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CARBON GAS FLUXES IN AN IRISH LOWLAND BLANKET BOG

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Declaration

I declare that this thesis has not been previously submitted as an excercise for a degree at the National University of Ireland or any other university and I further declare that the work embodied in it is my own.

Anna Laine

Summary

Peatlands have accumulated a significant amount of carbon (C) since the last ice age. Currently pristine peatlands affect the atmospheric concentration of greenhouse gases by being a small sink of carbon dioxide (CO_2) and a source of methane (CH_4). However, large spatial variation has been observed in the flux rates within and between peatlands, which is linked to water level and vegetation characteristics. In this study, CO_2 and CH_4 exchange was studied in a lowland blanket bog. Fluxes were measured in four different vegetation communities along a water level gradient, namely hummocks, high lawns, low lawns and hollows. Lawns were the most common vegetation community in the bog. During the study period the bog acted as a moderate C sink. The net ecosystem CO_2 exchange varied between the vegetation communities in the order hummock > high lawn > low lawn > hollow and the CH_4 flux varied in the order hollow > low lawn > high lawn > hummock. The spatial variation in fluxes was primarily controlled by the water level. The seasonal dynamics in the gas fluxes followed the changes in temperature and vegetation cover. Flux rates were lowest, but still noteworthy, during winter and highest during the second half of the summer. The peatland C balance is sensitive to changes in hydrological conditions; therefore it is projected that climate change will affect peatlands via changes in water level. The water level was raised and lowered experimentally, following which, gas fluxes were monitored during one year. Water level drawdown increased ecosystem respiration and gross photosynthesis and decreased the CH_4 flux in all vegetation communities. When the water level was raised, the ecosystem respiration and gross photosynthesis decreased and the CH_4 flux increased. Low lawns were an exception, insofar that their gross photosynthesis increased after water level was raised.

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1 Introduction

Globally peatlands cover circa 4 million km^2 (Lappalainen, 1996). This is equivalent to 2.7 % of the earth's land area. Despite the small coverage, peatlands are an important soil carbon (C) store. Since the last ice age northern peatlands have accumulated 450 Pg of C into peat; this represents 1/3 of the global soil carbon pool (Gorham, 1991). The C cycle in peatlands involves processes such as primary production (i.e. carbon dioxide (CO_2) uptake), plant and soil respiration (i.e. CO_2 release) and methane (CH_4) production and consumption. The high water level, characteristic of peatlands, prevents the complete decomposition of plant litter and favours the accumulation of organic matter as peat (Moore, 1975).

A typical feature of many peatlands is a patterned surface structure composed of microforms (ridge, hummock, lawn, hollow, pool) (Foster and Glaser, 1986; Lindsay, 1995). The microforms have distinct vegetation communities, which are supported by different water levels. Due to the differences in water level and vegetation, CO_2 and CH_4 fluxes differ between microforms (e.g. Alm et al., 1997; Heikkinen et al., 2002a).

During the past decades the atmospheric concentrations of greenhouse gases (GHG) have increased noticeably, which is causing climate change (IPCC, 2001). The role of peatlands in regulating climate is many faceted. On one hand peatlands are a C sink and have removed a large quantity of CO_2 from the atmosphere. On the other hand pristine peatlands are a large source of $CH_{4,}$ which is a powerful GHG (Lelieved et al., 1998). Since the C cycle in peatlands is sensitive to changes in climate, especially changes in hydrological conditions (e.g. Alm et al., 1999b) climate change also affects peatland functioning.

CO_2 and CH_4 flux dynamics in blanket bogs are poorly understood and the majority of studies have been carried out in the UK (e.g. Chapman and Thurlow, 1996; Hargreaves and Fowler, 1998; MacDonald et al., 1998). Studies at a blanket bog in southwest Ireland have been ongoing since August 2002. Eddy covariance (EC) has been used to measure net ecosystem exchange (NEE) (Sottocornola and Kiely,

2005) and an extensive vegetation survey was carried out in August 2005 (Unpublished data, Sottocornola 2005). In addition measurements of DOC in surface runoff water commenced in 2004. The research described here is based at the same site.

In this study we first selected 21 sample plots representative of the different vegetation communities (microforms). Using chamber methods we measured CO_2 and CH_4 fluxes at regular intervals over a 29 month time period (June 2003 – September 2005), which covered three growing seasons. The overall aim of the study was to measure the atmospheric exchange of greenhouse gases, CO_2 and CH_4, and to examine the role of these gas fluxes in the C budget of different vegetation communities. The measurements were made in the vegetation community level, since this is the scale of the spatial variation in peatland C gas exchange. The study was divided into four complementary sub-projects, with each sub-project having specific aims:

1. Pattern in vegetation and CO_2 dynamics along water level gradient in a lowland blanket bog (Chapter 4)
    1. Characterize the moisture gradient in vegetation
    2. Examine the controls on gross photosynthesis (P_G) and ecosystem respiration (R_E) along the moisture gradient
    3. Study the temporal variation in CO_2 exchange.

2. Methane flux dynamics in an Irish lowland blanket bog (Chapter 5)
    1. Define the environmental controls on spatial variation in CH_4 flux
    2. Quantify the CH_4 flux of different vegetation communities
    3. Investigate seasonal variation in CH_4 efflux.

3. The impact of changed water level on CO_2 and CH_4 fluxes along the vegetation gradient in a lowland blanket bog (Chapter 6)
    1. Study the impact of water level drawdown on vegetation, CO_2 and CH_4 fluxes
    2. Study the impact of flooding on vegetation, CO_2 and CH_4 fluxes

4. Estimating net ecosystem exchange in a patterned ecosystem: example from blanket bog (Chapter 7)

1. To investigate the variation in NEE between microforms
2. To compare the EC and chamber estimates of NEE over short (half-hour, day) and long (month, year) time periods
3. To investigate the effect of different environmental conditions on the reliability of the methods
4. To investigate how the patterned microform structure and shifting footprint affects the performance of the EC method

2 Literature review

2.1 Greenhouse gases and climate change

The thin and fragile envelope of air, the atmosphere, plays an important role in life on Earth, since it greatly affects the environment in which we live. The atmosphere is mainly composed of nitrogen (N_2) and oxygen (O_2), however, it is the trace gases such as water vapour (H_2O), carbon dioxide (CO_2) and methane (CH_4) that cause the greenhouse effect and maintain the Earth's temperature suitable for life (Brasseur et al., 1999). In the greenhouse effect the atmosphere permits the entry of short wave radiation but does not allow longer wave radiation to exit (Wayne, 2000). Therefore, the lower atmosphere and surface remains warm. The atmospheric concentrations of greenhouse gases (GHG) that trap radiation and heat in the atmosphere, are increasing (IPCC, 2001). This is causing global warming, which in turn causes climate change with potential consequences for every aspect of life. Carbon dioxide (CO_2) and methane (CH_4) are the most important GHG and since 1750, the atmospheric concentrations of these gases have increased by 31 and 151 %, respectively, (IPCC, 2001). Terrestrial ecosystems and the climate system are closely coupled since in the biological cycle CO_2 is taken up in photosynthesis and released in respiration of vegetation, while both CO_2 and CH_4 are produced in and released from soils as an end product of the decomposition processes. The human induced effect on climate change is superimposed on natural climate variation (Brasseur et al., 1999), however, there is little doubt that the major share of the changes in GHG concentrations is caused by anthropogenic emissions: fossil fuel burning and land use change (IPCC, 2001).

The global climate has been in a state of change for 420,000 years and the temperatures closely correlate with the atmospheric concentrations of CO_2 and CH_4 (Petit et al., 1999). The distinctive difference in the current trend in global warming is its magnitude and that it is induced by human activity (IPCC, 2001). The human influence started some 2000 years ago with the clearing of forest for agricultural land (Brasseur, et al. 1999). The most dramatic changes in the chemical composition of atmosphere occurred after the industrial revolution (Brasseur et al.,

1999) so much so that the increase in the atmospheric concentrations of CO_2 and CH_4 in the intervening period are unprecedented during the past 420,000 years (Petit et al., 1999).

Globally, the average surface temperature is predicted to increase by 1.4 to 5.8 °C by 2100 and also precipitation is projected to increase (IPCC, 2001). Moreover, the extreme events, such as intense precipitation, summer heat waves and gale events are also likely to increase (IPCC, 2001). The changes can already be seen in the forms of intense El Niño events, summer droughts in America and hot summers and violent winter storms in Europe (Wayne, 2000). Ireland is mirroring the global changes in climate with a delay due to the buffering of the Atlantic Ocean (Sweeney et al., 2002). Similar to global trends, changes in temperatures and precipitation and hence in evapotranspiration are projected to occur. Both winter and summer temperatures are expected to rise. The increases in January temperatures are projected to be about 1.5 ºC by 2050 and approximately 2.5 ºC by 2075, while the increase in summer temperature would be approximately 2 ºC by 2050 (http://unfccc.int/resource/docs/natc/irenc03.pdf). The change is projected to be stronger in the midlands than in the western part of the country (Sweeney and Fealy, 2002). Winter precipitation is expected to increase, especially in the north west, while summers become drier, especially in the south and east (Sweeney et al., 2002). This would intensify the moisture gradient within the country. Increased summer temperatures may result in higher evapotranspiration and together with reduced summer precipitation this may cause soil moisture deficits and drought stress, especially in the midlands and eastern part of the country.

The North Atlantic Oscillation (NAO) has a strong impact on the climate weather conditions in Europe, but especially in western Ireland where NAO explains 30 to 50% of variation in wintertime temperatures (Sweeney et al., 2002). Over the last 30 years the trend has been towards a positive phase of NAO, which means warmer and wetter than average conditions are likely to prevail in northern Europe (Visbeck et al., 2001). The interaction between human driven climate change and NAO are not well known (Mc Grath et al., 2005).

2.2 Peatlands in global carbon cycle

Peatlands have a key role in controlling the terrestrial carbon (C) cycle, with a dual effect on atmospheric C gas concentrations. Peatlands act as a long-term sink of C, owing to the CO_2 uptake in photosynthesis and incomplete decomposition of the organic matter in water logged, cold and acidic conditions (Moore, 1975). The residual organic matter, peat, has a high C content of about 50 % (Clymo, 1983; Malmer and Wallén, 2004). Estimates of the C reservoir in the northern (boreal and arctic) peatlands alone range from 270 to 455 Pg of C (Gorham, 1991; Turunen et al., 2002). These estimates include ~ 80 % of world's peatlands. For Irish peatlands an estimate of 1.07 Pg is given by Tomlinson (2005). The long term average annual C accumulation rate in different boreal peatlands has ranged from 17 to 29 g m^{-2} (Clymo et al., 1998; Gorham, 1991; Laine et al., 1996; Turunen et al., 2002). The estimation of the C reservoir of peatlands is, however, difficult due to the lack of comprehensive and comparable data on peatland distribution and coverage and also due to the large spatial variation in peat depth (Joosten and Clarke, 2002). Some reasons for the lack of knowledge are that peatlands form a complex landscape mosaic together with non-peatlands; they can be difficult to identify from the air and may be inaccessible on the ground. In addition, their depth and profile bulk density cannot be determined by remote sensing means (Clymo et al., 1998; Gorham, 1991).

The climate cooling effect of peatlands by reducing the atmospheric CO_2 concentration has been emphasized (Franzén, 1994). However, it should not be forgotten that peatlands are an important natural source of CH_4 (Huttunen et al., 2003; Lelieved et al., 1998), which has a higher instantaneous infrared absorption but a relatively short lifetime compared to CO_2 (IPCC, 2001). Globally wetlands, a group into which peatlands belong, contribute 20 to 30 % of the total CH_4 emissions (IPCC, 2001). Similar to C sequestration, the estimates of CH_4 emissions are questionable and are likely to underestimate fluxes due to the high spatial and temporal variation in flux source (Huttunen et al., 2003). Different studies have found strongly varying emissions especially between the geographic regions. Crill, et al. (1988) and Cao, et al. (1996) estimated annual global CH_4 emission of 70 to

96 Tg yr^{-1}. Huttunen, et al. (2003) however, estimated similar emission rates solely for Fennoscandian peatlands as Cao, et al. (1996) did for the whole northern boreal and tundra peatlands. The estimate of Lelieved, et al. (1998) is somewhat higher, with wetlands estimated as emitting globally 145 ±30 Tg yr^{-1}, of which 60 % comes from tropical wetlands and most of the prevailing 40 % from boreal wetlands.

Global Warming Potential (GWP) is often used to compare the climate impacts of different GHGs (IPCC, 2001). GWP describes the radiative effect of pulse emission over a specified time horizon (IPCC, 2001). The GWP of CH_4 is 62, 23 and 7 over 20, 100 and 500 years time horizons, respectively. Due to the CH_4 emissions, the GWP of peatlands is positive (i.e. warming) over a short time horizon (less than 100 yr) but over longer time horizons the GWP of peatlands can become negative (i.e. cooling) (Whiting and Chanton, 2001). Frolking et al. (2006) criticised the suitability of GWP in the case of pristine peatlands, since peatlands do not emit isolated annual gas pulses, but are persistent sinks of atmospheric CO_2 and sources of atmospheric CH_4. They suggested that the current and future radiative forcing of peatlands depends on all the previous gas emissions and that after the CH_4 emissions have reached equilibrium in the atmosphere (about 50 years of emissions) the continuing CO_2 sequestration would ultimately turn the effect of peatlands on climate into cooling.

2.3 Carbon gas dynamics in peatlands

2.3.1 Carbon gas cycle in peatland

A schematic representation of the C cycle in peatlands is shown in Figure 2.1. The cycle begins with the uptake of atmospheric CO_2 in plant photosynthesis. Approximately 50 % of the CO_2 is released back to the atmosphere in plant respiration (Ryan, 1991), while the rest is bound into organic matter. Plants and produce litter both above (leaves) and below (roots) the soil surface. In peatlands the water level divides the peat profile into aerobic and anaerobic sections. Above the water level the litter is decomposed in aerobic conditions, which produce CO_2.

When organic matter decomposes, its structure collapses and the density increases. The proportion of air filled pores decreases and microbes use all available oxygen. The gradually rising water level adds the increasingly poorly decomposable matter to the permanently anoxic zone, where decomposition continues at an ever decreasing rate (Belyea and Clymo, 1998). Only 2 to 20 % of the litter ends up in these anaerobic conditions (Francez and Vasander, 1995; Päivänen and Vasander, 1994). Decomposition in oxic conditions is two to three orders of magnitude faster than in anoxic conditions (Clymo, 1984). The anaerobic decomposition is carried out by methanogenic archeae and results in CH_4 production. The CH_4 flux to the atmosphere is affected by the CH_4 oxidation process occurring above the water level and also by the speed of the transport pathway. The following sections introduce the C cycle processes in detail.

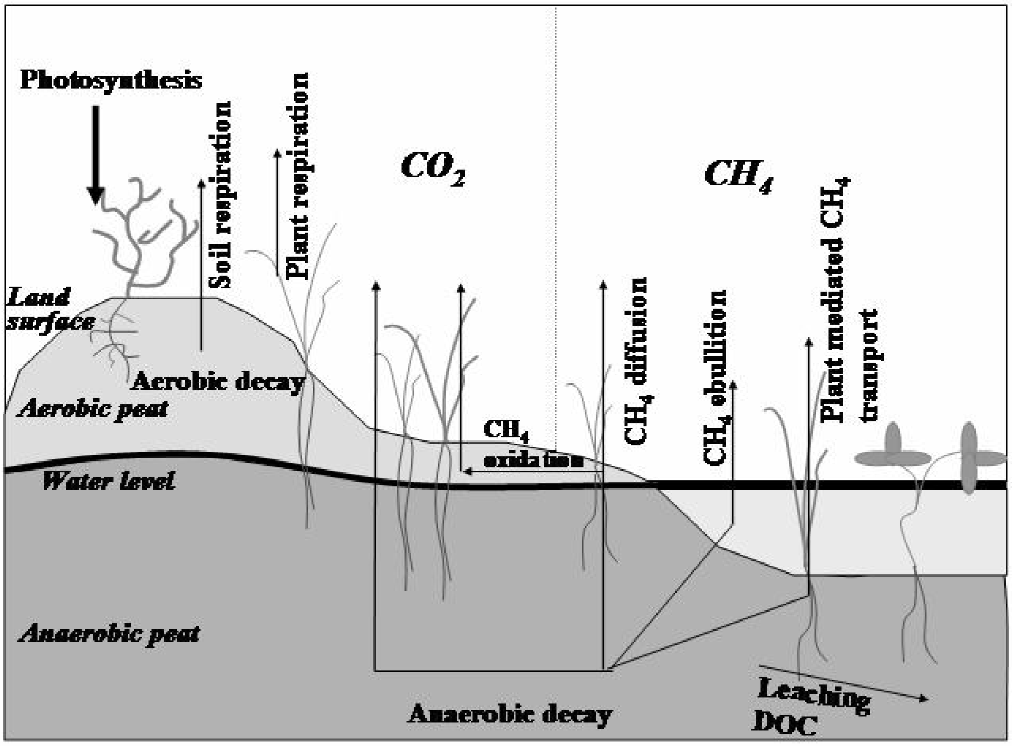

Figure 2.1 Schematic representation of the carbon cycle in peatland ecosystem.

2.3.2 Uptake of carbon dioxide

The plants growing in peatlands and especially in bogs must tolerate relatively cool and wet conditions, in addition to rooting media with low nutrient availability, poor aeration and high adicity (Bradbury and Grace, 1983). For this reason treeless peatlands are low productivity ecosystems, where the primary production that indicates the rate of CO_2 uptake, is as low as 114 – 868 g m^{-1} yr^{-1} (Bartsch and Moore, 1984; Doyle, 1982; Forrest and Smith, 1975; Reinikainen et al., 1984; Vasander, 1982). Correspondingly, the rate of photosynthesis is low in peatlands when compared to ecosystems such as grasslands or forests (Frolking et al., 1998).

The rate of photosynthesis is controlled by biotic and abiotic factors such as, irradiation, water level (WT), vegetation structure, CO_2 concentration and temperature (Begon et al., 1996). Irradiation or PPFD is the source of energy for the photosynthesis reaction (Begon et al., 1996). The processes are, however, complex due to the interactions between controlling factors. Through stomatal conductance, WT directly influences photosynthesis by controlling the CO_2 intake into cells. In addition, WT affects the vegetation structure, which defines the photosynthesising leaf area. These factors together control the ability of vegetation to use photosynthetic photon flux density (PPFD) and to photosynthesise (Tuittila et al., 2004). The photosynthesising leaf area is also affected by factors such as nutrient and CO_2 concentration (Cowling and Field, 2003). The different functional plant groups vary in their relationship to these factors. For example, for the growth of *Sphagnum* mosses, the CO_2 concentration in surface soil may be more important than the atmospheric CO_2 concentration since the mosses are able to recycle the CO_2 released directly from the surrounding substrate (Domisch et al., 1998; Domisch et al., 2000; Smolders et al., 2001).

Spatial variation is a typical feature of photosynthetic fluxes because the environmental conditions vary within and between peatland ecosystems. The peatland vegetation varies spatially along the ecohydrological gradient formed by the WT and water quality (Laine et al., 2002; Wheeler and Proctor, 2000). In general, the vegetation of treeless peatlands is dominated by shrubs, sedges or bryophytes, depending on the ecohydrological conditions. These functional plant groups have different capacities to photosynthesise (Bubier et al., 1998). Variation in the ecohydrology causes differences between peatlands (bog / fen). Bogs receive water and nutrients solely from the atmospheric inputs while fens receive additional input from the runoff water flowing from higher elevation areas and therefore have higher nutrient status and pH. This triggers higher photosynthesis and productivity for fens than for bogs (Frolking et al., 1998). Within a peatland the variation in water level (WT) is a more important determinant of spatial variation than variation in nutrient status. WT gives rise to different vegetation communities, often referred to as microforms. Gross photosynthesis (P_G), which is the total amount of photosynthesis by vegetation, of these communities has a unimodal relationship with WT (Tuittila et al., 2004). P_G is low in the wet vegetation communities with small leaf area and increases until in dry vegetation communities the low WT begins to limit photosynthesis. As an example, in boreal bogs annual P_G varied from 171 to 235 g C m^{-2} yr^{-1} (Alm et al., 1999b).

Photosynthesis is sensitive to changing conditions and therefore it varies on a daily and seasonal basis (Griffis et al., 2000a). Seasonality follows the cycle of PPFD and temperature as well as the development of leaf area; these variables and therefore also the flux rates are usually highest in late summer. Moisture conditions affect the dormancy and phenology of plants (Griffis and Rouse, 2001), thus, the microforms may have different seasonality in fluxes due to vegetation community structure. Evergreen plants are able to photosynthesise as soon as temperature and light levels are suitable, while deciduous plants need to grow new leaves, which takes time (Bubier et al., 1998).

2.3.3 Plant respiration

Respiration is oxidation of organic substrate by certain metabolic pathways, a process proceeding continuously in all active living cells (Opic, 1980). Plants respire in order to maintain the complex tissue components, to take up ions and to construct new cells (Ryan, 1991). As an enzymatic process, plant respiration is affected by temperature, having an optimum at 25 to 30 °C, and is affected by O_2 and CO_2 concentrations (Opic, 1980). In a plant community the respiration rate is linked with the amount of respiring plant biomass, which is derived from photosynthesis, therefore photosynthesis and respiration are closely coupled. Plant respiration reacts to water stress in a similar manner to photosynthesis and consequently is highest in the water level range where photosynthesis (plant activity) is highest (Tuittila et al., 2004). Johnson and Shaver (2000) estimated that plant respiration constitutes 2/3 of the ecosystem respiration.

2.3.4 Soil respiration

Soil respiration, also referred to as heterotrophic respiration is a result of the aerobic decomposition process, where dead plant material is broken down into chemical components by micro-organisms. The rate of respiration depends on substrate quality, decomposers present, available nutrients and environmental condition (Laiho, 2006). From the environmental conditions the water level is the principal controller of soil respiration since it determines the depth of the aerobic layer (Bubier et al., 1998; Szumigalski and Bayley, 1996; Tuittila et al., 2004). Respiration increases rapidly with lowering WT until the peat surface dries out (30 cm) (Silvola et al., 1996; Tuittila et al., 2004). This causes spatial variation in respiration rates in peatlands that have a surface composed of microforms of different height above water level. Fluxes are higher in microforms with low WT and lowest in wet or inundated microforms (Alm et al., 1997; Heikkinen et al., 2002b). Spatial variation is increased by the differences in the decomposability of the organic matter. Decomposability varies between peatland types (fen > bog) (Szumigalski and Bayley, 1996) and between microforms within peatlands (hollow > hummock) (Johnson and Damman, 1991) due to the varying vegetation composition.

The rate of soil respiration varies seasonally following changes in temperature. Seasonality effects on respiration are, however, weaker than in photosynthesis. Soil respiration correlates positively with temperature, however respiration may occur even at temperatures below 0 ºC (Roehm and Roulet, 2003). Therefore, wintertime fluxes are important even in the northern hemisphere (Aurela et al., 2002; Roehm and Roulet, 2003; Zhang et al., 2005). Due to measuring technique and difficulties in separating plant and soil respiration, they are often expressed together as ecosystem respiration (R_E)

2.3.5 CH_4 emissions

CH_4 flux into the atmosphere is the difference between CH_4 production and oxidation and is strongly affected by the transport route to the atmosphere (Fig 2.1). CH_4 production (i.e. methanogenesis) occurs below the water level, where the decomposition of peat is continued by the methanogenic archae that require strictly anoxic conditions (Kettunen, 2002). In addition to creating the anoxia, WT controls the rate of methanogenesis by affecting the quantity of easily available substrate. The distribution of substrate in the peat profile depends on plant species composition and therefore on peatland type. In raised ombrotrophic bogs where shrubs and *Sphagna* dominate, the litter is distributed on the surface of the bog and is generally fresher closer to the surface. However, methanogens can only use substrate that is below the WT; therefore more substrate is available when the WT is closer to the surface. In contrast, in peatlands (fen, marsh) where the vegetation is composed of deep rooting graminoid species, fresh organic matter, in the form of root exudates, is distributed also below the water level, where it is available for the methanogens. This readily increases CH_4 production.

Correlating with the substrate availability, the largest quantity of methanogenesis is found right below the water level (Edwards et al., 1998; McDonald et al., 1999; Roulet et al., 1993) or 10-15 cm below water level (Daulat and Clymo, 1998; Galand et al., 2003). Methanogens are attached to peat particles and remain in the same layer even when the WT changes. Therefore the production potential reacts slowly to WT fluctuation, both upward and downward (Kettunen et al., 1999). A time lag of 12 hours has been noted before CH_4 production returns to the original level after the re-establishment of the reference water level (Lloyd et al., 1998). This phenomenon is called hysteresis. The methanogens seem to retain their viability in unsaturated conditions even if their growth is inhibited (Kettunen et al., 1999).

As a microbial process methanogenesis is dependent on temperature, with a Q_{10} value of ~5.3 and temperature optima in the range 25 to 30 ºC (Dunfield et al., 1993). The impact of temperature is higher in the presence of vascular plants, since photosynthesis is increased at higher temperatures (Granberg et al., 2001b). The rate of photosynthesis affects the supply of available substrate for methanogens (Ström et al., 2003). Methanogenesis is also affected by pH (Crill et al., 1988; Duval and Goodwin, 2000), with most of the methanogenic communities having the pH optimum at 6 (Williams and Crawford, 1984), which is higher than commonly found in ombrotrophic peatlands (Dunfield et al., 1993). However, Bubier (1995) suggested that in peatlands the effects of pH and nutrient status is overridden by the effect of WT. Another factor affecting CH_4 production is the existence of competing electron acceptors, such as sulphate reducing bacteria. High concentrations of SO_4^{2-} suppress CH_4 fluxes (Crozier et al., 1995; Dise and Verry, 2001; Dowrick et al., 2005; Gauci et al., 2004; Granberg et al., 2001b). The effect is stronger at low temperatures (<15 ºC) (Gauci et al., 2004) and also during drought, since sulphate concentrations are increased in dry conditions (Dowrick et al., 2005).

CH_4, which is produced below the water level, has to move through the peat column before it reaches the atmosphere. The three main transport pathways are: diffusion, ebullition and transport through plants (Schütz et al., 1991). The relative importance of the pathways depends on organic loading, seasonal variation in temperature and the type and density of vegetation (Chanton, 2005). The passive diffusion follows the gas concentration gradient in peat and is relatively slow. It is the main pathway in vegetation communities without deep rooting aquatic plants.

Gas bubbles are formed when a gas is super saturated in a liquid and the partial pressure of the gas exceeds the value of the hydrostatic pressure (Chanton and Whiting, 1995; Schütz et al., 1991). When bubbles are large enough their buoyancy allows them to reach the surface and burst. Such ebullition dominates in shallow, non-vegetated and organic-rich aquatic environments (Chanton and Whiting, 1995;

Käki et al., 2001; Schütz et al., 1991; van der Nat and Middelburg, 1998). Ebullition is episodic and therefore it is difficult to estimate (Chanton, 2005). Yet, Christensen, et al. (2003) in a study using wetland monoliths estimated that ebullition may account for 18 to 50 % of CH_4 flux, depending on vegetation properties and temperature.

Certain plant species facilitate CH_4 transport between the soil and the atmosphere. The gas is transported from the sediment through the continuous intercellular airspaces (aerenchyma) of aquatic plants (Conway, 1936; Conway, 1937; Evans, 2003). The cell structure has developed for transportation of oxygen (O_2) to the roots that are located in inundated environments (Armstrong, 1964; Conway, 1937). CH_4 molecules, which resemble O_2 molecules, are able to use the same pathway (Schütz et al., 1991). Transport can be passive molecular diffusion or in the case of certain plant species (e.g. *Typha Latifolia*, *Phragmites australis*) high-low pressure induced flow (Armstrong et al., 1996; Schütz et al., 1991; Whiting and Chanton, 1996). In both cases the transportation is faster than diffusion through the peat column. Plant mediated CH_4 transport is important in peatlands that have an abundant cover of vascular plants with aerenchymatic cell structure (Chanton and Whiting, 1995; Granberg et al., 2001a). Bowes and Hornibrook (2006) showed that in both *Sphagnum* and vascular plant dominated communities in blanket bog the flux was mainly transported via plants. Plant mediated transport may contribute up to 90 % of the CH_4 flux depending on species composition (Ding et al., 2005; Frenzel and Karofeld, 2000; Shannon et al., 1996; van der Nat and Middelburg, 1998; Wang and Han, 2005).

