterization and the form of exponential decay was used instead. The response to vascular green area was described as linear (term III). Term III was included when vascular plants were present. The form of the responses is illustrated in Fig. 1.

$CO_2$ exchange was reconstructed for the snow free season using the models (Papers **I** and **III**). $CO_2$ exchange during the snow covered season was reconstructed by linearly interpolating the fluxes between the winter measurement days (chamber or snow pack diffusion method) (Paper **III**). The last measurement at the end of and the first measurement at the beginning of the snow-free season were used as a starting and end values for the interpolation.

### *2.3.2 $CH_4$ flux measured using chamber method*

$CH_4$ fluxes were linearly interpolated between the measurement days to create a continuous time series (Papers **II** and **III**). The effect of linear interpolation was evaluated using the EC data and found to cause only a minor uncertainty in the seasonal flux estimate. Seven alternative sets of daily fluxes of every 7th day were extracted from the EC data and linearly interpolated to derive a seasonal estimate. These seven alternative estimates had a standard error of the mean that equaled 3% of the actual EC derived seasonal estimate (Paper **III**).

### *2.3.3 Scaling up from the plant community level to the ecosystem*

In Siikaneva, one of the aims was to study the effect of the spatial variation in the plant community level on the ecosystem C gas fluxes (Paper **III**). Plant communities in the site were defined with TWINSPAN cluster analysis, using the data from the vegetation inventory (Hill 1979, Hill and Šmilauer 2005). The analysis divided the vegetation into seven plant communities which we combined into five so that there were gas exchange sample plots in every community. The chamber measurements in different plant communities provided an estimate of the community specific C gas exchange. The proportion of each plant community within the ecosystem was determined based on the vegetation inventory. Community scale C gas exchange estimates were scaled to the ecosystem level by taking an area weighted mean. In case of $CO_2$, the differences between the vascular green leaf areas in the gas exchange sample plots and in the entire site were taken into account by reconstructing the $CO_2$ exchange using the corrected vascular green leaf areas. To test the effect of the fetch size on the results, the scaling was carried out for three observation radii (90 m, 120 m and 200 m radius from the EC mast). The upscaled estimates were compared with the EC derived estimates for the growing season 2005.

### *2.3.4 Processing of the eddy covariance flux data*

The EC data acquisition was carried out with an in-house Python program BARFLUX (Finnish Meteorological Institute). The fluxes were calculated as half-hourly covariances (Eq. 1) using block averaging. Systematic flux losses were corrected for with empirical functions (Aubinet et al. 2000, Laurila et al. 2005). After data screening, 55% ($CO_2$) and 66% ($CH_4$) data coverage remained for the calculation of the annual balances. Gaps in the time series were filled using regression models ($CO_2$) and linear interpolation ($CH_4$).

# 3 RESULTS AND DISCUSSION

## 3.1 Carbon fluxes at the plant community component scale

### *3.1.1 $CO_2$*

Photosynthesis at the plant community component scale was controlled by PAR, green area, temperature, and water level (Paper **I**). Based on the modeled responses, the optimum water level (parameter $WL_{opt}$ in Eq. 2) for the photosynthesis of *Sphagnum* mosses, sedges, and mixed sedge and shrub vegetation of the lawn level plant community was 8.5, 16, and 29 cm below the moss surface, respectively (Fig. 1, Paper **I**). The photosynthesis of *Sphagnum* mosses had the narrowest and sedges had intermediate tolerance to water level variation (parameter $WL_{tol}$ in Eq. 2). The very wide tolerance range of the mixed sedge and shrub vegetation indicated that such vegetation photosynthesizes equally efficiently in practically any hydrological conditions observed in the study. This wide tolerance range reflects the genuine lack of sensitivity of the shrubs to water level variation (Bubier et al. 2003a) but also may indicate a wider tolerance of mixed vegetation than a vegetation population consisting of only one functional group. Because of the high level of noise in the data, it was not possible to estimate the photosynthesis rate and parameterize the photosynthesis model separately for shrubs by subtracting the modeled sedge and *Sphagnum* photosynthesis from the measured values in the plots with shrubs present.