Up to 90 % of the CH_4 produced may be oxidized into CO_2 in the aerobic surface peat layer above the WT (Fechner and Hemond, 1992; Freeman et al., 2002). Methanotrophic bacteria are responsible for CH_4 oxidation and their functioning requires O_2. Methanotrophs are most abundant in conditions where CH_4 and O_2 concentration are high i.e. just above the WT (Edwards et al., 1998). Therefore, the maxima of CH_4 production and oxidation occur at approximately the same depth (Edwards et al., 1998; Freeman et al., 2002). Methanotrophs, however, can be found throughout the peat profile and may be activated when conditions become favourable (Edwards et al., 1998; Whalen and Reeburgh, 2000).

In contrast to methanogenesis, CH_4 oxidation is positively correlated with deepening WT. The thicker the oxic peat layer the more CH_4 is oxidized. However, when CH_4 production is reduced the supply of substrate for methanotrophs is also reduced and therefore the rate of oxidation decreases as well (Kettunen et al., 1999). Oxidation is considered to be less dependent on temperature than methanogenesis having a Q_{10} value in the range 1.4 to 2.1 and a temperature optima at 20 to 25 ºC, which is lower than that of methanogenesis (Dunfield et al., 1993). Since the aerenchyma contain oxygen, some CH_4 may be oxidized inside the plants. Vascular plants also induce CH_4 oxidation by releasing oxygen into the rhizosphere, even below the WT. This increases the depth of the oxidizing horizon. However, certain common peatland species such as *Eriophorum* sp. do not support CH_4 oxidation, even if they form a major pathway for CH_4 fluxes to the atmosphere (Frenzel and Rudolph, 1998).

Studies of the relative importance of CH_4 production or consumption in causing spatial variation in flux rates between microforms have produced contrasting results. Bubier et al. (1993) found higher CH_4 production capacity in hollows than in hummocks, indicating that production is the more important regulator. Freeman, et al. (2002) agreed with the theory that CH_4 oxidation has a minor role in regulating the CH_4 emission under changing hydrological conditions. Frenzel and Karofeld (2000), however, emphasized the importance of oxidation capacity in creating differences between vegetation communities, since they found similar CH_4 concentrations below the WT in hummocks and hollows. Correspondingly, Galand, et al. (2003) observed similar CH_4 production rates at the depth of maximum CH_4 production in different vegetation communities

Due to the relationships between CH_4 production, oxidation and transport processes and environmental variables, flux rates vary both temporally and spatially. Temporal variation in CH_4 fluxes has been observed on diurnal (Käki et al., 2001; Kim et al., 1998; Wang and Han, 2005), seasonal (Frolking and Crill, 1994; Saarnio et al., 1997) and interannual scales (Frolking and Crill, 1994; Granberg et al., 2001a). Diurnal variation is linked with temperature (Hargreaves and Fowler, 1998; Wang and Han, 2005) and with stomatal conductance of plant species, such as *Phragmites australis* and *Typha latifolia* that actively transport CH_4 through the oxic peat layer (Armstrong et al., 1996; Käki et al., 2001; Kim et al., 1998; van der Nat et al., 1998; Whiting and Chanton, 1996).

The seasonal dynamics in CH_4 flux involves an increase in fluxes during the summer in respect to an increase in soil temperature (Moore and Knowles, 1987). Summer fluxes are further increased by the development of vascular vegetation that increases the amount of substrate for methanogens and intensifies the gas transport. WT is an important control of CH_4 flux but hysteresis makes it difficult to interpret the temporal correlation (Lloyd et al., 1998; Moore and Dalva, 1993; Moore and Roulet, 1993). Similar to soil respiration, wintertime CH_4 fluxes are low but still important in the northern hemisphere (Alm et al., 1999a; Dise, 1992; Zhang et al., 2005), where they can constitute 5 to 33 % of the annual CH_4 flux (Alm et al., 1999a). The interannual variation can be large and is mainly controlled by the mean WT and soil temperature (Granberg et al., 2001a). Rather small changes in climate are enough to cause variation in flux rates (Bubier et al., 2005).

Lower CH_4 fluxes have been measured in acidic nutrient poor bogs compared to fens (Bubier et al., 1993; Saarnio et al., 1997; Waddington and Roulet, 1996), which have a richer vascular plant cover. Vegetation structure and pH influence the CH_4 flux (Crill et al., 1988). The spatial variation is however, more linked to moisture conditions than to chemical parameters, insofar that in bogs and fens the vegetation communities, with similar WT, may have similar flux rates (Bubier, 1995; Bubier et al., 1995). Within a peatland the different vegetation communities have a large variation in CH_4 fluxes (Bubier et al., 1993; Heikkinen et al., 2002b; MacDonald et al., 1998; van Huissteden et al., 2005). Fluxes follow the water level gradient being highest in wet communities (Bubier et al., 1993; Dalva et al., 2001; Dise et al., 1993; MacDonald et al., 1998; Waddington and Roulet, 1996). The variation is also explained by vegetation properties (Strack et al., 2006b; van Huissteden et al., 2005) and by plant species (Christensen, 1993). Particularly in wet conditions the CH_4 flux correlates positively with plant production (Saarnio et al., 1997; Strack et al., 2004; Strack et al., 2006b). This is supported by the small CH_4 flux rates measured from communities with permanent standing water and low vascular plant cover (Juutinen et al., 2003; Strack et al., 2004). MacDonald et al.

(1998) observed different CH_4 flux rates between blanket bog pools with or without *Menyanthes trifoliata*, which is known to transport CH_4 efficiently (Daulat and Clymo, 1998). Overall, CH_4 flux is more closely linked to the living vegetation, in terms of substrate and transport pathway, than to the decomposition of peat in deeper layers (Chanton et al., 1995; Ström et al., 2003). Therefore, peatlands that have deep rooting vascular plants (e.g. fens) and input fresh organic matter straight into the lower peat layers often have higher CH_4 fluxes.

Of net ecosystem exchange (NEE) (as carbon), 2.3 % and 4.2 % in northern and temperate wetlands, respectively, may be decomposed and released into the atmosphere as CH_4 (Cao et al., 1996). Annual CH_4 flux estimates for different peatland ecosystems range between 1 and 21.2 g CH_4 m^{-2} (Cao et al., 1996; Granberg et al., 2001a; Huttunen et al., 2003; Nykänen et al., 2003). The only annual estimate given for blanket bogs are 4.9 g CH_4 m^{-2} (Chapman and Thurlow, 1996) and 6.9 g CH_4 m^{-2} a^{-1} (Hargreaves and Fowler, 1998).

2.3.6 Spatial variation in C flux sources

As noted, all C gas flux components experience spatial variation within and between peatlands. Spatial variation occurs in peatlands at many different scales: macroscale is due to landforms, mesoform by large scale surface patterns (pools, ridges, lawns) and microscale in forms of hummocks and hollows (Waddington and Roulet, 1996). This spatial variation is controlled by environmental conditions and also causes different conditions that affect C gas fluxes (Waddington and Roulet, 1996). Ecohydrology varies strongly within and between peatlands thereby affecting the vegetation composition and being the principal creator of the surface pattern. The nutrient status, pH and concentrations of ions such as SO_4^{2+} and Fe vary more between peatlands, while WT is the cause of small scale variation within a peatland.

The surface pattern of microforms, with horizontal dimensions of 1 to 10 m and vertical dimensions of < 1 m is a common feature of all northern peatlands (Foster and Glaser, 1986; Lindsay, 1995). The surface pattern is, however, a secondary feature and it has been shown that in a Scottish blanket bog the microforms started to develop on a relatively featureless surface about 2200 years ago due to differential peat accumulation rates (Tallis, 1994; Tallis and Livett, 1994). Once developed the microforms tend to prevail in the same position growing and shrinking both laterally and horizontally in response to the changes in hydrology (Belyea and Clymo, 2001).

The variation in C accumulation rates between microforms are due to differences in productivity, decomposability of litter and the depth of oxic peat layer. High hummocks and wet hollows accumulate less C compared to lawns with intermediate WT (Alm et al., 1997). In hummocks the productivity may be high, but the C circulates rapidly due to the high respiration rate (Heikkinen et al., 2002a). In hollows the productivity is low due to the sparse vascular plant cover caused by high WT (Vasander, 1982).

2.4 Effects of climate change on peatlands

2.4.1 General impacts of climate change on peatlands

Peatlands act as a long-term C store, however, the changing climate may threaten this storage capacity by affecting the functions of peatland ecosystems directly and indirectly through environmental factors (Gorham, 1991). The question is how changing climate affects the peatland carbon gas dynamics, which are known to be sensitive to weather conditions (Alm et al., 1999b; Aurela et al., 2004; Griffis et al., 2000a). As was noted by Christensen, et al. (1999), the possible impacts and feedback mechanisms of climate change on peatlands are complex and involve every stage of the C cycle.

Most peatlands are characterized by a considerable topographic heterogeneity at several scales (Lindsay, 1995; Tallis, 1969) and at each of these scales the characteristics of hydrology, vegetation, nutrients and gas fluxes may exhibit differential responses to future environmental conditions (Belyea and Malmer, 2004; Gorham, 1991; Waddington and Roulet, 1996). The inherent changeability of wetland communities (Tallis, 1983) may be the key factor in the response of peatland communities to climate change. The microform distribution that is essential for C dynamics, shifts along with moisture conditions; in wet years hollows expand and conversely in dry years hummocks expand (Belyea and Clymo, 2001; Walker and Walker, 1961). In both, dry and wet conditions, the C sequestration rate decreases compared to intermediate conditions, because of the increased decomposition and decreased productivity, respectively (Belyea and Malmer, 2004). Waddington, et al. (1998) however, projected that drier conditions may actually increase C accumulation in peatlands with high WT, since presently the drier microforms have higher C uptake. The contrasting impacts of climate change on C flux components in different microforms, is largely due to the dissimilar responses of vegetation communities on changing conditions (Strack et al., 2004; Strack et al., 2006b). Therefore, an understanding of how the vegetation and surface structure interact with climate is necessary to understand the effect of climate change on peatland C dynamics.

Direct impacts of climate change result from increasing temperature and CO_2 concentration. Temperature is an important controller of many ecological and physical functions. For example primary productivity and microbial activities (e.g. CH_4 production, respiration) are controlled to a certain extent by temperature (Begon et al., 1996). Cool and moist environments (for example the UK and Ireland) seem to be most sensitive to warming, though in many cases the increase in plant growth is most likely to be manifested as a longer growing season, rather than an increase in photosynthesis rate (Penuelas et al., 2004). Longer growing seasons are already observed in southwest Ireland (Sweeney et al., 2002). In addition to increased production rates, the warmer temperatures can directly increase respiration, CH_4 production and to some extent CH_4 oxidation (Dise et al., 1993; Dunfield et al., 1993; Moore and Dalva, 1993).

Increasing atmospheric CO_2 concentration can increase productivity (Begon et al., 1996; Cao and Woodward, 1998; Norby et al., 1999), since photosynthesis is limited by CO_2 concentration in optimal weather conditions. The leaf area that defines the photosynthesising surface has been shown to be limited by CO_2 only in conditions when concentrations are less than ambient (Cowling and Field, 2003).

The effect of increasing CO_2 concentration may also be species specific; for example, the growth of *Sphagnum*, an important component of peatland vegetation, is not affected by increased CO_2 supply (Berendse et al., 2001) and has been found to suffer from the combination of increased CO_2 concentration and warm temperature (Heijmans et al., 2002). Conversely, Jauhiainen and Silvola (1999) measured increased photosynthesis in *Sphagnum fuscum* exposed to raised CO_2 concentration. In peatlands, small increases have been detected in photosynthesis and respiration (Kang et al., 2001; Saarnio et al., 2003), CH_4 emissions (Saarnio et al., 2000) and DOC release (Freeman et al., 2004) under increased CO_2. The effect is probably stronger in nutrient rich fens compared to bogs where processes are nutrient-limited (Freeman et al., 2004; Kang et al., 2001).

The most significant effect of climate change for peatlands is the lowering water level caused by changes in precipitation regime and increasing evapotranspiration at higher temperatures (Gorham, 1991; Trettin et al., 2006). Roulet et al. (1992) estimated that according to the 2 x CO_2 scenario, the water level in a boreal peatlands would drawdown approximately 14 - 22 cm even when the increasing annual precipitation rate is considered.

Water level is the most important determinant of the interannual differences in CO_2 balance (Lafleur 2003) and CH_4 emissions (Granberg et al., 2001a). During a dry year a C accumulating bog can turn into a C source (Alm et al., 1999b). However, it is not solely the annual rainfall that is important but also the frequency and intensity of precipitation events. Spring and peak growing season conditions are the most important for the C uptake rate (Aurela et al., 2004; Griffis and Rouse, 2001; Hunt et al., 2004; Waddington and Roulet, 2000). The effect of climate change is pronounced since it is projected to decrease the summer precipitation rates (IPCC, 2001). Alm, et al. (1999b) suggested that the ratio between moist and dry summers should be at least 4:1 to retain a positive C balance and 5:1 to retain the average long-term accumulation rate of 25 g C m^{-2} yr^{-1}. Changes in water level affect all processes of the C cycle in peatlands.

2.4.2 Impact of changing water level on vegetation community

Plants have adapted in varying degrees to the reduced conditions caused by the high WT. Many species have adapted to a specific WT range and therefore the vegetation is a mosaic of communities with certain niches along the WT gradient (Lumiala, 1944; Rydin and McDonald, 1985). For this reason the changing WT has a strong impact on the vegetation composition of peatlands. The adaptation to the changing environmental conditions can be viewed to occur in two stages. First the existing community responds to the change (Weltzin et al., 2000) and secondly, in the long-term, the community structure changes since the species better adapted to the new conditions become dominant (Laine et al., 1995). Different and even opposite responses of species and lifeforms to WT elevations indicate individualistic responses of species to change (Weltzin et al., 2003). For example biomass production in bog and fen plant communities or in above and below ground compartments respond differently to WT drawdown (Weltzin et al., 2000).

Many *Sphagnum* species are most abundant in wet conditions and production decreases with increasing depth to WT (Vasander, 1982; Weltzin et al., 2001). The dry and warm conditions benefit shrubs, while the opposite applies to graminoid species (Weltzin et al., 2003; Weltzin et al., 2000). Consequently the plants living on wet surfaces are the first ones to disappear after WT drawdown, whereas the hummock-dwelling shrub species may benefit from the drying of surface soil (Laine and Vanha-Majamaa, 1992; Minkkinen et al., 1999). The change from sedge to shrub dominated vegetation can happen over a short time period (Bubier et al., 2003b). In a peatland with a patterned surface structure the vegetation communities may respond differently to WT drawdown (Strack et al., 2006b). The previously inundated sites may undergo colonisation by mosses and sedges, with increasing productivity, while in drier sites (hummocks) WT drawdown decreases moss cover. On the other hand, mosses may retain their importance after adaptation at the community level has occurred and species more suitable for lower WT have out competed other species (Laiho et al., 2003). In the long-term the drying of the surface soil initiates a secondary succession whereby the original wetland species are gradually replaced by species that are typical of forests and heathlands (Laine and Vanha-Majamaa, 1992; Laine et al., 1995).

Plant macrofossile and peat humification stratigraphy can be used as indicators of past climate change (Mauquoy and Barber, 1999). Vegetation composition has varied during peatland development following hydrological conditions (Mauquoy and Barber, 1999) and the drier and wetter climatic eras have especially affected the abundance of *Sphagnum* species in blanket bog (Tallis, 1994). The rate of impact varied so that the water collecting areas recovered from the changes faster than the drier areas (Tallis, 1994). Overall, blanket bogs have been sensitive to past changes in climate (Ellis and Tallis, 2000; Tallis, 1998). These changes have, however, been small compared to the projected future change, induced by anthropogenic activity (IPCC, 2001; Petit et al., 1999). Therefore, severe impacts on blanket bog development can be expected in the future (Ellis and Tallis, 2000).

2.4.3 Impact of changing water level on CO_2 fluxes

The effect of WT drawdown on photosynthesis is complex, since different vegetation communities respond differently to changes (Bubier et al., 2003a; Strack et al., 2006b). Photosynthesis of shrubs may increase while in sedge and moss communities it is reduced (Bubier et al., 2003a). The WT during the growing season is most important for the vegetation (Päivänen, 1984), therefore the projected increase in wintertime precipitation would not have as large an impact as increased evapotranspiration and consequent WT drawdown in summertime (Laiho et al., 2003).

Over a long timescale vegetation succession affects photosynthesis and productivity (Strack et al., 2006b). Different vegetation types have different rates of photosynthesis: sedges and herbs support higher maximum net photosynthesis than deciduous shrubs while the evergreen shrubs have the lowest maximum photosynthesis (Bubier et al., 1998). Thus, the increased proportion of shrubs might decrease C accumulation in the long-term. However, if tree growth is stimulated by WT drawdown, productivity increases (Laiho et al., 2003; Vasander, 1982). The same applies for microforms. Inundated vegetation communities, such as hollows and pools have low productivity since their vegetation is often sparse. A succession of sedges and mosses induced by WT drawdown of hollows and lawns increased gross photosynthesis (Strack et al., 2006b). Therefore the changing microform composition towards drier communities may accelerate productivity (Waddington et al., 1998).

The effect of WT drawdown on respiration is crucial (Moore and Dalva, 1993), insofar that the high WT is the main reason for low respiration rates and incomplete decomposition in peatlands. The respiration rate is 4.3 - 20 times greater under oxic compared to anoxic conditions (Bergman et al., 1999; Scanlon and Moore, 2000) and a WT drawdown of 14-22 cm has increased respiration rates by 50-100 % (Bubier et al., 2003b; Silvola et al., 1996). This increase is mainly derived from soil respiration (Tuittila et al., 1999), since plant respiration is indirectly affected by moisture conditions. Plant respiration depends on the physical activity of plants and correlates positively with photosynthesis (Bubier et al., 2003b; Tuittila et al., 2004) that is affected by WT. WT drawdown increases soil respiration up to a threshold level after which it becomes water limited and the rate of decomposition decreases (Chimner and Cooper, 2003; Tuittila et al., 2004). WT drawdown increases the respiration rate in a similar manner in all microforms (Bubier et al., 2003a; Bubier et al., 2003b; Strack et al., 2006a).

Since the respiration is strongly dependent on temperature (Lloyd and Taylor, 1994), the interaction of increased temperatures and reduced WT could be expected to increase respiration significantly. However, Silvola, et al. (1996) noticed that the effect of temperature is less strong after WT drawdown and therefore an increase in temperature would increase respiration rate less in drier ecosystems. In addition, Christensen, et al. (1999) observed that the sensitivity of decomposition to temperature decreases in deeper recalcitrant peat layers. According to Oechel, et al. (1993) WT drawdown rather than the direct effect of increasing temperature is the principal reason for an Arctic tundra ecosystem converting into a C source. In the long-term the changing vegetation composition affects soil respiration via changes in the amount of produced litter as well as the decomposability of the litter (Laiho, 2006). Shrub litter decomposes slower than sedge litter (Hobbie, 1996).

2.4.4 Impact of water level drawdown on CH_4 flux

The effect of WT drawdown on CH_4 flux is opposite to that on respiration, therein the CH_4 emissions decrease after WT drawdown (Moore and Dalva, 1993; Roulet et al., 1992). Several reasons for the decrease are acknowledged. One is the changing vegetation community that alters the substrate flux to anoxic layers, which consequently decrease CH_4 production (Freeman et al., 2002). The change from sedge to shrub-dominated communities would also decrease the amount of plant-mediated transport. The thicker aerobic layer enhances the area where CH_4 oxidation can occur (Roulet et al., 1993). In a nutrient poor fen in Canada a 20 cm drop in WT reduced CH_4 flux on average by 55 % (Strack et al., 2004). Overall, the location of WT 10 to 20 cm below the peat surface is seen as a threshold for CH_4 flux in northern peatlands; below this depth the CH_4 flux is reduced to near-zero (Trettin et al., 2006 and references therein)

The CH_4 flux of different microforms can have different responses to WT drawdown, depending on the vegetation succession. For example, if the drainage of hollows with permanent standing water results in colonisation by vascular plants, the CH_4 flux could remain unchanged, while fluxes in originally drier vegetation communities decrease (Strack et al., 2004). However, colonisation by sedges maintain the pre- WT drawdown flux rates only following large or continuous rain events, when high WT together with high sedge cover increase CH_4 fluxes. In dry conditions CH_4 flux in these communities is low compared to pristine conditions, which indicates the dominating control of WT over vegetation (Strack et al., 2006b).

As a conclusion, the effect of climate change on peatland C flux balance depends on the rate of change in the opposing processes: increasing respiration, decreasing CH_4 emission and the more variable response of photosynthesis that depends on the direction of the vegetation succession. It has been suggested that after WT drawdown, the reduced CH_4 emissions, together with an increase in tree biomass and a fairly small change in carbon sequestration into peat, would decrease the greenhouse effect of some peatland ecosystems in a long time scale (Laine et al., 1996).

2.5 Peatlands in Ireland

The original peatland cover in the island of Ireland was 1.34 million ha (Hammond, 1981) of which 1.18 million ha were in the Republic of Ireland (Foss et al., 2001). Over the past 400 years little value was given to pristine peatlands and therefore peatlands have been managed and improved for agriculture, turf cutting and in past decades for forest amelioration purposes. Nowadays only 18 % of the original peatland area remains in a near-natural condition (Foss et al., 2001).

Peatlands are classified into fens and bogs according to their ecohydrology. Nowadays in Ireland undisturbed fens are rare and cover only 19,656 ha of the republic (Foss et al., 2001). The more numerous bogs are divided into raised bogs and blanket bogs. The former develop on flat ground or in depressions as a continuing development after a fen stage, while the latter overlay mountain and hill slopes. Raised bogs covered an area of 308,742 ha (Foss et al., 2001) and were located mainly in the midlands. Only a few remain in near-natural state, as 74 % of them were man-modified already two decades ago (Hammond, 1981). Peat harvesting is mainly concentrated in the midlands and is one of the most important usage forms of raised bogs.

The development of blanket bogs requires extremely humid conditions with minimum rainfall of 1250 mm over more than 250 rain days (Hammond, 1981) or 160 wet days (Moore, 1993) (rain day > 0.2 mm; wet days > 1 mm precipitation (Sweeney et al., 2002)). Worldwide, blanket bogs are rare ecosystems being restricted to extremely maritime conditions. They can be found in Norway, Newfoundland, Alaska, Kamchatka, Japan, Tierra del Fuego, the Falkland Islands, Tasmania, New Zealand, Britain and Ireland (Lindsay, 1995). The vegetation communities in blanket bogs vary between geographical areas: in the northern hemisphere blanket bogs are largely built from Poaceae and Cyperaceae, while in New Zealand and Tasmania they are built from Restionaceae (Agnew et al., 1993).

Globally blanket bogs cover only 10 million hectares. They are, however, locally important in Ireland, where they occupy some 908,117 ha (Foss et al., 2001). They are found in the western seabord where they are the most distinctive landscape feature (O'Connor and Skeffington, 1997) and in mountain areas throughout the country. Ireland has the greatest amount of blanket bogs in Europe.

Blanket bog ecosystems are considered to be extremely sensitive to changes in ecohydrology (Bragg and Tallis, 2001) and have been modified by grazing and trampling due excessive sheep stocking, peat extraction, afforestation and agricultural reclamation (Douglas, 1998). Only about 21 % of the Irish blanket bogs remain in a natural to near natural state (Foss et al., 2001). In contrast to raised bogs, the lowest peat layers in blanket bogs are not generally of fen peat origin, but are largely ombrogenous from the beginning (Hammond, 1981). Another difference from raised bogs is that *Sphagnum* species do not occur in the peat profile with the same abundance (Hammond, 1981). Blanket bogs are further divided into mountain and lowland blanket bogs (Hammond, 1981). The focus of this study is in lowland blanket bogs, which are described in more detail.

2.6 Lowland blanket bogs

Lowland blanket bogs are located in moderately sloping to flat surfaces at less than 200 m asl. (Doyle, 1982). They are an extreme type of blanket bog insofar that they require more humid climate conditions than mountain blanket bogs (in Ireland precipitation > 1300 mm yr^{-1}, 235 rain days (Doyle and Moore, 1980)). Therefore, in Ireland they are restricted to the west coast, where the rainfall is high and temperature is more uniform, with lower summer and higher winter temperatures, than in the more continental locations (Sparling, 1967). Lowland blanket bogs originally covered an area of 382,000 ha in the Republic of Ireland and together with the Scottish lowland blanket bogs they constitute the major representation of this habitat in the world (Douglas, 1998).

The nutrient status in lowland blanket bogs is low, similar to other ombrotrophic bogs, but the concentrations of maritime salts Cl, Mg, Na, SO_4^{2+} are higher due to the excessive maritime rainfall (Sparling, 1967). This is not surprising, since sea salt is known to account for ~80 % of the total ionic concentration in precipitation in western Ireland (Aherne and Farrell, 2002). In blanket bogs the saturation deficit is low and the WT generally remains near the surface (Sparling, 1967). Due to the more reduced conditions caused by consistently high WT and high electrolyte concentration and possibly due to the activity of sulphur oxidizing bacteria the pH is high compared to continental bogs (Sparling, 1967), ranging from 4.4 to 4.9 (Doyle, 1982; Shotyk, 1997). In continental bogs the pH is normally less than 4.0 (Laine et al., 2002).

Owing to the special ecohydrological conditions caused by the abundant sea spray, the vegetation of lowland blanket bogs shares characteristics of flushes and fens of Britain and continental Europe. This is indicated by the occurrence of species such as *Schoenus nigricans, Rhynchospora fusca* and *Potentilla erecta* (O'Connor and Skeffington, 1997; Osvald, 1949). The occurrence of *Schoenus nigricans* in the Irish lowland blanket bogs distinguishes them from similar habitats in Scotland (Doyle and Moore, 1980), making them a unique ecosystem worldwide.

The peat depth in lowland blanket bogs varies from a few centimetres to metres depending on the surface structure of the underlying mineral soil (Doyle, 1990). Consequently, the blanket bog complex can have varying topographic features from water shedding to water collecting areas (Doyle, 1990; Lindsay, 1995). The vegetation of the drainage features varies being influenced by peat depth, degree of water logging, nutrient supply (Doyle and Moore, 1980) and in many areas also by the grazing intensity (Cooper et al., 2001). Traditionally the phytosociological approach has been used to classify the peatland vegetation in Ireland, nevertheless, only a few studies have been carried out in lowland blanket bogs (e.g. Doyle, 1982; Doyle, 1990; Doyle and Moore, 1980; MacGowan and Doyle, 1997).

Since the habitat conditions are far from uniform, a number of vegetation communities can be identified (Doyle, 1982). The typical blanket bog vegetation in Ireland is co-dominated by *Schoenus nigricans* and *Molinia caerulea*, while the ericoid shrubs are stunted (Doyle and Moore, 1980). The *Sphagnum* cover, which is a dominating feature of most ombrotrophic peatlands, is generally poorly developed (Doyle and Moore, 1980; Tallis, 1969), except in hummocks and in some depressions (Doyle, 1990). There does not seem to be a simple reason for the undeveloped *Sphagnum* cover. In west Galway and Mayo the bog surface is typically covered by a dense mat of algal material that seems to bury bryophytes (Doyle, 1982). On the other hand, bryophytes are sensitive to trampling (MacGowan and Doyle, 1998) and therefore even occasional sheep grazing may have impacted the *Sphagnum* cover. Historically, the wild fires and changing weather conditions may have affected the *Sphagnum* cover (Tallis, 1994). This may be reflected in the present situation.

Most blanket bogs have a mosaic surface structure of microforms: hummocks, high and low ridges (or lawns), hollows and pools (Lindsay, 1995). They differ from each other in terms of WT, vegetation composition and pH. The phytosociological vegetation classification, however, tends to focus on synthesis of communities and does not aim to separate the microscale vegetation patter (Guinan et al., 1998) that has shown to be crucial in determining C gas fluxes in raised bogs (Waddington and Roulet, 1996).

Lawns and hummocks of the typical ombrotrophic parts of lowland blanket bogs in Ireland belong to the Pleurozio purpureae-Ericetum tetralicis association (Doyle, 1982; Doyle, 1990; Doyle and Moore, 1980). According to Doyle and Moore (1980) the character species of this association are *Schoenus nigricans, Pleurozia purpurea* and *Campylopus atrovirens*. The differential species include *Potentilla erecta, Pedicularis sylvatica, Polygala serpyllifolia* and *Pinguicula lusitanica*, while alliance diagnostic species include *Calluna vulgaris, Erica tetralix, Molinia caerulea, Narthecium ossifragum, Myrica gale, Campylopus paradoxus, Sphagnum subnitens, Cephalozia bicuspidata, Diplophyllum albicans, Mylia anomala, Cladonia impexa* and *Cladonia uncialis*. The vegetation associations of hollows are more varied (Doyle, 1990) but typically include species such as *Rhyncosphora alba, Rhyncosphora fusca, Sphagnum cuspidatum, Sphagnum recurvum, Sphagnum auriculatum* and *Menyanthes trifoliata* (Doyle, 1990). The typical companion species, though having a low cover, are *Molinia caerulea* and *Eriophorum angustifolium*. The vegetation of the different drainage features and edges of the peatland complexes differs from the typical association (Doyle, 1990).

Guinan, et al.(1998) viewed the blanket bog vegetation as a gradient ecosystem, where overlaps between phytosociological classes occur. The indicators of drier (*Calluna vulgaris*, *Hypnum jutlandicum*) and wetter (*Narthecium ossifragum*, *Rhynchospora alba*) conditions are present in the whole lawn vegetation gradient and consequently the species number is highest in lawns (Guinan et al., 1998). Vegetation tends to be taller and denser in hummocks and lawns compared to wetter habitats, and similarly the biomass is larger in drier habitats (Doyle, 1982). The above ground production of a lowland blanket bog in Galway was 360 g m^{-2} yr^{-1} (Doyle, 1982).

Lowland blanket bogs account for 19 % of the soil C stock in Ireland (Tomlinson, 2005). Still, little attention has been focused on the C gas fluxes in these ecosystems. Studies from various peatlands have shown large spatial variation in C fluxes between and within peatlands. Therefore the differences in vegetation, climate and WT regime raises the question whether C flux dynamics are similar in blanket bogs than in the continental peatlands. The more vigorous growth of cyperaceous plants, a stunted growth form of ericaceous shrubs and the sparse moss cover differentiate blanket bogs from raised bogs. Furthermore, the maritime climate, in which blanket bogs exists, offers different conditions from continental, boreal and arctic areas, where most flux studies have been carried out. For these reasons it is necessary to increase the understanding of blanket bogs in the C cycle and to study the response of C fluxes to changing environmental conditions in these ecosystems.

To date a limited number of C flux studies have been made in blanket bogs and the majority of these were located in mountain blanket bogs in the UK. Fowler, et al. (1995) used the eddy covariance method and Chapman and Thurlow (1996) the chamber method to measure CO_2 and CH_4 fluxes. Hargreaves and Fowler (1998) used the eddy covariance method to study continuous CH_4 flux over a 14 days period. They related the fluxes to temperature and water level and estimated an annual flux of 6.9 g m^{-2} yr^{-1}. MacDonald, et al. (1998) measured CH_4 fluxes from different microforms using chamber method; they made measurements both in the field and in the laboratory and linked fluxes with vegetation, temperature and water level. Sottocornola and Kiely (2005) studied the net ecosystem CO_2 exchange over a two year time period.

Excluding Sottocornola and Kiely (2005), all studies have been made in Scotland, where the vegetation is somewhat different to the Irish lowland blanket bogs (Doyle and Moore, 1980). Studies on CH_4 flux were based on short or irregular measurements campaigns or did not cover the large spatial variation existing in blanket bogs. The studied relationships between fluxes and environmental conditions are mainly based on laboratory studies, and may not reflect the situation in the field. Carbon dioxide fluxes have not been studied at vegetation community level and therefore the spatial variation is not well understood. In addition, no estimates of gross photosynthesis exist.

3 Materials and Methods

3.1 Study area

The study was located in an extensive lowland blanket bog in Glencar, Co Kerry, Ireland (51°55´N, 9°55´W), at 150 m asl (Fig. 3.1). The nearest synoptic weather station is located at Valentia, 30 km west of the study area and beside the Atlantic Ocean. The weather conditions are rather different between the study area and Valentia. The mean annual precipitation over the past 30 years was 1430 mm in Valentia, whereas in the study area the precipitation in the three studied years was 2510, 2356 and 2459 mm yr^{-1} in 2003, 2004 and 2005 respectively. This was on average 1134 mm more than in Valentia during the same period. During the same three-year period the average air temperature in the study area for the warmest month, July was 14.6 °C and in the coldest month, February was and 6.1 °C. The long-term average temperature in Valentia was 14.8 ºC in July and 6.6 ºC in February (ref. http://www.meteireann.ie/climate/valentia.asp).

Figure 3.1 Location of the Glencar study site

The vegetation was typical of lowland blanket bogs as characterised by Doyle (1982). The surface of the bog was a continuum of vegetation communities ranging from dry hummocks to permanently inundated hollows and pools. **Hummocks** (HU) had the deepest water level and they were covered by dense bryophyte carpet (e.g. *Sphagnum rubellum, Sphagnum papillosum, Racomitrium lanuginosum*) and had *Molinia caerulea* and dwarf scrubs *Calluna vulgaris* and *Erica tetralix* as dominant vascular plant species. Also *Schoenus nigricans* and *Narthecium ossifragum* were common in hummocks. The Inundated **hollows** (HO) varied in shape and size and were more abundant in the water collecting depressions than on the higher ground. Hollows can be divided into mud-bottom and *sphagnum* hollows. The former had a scattered cover of vascular plants such as *Rhynchospora alba, R. fusca, Eriophorum angustifolium, Menyanthes rifoliata* and *Schoenus nigricans*. In addition to these species the latter were covered by bryophytes (*Sphagnum cuspidatum, Sphagnum. auriculatum*). **Lawns** (i.e. the flat areas between hummocks and hollows) were divided into two categories. The **high lawns** (HL) were drier and had a dense stand of *M. caerulea* and *S. nigricans* in additions to various other species common in both hummocks and hollows. The **low lawns** (LL) had a WT closer to, and occasionally above, the soil surface. Vegetation in this community was dominated by *Rhynchospora alba*. The leaf area of low lawns was lower than that in high lawns and the moss cover was sparse in both lawns types.

The water chemistry varied little between and within vegetation communities in the study area. As an example, pH ranged between 3.5 and 5.1; calcium concentration was 0.27 to 2.8 mg l^{-1}, sodium varied between 4.3-11.5 mg l^{-1} and sulfate concentration was 0.6 to 3.8 mg l^{-1} (Unpublished data, M. Sottocornola 2005). Samples were taken from HU (n = 20), HL (n = 41), LL (n = 15) and HO (n = 9) in December 2005. Ca, Na, and SO_4^{2+} concentrations were analysed using flow injection analysis and ion chromatography (QuikChem IC+FIA 8000 series, Lachat Instruments, Milwaukee, USA), while pH was determined on site (WTW pH 320 model, Geotech Environmental Equipment, Inc, Colorado, USA).

3.2 Study site

The study site was established in June 2003. To facilitate the gas flux measurements 18 stainless steel collars (0.6 × 0.6 × 0.15 m) were permanently inserted into the peat to cover the spatial variation in vegetation continuum from hummocks to low lawns. In March 2004 three additional sample plots were established to widen the range into hollow vegetation. Each collar had a water channel at the top to allow water sealing during gas sampling. Boardwalks were constructed around the sample plots to minimize disturbance. A perforated PVC pipe was inserted into the peat next to each sample plot to facilitate WT measurements.

The sample plots were divided into four groups: hummocks (HU), high lawns (HL), low lawns (LL) and hollows (HO). In each group the sample plots were coded from 1 to 6 according to their median water level (WT_{MED}) (Fig. 3.2).

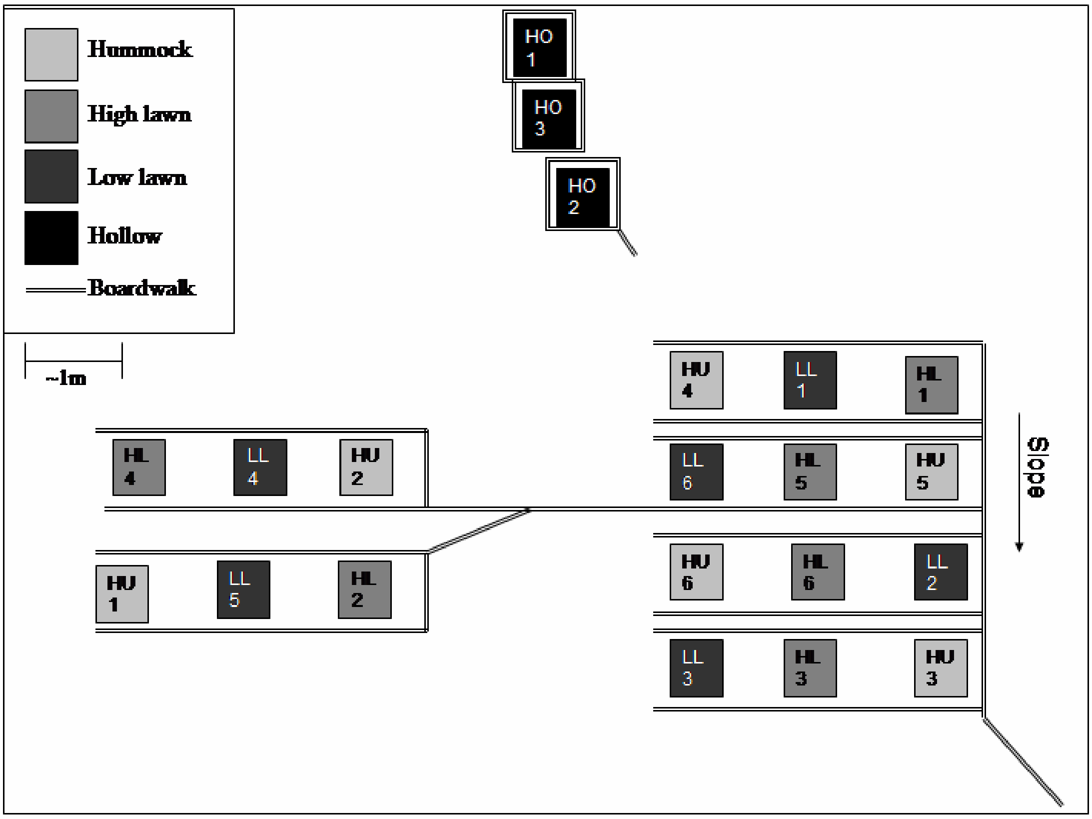

Figure 3.2. Plan set out of the study site.

3.3 Gas exchange measurement techniques

3.3.1 Chamber method

Ecosystem chambers are widely used for measurements of land surface-atmosphere gas exchange (e.g. soil respiration, photosynthesis and methane emissions) (e.g. Alm et al., 1997; Dalva et al., 2001; Juutinen et al., 2003; Larmola et al., 2003; McDonald et al., 1999; Nykänen et al., 2003; Strack et al., 2004; Tuittila et al., 1999; Waddington and Roulet, 1996). According to the operational properties, chambers are divided into closed and open top chambers and into steady-state and non-steady-state chambers (Livingston and Hutchingson, 1995). The limited size of the chambers has restricted the use of them to ecosystems with low stature vegetation, such as treeless peatlands.

The advantages of chambers are that they are relatively low in cost and simple to operate (Livingston and Hutchingson, 1995). For several purposes it is desirable to be able to explain the relationship between gas fluxes and the physical, chemical and biological factors that control the fluxes (Angell et al., 2001; Laville et al., 1999; Matson and Harris, 1995; Waddington and Roulet, 2000). Small scale enclosures that enable discrete observations in space and time (Livingston and Hutchingson, 1995), are necessary to achieve this aim, due to the small scale spatial variation in trace gas exchange that is a common feature of many ecosystems, especially peatlands (Waddington and Roulet, 2000). Chamber flux measurements dominate the body of empirical data available on environmental and climatic controls on wetland CH_4 emissions (Christensen et al., 2003).

Chamber techniques are susceptible to a number of measurement errors. These errors are mainly caused by modifications of the chamber microenvironment (air temperature, humidity, pressure and mixing of air) during the measurement cycle (Dore et al., 2003; Griffis et al., 2000b). The use of chambers eliminates the air turbulence that would naturally occur at the land-atmosphere interface and the composition of gas within the chamber changes as well (Griffis et al., 2000b). This may impact the gas diffusion by changing the concentration gradients. The errors should be minimized by (a) keeping the mixing inside the chamber similar to that prior to chamber deployment, (b) by taking care not to alter pressure when installing the chamber or taking the sample and (c) by allowing sufficient time between consecutive measurements from the same plot (Hutchinson et al., 2000). The performance of the chamber is improved also if the soil is fine-textured, wet and uniform (Hutchinson et al., 2000), this applies to wet peat. The air temperature inside the chamber, which tends to increase during measurement, can be controlled with a cooling system (Alm et al., 1997).

In addition to measurement errors, chamber methods encounter problems when fluxes are integrated over time and space. Since chambers can only cover a small area relative to the spatial variation that occurs in most environments, they are less effective for quantifying fluxes at landscape level than micrometeorological methods (Laville et al., 1999). Therefore, a large effort is required to collect a sufficient amount of measurements spatially and temporally to scale chamber measurements to the ecosystem level (Lavigne et al., 1997). A limited number of sampling points and restricting measurements to the early morning or afternoon may cause an underestimation of NEE, for example (Griffis et al., 2000b). In case of CH_4 emission problems occur when dealing with episodic fluxes (Christensen et al., 2003).

3.3.2 Eddy covariance method

The eddy covariance (EC) method was first applied in the 1980s in limited field campaigns until the reliability of the instrumentation and the power of hardware was increased enough in the 1990s for measurements to be made on a long-term scale (i.e. annual) (Baldocchi, 2003; Baldocchi et al., 2001). Currently EC is a widely used technique all over the world (e.g. Aubinet et al., 2001; Aurela et al., 1998; Baldocchi et al., 2001; Lohila et al., 2004; Sottocornola and Kiely, 2005; Suyker et al., 1997).

As a micrometeorological method, EC calculates or measures fluxes using measurements of atmospheric elements above the land surface. It provides a direct measure of net C fluxes between vegetation and the atmosphere by using micrometeorological turbulence theory to interpret measurements of the covariance between vertical wind velocity and scalar concentrations of fluctuations (Baldocchi et al., 1988). In contrast to the chamber method, EC does not modify the microenvironmental conditions of the surface and it provide spatially and temporally integrated measurements (Baldocchi et al., 2001; Baldocchi et al., 1988). Eddy covariance allows sub hourly to decadal scale estimates of NEE by integrating quasi-continuous short-term measurements (Aurela et al., 2004; Baldocchi et al., 2001; Barford et al., 2001; Lafleur et al., 2003).

Reliable flux measurements can be made using micrometeorological techniques, as long as the users work within the theoretical framework (Baldocchi et al., 1988). The method assumes horizontal homogeneity of fluxes (Baldocchi et al., 1988); this is the weakness of the method (Baldocchi et al., 2001) since it makes EC most applicable over a flat terrain, when environmental conditions are stable and the vegetation is homogeneous for an extended distance upwind (Baldocchi, 2003). If the latter does not apply, footprint models can be used to separate the contributions of different ecosystems (e.g. conifer/beech forest (Aubinet et al., 2001)). Footprint analysis helps to develop relationships between the emission pattern and the measured fluxes, which is the key step in interpreting the flux measurements (Laville et al., 1999). The footprint is the source area of the flux. Several models and solutions for defining the footprint have been developed (Horst and Weil, 1992; Hsieh et al., 2000; Schuepp et al., 1990).

Reliable EC measurements require adequate mixing of air in the ecosystem, but when thermal stratification of the atmosphere is stable, turbulent mixing is weak and hence the turbulence assumption is violated (Baldocchi et al., 2001). These conditions are common at night (Baldocchi, 2003; Baldocchi et al., 1997; Goulden et al., 1996). This can lead to underestimation of respiration (Goulden et al., 1996) and consequently, overestimation of NEE. Unsatisfactory conditions result in rejection of data and also due to system failures. The average data coverage during a year is between 65 % and 75 % (Falge et al., 2001). The missing data needs to be filled in, however, the proper gap filling procedures do not provide a significant source of bias error (Baldocchi et al., 2001)

The EC method is typically operated from a tower, but aircraft based EC measurements are also made. The aircraft based measurements give good information on the spatial variation of C gas fluxes across large area, but do not provide continuous time series (Baldocchi et al., 2001; Matson and Harris, 1995). The small scale spatial variation in gas fluxes in peatlands occurs on a much smaller scale than can be detected in spatially integrated flux estimates using EC (Waddington and Roulet, 2000), therefore the landscape level measurements are not adequate to describe the responses of flux components to varying environmental conditions in this scale (Griffis et al., 2000b).

Micrometeorological measurements have most commonly been applied for studies of NEE, but also measurements of CH_4 fluxes are increasing in number (e.g. Fowler et al., 1995; Hargreaves and Fowler, 1998).

3.4 CO_2 flux measurements

In this study the aim was to investigate CO_2 gas fluxes at vegetation community scale and to link the fluxes to environmental parameters. Therefore, the chamber method was used. Carbon dioxide exchange measurements began in July 2003 and were made using the closed non-steady-state chamber method. The chamber was made of transparent plexiglas (0.6 × 0.6 × 0.33 m) (Fig. 3.3). It included a cooling system (Alm et al. 1997) to regulate the inside temperature that tended to increase during measurements. A battery operated fan ensured the air circulation inside the chamber. The CO_2 concentration inside the chamber was monitored with a portable infrared gas analyser (EGM-4, PP Systems, UK). A set of coupled measurements were carried out for each sample plot. The instantaneous net CO_2 exchange (NEE) was first measured under a stable ambient illumination at 15 second intervals over a 60-240 second period. This was then repeated with the chamber covered with an opaque canvas cover, in order to get an estimate of the instantaneous ecosystem respiration rate (R_E). Between the measurements of NEE and R_E the chamber was removed from the collar for a short time period to allow the gas concentration to return to ambient levels. Carbon dioxide flux rates were calculated from the linear change in gas concentration as a function of time. The ecological sign convention, in which fluxes from the biosphere to the atmosphere are negative, was used. Gross photosynthesis (P_G) was estimated as the sum of flux rate values measured in light (NEE) and dark (R_E).

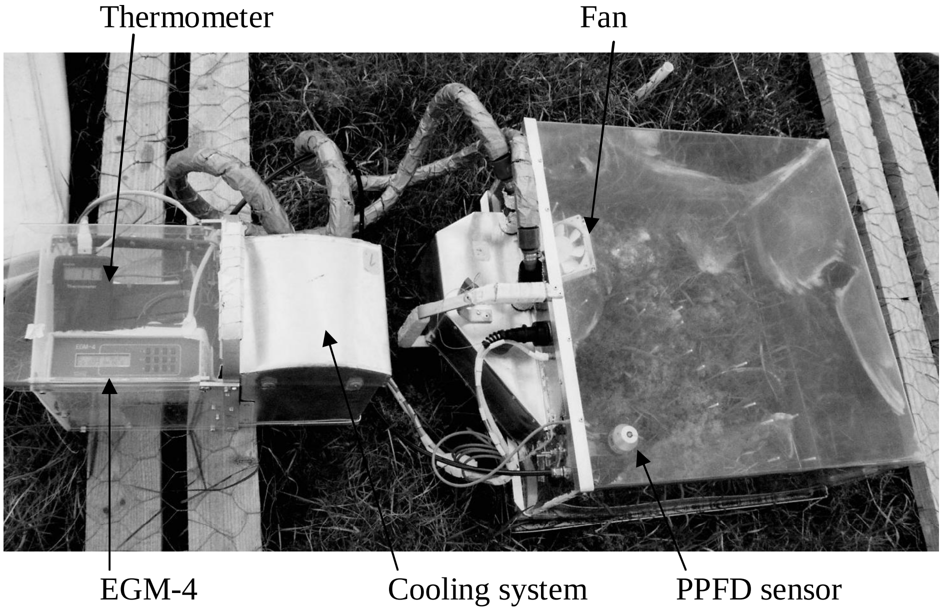

Figure 3.3 CO_2 flux chamber equipped with a cooling system and a fan. Infrared gas analyser (EGM-4) measures CO_2 concentration. Photosynthetic photon flux density (PPFD) and air temperature are measured inside the chamber.

3.5 CH_4 flux measurements

Methane measurements began in August 2003 and were carried out at biweekly to monthly intervals until September 2005. The closed chamber method was used (Saarnio et al., 1997). Each chamber (0.6 m × 0.6 m × 0.25 m) (Fig. 3.4) had a vent to ensure pressure equilibration; the vent was closed only after the chamber had been placed on the collar. A fan ensured the circulation of the air inside the chamber. Four 40 ml air samples were taken into plastic syringes equipped with three way stopcocks, at five minute intervals. A 10 minute interval was used in wintertime when low flux rates were expected due to cold temperatures and low vascular plant cover. Samples were analysed within 48 hours on a Shimadzu GC-

14-B gas chromatograph equipped with a flame ionisation detector (FID). Column, injector and detector temperatures were set to 40 °C, 100 °C and 330 °C, respectively and nitrogen was used as the carrier gas. Methane standards (4 ppm; BOC Gases Ireland Ltd.) were used. In order to remove moisture, samples and standards were injected through a 12 cm long Tygon tubing (6 mm diameter) filled with drierite (10 / 20 mesh) prior to entering the 2 ml sample loop. The flux rate was estimated as the linear rate of change in gas concentration over time. Due to the small flux rates, the unit of mg CH_4 m^{-2} day^{-1} was used.

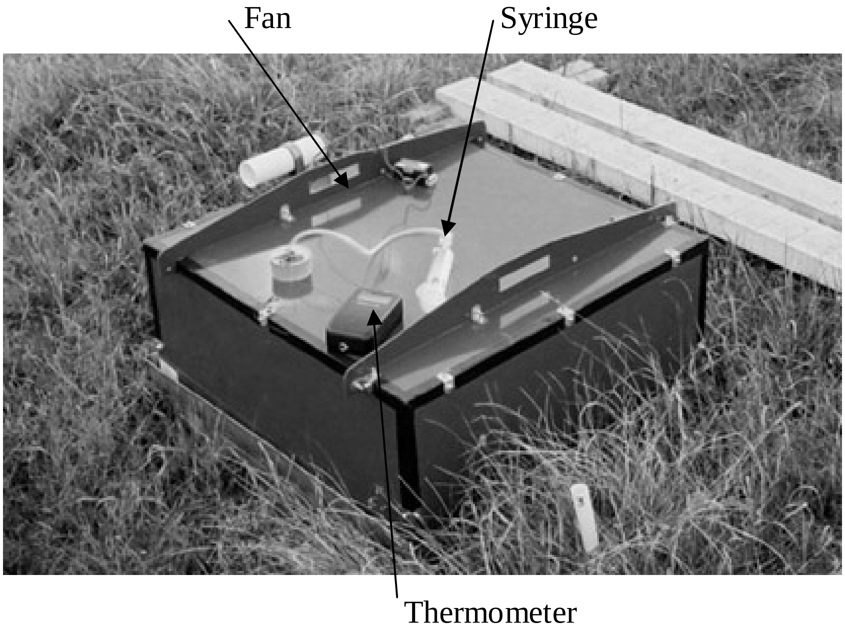

Figure 3.4 CH_4 flux chamber equipped with battery operated fan. Thermometer is used to measure air temperature inside the chamber. Samples are taken by plastic syringes.

3.6. Environmental measurements

In order to relate the CO_2 and CH_4 gas fluxes to prevailing environmental conditions, a set of parameters were measured in connection with the gas exchange measurements. The photosynthetic photon flux density (PPFD) was measured with a quantum sensor in µmol m^{-2} s^{-1} (PAR-1, PP-Systems, UK) simultaneously with CO_2 readings. Air temperature (T_{AIR}) inside the chambers was recorded simultaneously with CO_2 and CH_4 readings. At the same time, soil temperature and water level (WT) were measured adjacent to each sample plot. Soil temperatures were measured at 5, 10, 20 and 30 cm depths with a soil temperature probe, while WT was measured from perforated PVC pipes. Negative WT values indicate WT below soil surface.

Continuous meteorological measurements were carried out at an onsite weather station, located circa 200 meters south from the sample plots. Photosynthetic photon flux density (PPFD) (PAR Lite, Kipp & Zonen, Delft, The Netherlands) and air temperature (HMP45C, Vaisala, Vantaa, Finland) were measured at 2 m height. Soil temperature was recorded at 20 cm depth (107, Campbell Scientific Ltd. Loughborough, UK) below HL vegetation. Precipitation was measured with two tipping bucket rain gauges (ARG100, Environmental Measurements Ltd., Sunderland, UK and Obsermet OMC-200, Observator BV, Ridderkerk, The Netherlands). The averaging time for the meteorological data was 30 minutes.

3.7 Vegetation

3.7.1 Vascular Green Area index

Vascular Green Area index (VGA, m m^{-2}), which represents the surface area of green vascular plant material, was used in the gas fluxes modelling to relate gas fluxes to the seasonal dynamics of plant growth and senescence. VGA was calculated for each sample plot individually following Wilson, et al. (in Press-a). Five sub sample plots (8 × 8 cm) were established within each sample plot. The number of leaves of each vascular plant species was measured from these sub sample plots at two to four week intervals throughout the study period. In order not to disturb the vegetation in the sample plots three to five individuals of each vascular species were selected and ringed outside the sample plots to facilitate the leaf size measurements. The length and width of each leaf was measured non-intrusively and an average leaf size was calculated for each species. These measurements were made during the same dates as leaf numbers were counted. The green area (GA) of each species was calculated by multiplying the number of leaves by the size of an average leaf. Non-linear regression analysis was used to interpolate the green area (GA) of each species between measurements. This was made in order to describe the seasonal dynamics in GA and was carried out separately for each year. Equation 3.1 or 3.2 was used in interpolation based on the shape of development of GA

$$Daily\ GA = y_0 + a\, e^{\left(-0.5\left(\frac{julian\ -\ \mathrm{x}_{\max}}{b}\right)^2\right)} \tag{3.1}$$

$$Daily\ GA = y_0 + a\ e^{\left(-0.5\left(\frac{\ln\left(\frac{julian}{\mathrm{x}_{\max}}\right)}{b}\right)^2\right)} \tag{3.2}$$

where y_0 is a constant, julian is julian day, a is maximal GA during the season, x_{max} denotes the julian day when maximal GA occurs and b denotes the shape of the curve. Daily community VGA was calculated by summing the GA values of each species i within the sample plot (Equation 3.3).

$$Daily\ VGA = \sum_{i=1}^{n} GA_i \tag{3.3}$$

3.7.2 Vegetation characteristics

The vegetation community structure was analysed from each sample plot as a means of projection cover of each vascular and moss species (%). This was carried out at the end of July in each year. The nomenclature of vascular plants, mosses and liverworts follows Stace (1997), Smith (2004) and Smith (1990), respectively.