Differences in the water level responses were reflected in the contribution of the groups to the whole community photosynthesis (Paper **I**). In hydrologically normal conditions, *Sphagnum* mosses were an important component of the plant community, contributing approximately 28% of the community photosynthesis. Their role was emphasized in the beginning and at the end of the growing season when the green area of the vascular plants was low (Fig. 1). However, because of the sensitivity of *Sphagna* to drought, their contribution was reduced to approximately 10% during water level drawdown conditions (Paper **I**). The results agree with earlier observations on the sensitivity of *Sphagnum* photosynthesis to moisture conditions (Silvola and Aaltonen 1984, Rydin and McDonald 1985a, Schipperges and Rydin 1998).

Both the annual (Paper **I**) and seasonal (Fig. 2) variation in the photosynthesis of sedges was mostly related to the variation in their green area, but water level conditions also had an impact. Sedge photosynthesis was slightly suppressed in water level drawdown conditions. Furthermore, as shrub photosynthesis increased in drier conditions, the relative contribution of sedges to the community photosynthesis changed from 60% in hydrologically normal conditions to 30% in water level drawdown conditions (Paper **I**).

Respiration at the plant community component scale was controlled by temperature, water level and vascular green area (Paper **I**). Because of the high level of noise in the respiration measurements, the models could not be parameterized for the different components, using the subtraction method, but they were parameterized by the plot types. All plot types showed similar temperature and water level responses.

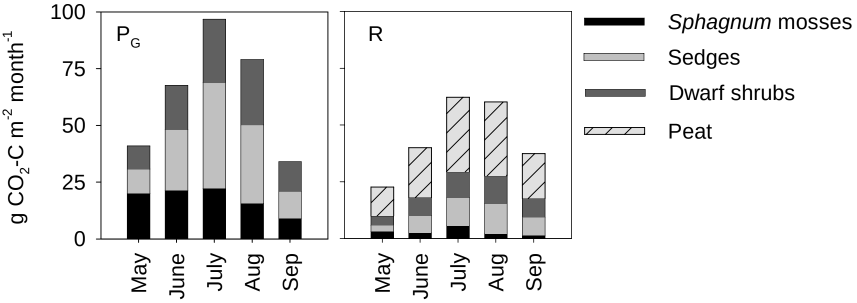

**Figure 2.** Monthly gross photosynthesis ($P_G$) and respiration (R) in Lakkasuo site, calculated as four year means. The fills in the bars show the contribution of each plant community component (*Sphagnum* mosses, sedges, dwarf shrubs and the underlying peat) to the total fluxes.

Both in Lakkasuo (Paper **I**) and Siikaneva (Paper **IV**), peat respiration accounted for approximately 50% of the total respiration in hydrologically normal conditions. Similar ratios between autotrophic and heterotrophic respiration have been obtained in earlier studies (Moore et al. 2002, Crow and Wieder 2005). Peat respiration and vascular plant respiration showed a clear seasonal pattern and their ratio was rather consistent throughout the growing season (Fig. 2). Relative to the amount of leaf area, shrubs had a higher respiration rate than sedges (Paper **I**), woody tissue constituting a significant proportion of the shrub respiration (Levy and Jarvis 1998, Saveyn et al. 2008). Peat respiration increased in water level drawdown conditions, while plant-derived respiration showed little variation between conditions (Papers **I** and **IV**).

### *3.1.2 Methane*

Sedges were the most important plant group in regulating $CH_4$ fluxes (Paper **II**). In hydrologically normal conditions, the presence of sedges had a major impact increasing the $CH_4$ fluxes. $CH_4$ emissions were more than twice as high in the plots where sedges were present than in the plots where they had been removed. Similarly, in other sedge dominated sites, plant-mediated flux has been observed to account for 75 to 97% of the total flux (Whiting and Chanton 1992, Schimel 1995, Kelker and Chanton 1997). However, only the presence, rather than the number of sedges was significant within the range of sedge green leaf areas observed in this study (Fig. 3).