3.8 Water level experiment

A WT experiment was carried out to mimic the possible effects of climate change on peatland C fluxes. The period from October 2003 to September 2004 was considered as a calibration year. The experimental year began in October 2004 when the sample plots were divided into three experimental sites: control, WT drawdown and flooding sites. The six sample plots (two of each microform (HU, HL, LL)) within the WT drawdown site were surrounded by a narrow drainage ditch. The excess water was led towards the six sample plots located down slope in the flooding site. The runoff from the flooding site was blocked by a dam that was inserted 50 cm into the peat profile. The other sample plots remained intact, forming a control site. The aim of the experiments was to moderately decrease and increase WT by 5 to 10 cm. CO_2 and CH_4 fluxes were measured regularly until the end of September 2005.

3.9 Modelling of C flux components

3.9.1 Regression modelling

The use of the chamber method allowed us to create response functions between vegetation community C fluxes and environmental variables. The response functions were created to increase the understanding of the mechanisms behind C gas fluxes and to establish continuous time serious of gas flux components. Modelling was based on simultaneously measured gas exchange fluxes and environmental variables, which were corralated using ecophysiologically acceptable relationships. Regression modelling is a commonly used method in integrating P_G and R_E (Alm et al., 1997; Larmola et al., 2003; Nykänen et al., 2003; Tuittila et al., 1999; Tuittila et al., 2004) and CH_4 fluxes (Juutinen et al., 2003; Saarnio et al., 1997) measured by the chamber method. Modelling was performed with SPSS 12.0.1 for Windows. For the non-linear regression we applied the Levenberg-Marquardt method that uses the method of steepest descent in early iterations and then gradually switches to the Gauss-Newton approach, therein combining the best qualities of these methods was applied (Motulsku and Christopoulos, 2003).

3.9.2 CO_2 flux modelling

We modelled CO_2 flux components P_G and R_E separately, since they have different relationship with environmental variables and because we wanted to quantify the components separately. We followed the ecophysiological modelling approach of

Tuittila, et al. (2004), since it enables assessment of the different forms of relationships between fluxes and environmental parameters.

P_G is primarily controlled by irradiation (PPFD); this relationship is traditionally described by a Michaelis–Menten hyperbolic function (Stryer, 1988). Due to the use of the hyperbolic relationship, a non-linear regression has been widely used in the modelling of P_G (Alm et al., 1997; Bubier et al., 1998; Kettunen, 2000; Tuittila et al., 2004). The rate of P_G is connected to the photosynthesising leaf area, which varies within a year in accordance with the growth pattern of the plants. Bubier, et al. (1998) divided the growing season into three section and parameterized the P_G – PPFD model separately for each section. Alm, et al. (1997) added a linear term called the effective temperature sum index (ETI) to describe the seasonality. We, on the other hand used an actual leaf area parameter, VGA, in the models. Since the moss cover is generally more stable over time, VGA alone is often adequate to describe the changes in leaf area in the models. The correlation between P_G and VGA depends on the vegetation community structure. The correlation is generally saturating, however in cases when no self-shading occurs, it can be expressed with a linear form (Wilson et al., in Press-a). P_G depends on moisture conditions: the water balance regulates the stomatal opening and therefore controls the CO_2 uptake and also the metabolic processes may be water restricted (Farquhar and Sharkey, 1982; Hanson and Hitz, 1982). On the other hand, the high WT limits the productivity of many peatland plant species (Crawford, 1983). In peatlands, the WT is easy to measure and can be used to describe the moisture conditions. Tuittila, et al. (2004) established a unimodal relationship between P_G and WT in a *Sphagnum* community. The form of the correlations, however, depends on the range of measured variation in WT. In our study the WT range during the study period was small and remained in the linear part of the unimodal relationship. As a biological process, photosynthesis is also regulated by temperature. In both sides of the temperature optimum photosynthesis is reduced: low temperatures reduce the activity of Rubisco and the capacity for electron transport, while high temperatures reduce electron transport capacity and also increase the rates of CO_2 evolution from photorespiration (Farquhar and Sharkey, 1982). We used a unimodal relationship between air temperature and P_G.

R_E is the sum of autotrophic plant respiration and heterotrophic soil respiration; in this study the two processes were not separated. R_E is principally related to temperature. However, WT and leaf area also affect the flux rate. Exponential functions have been used to describe the relationship between R_E and temperature (Fang and Moncrieff, 2001; Lloyd and Taylor, 1994). The correlation is shown to be stronger in moist conditions compared to dry conditions (Silvola et al., 1996). Due to the exponential nature of the relationship, logarithmic transformation and linear regression were commonly used in modelling (Alm et al., 1997). Non-linear regression offers a possibility to describe the relationships between R_E and environmental variables more accurately. WT, for example, has a saturating relationship with soil respiration: lowering the WT increases soil respiration rapidly until at a certain depth (-30 cm) the peat surface becomes too dry and respiration saturates (Tuittila et al., 2004). Plant respiration is connected to metabolic activity of plants and has a similar unimodal WT response as P_G (Tuittila et al., 2004). As stated above, we did not separate soil and plant respiration, but modelled the R_E. During the study period the WT remained in a limited range and we only detected a linear relationship between R_E and WT. VGA was included in R_E models, since it directly affects the plant respiration rate and via litter production it affects also the soil respiration. It has been shown that the correlations of daytime and nighttime R_E with temperature are similar and therefore it is possible to use the response curves based on daytime measurements for estimating the nighttime flux rates, as well (Larmola et al., 2003).

Depending on the goal of the modelling, the P_G and R_E models were parameterized separately for each sample plot (Chapters 4 and 6) or for sample plot groups representing the four microforms (HU, HL, LL and HO) (Chapter 7). The models used are described in detail in each of the chapters.

3.9.3 Modelling of CH_4 flux

Frolking and Crill (1994) used regression modelling to relate CH_4 flux with environmental parameters. Among others, Saarnio et al. (1997) and Juutinen (2003) widened the use of the response functions into the integration and reconstruction of seasonal CH_4 fluxes. Granberg, et al. (1997) and Kettunen, et al. (2000) noticed that the performance of the models increased, when data from separate vegetation communities was treated separately. For the same reason we parameterized models separately for each sample plot. Saarnio, et al. (1997) used a linear model where soil temperature and WT were independent variables and had a logarithmic relationship with the flux. Juutinen, et al. (2003) used non-linear functions that do not require data transformation and allow the use of different types responses between flux and independent variables.

CH_4 flux is the difference between CH_4 production and consumption. Both processes are temperature dependent, but have different Q_{10} values (Dunfield et al., 1993), which makes it difficult to establish an accurate relationship between temperature and CH_4 flux (Moore and Dalva, 1993). Also WT affects both processes but in opposing ways; deepening WT increases oxidation and decrease production. The flux is strongly affected by WT, however the time-lag between a change in WT and change in flux rate i.e. hysteresis as well as the release of pore water CH_4 complicates the relationship (Moore and Dalva, 1993; Moore and Roulet, 1993). For these reasons only a weak relationship has sometimes been observed between point measurements of CH_4 flux and temperature and WT (Dalva et al., 2001). Besides, the vegetation, especially the amount of vascular plants with aerenchymatic cell structure, influences the CH_4 flux by increasing substrate supply for methanogens and by offering a transport pathway for the gas. In field conditions it is not possible to separate CH_4 production and consumption processes, modelling has to find the ‘middle course’ in describing the CH_4 flux. We related the CH_4 to soil temperature at 20 cm depth, WT and VGA using non-linear regression. Models that were parameterized individually for each sample plot are described in detail in Chapters 5 and 6.

3.10 Reconstruction of fluxes

The fluxes were integrated over time by using the models created in conjuction with the continuous environmental data. Half hourly PPFD, T_{AIR} and T_{20} were obtained from the onsite weather station (Section 3.6). Daily WT was integrated for each sample plot from the WT measurements made during gas flux measurement campaigns. Daily VGA was calculated for each sample plot using Equations 3.1, 3.2 and 3.3 (Section 3.7.1).

3.11 Canonical Correspondence Analysis

Ordination methods are used to define and describe the patterns in communities (Leps and Smilauer, 2003). This is achieved by finding the axes of the greatest variability in the community composition for a set of samples. Ordination also can also be used to visualize the similarity structures between samples or species. With ordination the measured environmental variables can be correlated with the ordination axes and therein, connect the variables with community composition (Leps and Smilauer, 2003; ter Braak and Smilauer, 2002), as was done in this study. Several different ordination techniques have been developed (correspondence analysis (CA), canonical correspondence analysis (CCA), redundancy analysis (RDA)) (ter Braak, 1986). CA and RDA apply a linear species response model that is suitable when the observed variation is small and the gradient is short (ter Braak and Smilauer, 2002); CCA, on the other hand enables the use of unimodal (Gaussian) relationship that is common between species and environmental parameters (ter Braak, 1986). In our study, the variation was large enough for the use of CCA. The other advantage of CCA is that the constrained ordination axis corresponds to the direction of the greatest data set variation that can be explained by the environmental variables (Leps and Smilauer, 2003). We used CCA to define the water level gradient in the vegetation communities (Chapter 4) and to relate the vegetation communities with explanatory variables (CH_4 flux, NEE, WT, VGA and moss cover) (Chapter 5). The use of a Monte Carlo permutation test facilitates the evaluation of the statistical significance of the relationship between the species and the environmental variables (ter Braak and Smilauer, 2002).

4 Patterns in vegetation and CO_2 dynamics along a water level gradient in a lowland blanket bog

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4.1 Abstract

The surface of bogs is commonly patterned and composed of different vegetation communities, defined by water level. Carbon dioxide (CO_2) dynamics vary spatially between the communities. In assessing the role of bogs in global carbon cycling, an understanding of the controls on the high spatial variation of CO_2 dynamics is required. We described the water level gradient in vegetation in a blanket bog and estimated CO_2 exchange along the gradient using a combination of chamber based measurements and regression modelling. The aim was to investigate the controls on gross photosynthesis (P_G), ecosystem respiration (R_E) and net ecosystem CO_2 exchange (NEE) as well as spatial and temporal variation in these fluxes. Vegetation structure was strongly controlled by water level. The species with distinctive water level optima were separated into the opposite ends of the gradient using canonical correspondence analysis. The number of species and leaf area were highest in the intermediate water level range and these communities had the highest P_G. R_E, which includes decomposition, was less dependent on vegetation structure and followed the water level gradient more directly. Annual NEE varied from -35 to 195 g C m^{-2}, being lowest in wet and highest in dry vegetation communities. Temporal variation was most pronounced in P_G that decreased substantially during winter, when photosynthetic photon flux density and leaf area were lowest. R_E, which is dependent on temperature, was less variable and wintertime R_E fluxes constituted ~25 % of the annual flux.

4.2 Introduction

Blanket bogs are locally important ecosystems in areas with high and regular rainfall: for example in Ireland, Scotland, and costal areas of England and Norway. In Ireland blanket bogs cover 12 % of the land area and their carbon (C) stock is estimated to be 0.57 Pg or 28 % of the total soil C stock (Tomlinson, 2005). Globally peatlands are an important C store. Since the last Ice Age, northern peatlands have accumulated 270-455 Pg of atmospheric C (Gorham, 1991; Turunen et al., 2002). At present, pristine peatlands are, in general, a small sink of carbon dioxide (CO_2) (Gorham, 1991; Turunen et al., 2002) and a considerable source of methane (CH_4) (Bartlett and Harriss, 1993). The annual C budget of a peatland depends on the environmental conditions and interannually a peatland can change from being a sink to a source of C (Lafleur et al., 2003; Waddington and Roulet, 2000).

Studies carried out in peatlands of the boreal, arctic and cold temperate climate zones have shown that CO_2 exchange is dependent on vegetation structure and environmental factors such as hydrological conditions and weather phenomena (Alm et al., 1997; Lafleur et al., 2003). In ombrotrophic bogs CO_2 exchange varies spatially (Waddington and Roulet, 2000), as the surface is often a continuum of different vegetation communities commonly classified as microforms, namely hummocks, lawns and hollows (Lindsay, 1995). These vegetation communities are supported by different water levels that affect their species composition, biomass (Moore et al., 2002), and photosynthetic capacity (Bubier et al., 2003b). The response of CO_2 fluxes to environmental variables varies between communities (Bubier et al., 2003b). Therefore, an understanding of the interaction between different vegetation communities and climate is a vital prerequisite for the incorporation of peatlands into models of global C cycling (Belyea and Malmer, 2004).

Ireland has a humid temperate climate that is characterized by cool summers and mild winters, with only moderate seasonality (Collins and Cummins, 1996). The proximity of the Gulf Stream exerts a moderating influence on the climate. This provides conditions that are extremely favourable to peat formation. The major difference compared to more northern and continental regions is the lack of snow cover and soil frost development during winter. As a result the evergreen plants and mosses are able to function during the winter period. Only a few studies of CO_2 fluxes have been carried out in peatlands in this region (Laine et al., 2006; Sottocornola and Kiely, 2005). Consequently, the nature of CO_2 exchange of blanket bogs is not well understood.

The surface structure and vegetation composition of lowland blanket bogs, which are located in flat to moderately sloping terrain, resemble that of raised bogs (Guinan et al., 1998). However, the high oceanic rainfall and frequent rain days, required for the existence of these bogs, constitutes an important input of nutrients (Doyle, 1982). Similarly to raised bogs, the different vegetation communities in blanket bogs support different CO_2 exchange dynamics (Laine et al., 2006). However, the interaction between the factors controlling CO_2 fluxes and their spatial variation is poorly understood. In Ireland the longer growing season and mild winters may produce higher annual productivity, however, plant and soil respiration during winter may be high compared peatlands in more northerly regions (Wilson et al., in Press-b). This emphasises the need to investigate the contribution of wintertime CO_2 fluxes to the annual CO_2 balance, in this maritime temperate climate.

In this study we measured the CO_2 exchange along a water level and vegetation gradient in a lowland blanked bog. The use of the chamber method allowed us to study homogenous vegetation communities and to analyse the flux responses to varying environmental variables. These measurements captured both spatial and temporal variation in the components of CO_2 exchange: gross photosynthesis (P_G), ecosystem respiration (R_E) and net ecosystem exchange (NEE). Our aim was (1) to characterize the vegetation structure along the water level gradient, (2) to examine the controls on P_G and R_E along the gradient and (3) to investigate the temporal variation in CO_2 exchange.

4.3 Materials and methods

4.3.1 Site description

The study site was located in an extensive lowland blanket bog in Co Kerry, Ireland (51°55´N, 9°55´W). During 2003, 2004 and 2005 the annual rainfall was 2510, 2356 and 2459 mm yr^{-1}, respectively. In the same period the average air temperature for the warmest month, July and the coldest month, February were 14.6 and 6.1 °C, respectively.

The surface of the bog is a continuum of vegetation communities ranging from dry hummocks to permanently inundated hollows. Hummocks were covered by a dense bryophyte carpet (*Sphagnum* spp., *Racomitrium lanuginosum*) and had *Molinia caerulea* and dwarf scrubs *Calluna vulgaris* and *Erica tetralix* as dominant vascular plant species. Lawn level vegetation ranged from dense stands of *M. caerulea* and *Schoenus nigricans* in drier areas, to wet areas dominated by *Rhynchospora alba* that had a shorter growing season than most other plant species in the area. Moss cover was sparse in lawns. Inundated hollows supported bryophytes (*Sphagnum cuspidatum, S. auriculatum*) and a scattered vegetation of *R. alba, S. nigricans* and *Eriophorum angustifolium*.

4.3.2 Study site

The study site was established in June 2003. Eighteen stainless steel collars (0.6 m × 0.6 m × 0.15 m) were inserted into the peat to cover the spatial variation in vegetation from hummocks to low lawns. In March 2004 three additional sample plots were established to widen the range to include hollow vegetation. The sample plots were divided into four groups: hummocks (HU), high lawns (HL), low lawns (LL) and hollows (HO). In each group we coded the sample plots from 1 to 6 according to their median water level (WT_{MED}). Sample plot characteristics are given in Table 4.

Table 4.1 Characteristics of each sample plot. (a) Percentage cover of the five most abundant vascular plant species, (b) total moss cover (%), (c) median water level (WT_{MED}, cm below surface) and (d) maximum vascular green area (VGA_{MAX}, m^2m^{-2}) in years 2003 and 2004.

Sample plot	HU1	HU2	HU3	HU4	HU5	HU6	HL1	HL2	HL3	HL4	HL5	HL6	LL1	LL2	LL3	LL4	LL5	LL6	HO1	HO2	HO3
Drosera rotundifolia	0.5												0.5			0.5		0.1		0.2	
Drosera intermedia									1										0.1	0.1	
Erica cinerea	3	2	1	3	3	3	3	2		3	3	3		1	1	1	0.5				
Eriophorum angustifolium					1									1			0.5	0.5	0.5		
Molinia caerulea	5	5	12	6	7	10	10	10	7	5	4	8	3	2	4	2	2	1		0.5	0.1
Narthecium ossifragum	3	2	2	4	10	15	5		7	3	2	4		0.5	2	1	0.5	0.5			
Rhynchospora alba				1		3	25	3	10	17	35		25	20	15	20	20	3	0.1	2	0.5
Schoenus nigrican		15	2				1	7				8	3						0.5		0.1
Calluna vulgaris	4	8	4	7	8	4	7	4	3	5	1	6	1		1						
Menyanthes trifoliata																				15	10
Carex limosa																			0.1		0.1
Moss cover	100	60	97	96	91	22	27	22	6	54	8	53	10	2	1	6	15	2	25	15	10
WT_{MED}	-15	-14	-14	-13	-12	-11	-7	-6	-5.5	-4	-3	-3	-3	-2	-2	-1.5	-1.5	0	2.5	3.5	7
VGA_{MAX} 2003, m^2/m^2	0.7	1.5	0.6	0.9	1.1	1.1	1.5	1.1	1.0	1.1	1.0	0.9	0.7	0.9	0.9	0.9	0.7	0.6	0.1	0.4	0.5
VGA_{MAX} 2004, m^2/m^2	0.9	2.1	0.9	0.6	1.2	1.2	1.7	1.8	1.3	1.2	1.1	1.2	0.6	0.9	0.8	1.0	0.9	0.7	0.1	0.4	0.5

4.3.3 CO_2 flux measurements

CO_2 exchange measurements were made using a closed transparent plexiglas chamber (0.6 m × 0.6 m × 0.33 m). The chamber was vented and included a cooling system (Alm et al. 1997). The CO_2 concentration inside the chamber was monitored with a portable infrared gas analyser (EGM-4, PP Systems, UK). The instantaneous net CO_2 exchange (NEE) was first measured under a stable ambient illumination at 15 second intervals over a 60-240 second period. This was then repeated with the chamber covered with an opaque canvas cover, in order to measure the instantaneous ecosystem respiration rate (R_E). CO_2 flux rates were calculated from the linear change in gas concentration as a function of time. We used the ecological sign convention, in which fluxes from the biosphere to the atmosphere are negative. Gross photosynthesis (P_G) was calculated as the sum of flux rate values measured in light (NEE) and dark (R_E).

In order to relate the gas fluxes to prevailing environmental conditions, the photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}, PAR-1, PP-Systems, UK) and air temperature (T) inside the chamber were recorded simultaneously with NEE readings. At the same time water level (WT), relative to the sample plot surface, was measured. For sample plots HU1, HU2, HL2, HL4, LL4 and LL5 we used measurements carried out from July 2003 to August 2005; for sample plots HO1, HO2 and HO3 measurements from March 2004 until August 2005. For the other 12 sample plots measurements were made from July 2003 to September 2004.

4.3.4 Vegetation

We used Vascular Green Area index (VGA, m m^{-2}) in the CO_2 flux models in order to describe the changes in gas fluxes that were related to seasonal dynamics of plant growth. VGA was calculated for each sample plot according to Wilson et al. (in Press-a) and Laine et al. (2006). We counted the number of leaves of each vascular plant species present in each sample plot at two to four week intervals throughout the study period. We then multiplied this by leaf size, which was determined by measurement of the leaves of selected individual plants of each species on the same dates as the leaf numbers were counted.

For each sample plot, non-linear regression analysis was used to interpolate the green area (GA) of each species between measurements. This was made in order to describe the seasonal dynamics in the growth of the species. We used GA models described in Laine et al. (2006). Daily VGA was calculated by summing the GA values of each species within the sample plot.

In addition, the vegetation composition of the sample plots was surveyed in August of 2003 and 2004 by estimating the projection cover of each species (%). Nomenclature of vascular plants, mosses and liverworts follows Stace (1997), Smith (2004) and Smith (1990), respectively. We used constrained ordination to characterize the moisture gradient in vegetation. Canonical Correspondence Analysis (CCA) using CANOCO for Windows 4.5 program (ter Braak and Smilauer, 1998) was performed for plant community data gathered in August 2004. We applied median, mean, minima and maxima water level as explaining variables. A Monte Carlo permutation test was performed to evaluate the significance of the model and the partial effect of each explaining variable.

4.3.5 Modelling of CO_2 exchange components

We constructed CO_2 exchange component (P_G, R_E) models separately for each sample plot. Following the approach of Tuittila et al. (2004), we used a multiplicative model format in which the sub-models, representing the responses of fluxes to different environmental variables, were multiplied by each other. Due to differences in the vegetation composition between the sample plots (Table 4.1), it was not possible to use the same model format for every sample plot.

We used the Michaelis-Menten relationship (Stryer, 1988) to describe the light dependence of P_G for all sample plots (Fig. 4.1a). Photosynthesis is related to the amount of photosynthesizing green leaf area, which has strong seasonal dynamics. Since the moss cover remained constant over the study period, VGA was used to describe seasonal changes in P_G. For the majority of the plots the relationship between P_G and VGA was linear (Fig. 4.1b). We applied parameter s (Equation 4.1) to describe the contribution of mosses to the total green area. Moss cover in plots LL2 and LL6 was negligible and therefore parameter s was not necessary (Equation 4.2). In the wettest plots HO1, HO2 and HO3 P_G showed a saturating response to VGA, therefore we used a hyperbolic curve to describe the relationship (Equation 4.3). Photosynthesis has a unimodal response to temperature i.e. photosynthesis increases with increasing temperature until it becomes restricted at high temperatures. We related P_G to air temperature (T) (Fig. 4.1c) by using a gaussian response (Equation 4.1). In LL2 and LL6 VGA was highly associated with temperature; accordingly temperature did not improve the models (Equation 4.2). Within the drier sample plots the water level (WT) range was small during the study period and was excluded from the models. However, in the hollow plots (HO1, HO2 and HO3) WT had a strong impact on photosynthetic rate, which we described using a linear relationship (Equation 4.3).

The general P_G model format was as follows:

$$P_G = Q\left(\frac{PPFD}{k + PPFD}\right)(s + VGA)\exp\left(-0.5\left(\frac{T-u}{p}\right)^2\right) \tag{4.1}$$

The P_G model format for plots LL2 and LL6 was as follows:

$$P_G = Q\left(\frac{PPFD}{k + PPFD}\right)VGA \tag{4.2}$$

The P_G model format for plots HO1, HO2 and HO3 was as follows:

$$P_G = (b + b_1 WT)\left(\frac{PPFD}{k + PPFD}\right)\left(\frac{VGA}{k_{VGA} + VGA}\right)\exp\left(-0.5\left(\frac{T-u}{p}\right)^2\right) \tag{4.3}$$

P_G model parameters for each plot are given in Table 4.2.

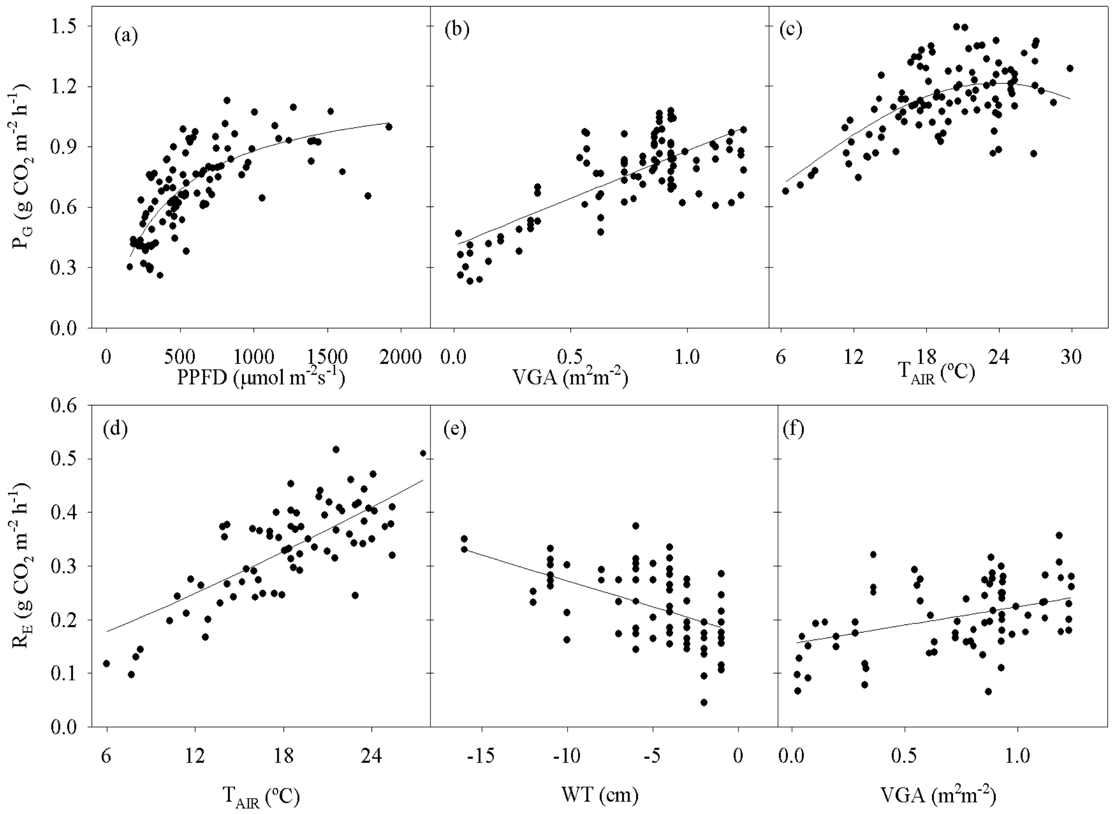

Figure 4.1 An example of environmental controls on P_G and R_{TOT} in sample plot HL6. Response of P_G to (a) photosynthetic photon flux density (PPFD), (b) vascular green area (VGA) and (c) air temperature. Response of R_{TOT} to (d) air temperature, (e) water level (WT) and (f) VGA. During 2003-2004 measured P_G values were adjusted to (a) VGA = 1 and T_{AIR} = 10 °C, (b) PPFD = 1000 μmol m^{-2} s^{-1} and T_{AIR} = 10 °C, (c) PPFD = 1000 μmol m^{-2} s^{-1} and VGA = 1 using Equation 4.1. During 2003-2004 measured R_{TOT} values were adjusted to (d) WT = -5 cm and VGA = 1, (e) T_{AIR} = 10 °C and VGA = 1, (f) T_{AIR} = 10 and WT = -5 cm using Equation 4.5.

Table 4.2 Estimated parameter values and goodness of fit (R^2) for gross photosynthesis (P_G) model of each sample plot. Number of the used Equation is given for each sample plot.

	Q (g m^{-2} h^{-1})	k (μmol m^{-2} s^{-1})	s/k_{vga} (m^2 m^{-2})	u (ºC)	p (ºC)	b (g m^{-2} h^{-1})	b_1	R^2	Eq no.
HU1	1.57 (0.24)	405.18 (103.86)	0.31 (0.08)	22.89 (1.27)	13.50 (1.93)			0.81	3.1
HU2	0.63 (0.09)	241.98 (58.06)	1.23 (0.30)	23.45 (0.77)	10.44 (1.10)			0.79	3.1
HU3	1.21 (0.19)	358.49 (84.37)	0.78 (0.16)	23.48 (1.16)	13.63 (1.74)			0.79	3.1
HU4	1.46 (0.23)	633.35 (127.21)	0.49 (0.09)	20.00 (0.94)	11.87 (1.52)			0.84	3.1
HU5	0.95 (0.10)	392.79 (66.10)	0.95 (0.14)	23.75 (1.01)	13.51 (1.73)			0.91	3.1
HU6	1.50 (0.17)	527.92 (87.10)	0.38 (0.08)	18.79 (5.55)	27.85 (15.03)			0.88	3.1
HL1	0.86 (0.10)	397.62 (83.74)	0.46 (0.13)	23.33 (0.87)	10.88 (1.22)			0.84	3.1
HL2	0.59 (0.09)	223.57 (66.63)	1.34 (0.29)	24.97 (0.78)	9.87 (0.87)			0.81	3.1
HL3	0.83 (0.11)	328.84 (74.35)	0.75 (0.17)	23.64 (1.01)	12.23 (1.72)			0.81	3.1
HL4	1.04 (0.12)	406.37 (69.70)	0.38 (0.06)	32.05 (20.25)	36.96 (38.50)			0.90	3.1
HL5	1.24 (0.11)	453.53 (77.39)	0.20 (0.05)	22.98 (0.88)	12.49 (1.91)			0.92	3.1
HL6	0.91 (0.11)	395.15 (72.71)	0.86 (0.16)	23.72 (1.99)	17.06 (3.98)			0.83	3.1
LL1	0.91 (0.11)	201.28 (74.50)	0.22 (0.06)	24.64 (1.42)	13.56 (2.99)			0.82	3.1
LL3	0.81 (0.09)	425.07 (81.28)	0.51 (0.09)	24.18 (0.63)	10.70 (1.18)			0.88	3.1
LL4	0.66 (0.09)	313.12 (96.30)	0.34 (0.09)	24.01 (1.28)	10.75 (2.36)			0.78	3.1
LL5	0.73 (0.09)	187.34 (69.79)	0.36 (0.09)	26.04 (1.94)	11.42 (2.60)			0.79	3.1
LL2	1.37 (0.13)	420.33 (98.69)						0.79	3.2
LL6	0.57 (0.07)	326.49 (113.11)						0.63	3.2
HO1		212.45 (102.29)	0.01 (0.00)	27.70 (1.65)	14.79 (2.87)	0.16 (0.02)	-0.01 (0.00)	0.77	3.3
HO2		253.32 (109.78)	0.51 (0.21)	24.86 (2.35)	16.64 (3.63)	1.02 (0.31)	-0.06 (0.02)	0.86	3.3
HO3		195.60 (95.14)	0.06 (0.02)			0.28 (0.04)	-0.01 (0.00)	0.76	3.3

Ecosystem respiration (R_E) consists of soil and plant respiration, both of which are affected by temperature and water level (Silvola et al., 1996; Tuittila et al., 2004). We related R_E to air temperature (T) using an exponential relationship described by Lloyd and Taylor (1994) (Fig. 4.1d). In our study the WT fluctuation remained modest and we observed a linear relationship between R_E and WT (Fig. 4.1e). Along with temperature, the seasonality in the flux rate was described by VGA. Respiration increased linearly with increasing VGA (Fig. 4.1f). For R_E in HO1, HO2 and HO3, the effect of VGA was not significant and it was not used in the model. Therefore the R_E model for these three plots was:

$$R_E = (b + b_1 WT)\left[\exp\left(b_2\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)\right)\right] \tag{4.4}$$

The model format for the other plots was:

$$R_E = (b + b_1 WT)\left[\exp\left(b_2\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)\right)\right](s + VGA) \tag{4.5}$$

In Equations (4.4) and (4.5) T_{ref} was set at 283.15 K and T_0 at 227.13 K according to Lloyd and Taylor (1994). T_0 is the temperature minimum at which respiration reaches zero. Air temperature (T) is given in degrees Kelvin. The R_E model parameters for each sample plot are given in Table 4.3. SPSS 12.0.1 for Windows statistical package (SPSS, Inc.) was used in flux modelling.

Table 4.3 Estimated parameter values and goodness of fit (R^2) for ecosystem respiration (R_E) model of each sample plot. Standard errors of the estimates are given in brackets. Equation 4 was used for HO1-HO3 and Equation 5 for HU1-LL6

	b	b_1	b_2 (K)	s	R^2
HU1	0.029 (0.013)	-0.002 (0.001)	239.30 (20.27)	2.045 (0.756)	0.736
HU2	0.028 (0.008)	-0.001 (0.000)	184.21 (20.81)	2.908 (0.869)	0.702
HU3	-0.021 (0.015)	-0.005 (0.002)	159.69 (30.47)	2.667 (1.135)	0.797
HU4	0.046 (0.015)	-0.002 (0.001)	216.40 (34.19)	1.427 (0.475)	0.694
HU5	0.007 (0.005)	-0.003 (0.001)	195.35 (28.10)	3.931 (1.417)	0.762
HU6	0.039 (0.008)	-0.004 (0.001)	178.07 (26.45)	1.277 (0.282)	0.849
HL1	0.025 (0.006)	-0.002 (0.001)	229.05 (29.04)	2.696 (0.791)	0.792
HL2	0.033 (0.005)	-0.004 (0.001)	174.06 (17.68)	1.676 (0.333)	0.818
HL3	0.028 (0.007)	-0.004 (0.001)	190.23 (28.30)	1.935 (0.547)	0.824
HL4	0.023 (0.006)	-0.001 (0.000)	241.78 (21.96)	3.005 (0.796)	0.803
HL5	0.081 (0.013)	-0.013 (0.003)	119.90 (32.99)	0.616 (0.141)	0.829
HL6	0.054 (0.012)	-0.003 (0.001)	168.94 (27.59)	2.260 (0.622)	0.783
LL1	0.081 (0.020)	-0.010 (0.004)	183.96 (47.55)	0.674 (0.196)	0.739
LL2	0.086 (0.016)	-0.014 (0.004)	101.16 (42.63)	0.619 (0.156)	0.796
LL3	0.048 (0.010)	-0.006 (0.002)	212.03 (36.53)	0.987 (0.248)	0.822
LL4	0.082 (0.015)	-0.005 (0.002)	169.37 (33.53)	0.489 (0.120)	0.704
LL5	0.053 (0.012)	-0.008 (0.002)	157.01 (30.52)	0.955 (0.244)	0.725
LL6	0.046 (0.011)	-0.014 (0.004)	146.78 (48.48)	0.460 (0.160)	0.823
HO1	0.041 (0.010)	-0.007 (0.002)	148.03 (74.33)		0.450
HO2	0.091 (0.015)	-0.016 (0.003)	122.26 (50.36)		0.700
HO3	0.068 (0.016)	-0.007 (0.002)	145.69 (71.37)		0.615

Equations (4.1 – 4.5) were individually parameterised and used to calculate hourly P_G and R_E for each sample plot. P_G and R_E fluxes were reconstructed for the time period 1st October 2003 – 30th September 2004 to obtain annual fluxes using PPFD and air temperature data from an on-site weather station (Laine et al., 2006). Daily WT was interpolated for each plot from WT measurements made during the chamber measurement campaigns. Daily VGA was estimated for each plot using the VGA models (Laine et al., 2006). There were no measurements of WT or VGA of hollows from the period of October 1st 2003 to April 5th 2004. Therefore, the daily water level for the missing period was estimated from LL values using the difference in the relative altitude between microforms LL and HO. To estimate the average daily VGA of the HO for this period, the VGA models based on data from 2004 were used. Hourly NEE over the year was calculated as the difference between P_G and R_E.

4.4 Results

4.4.1 Environmental conditions

The seasonal dynamics in the average daily air temperature was noticeable but modest and during wintertime the daily air temperature often exceeded 10 ˚C (Fig. 4.2a). The average WT of the sample plots remained in the top 5 cm peat layer during most of the study period (Fig. 4.2a). However, in all three summers the WT periodically deepened, particularly in the summer of 2005. Daytime daily average PPFD (Fig. 4.2b) had stronger seasonal dynamics than air temperature or WT. The regularity of overcast days during all three growing seasons is pronounced. The environmental conditions in the study site in years 2003 and 2004 are described in more detail by Sottocornola and Kiely (2005).

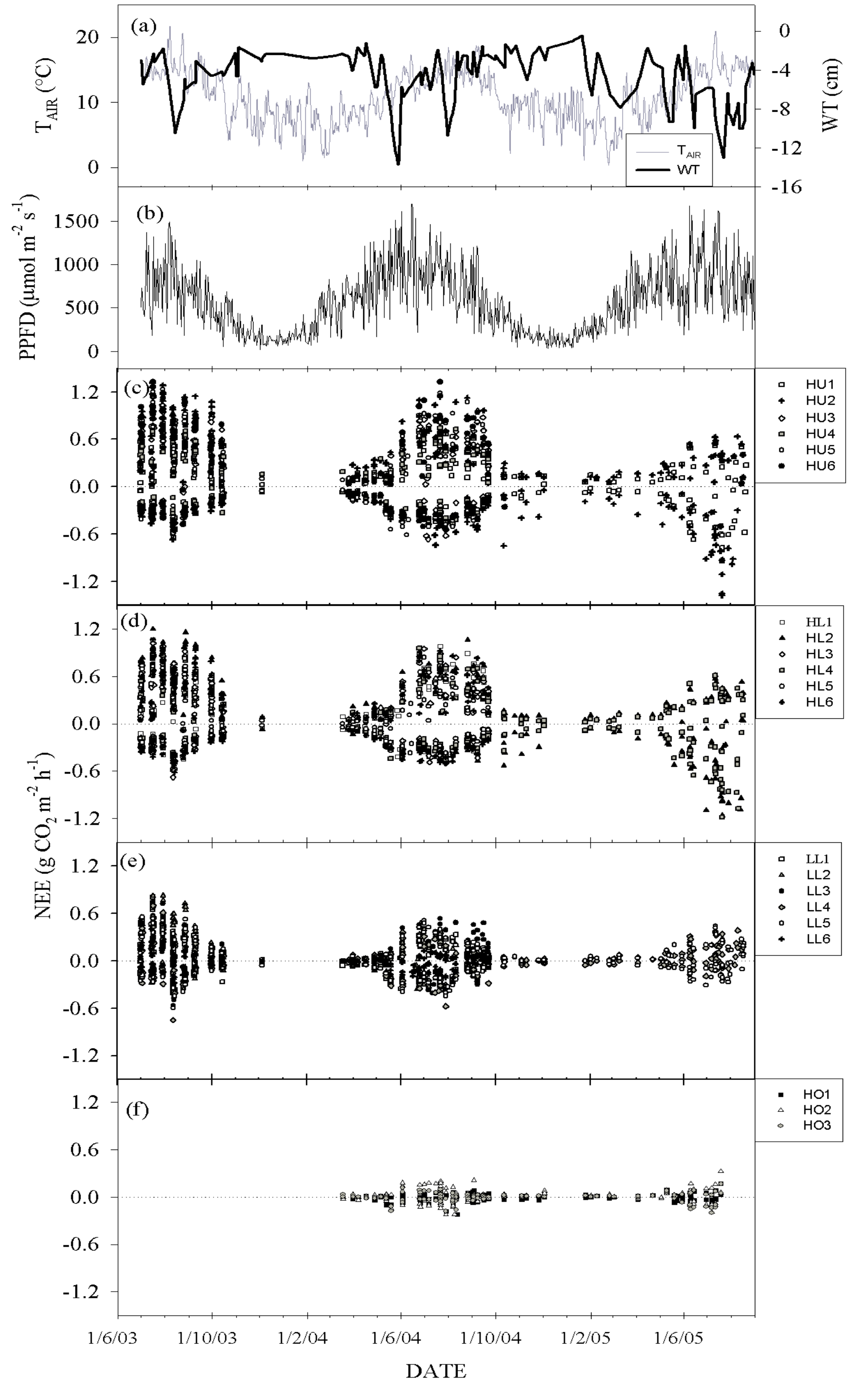

Figure 4.2. Daily average (a) air temperature (T_{AIR}) and average water level (WT) of the sample plots and (b) photosynthetic photon flux density (PPFD) during daylight hours. Measured net CO_2 exchange (light and dark measurements) in sample plots (c) HU1-HU6, (d) HL1-HL6, (e) LL1-LL6 and (f) HO1-HO3. Daily variation in fluxes is mainly due to variation between sample plots and differences in light levels between measurements.

4.4.2 Moisture gradient in vegetation

Canonical Correspondence Analysis (CCA) for vegetation communities using water level parameters as explanatory variables indicated strong correlation between water level parameters. After including a single WT parameter into the model, the partial effect of other parameters was very low and they did not improve the model. We selected median water level (WT_{MED}) as a representative variable, which had a significant relationship with plant community data ($p = 0.002$) and alone explained 20.3 % of the variation in species distribution.

The first axis separated sample plots forming a continuum from HU to HO (Fig. 4.3). Along this WT gradient there was a clear separation of species between HU and HO species (Fig. 4.3). In the dry end of the gradient the hummock forming mosses such as *Sphagnum rubellum* were associated together with lichens and a dwarf scrub *Calluna vulgaris*. A forb, *Menyanthes trifoliata* had its optimum in the wet end of the gradient together with hollow *Sphagna* (*Sphagnum cuspidatum*, *Sphagnum auriculatum*). Although *Rhynchosphora alba* was the only species having its optimum in lawns (Fig. 4.3), the highest VGA was associated with lawn communities (Fig. 4.4a); the maximum vascular green area (VGA_{MAX}) had a unimodal relationship with WT_{MED} having the optimum at WT 9 cm below the surface (Fig. 4.4a). Unlike the vascular plants, mosses were most abundant in hummocks (Fig. 4.4b), which had WT_{MED} below the optimal conditions for VGA (Fig. 4.4a). None of the bryophytes had their optimum in the intermediate water level conditions (Fig. 4.3). Reflecting the moss species distribution along the WT gradient, moss cover had a bimodal response to WT_{MED}, although the peak in the wetter end was much lower than in the drier end (Fig. 4.4b). The species abundance was highest in the communities in the hummock – lawn interface and decreased with increasing moisture (Fig 4.4c). The second axis of CCA was related to internal variation within the groups, especially HU showed large variation along the second axis (Fig. 4.3).

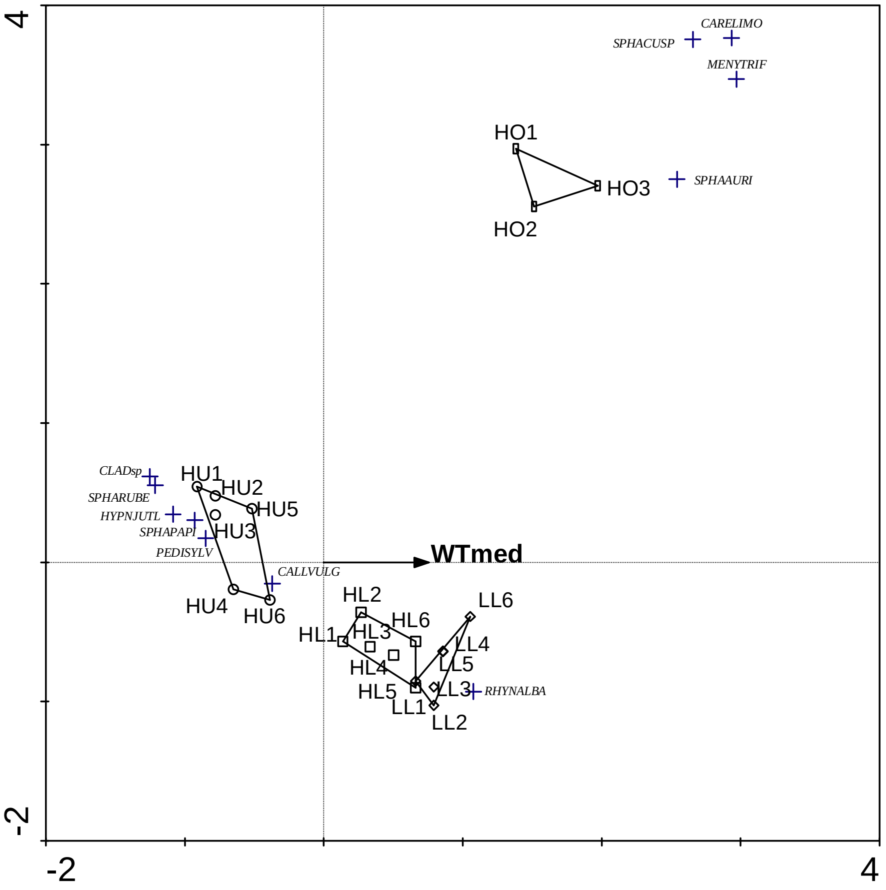

Figure 4.3 Canonical correspondence analysis (CCA) of the interaction between species and median water level (WT med). The eigenvalue of axis 1 is 0.57. Species with 15 % lower axis minimum fit are included in the figure. The second, unconstrained, axis that describes residual variation, which is not related to WT$_{MED}$, had a higher eigenvalue (0.75) than the first axis. CALLVULG = *Calluna vulgaris*; CARELIMO = *Carex limosa*; CLADsp = *Cladonia* sp; HYPNJUTL = *Hypnum jutlandicum*; MENYTRIF = *Menyanthes trifoliata*; PEDISYLV = *Pedicularis sylvaticum*; RHYNALBA = *Rhynchospora alba*; SPHAAURI = *Sphagnum auriculatum*; SPHACUSPI = *Sphagnum cuspidatum*; SPHAPAPI = *Sphagnum papillosum*; SPHA RUBE = *Sphagnum rubellum.*

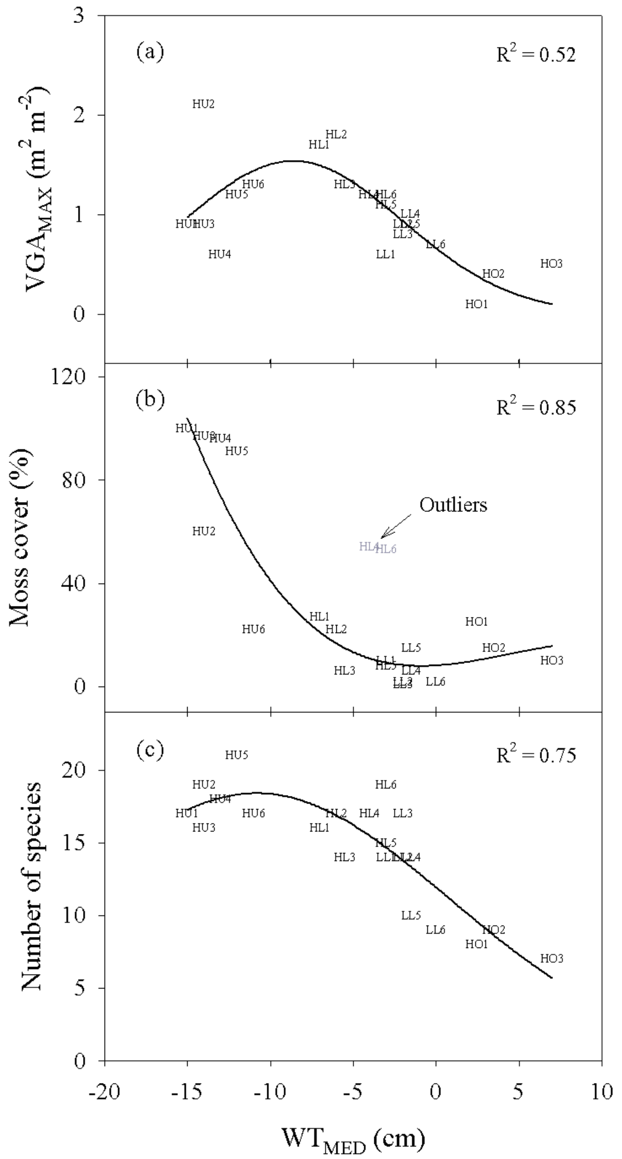

Figure 4.4 Correlation between median water level (WT_{MED}) and (a) maximum vascular green area (VGA_{MAX}), fitted with a unimodal gaussian model (R^2 = 0.52; SE = 0.35; F = 9.6; P = 0.002) and (b) moss cover, fitted with a cubic (3rd degree polynomial) model (R^2 = 0.85; SE = 15.6; F = 27.5; P <0.0001) and (c) number of species, fitted with a gaussian curve (R^2 = 0.75; SE = 2.1; F = 26.5; P <0.0001). In (b) sample plots HL4 and HL6 were excluded from the curve fitting as outliers.

4.4.3 Model performance

On average, the regression models explained 82 % of the variation in P_G fluxes (Table 4.2). The models tended to slightly overestimate small and underestimate high fluxes. The slope of the estimated versus observed data regression, which describes the departure from 1:1 line, varied between 0.64 – 0.90.

On average 75 % of the variation in R_E fluxes was explained by the models (Table 4.3). Similarly to P_G models, R_E models overestimated small and underestimate high fluxes. The slope of the estimated versus observed data regression varied between 0.62 – 0.81.

4.4.4 Controls of CO_2 exchange along the moisture gradient

The measured CO_2 exchange, both in light and dark, followed the moisture gradient, being highest in HU (Fig. 4.2c) and lowest in HO (Fig. 4.2f). However, variation between the sample plots was large.

The reconstructed annual P_G flux followed the WT gradient with a unimodal relationship showing the highest P_G in WT of –10 cm (Fig. 4.5a). The reconstructed annual R_E (Fig. 4.5b) saturated at the driest end of the water level gradient. The fastest changes between sample plots in R_E fluxes occurred between the WT range from 0 to –5 cm. Similar to VGA_{MAX} and P_G, the reconstructed annual NEE (Fig. 4.5c) had a unimodal relationship with WT. However, the correlation was weaker and the flux rates saturated when the WT was close to the soil surface. Both annual P_G and annual R_E showed a saturating relationship to VGA_{MAX} (Fig. 4.6a, b), but only a weak linear correlation was observed between NEE and VGA_{MAX} (Fig. 4.6c). The species diversity (amount of species in the sample plot) had a strong linear correlation with both annual P_G (Fig. 4.6d) and annual R_E (Fig. 4.6e), while the correlation with NEE was weaker (Fig. 4.6f).

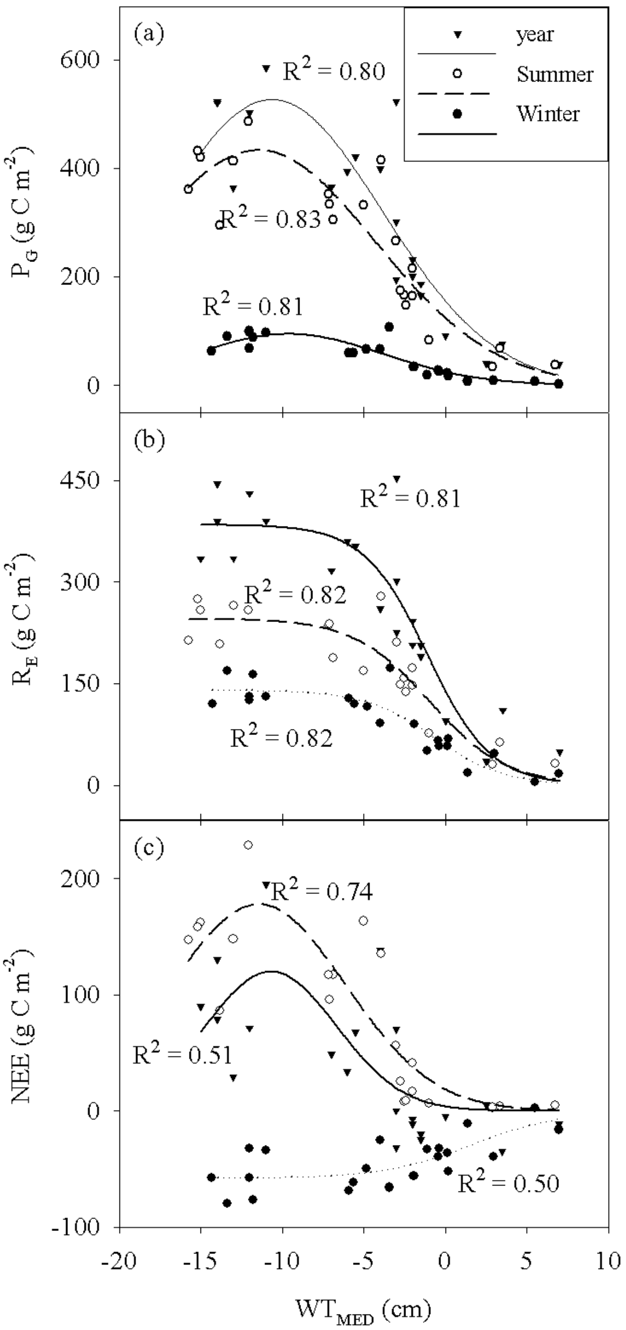

Figure 4.5 The relationship between sample plot's median water level (WT) and reconstructed annual, summer (April-October) and winter (November-March) (a) gross photosynthesis (P_G), fitted with a gaussian curve ($R^2 = 0.81$; SE = 83.6; F = 23.4; $P < 0.0001$), (b) ecosystem respiration (R_E), fitted with a sigmoidal curve ($R^2 = 0.81$; SE = 60.2; F = 38.3; $P < 0.0001$) and (c) net ecosystem exchange (NEE) fitted with a gaussian curve ($R^2 = 0.51$; SE = 46.34; F = 9.5; $P < 0.0015$).

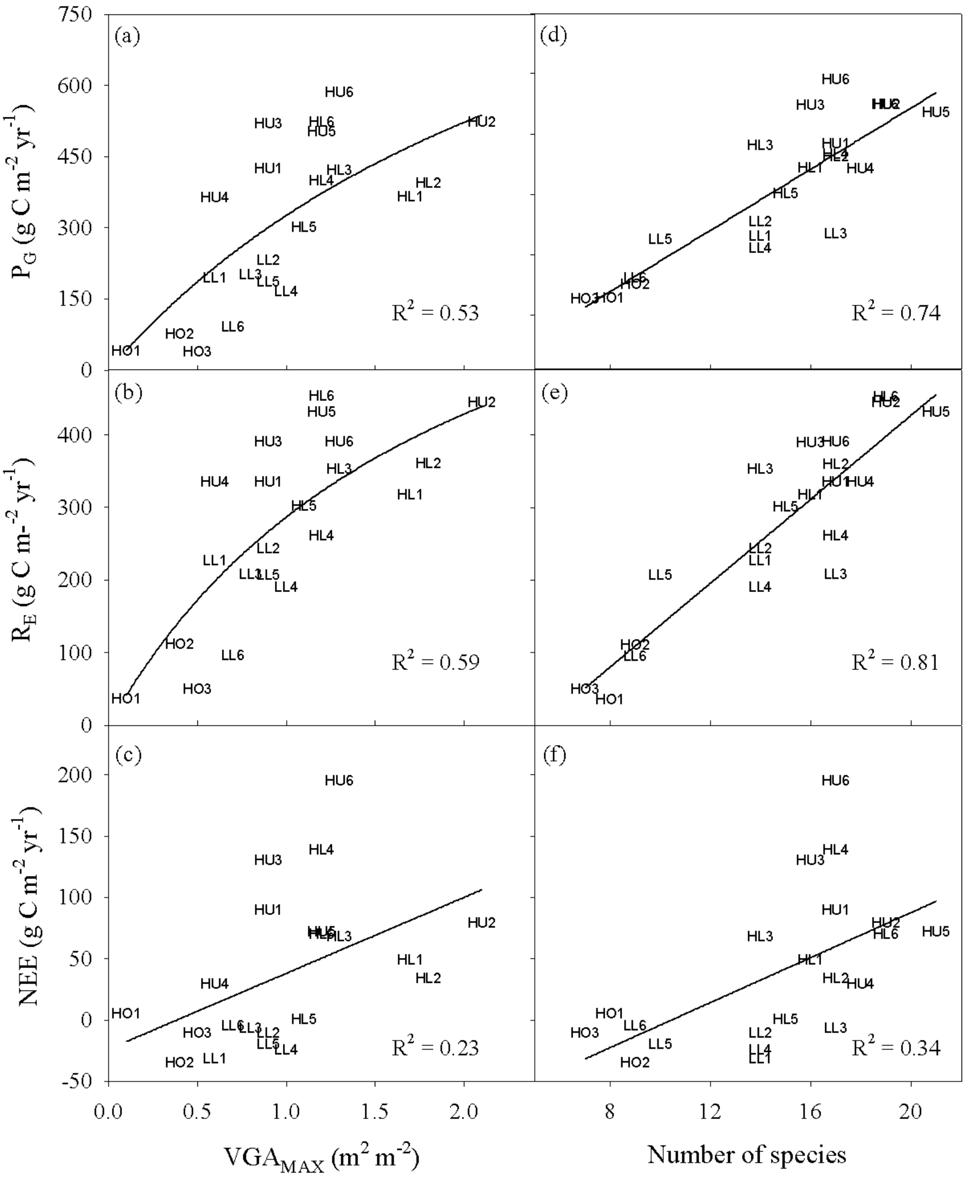

Figure 4.6 Relationship between sample plot's maximum vascular green area (VGA$_{MAX}$) and (a) annual gross photosynthesis (P$_G$) with a hyperbolic fit (R^2 = 0.53; SE = 122.9; F = 21.5; P <0.0002), (b) annual ecosystem respiration (R$_E$) with a hyperbolic fit (R^2 = 0.59; SE = 85.6; F = 27.9; P <0.0001) and (c) annual NEE with a linear fit (R^2 = 0.22; SE = 57.1; F = 5.3; P <0.001). Relationship between number of species and (d) annual P$_G$ with a linear fit (R^2 = 0.74; SE = 92.0; F = 53.3; P <0.0001), (e) annual (R$_E$) with a linear fit (R^2 = 0.81; SE = 57.2; F = 79.3; P <0.0001) and (f) annual NEE with a linear fit (R^2 = 0.34; SE = 52.9; F = 9.33; P = 0.006).