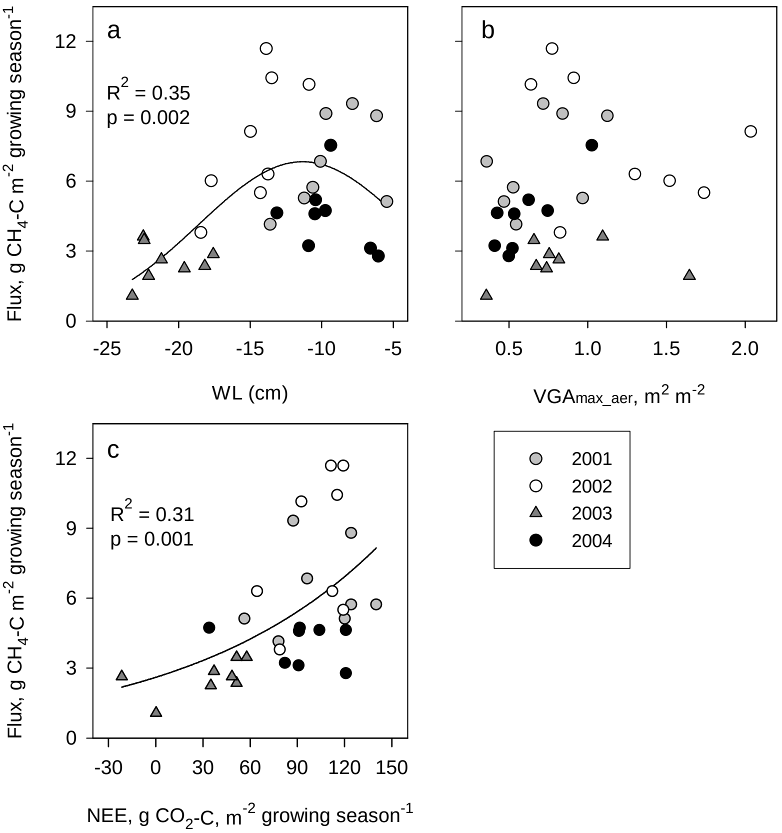

**Figure 3.** The relationship between the plot-wise seasonal (June-September) CH$_4$ emission and **a)** seasonal mean water level (WL), **b)** peak season vascular green area of aerenchymatous plants (VGA$_{max}$_aer) and **c)** seasonal net ecosystem CO$_2$ exchange (NEE). Water level is negative when it is below the moss surface. NEE is positive when the system is a sink of atmospheric CO$_2$. In **a)** a Gaussian and in **b)** an exponential curve was fitted, using data points from all years. R$^2$ and p are the coefficient of determination and the significance level of the regression, respectively. Data from Lakkasuo control subsite, plots with unmanipulated vegetation.

The vegetation removal treatments suggested that the presence of shrubs may have a slightly attenuating effect on CH$_4$ fluxes (Paper **II**). The possible reasons behind these indicative results are the decreased substrate supply to the anaerobic decomposition chain due to the increased biomass allocation of sedges from the roots to the shoots in the presence of shrubs (Aerts et al. 1991), and the chemical suppression of methane fluxes by certain lignin compounds (Yavitt et al. 2000) that might be linked to the presence of shrubs (Paper **II**). However, more research on this topic needed.

During water level drawdown, the presence or absence of the vegetation components had no effect on the fluxes (Paper **II**), supporting the findings by Waddington and others (1996) and Strack and others (2006b). The fluxes were equally low in all vegetation treatment types. Only a small fraction of the sedge roots reach the $CH_4$ production zone in water level drawdown conditions. As a result, most of the recently fixed carbon, which is a more easily decomposable substrate for the anaerobic decomposition chain than the old, recalcitrant peat, is not available for $CH_4$ production. Water level acts as a switch. Only after passing through the water level control can the vegetation composition have an impact on the fluxes.

## 3.2 Carbon fluxes at the plant community scale

### *3.2.1 CO$_2$*

The plant communities in Siikaneva differed in their $CO_2$ exchange (Paper **III**). Photosynthesis varied more between the communities than respiration, thus controlling the variation in NEE. *Carex lasiocarpa* lawns and hummocks had the highest, *Eriophorum vaginatum* lawns and *Carex rostrata* lawns had intermediate and hollows had the lowest NEE. This pattern is similar to the pattern in peak season VGAs. Besides spatial variation, temporal variation in the fluxes was considerable. The four-year study in Lakkasuo showed marked annual variation in the fluxes. The growing season NEE averaged 120 g $CO_2$-C during the years 2001, 2002 and 2004, but only 34 g $CO_2$-C during the dry year 2003 (Paper **I**). The $CO_2$ exchange estimates in Lakkasuo in hydrologically normal conditions were similar to the estimates in the Siikaneva lawn level communities. The experimental water level drawdown in Lakkasuo (Paper **I**) and the drought period in Siikaneva (Paper **IV**) caused a decrease in photosynthesis and an increase in respiration, resulting in a reduced $CO_2$ sink function.

### *3.2.2 Methane*

The $CH_4$ emissions from the Siikaneva plant communities ranged from 6 (hummocks) to 19 (*Carex lasiocarpa* lawns) g $CH_4$-C growing season$^{-1}$ (June-September) (Paper **III**), and they were slightly higher in 2004 than in 2005. In Lakkasuo, the seasonal $CH_4$ emission in the control site was on average 6.5 g $CH_4$-C growing season$^{-1}$ during the hydrologically normal years (2001, 2002 and 2004) and only 2.5 g $CH_4$-C growing season$^{-1}$ during the dry year 2003. Although the $CO_2$ fluxes in Lakkasuo site were similar to those in Siikaneva lawns, they showed lower $CH_4$ fluxes, despite their similar VGAs and WLs. This demonstrates how large the site-to-site variation can be, even between peatlands located in the same region. Spatial variation in $CH_4$ fluxes was related to water level and NEE (Fig. 3). The water level response was unimodal, similar to Strack et al. (2004). In peatlands, the plant communities in the wettest microforms are often associated with the sparsest vascular plant cover and lowest net $CO_2$ uptake rate (Paper **III**, Waddington and Roulet 2000, Laine et al. 2007b). Thus, less substrate for $CH_4$ production is available in those communities.

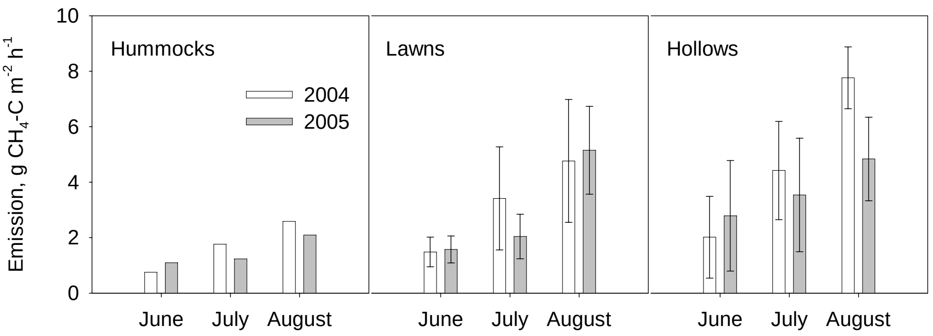

**Figure 4.** Mean measured methane emission in hummocks, lawns and hollows in Siikaneva site in mid-June, Mid-July and Mid-August. Water level during the drought period in July 2005 was 20 cm lower than in July 2004.

Both the experimental water level drawdown and natural droughts had an attenuating effect on the fluxes. The experimental water level drawdown in Lakkasuo significantly decreased the $CH_4$ fluxes, almost to zero (Paper **II**). In Siikaneva, the fluxes in all microforms were lower during the dry July 2005 than during the wet July 2004, while the differences were microform specific during the other months (Fig. 4).