4.4.5 Temporal variation in CO_2 exchange components along the water level gradient

A strong seasonal variation was measured in all sample plots, with small fluxes and less spatial variation occurring during the winter periods (Fig. 4.2c, d, e, f). The highest fluxes were measured in the second half of July in every year. Fluxes were quite similar during the two summers 2003 and 2004, although summertime NEE was higher in 2004. During summer 2005 the measured net CO_2 uptake was lower and release higher in sample plots HU1, HU2, HL2 and HL4 in comparison to two previous summers (Fig 4.2c, d).

Water level affected P_G and R_E fluxes in a similar manner during summer and winter. The highest P_G of 433.2 g C m^{-2} was reached at WT_{MED} of –11 cm in summer. In winter the highest P_G of 94.2 g C m^{-2} was reached at WT_{MED} of –10 cm (Fig. 4.5a). During summer and winter, the WT_{MED} level at which the greatest change in R_E occurred was the same (-2 cm; Fig. 4.5b). Seasonal NEE, conversely, had a different relationship with WT_{MED} during summer and winter (Fig. 4.5c). Similarly to $P_{G,}$ highest summertime NEE was reached in those vegetation communities where the WT_{MED} was 12 cm below the soil surface. In winter the NEE was highest in wet communities with WT_{MED} of –2.7 cm.

4.5 Discussion

4.5.1 Moisture gradient in the vegetation of a lowland blanket bog

The vegetation of the study site resembles the description of typical blanket bog vegetation by Doyle and Moore (1980). It is characterized by a co-domination of *Schoenus nigricans* and *Molinia caerulea*, stunted Ericoid shrubs and generally poorly developed *Sphagnum* cover. A surface pattern formed of different vegetation communities ranging from dry hummocks to hollows and pools is a typical feature of blanket bogs (Lindsay, 1995) and the sample plots of the current study formed a continuum along the consequent WT gradient. The plant species, which had a clear optimum along the WT gradient, were mostly HU and HO dwelling species, i.e. species having their highest abundance in the opposite ends of the gradient (Fig. 4.3). The permanently inundated HO that Doyle (1990) classified into a different plant physiological association than the common ombrotrophic bog vegetation, were clearly separated from other communities (Fig. 4.3). The lawn level vegetation was chiefly composed of vascular species, which have a wide niche width along the moisture gradient. Species, such as*, M. caerulea, S. nigricans* and *Eriophorum angustifolium* occur in all vegetation associations typical of lowland blanket bogs (Doyle, 1990) and in accordance, occurred in all vegetation communities in the study site. The *Sphagnum* species that have distinct WT optimums (Rydin and McDonald, 1985) and therefore describe the moisture gradient better were practically missing from the lawn communities in our study site, while the HU and HO *Sphagnum* species represented opposite ends of the WT gradient (Fig. 4.3). This is a typical feature of blanket bogs where *Sphagnum* cover is poorly developed except in hummocks and in some depression (Doyle, 1990).

In addition to species composition, the effect of WT on the quantity of vegetation was evident and conflicting at first sight. Although the optima of vascular plant species were at the extreme ends of the WT gradient (Fig. 4.3), the overlap of HU and HO species resulted in the highest leaf area in the intermediate WT range i.e. in HL communities (Fig. 4.4a). In blanket bogs where shrubs are often stunted (Doyle and Moore, 1980) and the vegetation tends to be taller and denser in lawns than in wetter habitats (Doyle, 1982) a unimodal relationship between WT and VGA as described in Figure 4.4a, is characteristic. The contribution of *Sphagnum* to production is often low in blanket bogs compared to raised bogs (Forrest, 1971). In the current study, the highest moss cover, ranging from 22 to 100 %, was observed in HU (Fig. 4.4b), while in raised bogs *Sphagnum* cover can be smaller in HU compared with the common occurrence of full cover in HO (Madden and Doyle, 1990; Vasander, 1982). While there were no great differences in the species composition within different lawn communities (Fig. 4.3), the amount of photosynthesising material varied (Fig. 4.4a, b). VGA and moss cover were lower in LL than in HL. The species diversity had a similar unimodal relationship with WT as VGA, however the highest diversity was observed in deeper WT, likely due to higher moss species abundance in hummock than in high lawns. In other blanket bogs the lawn vegetation was found to be richest in species compared to other microforms, especially hollows and pools (Guinan et al., 1998).

4.5.2 Factors controlling the spatial variation in P_G and R_E

Similarly to several other studies (e.g. Alm et al., 1997; Bubier et al., 1998; Waddington and Roulet, 2000) we found a strong spatial variation in CO_2 exchange between the vegetation communities. The magnitude of measured uptake and release varied between vegetation communities (Fig. 4.2) following the moisture gradient. The variability within each vegetation community group (HU, HL, LL, HO) (Fig. 4.2) suggests that vegetation forms a continuum of communities rather than clearly delineated groups. This is in line with Guinan et al. (1998), who described a blanket bog as an ecosystem with a gradient of overlapping vegetation communities. In contrast to this study Alm et al. (1997), observed higher CO_2 fluxes from lawns compared to hummocks. Also we noticed a decline in P_G and NEE and saturation in R_E after a certain WT threshold (Fig. 4.5) but on average the fluxes were highest in hummocks. A reason for this may be that the height of the hummocks included in this study was low, as is typical of bogs in oceanic conditions, being only 14 cm above the WT_{MED} on average. More so, they were the only sample plots with abundant moss cover that continued to photosynthesize at times when vascular plants had senesced. Then again, the annual P_G, R_E and NEE were higher in HU and HL, and lower in HO than those measured by Alm et al. (1997) in boreal conditions.

In this study, the strongest controllers of spatial variation in CO_2 fluxes were WT and vegetation structure (Figures 4.5 and 4.6). High WT is crucial for peat accumulation and lowering WT may turn a peatland into a C source (e.g. Alm et al., 1999b). WT controls the depth of the oxic peat layer where aerobic decomposition occurs (Clymo, 1983) and the thinner this layer is the lower is the decomposition rate (Moore and Dalva, 1993; Silvola et al., 1996). In accordance, we observed a strong correlation between the median sample plot WT and reconstructed annual $P_{G,}$ R_E and NEE (Fig. 4.5), with all flux components being lowest at the wet end of the WT gradient. The unimodal relationship we found between NEE and WT was similar to that described by Belyea and Clymo (2001), with maximum peat accumulation in WT ~ 10 cm below surface.

The vegetation structure in peatlands is controlled by ecohydrology (Laine et al., 2002) and therefore the abundance of vascular plants and mosses is strongly affected by WT (Fig. 4.4). The vegetation communities along the WT gradient have different levels of photosynthetic capacity and productivity (Belyea and Clymo, 2001; Wallén et al., 1988). In accordance, the VGA affected all CO_2 flux components (Fig. 4.6a-c). An increase in the VGA_{MAX} accelerated both P_G and R_E; however, the correlation of fluxes with VGA_{MAX} (Fig. 4.6a-c) was not as strong as with WT_{MED} (Fig. 4.5). The higher fluxes in HU sample plots compared to HL sample plots with higher VGA_{MAX} can be explained by the more abundant moss cover in HU (Fig. 4.4b). Therefore, the relationship between VGA_{MAX} and P_G and R_E was best described by a saturating curve. This is in accordance with Belyea and Clymo (1998) who found that the total net primary production increases with falling WT and increasing vascular species density until the mosses cannot transport water to their apices. Photosynthesis and respiration were highest in communities with the largest number of species (Fig. 4.6d and e). This may indicate that species diversity increases the productivity of the community.

4.5.3 Temporal variation in CO_2 exchange

The seasonal variation in CO_2 exchange, which we observed (Fig. 4.2c, d, e, f), is a well-reported phenomenon in boreal conditions (Lafleur et al., 2001). In all three summers, the fluxes were highest during July and August when the peak biomass of most vascular species present in the study site is known to occur in Ireland (Doyle, 1982; Madden and Doyle, 1990). The slightly higher NEE in summer 2004 may be due to the somewhat higher PPFD (Fig. 4.2b) and consequently higher VGA (Table 4.1) during summer 2004 compared to summers 2003. Temperature and WT were on average similar between the summers. In summer 2005 the increased respiration rates (Fig. 4.2c, d) were possibly due to WT, which remained low for a considerable time period (Fig. 4.2a). However, the same phenomenon was not observed in LL and HO sample plots (Fig 4.2e, f).

The relationships of cumulative P_G and R_E with WT were similar during summer and winter (Fig. 4.5a and b). P_G had a stronger seasonality than R_E (Fig. 4.5a and b). The seasonal changes in P_G are mainly controlled by irradiation and photosynthesizing leaf area that have a distinctive seasonality compared to air temperature (Fig. 4.2a and b), which controls R_E (Griffis et al., 2000a). Therefore, soil respiration continued throughout the winter when the summer-green plants had senesced and plant respiration ceased. The contribution of wintertime (November-March) respiration was from 8 to 33 % of annual respiration, which is in same range as reported by Roehm and Roulet (2003) and Martikainen et al (1995) in boreal conditions. This does not suggest increased respiration rates in snow and soil frost free conditions, as was observed by Wilson, et al. (in Press-b) in a restored Irish peatland. The high WT likely reduced wintertime respiration. Some photosynthesis took place during winter, as was observed by Sottocornola and Kiely (2005). The contribution of wintertime photosynthesis ranged from 2 to 20 % of the annual flux, which is noticeably lower than the contribution of wintertime respiration. NEE showed a dissimilar pattern along the WT gradient between the seasons (Fig. 4.5c). The difference between summer and wintertime NEE was greatest in the drier half of the WT gradient (Fig. 4.5c). The summertime NEE was highest at WT_{MED} of –11 cm, similar to summertime P_G (Fig. 4.5c). In wintertime the highest net loss of carbon (smallest NEE) was observed in the driest communities with high R_E fluxes triggered by the thick aerobic peat layer. In wet communities the high WT retarded R_E fluxes and the wintertime CO_2 losses were small (Fig. 4.5c).

The annual NEE was negative in LL and HO communities and it varied from –35 to 195 g C m^{-2} between all vegetation communities. Although this is within a range of estimates from various peatland ecosystems, with the constantly high WT and snow-free winters, higher NEE could be expected. Both P_G and R_E were lower when compared to a raised bog in Ontario, Canada (Lafleur et al., 2003), where the WT was markedly lower (-27 to -70 cm). The low P_G suggests that the vegetation in the Irish blanket bog may be less productive than in Canadian bogs. The main differences in the vegetation composition are the scattered *Sphagnum* cover and the less vigorous shrub canopy in the blanket bog than those associated with lower WT of continental bogs. Other reason for low productivity could be the regular cloudiness of the Irish climate that decreases the PPFD during the growing seasons (Fig. 4.2b) and limits photosynthesis.

4.6 Conclusions

Vegetation communities formed a continuum along the water level gradient. The hummock and hollow species had clear optima along the WT gradient, while conditions in lawns were suitable for a wide range of both hummock and hollow dwelling species. Vascular plants had the highest leaf area in high lawns, with intermediate WT, while moss cover was largest in hummocks with deep WT. The alpha diversity was highest in the intermediate communities with abundant moss cover and high VGA.

The CO_2 flux components followed the moisture gradient being controlled by WT and vegetation structure. Photosynthesis was high in conditions suitable for a large range of species rather than in conditions with small and specialized species composition. R_E was more dependent on WT, due to the soil respiration, which is independent of vegetation. Therefore, R_E showed only saturation while P_G already decreased at the dry end of the WT gradient. The annual NEE was highest in small hummocks, while low lawns and hollows showed negative annual fluxes (i.e. were sources of CO_2 to atmosphere).

The seasonal trend was more distinct in P_G, which is affected by variables such as PPFD and VGA, which experience strong seasonality, while R_E depends more on temperature, which in a maritime climate is less variable.

Acknowledgements

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5 Methane flux dynamics in an Irish lowland blanket bog

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5.1 Abstract

Pristine peatlands are a significant source of atmospheric methane (CH_4). Large spatio - temporal variation has been observed in flux rates within and between peatlands. Variation is commonly associated with water level, vegetation structure, soil chemistry and climatic variability. We measured spatial and seasonal variation in CH_4 fluxes in a blanket bog during the period 2003 - 2005. The surface of the bog was composed of different vegetation communities (hummocks, lawns and hollows) along a water level gradient. CH_4 fluxes were measured in each community using a chamber method. Regression modelling was used to relate the fluxes with environmental variables and to integrate fluxes over the study period. Water level was the strongest controller of spatial variation; the average flux rate was lowest in hummocks and highest in hollows, ranging from 3 to 53 mg CH_4 m^{-2} day^{-1}. In vegetation communities with permanently high water level, the amount and species composition of vegetation was also a good indicator of flux rate. We observed a clear seasonal variation in flux that was chiefly controlled by temperature. The annual average flux (6.2 g CH_4 m^{-2} yr^{-1}) was similar to previous estimates from blanket bogs and continental raised bogs. No inter-annual variation was observed.

5.2 Introduction

Pristine peatlands are a significant source of methane (CH_4) (Huttunen et al., 2003), the second most important greenhouse gas. Much of the research on CH_4 fluxes has focused on peatlands in the boreal and continental climatic zones (e.g. Bubier et al., 1993; Huttunen et al., 2003). In contrast, CH_4 fluxes in blanket bogs of the temperate zone have received relatively little attention (e.g. Fowler et al., 1995; MacDonald et al., 1998). Blanket bogs are ombrotrophic peatlands and occur in highly maritime areas with high and regular rainfall (in Ireland the requirement is at least 1250 mm distributed over more than 250 rain days per year (Hammond, 1981)). Blanket bogs differ from continental bogs in terms of water level, which remains close to the surface throughout the year due to the regular rain events (Sparling, 1967). In addition, the concentrations of maritime salts (Cl, Na, SO_4^{2+}) are high compared to the main nutrients (Adamson et al., 2001). Consequently, the pH in blanket bogs is relatively high, 4.4 - 4.9 (Shotyk, 1997) compared to other ombrotrophic bogs. These abiotic differences are reflected in the vegetation composition, which is a combination of species common in continental bogs and fens (O'Connor and Skeffington, 1997; Osvald, 1949).

The CH_4 flux depends on the height of the water level (Dise et al., 1993), vegetation structure (Bubier, 1995), pH (Williams and Crawford, 1984) and the presence of electron acceptors, such as sulphate reducing bacteria (Granberg et al., 2001b). The vegetation affects the flux rate through substrate quality and quantity (Ström et al., 2003) and by offering a fast transport pathway for the gas (Conway, 1937; Garnet et al., 2005). These properties vary between plant species; deep rooting sedges with aerenchymatic cell structure are generally associated with high CH_4 flux rates (Bubier et al., 1995). The controlling factors vary not only between but also within peatlands since the surface of bogs is often a mosaic of vegetation communities characterized by different water level (Daulat and Clymo, 1998). The small scale differences in species composition and water level has caused large spatial variation into CH_4 fluxes both in raised and blanket bogs (Bubier et al., 1993; MacDonald et al., 1998).

In addition to spatial variation the CH_4 efflux has been shown to vary diurnally (Käki et al., 2001), seasonally (Saarnio et al., 1997) and inter annually (Granberg et al., 2001a). In addition to water level, vegetation and other parameters, connected with spatial variation, the temporal variation is dependent on temperature (Granberg et al., 2001a).

To date, studies of CH_4 fluxes in blanket bogs have been based on short or irregular measurements campaigns (Chapman and Thurlow, 1996; Fowler et al., 1995; MacDonald et al., 1998) and no long-term studies exist. We measured CH_4 fluxes from different vegetation communities in an Irish lowland blanket bog over a 29-month period using a closed chamber method. The aims of this study are (1) to quantify the CH_4 flux of different vegetation communities, (2) to define the environmental controls on the spatial variation in CH_4 flux and (3) to investigate the seasonal variation in CH_4 efflux.

5.3 Materials and Methods

5.3.1 Site Description

The study site was located in an extensive lowland blanket bog in Glencar, Co Kerry, Ireland (51°55´N, 9°55´W). The surface of the bog is composed of different vegetation communities ranging from dry hummocks (HU) to permanently inundated hollows (HO). HU had a cover of mosses such as *Racomitrium lanuginosum*, *Sphagnum rubellum* and *Sphagnum papillosum* and vascular plants *Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea*. HO supported a sparse cover of species such as *Sphagnum cuspidatum, Sphagnum auriculatum, Menyanthes trifoliata, Schoenus nigricans, Carex limosa* and *Eriophorum angustifolium*. The flat surfaces between HU and HO were covered by lawn level vegetation, which we divided into two groups according to water level and the abundance of the vegetation. High lawns (HL) had a vigorous cover of *S. nigricans, M. caerulea, E. tetralix* and *Rhynchospora alba*. Low lawns (LL) had water level closer to the surface than HL and were dominated by *R. alba*.

Permanent sample plots were established by inserting six stainless steel collars (0.6 m × 0.6 m × 0.15 m) into the peat in HU, HL and LL, respectively in June 2003. To cover the entire vegetation community continuum, three sample plots were established in HO in March 2004. Each collar had a water channel at the top to enable air sealing during gas sampling. Boardwalks were constructed around the sample plots to minimize disturbance. For the purposes of analysis, within the vegetation community groups, the sample plots were coded according to their WT using numbers from 1 to 6. Consequently, HU1 was the driest and HO3 the wettest sample plot.

5.3.2 CH_4 flux measurements

CH_4 measurements began in August 2003 and were carried out at biweekly to monthly intervals until September 2004 when a water level manipulation experiment was started in 12 sample plots (data not shown). After this date measurements were continued until September 2005 in those plots that were not part of the water level manipulation experiment (i.e. HU1, HU2, HL2, HL4, LL4, LL5, HO1, HO2 and HO3). The closed chamber method was used (Saarnio et al., 1997). Each chamber (0.6 m × 0.6 m × 0.25 m) had a vent to ensure pressure equilibration, which was closed only after the chamber had been placed on the collar. A fan ensured the circulation of the air inside the chamber. Four 40 ml air samples were taken into plastic syringes equipped with three way stopcocks, at five minute intervals. A 10 minute interval was used in wintertime when low flux rates were expected due to cold temperatures and low vascular plant cover. Samples were analysed within 48 hours on a Shimadzu GC-14-B gas chromatograph equipped with a flame ionisation detector (FID). Column, injector and detector temperatures were set to 40 °C, 100 °C and 330 °C, respectively and nitrogen was used as the carrier gas. CH_4 standards (4 ppm; BOC Gases Ireland Ltd.) were used. In order to remove moisture, samples and standards were injected through a 12 cm long Tygon tube (6 mm diameter) filled with drierite (10 / 20 mesh) prior to entering the 2 ml sample loop. The flux rate was calculated as the linear rate of change in gas concentration over time (mg CH_4 m^{-2} day^{-1}).

To relate fluxes to environmental conditions, the temperatures inside the chamber and in the peat at 5, 10, 20 and 30 (T_5, T_{10}, T_{20}, T_{30}) cm depths were measured during CH_4 measurements. The water level (WT) was measured from perforated PVC pipes inserted into the peat adjacent to each sample plot.

The vascular green leaf area of CH_4 transporting species (*Carex limosa, Eriophorum angustifolium, Eriophorum vaginatum, Menyanthes trifoliata, Molinia caerulea, Rhynchospora alba, Schoenus nigricans, Trichophorum caespitosum*) (VGA_{AER}) was used to relate the CH_4 flux to the sample plot vegetation. VGA_{AER} was estimated by summing up the green leaf area (GA) of each species. GA was measured at biweekly to monthly intervals and regression models were used to describe the seasonal dynamics in GA. For a description of the measurement method see Laine et al. (2006). Coverage (%) of each moss species was estimated for each sample plot in August 2004. Nomenclature of vascular plants, mosses and liverworts follows Stace (1997), Smith (2004) and Smith (1990), respectively.

5.3.3 Modelling of CH_4 fluxes

Non-linear regression modelling was used in order to establish relationships between CH_4 fluxes and environmental variables and further to reconstruct CH_4 fluxes over the study period July 2003 to September 2005. Model was parameterised for each sample plot. T_{20} had an exponential relationship with CH_4 fluxes and was the main controlling variable, while the linear WT function was replaced with a variable *a* in sample plots HU2, HU3, HU4, HU5, HU6, LL1, LL3 and LL4 where it did not increase the explanatory power. The model took the form:

$$CH_4 = (c + dWT)(\exp(bT_{20})) \tag{5.1}$$

where *b*, *c* and *d* are parameters, *WT* is water level and T_{20} is soil temperature at 20 cm depth. The model parameters and R^2 for each plot are given in Table 5.1.

Table 5.1 Model parameters and R^2 for each sample plot

SP	a	b	c	d	R^2
HU1		0.106 (0.043)	0.167 (0.099)	0.003 (0.003)	0.24
HU2	0.084 (0.064)	0.143 (0.053)			0.29
HU3	0.055 (0.041)	0.073 (0.054)			0.17
HU4	0.001 (0.002)	0.458 (0.104)			0.73
HU5	0.013 (0.023)	0.270 (0.117)			0.40
HU6	0.002 (0.002)	0.431 (0.083)			0.73
HL1		0.3210 (0.0856)	0.0159 (0.0197)	0.0002 (0.0005)	0.73
HL2		0.299 (0.060)	0.018 (0.016)	0.0004 (0.0004)	0.71
HL3		0.418 (0.096)	0.004 (0.006)	0.0001 (0.0001)	0.81
HL4		0.521 (0.125)	0.0002 (0.001)	0.00001 (0.00002)	0.65
HL5		0.475 (0.096)	0.002 (0.003)	-0.00001 (0.0001)	0.84
HL6		0.243 (0.074)	0.028 (0.030)	0.001 (0.001)	0.57
LL1	0.003 (0.004)	0.446 (0.097)			0.72
LL2		1.155 (0.286)	2.8E-08 (1.2E-07)	-4.6E-09 (2.0E-08)	0.83
LL3	0.011 (0.017)	0.360 (0.108)			0.68
LL4	0.004 (0.006)	0.336 (0.097)			0.50
LL5		0.177 (0.073)	0.150 (0.154)	0.008 (0.009)	0.33
LL6		0.375 (0.066)	0.003 (0.003)	-0.0006 (0.001)	0.87
HO1		0.241 (0.056)	0.024 (0.019)	-0.001 (0.001)	0.69
HO2		0.177 (0.075)	0.295 (0.336)	-0.035 (0.043)	0.55
HO3		0.136 (0.055)	0.768 (0.649)	-0.066 (0.058)	0.66

5.3.4 CH_4 flux integration

An hourly time series of T_{20} were obtained from a weather station located ~250 m from the study site (Sottocornola and Kiely, 2005) and linear interpolation between the measurement campaigns was used to reconstruct the daily WT for each sample plot. Using these environmental data and sample plot specific models, the CH_4 flux was estimated for each hour of the study period. The annual CH_4 flux was integrated for each sample plot for from October 2003 to September 2004 and from April 2004 to May 2005 for the hollow sample plots. Fluxes were averaged for each of the vegetation community groups: HU, HL and LL. HO1 was treated separately, while fluxes of HO2 and HO3 were averaged and presented as HO2-3.

5.3.5 Environmental correlation of fluxes

Canonical Correspondence Analysis (CCA) was performed using CANOCO for Windows 4.5 to link the variation in vegetation with environmental variables: average CH_4 flux; median water level (WT_{MED}); moss cover; green area of CH_4 transporting plants (VGA_{AER}) and annual net ecosystem CO_2 exchange (NEE). The Monte Carlo permutation test was used to test the validity of the first canonical axes and also all canonical axes together.

5.3.6 Water chemistry analysis

Soil water chemistry samples were collected from the bog area in December 2005 (Unpublished data, M. Sottocornola). Samples were taken from HU (n = 20), HL (n = 41), LL (n = 15) and HO (n = 9), respectively. Samples were not taken from the gas flux sample plots. Samples were analysed for Ca, Na, Cl and SO_4^{2+} using flow injection analysis and ion chromatography (QuikChem IC+FIA 8000 series, Lachat Instruments, Milwaukee, USA), while pH was determined on site (WTW pH 320 model, Geotech Environmental Equipment, Inc, Colorado, USA).

5.4 Results

5.4.1 Environmental conditions

Environmental conditions were relatively similar during the three years of the study. During 2003, 2004 and 2005 the annual rainfall in the study site was 2510, 2356 and 2459 mm yr^{-1}, respectively. The average air temperature for the warmest month July and the coldest month February was 14.6 and 6.1 °C, respectively, during the three-year study period. The annual average air temperature varied from 10.3 to 10.7 °C between the years. The variation in average daily soil temperature at 20 cm depth (T_{20}) was modest (from 5.3 to 18 ºC) over the 29-month study period (Fig. 5.1a).