## 3.3 Carbon fluxes at the ecosystem scale

### *3.3.1 $CO_2$*

Siikaneva was a net sink of atmospheric $CO_2$ during the years 2004 and 2005 taking up, on average, 56 g $CO_2$-C $a^{-1}$ (Paper **IV**). The estimate agrees with the observations from other sedge dominated fens (Table 1). The seasonal cycle in the $CO_2$ exchange was considerable. The fen acted as a $CO_2$ sink during the five summer months (May-September) and as a small source of $CO_2$ to the atmosphere during the rest of the year. $CO_2$ fluxes had a clear diurnal pattern during the snow free season that followed the radiation conditions (Paper **IV**). Winter fluxes showed little variation (Paper **IV**). Their contribution to the annual NEE was, however, significant, approximately 25%.

By combining the photosynthetic and respiratory water level responses, it was concluded that the optimum water level for NEE in Siikaneva at the ecosystem scale was approximately -10 cm (Paper **IV**). This value matches the growing season average water level (-10 cm in 2004 and -13 in 2005), calculated from the water level measurements in the gas exchange sample plots. This optimum water level in Siikaneva is, interestingly, similar to that in an Irish blanket bog (Laine et al. 2007a) and in a Swedish poor fen (Yurova et al. 2007).

During July 2005 there was a short drought period, when the water level dropped to 25 cm below the surface. This deviation from the optimum water level was reflected as lower NEE (i.e. weaker net $CO_2$ sink) (Paper **IV**). The increase in respiration, mainly peat respiration, was the main factor in the lowered NEE, but also photosynthesis was slightly suppressed. Despite the short drought in 2005, the annual balances were quite similar during both study years (Paper **IV**).

### *3.3.2 Methane*

In Siikaneva, the annual $CH_4$ emission, measured by EC, was 9.4 g $CH_4$-C $m^{-2}$ (Paper **V**). The fluxes during the snow free period accounted for 91% of the annual flux. The annual and growing season $CH_4$ emissions from Siikaneva were typical for a northern fen (Table 1). $CH_4$ losses decreased the annual carbon balance estimate by 22% (Paper **V**).

The $CH_4$ fluxes showed a pronounced seasonal pattern (Papers **III** and **V**), but no diurnal variation (Paper **V**). Both the presence (Suyker et al. 1996, Juutinen et al. 2004) and the absence (Hyvönen et al. 1998, Kormann et al. 2001, Juutinen et al. 2004) of a diurnal cycle in wetlands has been previously observed. The diurnal cycle is strong in sites where the plant-mediated transport is based on pressured induced convection (Chanton et al. 1992, Kim et al. 1998). The $CH_4$ transport by *Carex* and *Eriophorum*, the dominant sedge genera in this study, is based on diffusion (Schimel 1995, Kutzbach et al. 2004). Besides transport through stomata that shows diurnal variation, cuticular conductance, not showing diurnal variation, is also an important mechanism of $CH_4$ release (Morrissey et al. 1993, Greenup et al. 2000). This would explain the absence of a diurnal pattern in Siikaneva.

Temporal variation in $CH_4$ fluxes at the daily scale was mainly controlled by peat temperature (Paper **V**). The temperature relationship was rather peculiar: no relationship could be seen at temperatures $> 12$ C (Paper **V**). These temperatures occurred from mid-July through August. A period of high fluxes that coincided with a rapid deepening of the water level was observed in mid-July. The change in water level probably caused a degassing of the methane pool in the soil. Simultaneously, the methane concentration in the soil, sampled using a semi-permeable silicon tubes, showed a marked decrease (Riutta et al. 2007).

Daily variation in $CH_4$ fluxes during the year 2005 was not controlled by the water level (Paper **V**) and the between-community variation in the fluxes was not directly linked to the water level of the community, either (Paper **III**). Nevertheless, the $CH_4$ emissions were lower during the drought period in July 2005 than during the wet July 2004 (Fig. 4). Treat and others (2007) found that the relationships between $CH_4$ fluxes and controlling factors are clearest in monthly, rather than daily, time scales, because time-averaging reduces noise in the data. Such analysis, however, requires multi-year data sets that were not yet available in Siikaneva site. Within a lawn community in Lakkasuo, the seasonal average water level and $CH_4$ flux had a relationship (Fig. 3). However, the water level explained the year-to-year variation in the fluxes rather than the spatial variation within a given year.

## 3.4 Scaling up from the plant community level to the ecosystem

As is typical of fen ecosystems, both the microtopographical variation and the variation in plant community composition in Siikaneva were modest (Paper **III**). The fen was dominated by lawn vegetation. Some hummocks and hollows were also present. Despite the modest variation in microtopography and vegetation, however, the study on the spatial variation on the C gas fluxes showed that plant communities differed markedly in their C gas exchange (Paper **III**). Consequently, to provide C gas exchange estimates for the entire fen ecosystem, it was important to take the spatial variation in fluxes and in vegetation composition into consideration. The results indicate that, were the proportion of the plant communities to change in a changing climate, it would have important consequences for the carbon balance of the mire (Paper **III**).

The chamber based estimates for the growing season NEE and $CH_4$ emission were in good agreement with the EC derived estimates (Paper **III**). However, the annual estimates differed more between the two methods. Outside the growing season, the sporadic measurements by the chamber and snowpack diffusion techniques were not representative for the entire autumn and winter period. The frequency of the winter measurements by the chamber and snow pack diffusion techniques was insufficient for the proper estimation of the winter time emissions. Rather, the measurements serve as an estimate of the magnitude of the fluxes during winter. Therefore, the annual fluxes estimated by the EC method (Paper **IV**, Paper **V**) are more reliable than those estimated by the chamber method (Paper **III**).

### 3.5 Synthesis of the water level drawdown impact

The experimental water level drawdown (Lakkasuo) and natural droughts (Lakkasuo during the growing season 2003 and Siikaneva during July 2005) caused changes in the carbon gas exchange. Of the plant community components, *Sphagnum* moss photosynthesis clearly decreased, sedge photosynthesis slightly decreased and dwarf shrub photosynthesis increased during water level drawdown (Fig. 5, Paper **I**). Because the responses of the components were compensatory, changes in photosynthesis and NEE were smaller at the plant community scale than at the plant community component scale (Fig. 5, Paper **I**). The results indicate that functional diversity buffers the ecosystem against environmental variability. If the drier conditions persist, the species abundance may gradually shift from sedge and *Sphagnum* dominance towards dwarf shrub dominance. Studies on the effects of the long-term water level draw-down (forestry drainage) on vegetation indicate that at the first stage of the drawdown induced succession, sedges decline and shrubs become more abundant (Laiho et al. 2003).

The water level drawdown resulted in a smaller $CO_2$ sink function, due to the decrease in photosynthesis and increase in respiration (Fig. 5, Papers **I** and **IV**). Because of the complementary responses of the plant groups, the reduced $CO_2$ sink function was mainly caused by the increase in peat respiration (Papers **I** and **IV**).

$CH_4$ fluxes decreased during the natural droughts and as a result of the water level drawdown treatment (Fig. 4, Fig. 5, Paper **II**). The moderate and short drought in Siikaneva during July 2005 had less impact on the fluxes than the long and severe drought in Lakkasuo from mid-June to September 2003. (Fig. 5). In Lakkasuo, the three-year experimental water level drawdown had a stronger impact than the natural drought. While $CH_4$ oxidation responds to environmental changes within a few days (Blodau and Moore 2003), $CH_4$ production recovers more slowly after a drought period, with an equilibration time of months (Freeman et al. 2002, Blodau and Moore 2003).