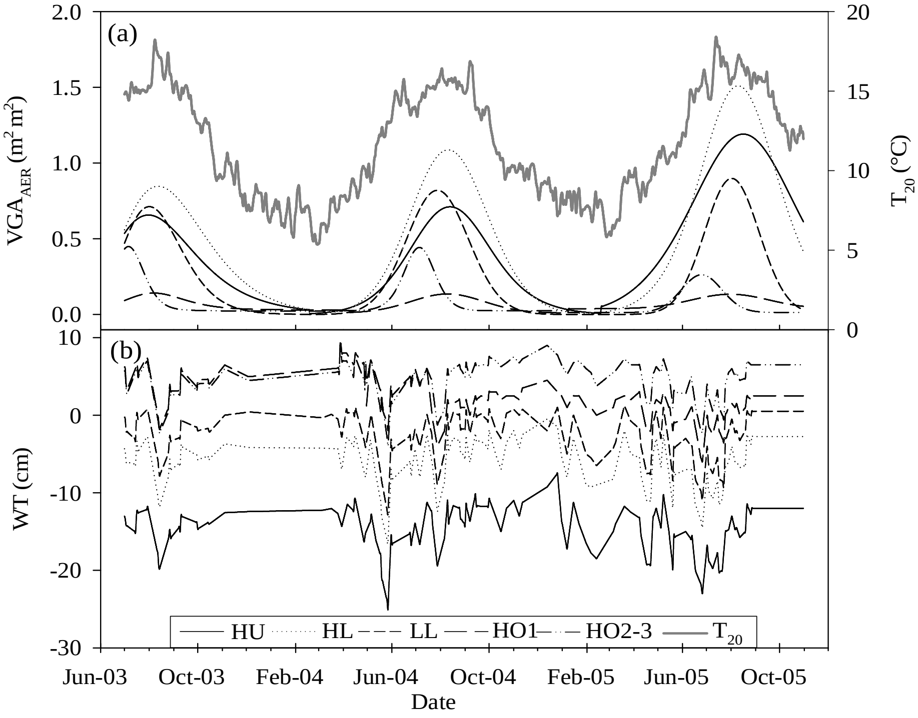

Figure 5.1 Environmental variables during the study period. (a) Vascular green leaf area of CH_4 transporting plants (VGA_{AER}) in vegetation communities hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO1, HO2-3) and average daily soil temperature at 20 cm depth (T_{20}). (b) Average daily water level (WT) in different vegetation communities.

VGA_{AER} followed the seasonal trend in temperature but peaked more distinctively than temperature during summers (Fig. 5.1a). VGA_{AER} varied between vegetation communities being highest in HL communities and lowest in HO1. The peaks in VGA_{AER} of HU, HL and LL were higher in summer 2005 than in summer 2003 (Fig. 5.1a). The VGA_{AER} of hollows was somewhat lower in the summer of 2005 compared to the two previous summers. The different vegetation communities were characterized by different water levels (WT). HU had the deepest WT, while hollows were regularly inundated (Fig. 5.1b). The WT varied moderately during the study period (Fig. 5.1b). The deepest WT was measured at the end of May 2004 when the WT in HU was 25 cm below the soil surface.

Soil water chemistry (pH, Na, Ca, Cl, SO_4^{2-}) within the bog area varied little between vegetation communities (Table 5.2). However, the pH of hollows (4.7) was somewhat higher than that of other communities (4.5 - 4.6) (Tukey, $p < 0.05$) and SO_4^{2-} concentration was higher in HL compared to LL and HO (Tukey, $p < 0.05$) (Table 5.2).

Table 5.2 Soil water chemistry in vegetation communities: hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO). Standard errors are presented in parenthesis.

	pH	Na (mg l^{-1})	Ca (mg l^{-1})	Cl (mg l^{-1}l)	SO_4^{2+} (mg l^{-1})
HU	4.5 (0.1)	6.4 (0.9)	0.9 (0.6)	8.6 (1.2)	1.8 (0.5)
HL	4.5 (0.1)	6.8 (1.4)	0.8 (0.4)	9.0 (1.2)	2.0 (0.5)
LL	4.6 (0.2)	6.3 (0.5)	0.8 (0.5)	8.8 (1.2)	1.6 (0.5)
HO	4.7 (0.2)	6.3 (0.5)	0.7 (0.4)	8.7 (0.7)	1.5 (0.5)

5.4.2 Spatial variation in CH_4 flux

The measured mean CH_4 flux varied between vegetation communities from 3 to 53 mg m^{-2} day^{-1} (Fig. 5.2). Fluxes were lowest in HU plots that had median WT more than 10 cm below the surface (Fig. 5.2). Variation within the HU plots was small compared to other vegetation communities (Fig. 5.2). Fluxes in lawns (HL, LL) were higher than in HU and had high variation between the sample plots. The mean fluxes in HL and LL communities were of similar magnitude (Table 5.3) ranging from 7.1 to 34.9 mg m^{-2} day^{-1} between sample plots (Fig. 5.2). The variation (SD) and the maximum flux was higher in LL than in HL (Table 5.3). HO1 with a low VGA$_{AER}$ and lacking *Menyanthes trifoliata*, had low CH_4 flux compared to other vegetation communities, while HO2-3 had the highest fluxes (Table 5.3).

Table 5.3 Methane flux statistics and median water level for vegetation groups (VG) hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO1, HO2-3). The annual fluxes for HU, HL and LL are calculated for time period 1st October 2003 – 30th September 2004. Annual fluxes for HO are calculated for time period 1st April 2004 – 31st March 2005. Standard error of the annual flux is given in parenthesis.

VG	Annual (g CH_4 m^{-2} yr^{-1})	CH_4 flux (mg m^{-2} day^{-1})					Water level (cm)
		Mean	SD	Min	Max	N	Median
HU	3.3 (0.5)	11.8	10.9	0.1	64.1	112	-13
HL	5.8 (1.1)	19.2	19.1	0.0	72.2	109	-5
LL	6.1 (1.4)	20.9	23.3	0.1	101.4	111	-1
HO1	3.5	11.6	9.4	1.7	31.8	23	3
HO2-3	13.0 (0.1)	50.4	54.6	0.3	263.0	50	5

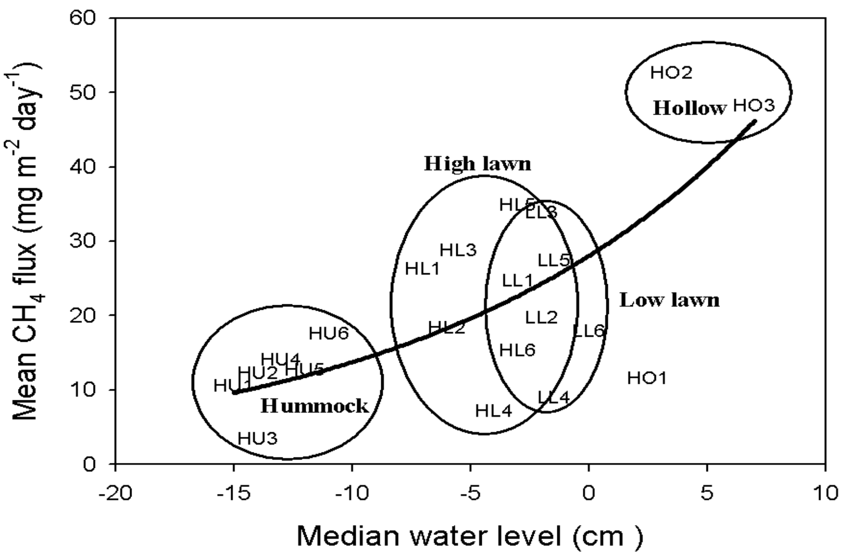

Figure 5.2 Relationship between mean CH_4 flux and median water level of each sample plot. Sample plots are grouped into vegetation communities: hummocks, high lawns, low lawns and hollows.

5.4.3 Seasonal patterns in CH_4 fluxes

Seasonality was evident in all vegetation communities (Fig. 5.3). Measured fluxes were low from December until May (Fig. 5.3) with an average of 7.9 mg m^{-2} day^{-1} (SE = 0.94, n = 132). The cumulative wintertime fluxes (November-April) at 0.7 g CH_4 m^{-2} were identical in HU, HL and LL communities being 26, 13 and 15 % of the annual flux, respectively. Winter fluxes in HO1 and HO2-3 were 0.5 and 1.4 g CH_4 m^{-2} and represented 31 and 10 % of the annual flux. Flux rates started to increase in early summer and peaked during August (Fig. 5.3). The study period included three summers (2003, 2004 and 2005) that showed no significant differences in cumulative peak season (July - September) CH_4 fluxes (one-way ANOVA, $p > 0.05$). Therefore, interannual variation was not observed.

5.4.4 Annual CH_4 flux

The annual CH_4 flux estimates were reconstructed for each sample plot using regression models. The average annual fluxes varied between vegetation communities: HO1 and HU had low fluxes; fluxes in HL were slightly higher than in LL; while HO2-3 were the hotspots of CH_4 (Table 5.3). The standard errors (SE) of the average annual fluxes of vegetation communities ranged from 0.1 to 1.3 (Table 5.3).

Laine et al. (2006) surveyed the distribution of vegetation communities within an area of ~ 28 ha in the bog; we used the same distribution (6, 62, 21 and 11 % for HU, HL, LL and HO respectively) to estimate the areal CH_4 flux. Since Laine et al. (2006) did not classify the hollow communities according to the occurrence of *Menyanthes trifoliata* we used an average flux of the three hollow plots (9.8 g CH_4 m^{-2} yr^{-1}) in the weighting procedure. The areal annual flux was 6.2 g CH_4 m^{-2} yr^{-1}.

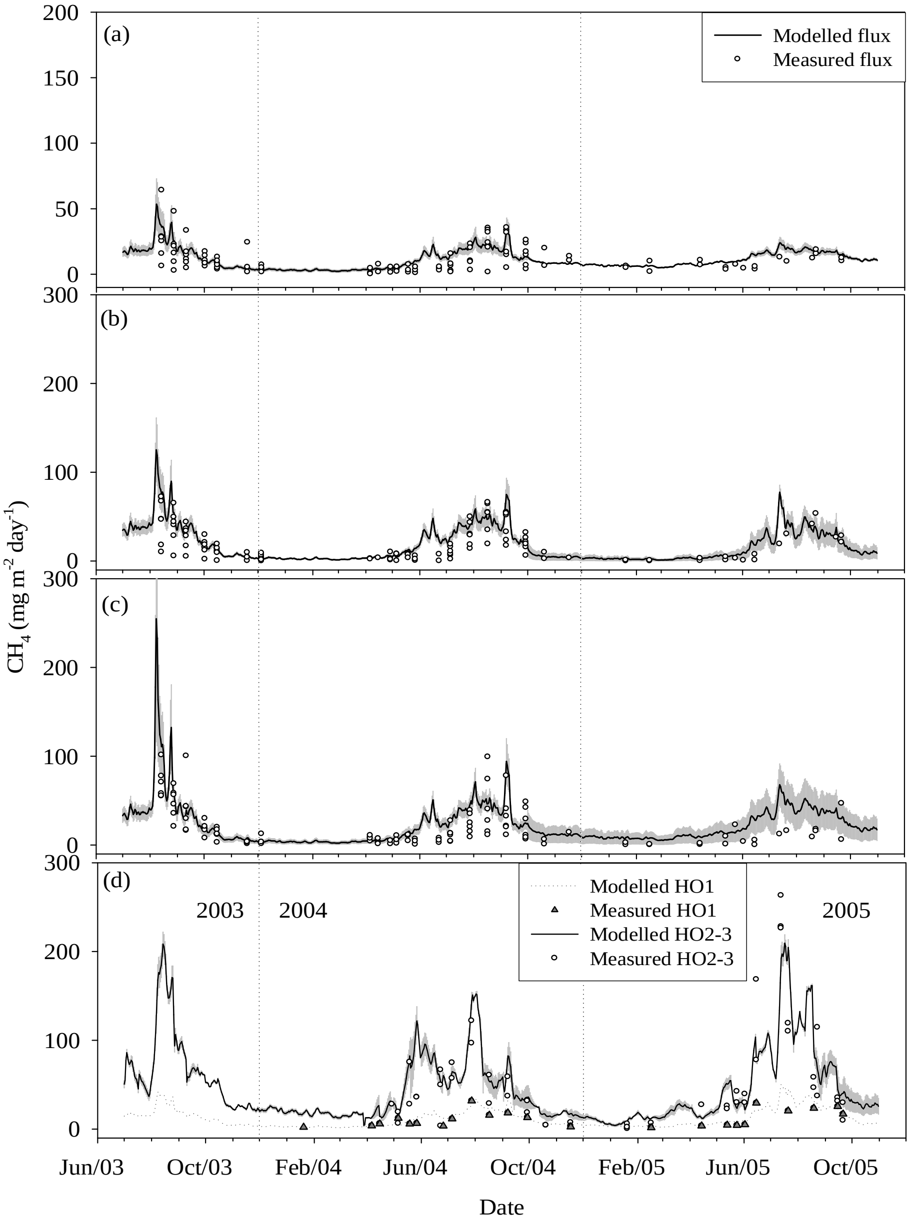

Figure 5.3 Measured (circles) and modelled (line) CH_4 flux in vegetation communities (a) hummocks, (b) high lawns, (c) low lawns and (d) hollows from July 2003 to October 2005. Grey shadow is the standard error of the modelled mean CH_4 flux of the sample plots. Starting from September 2004, only fluxes from sample plots HU1, HU2, HL2, HL4, LL4, LL5, HO1, HO2 and HO1 are shown. HO1 (grey triangles) is treated separately from the other two HO sample plots due to different plant species composition.

5.4.5 Factors controlling CH_4 flux

The spatial variation was most strongly related to WT. The relationship between median WT and mean CH_4 fluxes of sample plots was exponential (Fig. 5.2). Variation between HU plots was small but followed the WT gradient, except in HU3 that had a very low flux (Fig. 5.2). The fluxes in HL and LL sample plots varied irrespectively of WT. The small flux in HO1 cannot be explained by WT (Fig. 5.2).

Canonical correspondence analysis (CCA) (ter Braak, 1986) was used to visualize the similarity structure for the sample plots and species and to correlate the plant species composition with environmental parameters (CH_4 flux, median WT, VGA_{AER}, moss cover, net ecosystem CO_2 exchange (NEE) (NEE data unpublished A. Laine)) (Fig. 5.4). The first canonical axis had an eigenvalue of 0.66 and explained 23.6 % of the variation in the plant species composition and described the moisture gradient in vegetation; the inter set correlations of WT with axis 1 was 0.80. Species with clear optima in the wet end of the gradient, located on the right side of the ordination plot were typical hollow species (*Menyanthes trifoliata*, *Carex limosa*, *Sphagnum cuspidatum* and *Sphagnum auriculatum*). These species were also clearly related to the high CH_4 emissions as shown by the CH_4 vector. The close correspondence of the WT and CH_4 flux arrows indicate a high correlation between the variables, further supporting the relationship in Figure 5.2. The inter set correlations of axis 1 and CH_4 flux was 0.72. All canonical axes were statistically significant (Monte Carlo permutation $p = 0.02$).

VGA_{AER} and moss cover correlated negatively with axis 1 and therefore, were higher in drier sample plots, which also had higher NEE (Fig. 5.4). This indicates that the CH_4 flux correlated negatively with productivity. A closer investigation reveals an ambiguous relationship between VGA_{AER} and CH_4 flux (Fig. 5.5). VGA_{AER} had little effect on spatial variation in CH_4 fluxes, except in hollow communities where VGA_{AER} was positively correlated with CH_4 flux (Fig. 5.5).

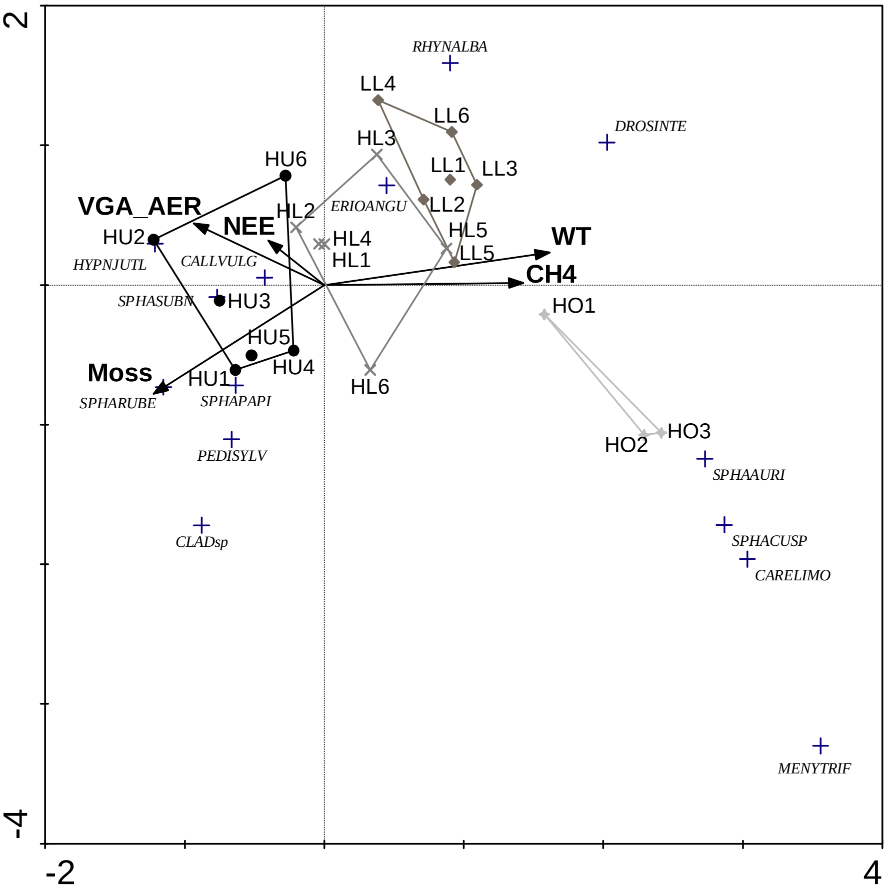

Figure 5.4 Canonical correspondence analysis (CCA) of species composition in sample plots in connection with mean CH_4 flux (CH4), median water level (WT), green area of CH_4 transporting plants (VGA_AER), Moss coverage (Moss) and annual net ecosystem CO_2 exchange (NEE). Eigenvalue of axis 1 and axis 2 were 0.66 and 0.34. Inter set correlations between axis 1 and CH_4, WT, VGA_AER, Moss and NEE are 0.72, 0.80, -0.49, -0.58 and -0.23, respectively. Species with 10 % lower axis minimum fit are included in the figure. CALLVULG = *Calluna vulgaris*; CARELIMO = *Carex limosa*; DROSINTE = *Drosera intermedia*; HYPNJUTL = *Hypnum jutlandicum*; MENYTRIF = *Menyanthes trifoliata*; PEDISYLV = *Pedicularis sylvaticum*; RHYNALBA = *Rhynchospora alba*; SPHAAURI = *Sphagnum auriculatum*; SPHACUSPI = *Sphagnum cuspidatum*; SPHA RUBE = *Sphagnum rubellum.*

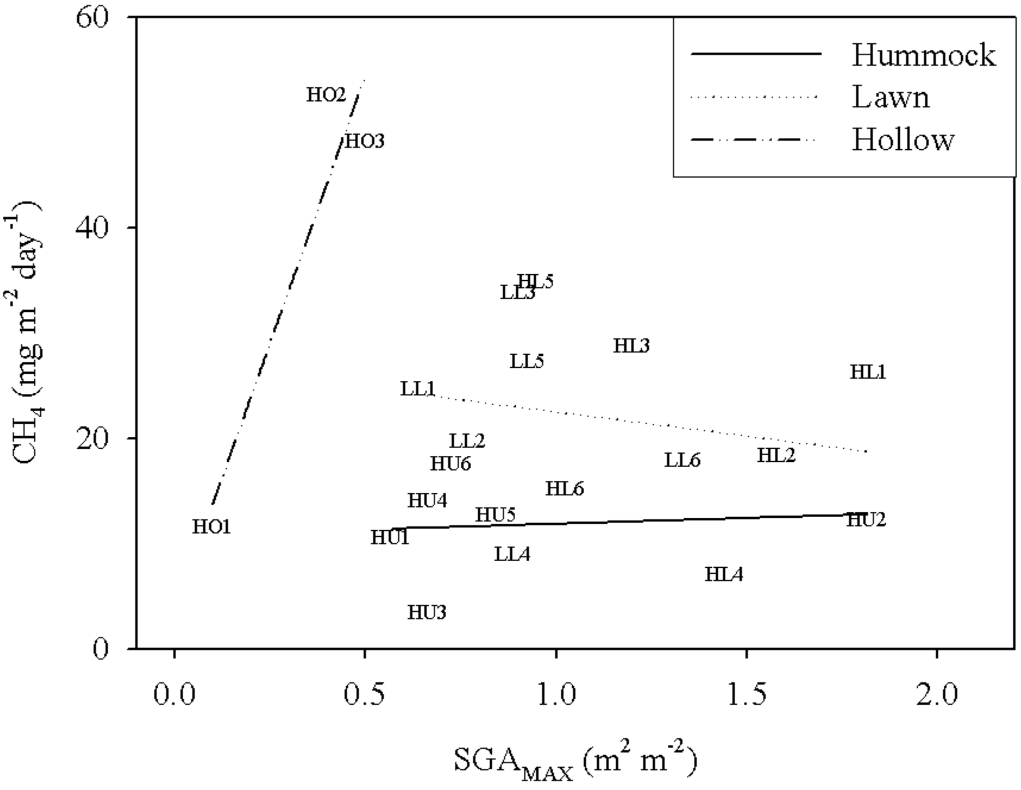

Figure 5.5 Relationship between mean CH_4 flux and maximum leaf area of CH_4 transporting species (SGA_{MAX}) of each sample plot. Separate relationship is defined for vegetation communities hummocks, lawns (high and low lawns) and hollows.

In the CH_4 flux model the seasonal variation in fluxes was explained by soil temperature at 20 cm depth (T_{20}) and WT. In all sample plots T_{20} explained most of the variation in CH_4 flux, while the effect of oscillating WT is less clear.

5.4.6 Model performance

The cumulative annual/seasonal flux estimates were based on modelled values. The modelled and measured fluxes agreed relatively well. The coefficient of determination (R^2) of the models varied from 0.17 to 0.87 (Table 5.1) and Figure 5.6 shows scatter, but no consistent over or under estimation between estimated and measured values. There were, however, two instances when the models failed to follow the measured fluxes. Firstly, the models over estimated fluxes in lawn communities in June 2004, when measured fluxes were particularly low (Fig. 5.3b, c). The modelled flux increases in June in response to increasing T_{20} and VGA, the measured fluxes, on the other hand, remain low in June and July, when WT oscillates strongly and reaches the lowest level of the whole study period (Fig. 5.7).

The second instance was in summer 2005 when the models estimated higher fluxes in LL communities than were measured (Fig. 5.3c); this phenomenon was not observed in other vegetation community groups. In 2005 the modelled and measured fluxes in LL were based on measurements made only from sample plots LL4 and LL5. The measured fluxes were lower in summer 2005 compared to measurements made during the two previous summers (Mann-Whitney $p = 0.005$). The soil temperature and VGA during measurements in summer 2005 were on average lower than during measurements in two previous summers ($T = 26$ and 23 °C; VGA = 0.6 and 0.4 m^2 m^{-2} in 2003 / 2004 and 2005, respectively). There was no difference in WT during the measurements between these years. There was no significant difference in environmental conditions during measurements between the summers. Similarly, the continuous temperature recordings that were used in flux integration showed no difference between the summers; also the difference in VGA was small. Therefore, the modelled flux in 2005 was similar to that in 2003 and 2004.

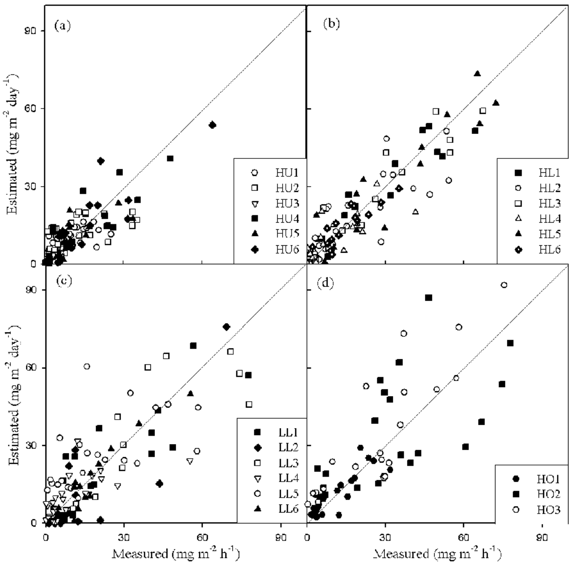

Figure 5.6 Estimated versus measured CH_4 fluxes in sample plots in (a) hummocks, (b) high lawns, (c) low lawns and (d) hollows.

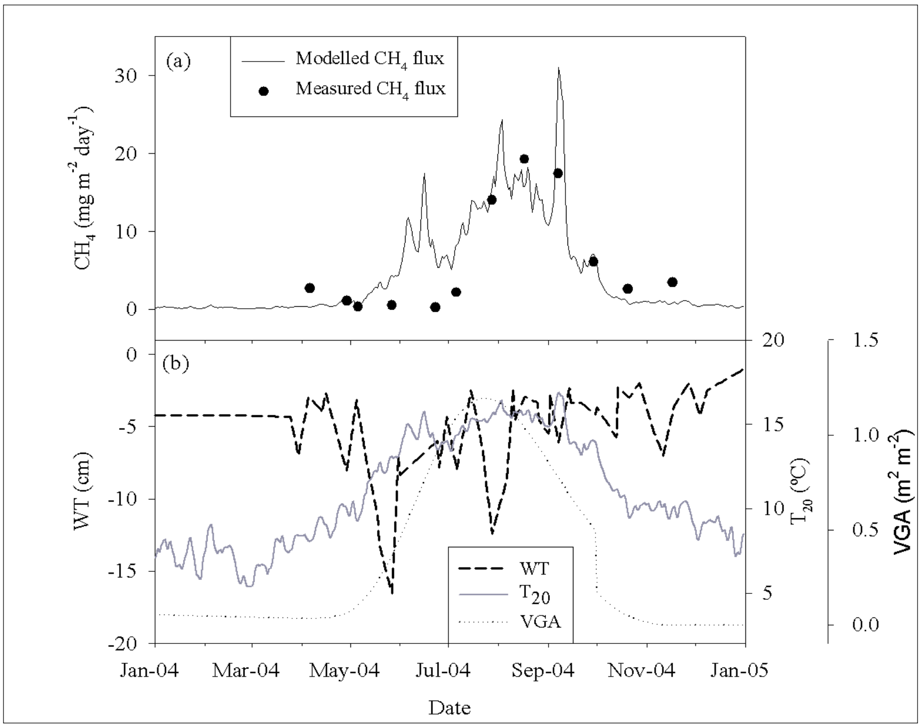

Figure 5.7 (a) Measured and modelled methane flux in sample plot HL4 in year 2004 and (b) vascular leaf area (VGA), soil temperature in 20 cm depth (T_{20}) and water level (WT) during the same time period.

5.5 Discussion

5.5.1 Spatial variation in CH_4 flux

In general methane fluxes followed the WT gradient being lowest in hummocks and highest in hollows (Fig. 5.2). In hollows the presence of *Menyanthes trifoliata* determined the flux level. HO1 with no *M. trifoliata* had low fluxes compared to other hollows. A similar pattern in CH_4 flux has been detected in many peatland ecosystems (e.g. Bubier et al., 1993; MacDonald et al., 1998). Compared to similar vegetation communities in a Scottish blanket bog (Fowler et al., 1995; MacDonald et al., 1998) our mean CH_4 fluxes were similar in hollows/pools, but were 270 % higher in hummocks and 47 % lower in lawns (Table 5.3). Compared to continental raised bogs the mean fluxes in different vegetation communities were in the same range as those measured in a Swedish bog by Granberg et al. (1997). However, Bubier et al. (1993) measured lower fluxes in hummocks (2.3 mg m^{-2} day^{-1}) and lawns (15.6 mg m^{-2} day^{-1}) in Canada than was observed in this study. The reason for the lower fluxes in the Canadian site is likely the noticeably lower WT that ranged from –15 cm in hollows to –46 cm in hummocks.

Although the two types of lawns (HL and LL) had different WT and VGA_{AER} (Fig. 5.1), they had similar measured and average annual CH_4 fluxes (Table 5.3). This is in contrast with the marked difference in net ecosystem CO_2 exchange (NEE) between the two communities (Laine et al. 2006). LL plots had negative annual NEE (i.e. were sources of CO_2), while HL plots had positive annual NEE. This suggests that the spatial variation in CH_4 and CO_2 fluxes is controlled by different mechanisms. The LL was dominated by almost pure stands of *Rhynchospora alba*. Although this community had low productivity, it appears that the plants were as effective at producing substrate for methanogens and in transporting CH_4 through the shallow aerobic peat layer as the more diverse and higher productivity HL vegetation.