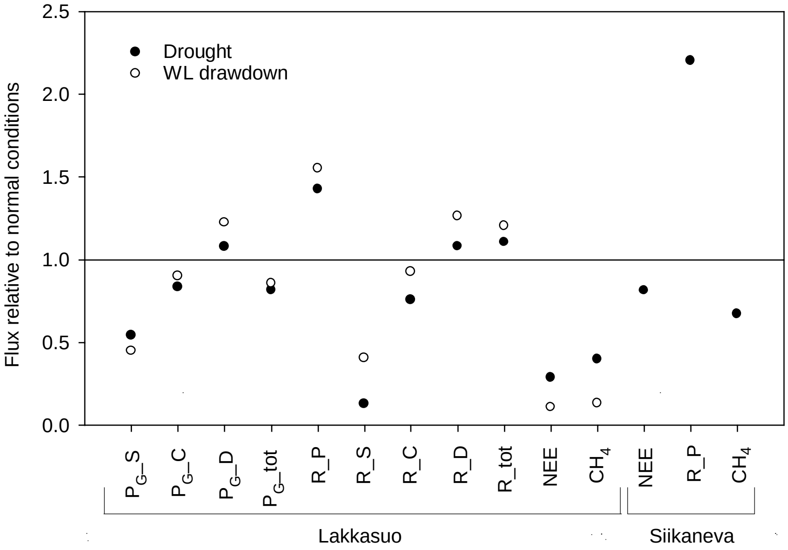

**Figure 5.** Impact of natural drought and experimental water level (WL) drawdown on photosynthesis ($P_G$), respiration (R), net ecosystem $CO_2$ exchange (NEE), and $CH_4$ emissions. The impact of the natural drought on the $CO_2$ and $CH_4$ fluxes in Lakkasuo is expressed as the ratio between the fluxes during the dry season 2003 and the average of the hydrologically normal seasons 2001, 2002 and 2004 in the control subsite. The impact of the experimental WL drawdown on $CO_2$ fluxes in Lakkasuo is expressed as the ratio between the average simulated fluxes in prevailing WL conditions and in the 14 cm WL drawdown conditions. The impact of the experimental WL drawdown in $CH_4$ fluxes in Lakkasuo is expressed as the ration between the fluxes during the WL drawdown treatment years (2002-2004) in the control and water level drawdown subsites. The impact of the natural drought in Siikaneva is determined as the ratio between the fluxes during the dry July 2005 and the hydrologically normal July 2004. In Lakkasuo, the impact is shown for the different plant community components (S-Sphagnum mosses, C-sedges, D-dwarf shrubs and P-peat) as well as for the whole community (tot). In Siikaneva, the NEE is measured by the eddy covariance technique and the peat respiration and $CH_4$ fluxes by chambers.

Deeper water levels do not necessarily stimulate $CH_4$ oxidation but the decrease in fluxes occurs mainly through changes in $CH_4$ production (Freeman et al. 2002) or transport. Furthermore, sulfate availability in the pore water increases during the low water level regime (Freeman et al. 1993, Dowrick et al. 2006), benefiting sulfate-reducing microorganisms that may out-compete methanogens for substrate (Yavitt and Lang 1990). Strack and others (2004, 2006b, 2007) showed that the water level response depends on the initial water level and on the plant community composition. For example, inundated hollows with sparse vascular cover may be colonized by sedges in drier conditions, causing no changes or an increase in $CH_4$ emissions (Strack et al. 2006b). This is in agreement with the Siikaneva results that the $CH_4$ fluxes are similar from lawns and hollows, the former having denser sedge cover and NEE and the latter having a higher water level and, therefore, larger $CH_4$ production zone (Paper **III**).

The results of this study examine the short term responses of a fen ecosystem and its components to water level drawdown. The results are applicable to climatic situations where droughts become more frequent but wet periods are still frequent enough as to maintain the fen vegetation composition relatively unchanged, consisting of *Sphagnum* mosses, sedges and dwarf shrubs. In case of a permanent water level drawdown, the changes in vegetation composition will mediate the changes in the carbon gas dynamics. The photosynthesis rate may recover when species adapted to drier conditions become more abundant and the decomposition rate may slow down due to the more recalcitrant litter (Laiho 2006). Therefore, the results of this study do not reflect the peatland carbon cycle in permanently drier climate.

### 3.6 Uncertainty in the estimates

The uncertainty in the flux measurements is considerable. In Siikaneva, the uncertainty in the EC-derived annual NEE and $CH_4$ emissions was estimated to be 25 and 3% for $CO_2$ and $CH_4$, respectively (Papers **IV** and **V**). The uncertainty analysis of the $CO_2$ fluxes considered more sources of error than that of the $CH_4$ fluxes and it is therefore a more realistic estimate of the magnitude of the uncertainty. The uncertainty was related to the instrumental errors, chosen filtering criteria, and gap-filling technique. Baldocchi (2003) estimated the error in EC derived annual NEE to be less than 50 g C $m^{-2}$ when measurements come from nearly ideal sites. This is a high figure relative to the typical annual NEE in fens (Table 1).

The uncertainty in the chamber derived estimates was even larger because of the limited spatial and temporal coverage and uncertainty in the temporal interpolation and spatial upscaling that were needed to estimate the ecosystem scale fluxes (Paper **III**). Both the reconstruction of the continuous time series and the upscaling caused considerable uncertainty in the estimates (Table 3 in Paper **III**). In addition, spatial variation, an inherent characteristic of a peatland ecosystem, was a source of further uncertainty. The total uncertainty in the seasonal NEE and $CH_4$ emissions was estimated to be 40% and 15%, respectively (Paper **III**). The uncertainty analysis did not take into account all sources of error, for example instrumental uncertainties. These values should, therefore, be only considered as indicative.

In Lakkasuo, the main aim was to reliably determine the impact of the water level drawdown, rather than to derive as accurate $CO_2$ exchange estimates as possible. As the results on the response of $CO_2$ exchange to water level drawdown were based largely on modeling, the uncertainty in the results that was related to the uncertainty in the model parameters was assessed (Paper **I**). The exercise showed that the impact of the water level drawdown and the role of the plant community components were evident enough as not to be obscured by the small changes in the model parameter values. In the Lakkasuo study (Papers **I** and **II**), the largest source of uncertainty is related to the vegetation removal treatments: the manipulations can never fully represent the vegetation components of an intact ecosystem. However, the results are consistent with the previous observations on the role of peat respiration (Crow and Wieder 2005), the sensitivity of *Sphagnum* mosses to variation in moisture conditions (e.g. Rydin and McDonald 1985b), the response of sedges and shrubs to drought (Bubier et al. 2003b), and the role of vegetation in $CH_4$ fluxes under different water level regimes (Waddington et al. 1996). Therefore, the results can be considered at least qualitatively reliable.

# 4 CONCLUSIONS

Fen ecosystem $CO_2$ and $CH_4$ dynamics during changing hydrological conditions was studied at different spatial scales, namely plant community component (*Sphagnum* mosses, sedges, dwarf shrubs and the underlying peat), plant community (hummocks, lawns and hollows) and ecosystem scale. The study shows that vegetation composition and water level impact are closely coupled. The response of the system to variations in hydrological conditions depends on the plant community composition. The photosynthesis of *Sphagnum* mosses and sedges decreases during water level drawdown conditions whereas the photosynthesis of dwarf shrubs increases. Consequently, functional diversity buffers the ecosystem against environmental variability. Because spatial variation between in C gas dynamics between the plant communities is considerable, their proportions determine the ecosystem scale fluxes. Thus, a shift in the community proportions during changing climatic conditions modifies the ecosystem fluxes.

The water level drawdown has a dual impact on the peatland ecosystem, and as a result, on the climate system. In water level drawdown conditions, the fen ecosystem becomes a smaller $CO_2$ sink and smaller $CH_4$ source to the atmosphere. However, if the drier conditions persist, changes in vegetation composition will mediate the changes in the carbon gas dynamics. Therefore, the results of this study are applicable to the short term impacts of the water level drawdown and to climatic situations where droughts become more frequent but there are still enough wet periods to maintain the fen vegetation composition relatively unchanged, consisting of *Sphagnum* mosses, sedges and dwarf shrubs.

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