5.5.2 Seasonal variation in CH_4 flux

The seasonal dynamics in CH_4 fluxes were similar in all vegetation communities (Fig. 5.3) and followed the changes in temperature and leaf area (Fig. 5.1a), being highest in late summer. Similar seasonality has been observed in blanket bog (Chapman and Thurlow, 1996) and other peatlands (e.g. Saarnio et al., 1997).

The summertime fluxes were at the same level in all three years and no interannual variation was observed (Fig. 5.3). This reflects the similarity in environmental conditions during the three years of study. Most of the interannual variation is caused by differences in hydrological condition and temperature (Granberg et al., 2001a). In our study the difference in precipitation between the driest and wettest year was only 150 mm and the annual average temperature varied by only 0.3 °C. The interannual differences in weather conditions are generally small in Ireland compared to continental areas; during the past 20 years the average annual temperature has varied within 2 ºC and rainfall within 300 mm yr^{-1} (Sweeney et al., 2002). As an example, in Finland during the same time period the variation in average annual temperature was ~ 4 ºC and in rainfall ~ 500 mm yr^{-1} (http://www.fmi.fi/saa/tilastot_99.html#1).

The contribution of wintertime flux (November-April) to the annual flux was similar to that measured in bogs in Finland (Alm et al., 1999a). The contribution of wintertime was highest in HO1 with low annual flux and little temporal variation and lowest in HO2-3, which had a distinctive growing season peak flux resulting from the growth pattern of *Menyanthes trifoliata*. The spatial variation between vegetation communities was less pronounced during winter (Fig. 5.3), when HU, HL and LL in particular had nearly identical fluxes.

5.5.3 Annual CH_4 flux

Our estimate of the average annual flux for the blanket bog is 6.2 g CH_4 m^{-2} yr^{-1}. This value resembles the few existing estimates for blanket bogs that are 4.9 g CH_4 m^{-2} yr^{-1} (Chapman and Thurlow, 1996) and 6.9 g CH_4 m^{-2} yr^{-1} (Hargreaves and

Fowler, 1998). Overall, the estimates (3.3 to 13.0 g CH_4 m^{-2} yr^{-1}) for different vegetation communities are in the low end of the range measured in different wetlands. The CH_4 flux estimates vary largely ranging from 3.6 g CH_4 m^{-2} yr^{-1} in non forested bog to 80 g CH_4 m^{-2} yr^{-1} in temperate marsh (e.g. Cao et al., 1996; Granberg et al., 2001a; Huttunen et al., 2003; Kim et al., 1998).

Due to the maritime impact, blanket bog vegetation share some characteristics with fens (O'Connor and Skeffington, 1997; Osvald, 1949); in the study site this is indicated by the high proportion of sedges compared to continental bogs. For the same reason blanket bogs have higher pH than continental bogs (Shotyk, 1997). The pH in ombrotrophic bogs is usually < 4 (Laine and Vasander, 1996), while in the study site pH ranged from 4.2 to 5.1. pH is one of the factors affecting CH_4 flux (Crill et al., 1988), with most methanogens having optimum at pH 6 (Williams and Crawford, 1984). The quality of vegetation and pH in the blanket bog did not, however, produce as high CH_4 fluxes as has been measured in fens (Huttunen et al., 2003; Saarnio et al., 1997). High sulphate (SO_4^{2+}) concentrations have been shown to suppress CH_4 flux due to competition of sulphate reducing bacteria. SO_4^{2+} concentrations are, however, seldom expressed together with CH_4 fluxes, and they also vary considerably throughout the year. The SO_4^{2+} concentration in the studied bog was low (0.52 - 3.81 mg l^{-1}) compared to other measurements in blanket bogs in Ireland and the UK (3.5 - 4.7 mg l^{-1}) (Adamson et al., 2001; Proctor, 2006; Shotyk, 1997) but higher than in peatlands in Ontario (Vitt and Bayley, 1984). We measured SO_4^{2+} concentration in December when wet conditions may have suppressed the SO_4^{2+} concentrations (Proctor, 2006). Therefore, the summer SO_4^{2+} concentration may be noticeably higher, which may have reduced the CH_4 fluxes.

The CH_4 fluxes might be underestimated, since the estimate does not consider ebullition that may be abundant in the mud bottom hollows. Estimating the amount and importance of the episodic ebullition is difficult (Chanton, 2005). Yet, Christensen, et al. (2003) estimated that ebullition may account for 18 to 50 % of CH_4 flux in wetland monoliths, depending on vegetation properties and temperature. We did not encounter ebullition during the chamber measurements. The diurnal variation was not considered as its importance is likely to be small, as was found in a Scottish blanket bog (Fowler et al., 1995). The study site did not include plant species that are known to have a pronounced effect on diurnal dynamics of CH_4 flux e.g. *Phragmites australis* and *Typha latifolia* (Armstrong et al., 1996; Whiting and Chanton, 1996).

5.5.4 Environmental controls on CH_4 flux

Correlation between sample plot vegetation, WT and CH_4 flux is evident (Fig. 5.4). Within the WT range experienced in this study (from –15 to 7 cm) the CH_4 flux increased exponentially (Fig. 5.2). A similar relationship has been observed, for example, by Moore and Roulet (1993) and Saarnio et al. (1997). WT induces the anaerobic conditions required for CH_4 production and therefore controls the size of the microbial population (Dise et al., 1993). WT also affects the oxidation capacity of methanotrophs (Frenzel and Karofeld, 2000) and through vegetation, the substrate quality and quantity (Moore and Dalva, 1993).

The effect of WT on seasonal CH_4 flux dynamics was more complex. Throughout the study period the variation in WT was less than 20 cm, with more oscillation during summer and a rather stable high level during winter (Fig. 5.1). The high winter WT did not cause high CH_4 fluxes due to the contrasting effect of low temperature and low substrate input for methanogens during the non-growing season. In addition, the regression models were unable to capture the effect of the oscillating WT especially in June/July of 2004 (Fig. 5.3). Moore and Roulet (1993) found it difficult to explain the temporal pattern between WT and CH_4 flux, as well. This may be due to the well described hysteresis phenomena (Lloyd et al., 1998; Moore and Dalva, 1993), where there is a considerable lag between changes in WT and CH_4 flux.

Bowes and Hornibrook (2006) measured significantly higher flux rates in plots with dense vascular plant cover and concluded that passive plant-mediated transport was responsible for the majority of CH_4 flux in a blanket bog. In our study the effect of vegetation was unclear and connected to WT. VGA_{AER} and moss cover were highest in the dry end of the WT gradient, which consequently had the highest net ecosystem CO_2 exchange (NEE), as well (Fig. 5.4). The deep WT was much more important than the effect of vegetation in these communities and CH_4 fluxes were low. Therefore, no relationship was found between VGA_{AER} and CH_4 flux in lawn and hummock communities (Fig. 5.5).

The importance of vascular plants is, however, obvious in the inundated vegetation communities (Fig. 5.5). The existence of *Menyanthes trifoliata* in HO2-3 initiated substantially higher flux rates than in HO1 (Fig. 5.5). The importance of *M. trifoliata* for CH_4 fluxes was observed also in a Scottish blanket bog (MacDonald et al., 1998). *M. trifoliata* is an efficient transporter of CH_4 and the emission occurs through the stems (MacDonald et al., 1998). Frenzel and Karofeld (2000) found large differences in CH_4 dynamics between different types of hollows and pools and considered vascular plants to indicate hotspots for CH_4 emissions, while in *Sphagnum* covered and mud-bottom hollows oxidation decreased flux rates significantly since CH_4 transport through vascular plants did not occur.

Temperature was the driver of seasonal variation in CH_4 fluxes. It affects the metabolic rate of the microbial communities (Dise et al., 1993) and since methanogens are more sensitive to temperature than methanotrophs (Dunfield et al., 1993), the seasonality is accentuated. The seasonal development of VGA_{AER} is closely coupled with temperature (Fig. 5.1) and even if it was not included in the CH_4 flux model it is likely to affect the seasonal flux dynamics

Within the bog the variation in soil water chemistry between the vegetation communities was small (Table 5.2) and hardly able to explain the spatial variation in flux levels. The high variation in CH_4 fluxes in lawn communities was not connected with WT, vegetation or water chemistry.

5.5.5 CH_4 flux in relation to net ecosystem CO_2 exchange (NEE)

The areal annual CH_4 flux was 5.8 % of the areal NEE (Laine et al., 2006). Despite the small CH_4 flux rate, this is more than was estimated by Cao, et al. (1996) (4.2 %) for temperate wetlands. For each vegetation community group the CH_4 flux was 1.9 %, 3.7 % and 30 % of NEE in HU, HL and HO, respectively. For LL, which was a net source of CO_2, the CH_4 flux increased the C source strength by 47 % from 9.8 to 14.3 g C m^{-2}. This result highlights the importance of CH_4 fluxes in the wet and low productivity communities of the bog.

The global warming potential (GWP) of the study site was calculated for different time periods using the annual CO_2 and CH_4 emissions. GWP in 20, 100 and 500 years time horizon was 117.6, -108.6 and -201.4 g CO_2 eq., respectively. Whiting and Chanton (2001) estimated GWP for seven subtropical, temperate and boreal wetland sites using different time horizons. All sites had positive GWP in a 20 year time horizon and negative GWP in 500 year time horizon, while in a 100 year horizon the subtropical and temperate sites had negative and boreal site positive GWP. Similarly, a Siberian bog was a source of GHG's over 20 and 100 year time horizons (1216 and 202 g CO_2 eq. m^{-2}, respectively), but was considered a sink over a 500 year time horizon (Friborg et al., 2003).

5.6 Conclusions

In this study, the CH_4 fluxes in a blanket bog is at a similar level to those in raised bogs, even if the consistently high WT, the large proportion of sedges in vegetation and the higher pH than in most bogs would suggest higher fluxes. Seasonal variation is strong and winter fluxes are similar to those of boreal bogs, although the temperature was significantly milder in maritime Ireland.

The CH_4 flux is ~70 % lower in hummocks than in hollows. The controls on the spatial variation in CH_4 fluxes in maritime blanket bog are similar to those in continental raised bogs. Water level is the most important controller, while in inundated communities also vegetation composition, particularly the presence of *Menyanthes trifoliata* has an impact on the flux rate. The hollows with this species are hotspots for CH_4 emission.

CH_4 flux has modest importance for the carbon gas budget in dry, high productivity communities (hummock, low lawn), while the impact is significant in the low productive communities with high water level (low lawns and hollows). In the studied blanket bog the average areal annual CH_4 flux was 6.8 % of the average annual NEE.

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6 The effect of changed water level on carbon fluxes in a blanket bog

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6.1 Abstract

Peatlands play an important role in the global carbon (C) cycle, by acting as a large, long-term C sink. The C sink is sustained by a high water level that prevents the complete decomposition of organic matter. The C gas dynamics are therefore sensitive to changes in water level, and in climatically different years a peatland can vary from a sink to a source of C. We measured carbon dioxide (CO_2) and methane (CH_4) fluxes from vegetation communities ranging from hummocks to low lawns in a blanket bog. After a one-year calibration period the water level was experimentally raised in one area of the bog and lowered in another area of the bog and the changes in vegetation composition and gas fluxes were monitored during the following year. Before the experiments the C gas balance was highest in hummocks and lowest in low lawns. The water level drawdown increased the respiration rate and decreased methane emission in all vegetation communities. The rate of photosynthesis decreased in most communities, as well; however, the response was dependent on species composition. The raised water level decreased respiration and increased methane emissions. The effect on photosynthesis depended on species composition, hummocks species suffered, while *Rhynchospora alba* benefitted from the rising water level. The conclusion of this study is that climate change in form of water level changes has a considerable effect on the CO_2 and CH_4 fluxes of blanket bog.

6.2 Introduction

Globally peatlands cover circa 4 million km^2 (Lappalainen, 1996). Since the last ice age northern peatlands have accumulated 270 to 450 Pg of C into peat (Gorham, 1991; Turunen et al., 2002). This represents ~ 1/3 of the global soil carbon pool (Gorham, 1991). Peatlands play an important role in atmospheric C gas concentrations; on one hand they remove carbon dioxide (CO_2) from the atmosphere by photosynthesis and on the other hand produce CO_2 and methane (CH_4) in decomposition processes. Even if in the long-term peatlands have acted as C sinks, the C gas dynamics are sensitive to interannual changes in moisture conditions and between years a site can switch from being a sink to a source of C (Lafleur et al., 2003). Throughout the developmental history of peatlands, changes in climate have altered moisture conditions, which in turn has led to changes in vegetation communities and C accumulation rates (Ellis and Tallis, 2000). Historical changes in climate have, however, been modest compared to the changes currently projected for the future (Petit et al., 1999).

The climate is changing due to increasing atmospheric concentrations of greenhouse gases, which are primarily derived from anthropogenic activities (IPCC, 2001). The predicted changes for Europe are (1) warmer temperatures, especially during summers, (2) higher winter and lower summer precipitation and (3) increased occurrence of extreme weather events (storms, drought) (IPCC, 2001). Similar changes are expected for Ireland, but with a delay due to buffering by the Atlantic Ocean (Sweeney et al., 2002). The changes are expected to be stronger in the midlands and smallest on the west coast (Sweeney and Fealy, 2002).

Blanket bogs are sensitive ecosystems, supported by high water level. Any change in moisture conditions, whether natural or anthropogenic, may disturb their functioning (Bragg and Tallis, 2001). The C gas fluxes of maritime peatlands, and especially blanket bogs, have received relatively little attention compared to northern continental peatlands. Some insights may be gained from studies of bogs drained for forestry or agricultural purposes. Such changes in blanket bogs have affected hydrology (Anderson et al., 2000), vegetation composition (Cooper et al., 1997; MacGowan and Doyle, 1997), peat properties (Anderson et al., 2000; Burke, 1978) and carbon (C) fluxes (Byrne and Farrell, 2005; Fowler et al., 1995). The degree of climate change in the main region of blanket bogs may not be as severe as in continental areas, and increased rainfall may be experienced. Blanket bogs have developed in particular climatic conditions and therefore even small changes may be detrimental for these ecosystems.

In northern peatlands the main effect of climate change is expected to be water level drawdown, caused by the increased evaporation and decreased summer precipitation (Gorham, 1991). Water level drawdown increases aerobic respiration (Bubier et al., 2003b; Silvola et al., 1996) and decreases CH_4 emission (Moore and Dalva, 1993; Roulet et al., 1992). The effect on photosynthesis depends on the vegetation community (Bubier et al., 2003b) and its ability to adjust to the new conditions. In ombrotrophic bogs, with low nutrient status and defined microform composition, hummock vegetation may become more abundant (Weltzin et al., 2003), while nutrient rich fen sites may develop towards forest vegetation (Laine et al., 1995). Overall, climate change may increase the abundance of woody plants (Welzin et al. 2000, Trettin et al. 2006) and the increased frequency of dry growing seasons may threaten the C sink function of peatlands (Alm et al., 1999b). In western Ireland, where the winter precipitation is projected to increase by 10 %, with minor changes in temperature (Sweeney and Fealy, 2002), the behaviour of water level is less certain and a rise in water level is possible.

The characteristic patterned surface structure of many peatlands causes spatial variation in C fluxes (Alm, 1997) and as a result different vegetation communities may respond differently to changing conditions (Belyea and Malmer, 2004). In order to assess the response of peatlands to climate change it is necessary to study the changes at the vegetation community level.

In this study we aim to investigate how a moderate change in ecohydrology (water level drawdown and flooding) affects the carbon gas fluxes (CO_2 and CH_4) in a blanket bog over a short time period (one year). We monitored vegetation and C flux components for one year before and after the experiments were carried out and used regression modelling to integrate the chamber flux measurements over the study period. We postulate that, similar to continental bogs, water level drawdown increases ecosystem respiration rate and decreases CH_4 flux in blanket bog. Flooding, conversely, decreases ecosystem respiration rate and increases CH_4 flux. The changes in vegetation and photosynthesis are expected to be small in such a short time period.

6.3 Material and methods

6.3.1 Site description

The study site was located in an extensive lowland blanket bog in Glencar, Co Kerry, Ireland (51°55´N, 9°55´W). The surface of the bog is a mosaic of vegetation communities, namely hummocks, lawns and hollows.

The study site was established in June 2003. 18 stainless steel collars (0.6 × 0.6 × 0.15 m) were permanently inserted into the peat. Each collar had a water channel at the top to enable air sealing during CO_2 and CH_4 measurements. Boardwalks were constructed around the sample plots to minimize disturbance. The sample plots were divided into three groups: hummocks (HU), high lawns (HL) and low lawns (LL) and ranked from 1 to 6 according to their median water level (WT_{MED}) (Fig. 6.1).

Following a calibration period from June 2003 to September 2004, the water level (WT) experiments were initiated. Sample plots HU4, HU5, HL1, HL5, LL1 and LL6 were surrounded by a narrow drainage ditch in order to decrease the WT. These six plots form the WT drawdown experiment (Fig. 6.1). The excess water was directed to flow towards the lower lying plots HU3, HU9, HL3, HL6, LL2 and LL3. A dam was constructed below these sample plots in order to retain the runoff and raise the WT. Due to the proximity of the drainage ditch, the WT did not rise in plots HU6, HL6 and LL2 and they were excluded from the data analysis. The three remaining plots formed the flooding experiment. The remaining six sample plots formed the control site (Fig. 6.1).

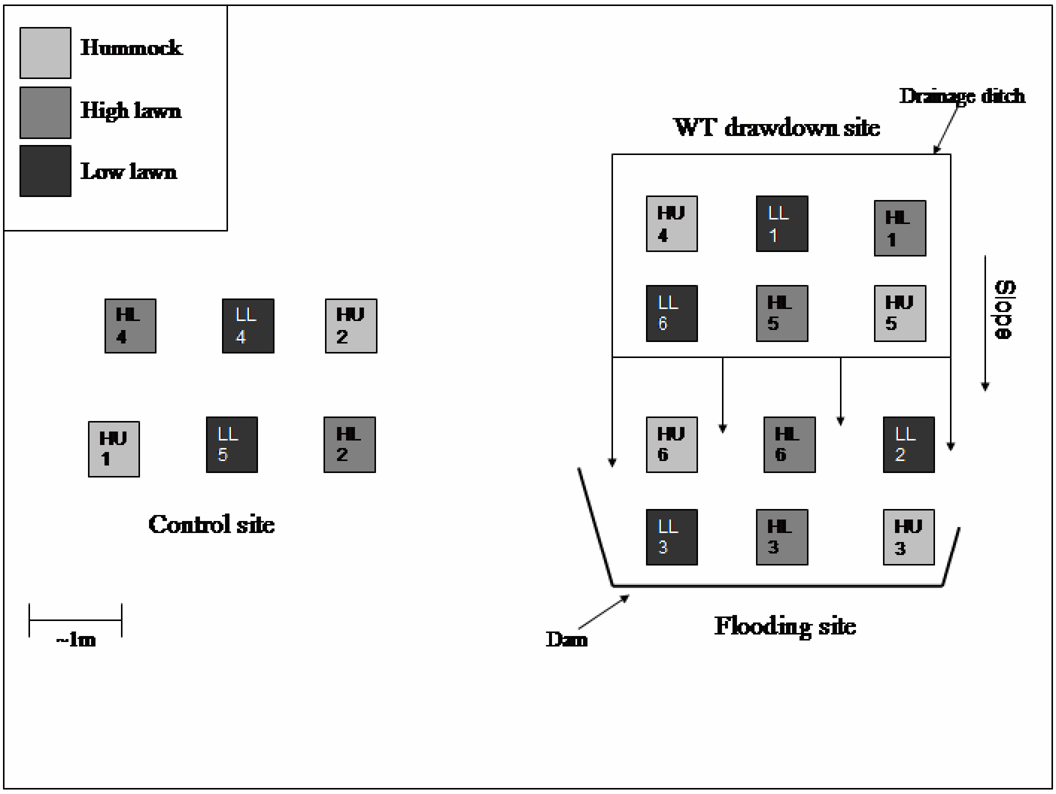

Figure 6.1 Schematic representation of the study site. Sample plots representing each vegetation community are ranked from 1 to 6 according to their median water level. The WT drawdown experiment site is surrounded by a drainage ditch and the flooding experiment site is surrounded by a dam. HU6, HL6 and LL2 were not included in data analysis, since their WT did not rise after the flooding was initiated.

6.3.2 Gas flux measurements

6.3.2.1 CO_2 exchange measurements

CO_2 exchange measurements were carried out at weekly intervals from July 2003 until September 2005. Measurements were made using a closed transparent plexiglas chamber (0.6 × 0.6 × 0.33 m). The chamber was vented and included a cooling system (Alm et al. 1997). The CO_2 concentration inside the chamber was monitored with a portable infrared gas analyser (EGM-4, PP Systems, UK). The instantaneous net CO_2 exchange (NEE) was first measured under a stable ambient illumination at 15-second intervals over a 60-240 second period. This was then repeated with the chamber covered with an opaque canvas cover, in order to get an estimate of the instantaneous ecosystem respiration rate (R_E). Carbon dioxide flux rates were calculated from the linear change in gas concentration as a function of time. We used the ecological sign convention, in which fluxes from the biosphere to the atmosphere are negative. Gross photosynthesis (P_G) was calculated as the sum of flux rate values measured in light (NEE) and dark (R_E).

6.3.2.2 CH_4 flux measurements

CH_4 measurements were carried out at biweekly to monthly intervals during the period August 2003 to September 2005 using a closed chamber method (Saarnio et al., 1997). Each chamber (0.6 m × 0.6 m × 0.25 m) had a vent to ensure pressure equilibration, which was closed only after the chamber had been placed on the collar. A fan ensured the circulation of the air inside the chamber. Four 40 ml air samples were taken by plastic syringes, fitted with three way stopcocks, at five minute intervals starting five minutes after chamber closure. A 10 minute interval was used in wintertime when low flux rates were expected due to cold temperatures and low vascular plant cover. Samples were analysed within 48 hours on a Shimadzu GC-14-B gas chromatograph equipped with a flame ionisation detector (FID). Column, injector and detector temperatures were set to 40 °C, 100 °C and 330 °C, respectively and nitrogen was used as the carrier gas. CH_4 standards (4 and 10 ppm) from BOC Gases Ireland Ltd. were used. In order to remove moisture, samples and standards were injected through a 12 cm long Tygon tubing (6 mm diameter) filled with drierite (10 / 20 mesh) prior to entering the 2 ml sample loop. Flux rate (mg CH_4 m^{-2} day^{-1}) was calculated as a linear rate of change in gas concentration with time.

6.3.3 Environmental measurements

In order to relate the gas fluxes to prevailing environmental conditions, the photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) was recorded simultaneously with NEE readings using a quantum sensor (PAR-1, PP-Systems, UK). Air temperature inside the chamber was recorded simultaneously during CO_2

and CH_4 flux measurements. WT was measured from perforated pipes inserted into the peat adjacent to each sample plot. Soil temperature at 5, 10, 20 and 30 cm depth were measured adjacent to each sample plot during flux measurements.

Vascular green area (VGA), which accounts for the green leaf area of vascular plants (Wilson et al., in Press-a), was estimated at biweekly to monthly intervals. Non-linear regression models were used to describe the seasonal dynamics in green leaf area (GA) of each species. For each sample plot, the daily GA of all species was summed up to VGA. For a description of the measurement method see Laine et al. (2006). Plant species composition was determined for each sample plot during July in 2004 and 2005 by estimating the cover (%) of each species. Nomenclature of vascular plants, mosses and liverworts follows Stace (1997), Smith (2004) and Smith (1990), respectively.

Continuous time series of meteorological parameters (PPFD, air temperature (T_{AIR}) soil temperature at 20 cm depth (T_{20}), precipitation) were obtained from an onsite weather station (Laine et al., 2006). Linear interpolation between the WT measurements made during gas flux measurements was used to derive a continuous time series of daily WT for each sample plot. Daily VGA was estimated for each sample plot using the GA models of each species (see Laine et al., 2006).

6.3.4 Modelling of gas fluxes

6.3.4.1 CO_2 exchange components

We constructed CO_2 exchange component (P_G, R_E) models separately for each sample plot. We used a multiplicative model format in which the sub-models, representing the response of fluxes to different environmental variables, were multiplied by each other. The approach and functions were based on Tuittila et al. (2004). Due to differences in the vegetation composition between the sample plots, it was not possible to use the same model format for every sample plot.

P_G was related to PPFD, VGA and T_{AIR}, using saturating, linear and unimodal sub-models, respectively. The models were parameterised separately for the calibration and experimental years. This was done since WT, which represented the major difference between the years, was not included in the models.

The P_G model format was as follows:

$$P_G = Q\left(\frac{PPFD}{k + PPFD}\right)(s + VGA)\exp\left(-0.5\left(\frac{T-u}{p}\right)^2\right) \tag{6.1}$$

where *Q* is the rate of maximum photosynthesis that is dependent on PPFD, VGA and T_{AIR}. Parameter *k* is the level of PPFD at which half of the maximum rate of photosynthesis is reached; *u* denotes the optimal air temperature for P_G, while *p* denotes the temperature tolerance. For sample plot LL3, VGA and T_{AIR} correlated strongly with each other, therefore only VGA was included in the model that took the format:

$$P_G = Q\left(\frac{PPFD}{k + PPFD}\right)VGA \tag{6.2}$$

P_G model parameters for control site sample plots and for WT drawdown and flooding site sample plots for calibration year are given in Table 5.2; model parameters for WT drawdown and flooding site sample plots for experimental year are given in Table 6.1.

Table 6.1 Estimated parameter values and goodness of fit (R^2) for gross photosynthesis (P_G) model for experimental year for the sample plots in the WT drawdown and flooding sites. Number of the used Equation is given for each sample plot.

	Q (g m^{-2} h^{-1})	*k* (µmol m^{-2} s^{-1})	s/k_{vga} (m^2 m^{-2})	*u* (ºC)	*p* (ºC)	R^2	Eq no.
HU3	1.71 (0.33)	358.96 (101.86)	0.35 (0.11)	41.50 (15.28)	30.43 (16.44)	0.86	6.1
HU4	1.80 (0.20)	356.44 (74.12)	0.14 (0.04)	24.43 (31.60)	31.60 (11.59)	0.93	6.1
HU5	1.16 (0.09)	505.78 (74.14)	0.67 (0.06)	25.14 (1.72)	21.75 (3.30)	0.96	6.1
HL1	0.81 (0.08)	467.25 (92.88)	0.35 (0.12)	32.35 (4.22)	24.99 (8.47)	0.93	6.1
HL3	0.99 (0.06)	338.00 (101.86)	0.01 (0.04)	30.43 (1.10)	16.20 (2.22)	0.96	6.1
HL5	0.76 (0.08)	436.85 (100.64)	0.33 (0.08)	28.11 (2.07)	20.57 (5.16)	0.92	6.1
LL1	1.03 (0.07)	461.47 (70.50)	0.21 (0.03)	27.34 (1.61)	20.62 (3.78)	0.95	6.1
LL3	1.51 (0.09)	553.05 (78.00)	0.05 (0.02)			0.94	6.2
LL6	0.17 (0.02)	250.68 (65.20)	0.55 (0.14)	28.92 (1.40)	16.11 (2.68)	0.86	6.1

Ecosystem respiration (R_E) consists of soil and plant respiration, which are both affected by temperature and WT. We related R_E to air temperature (T_{AIR}) using an exponential relationship described by Lloyd and Taylor (1994). In our study the WT fluctuation remained modest and we observed a linear relationship between R_E and WT. VGA was used to describe the seasonality in the flux rates. The model was parameterised separately for each sample plot for the whole study period.
The model format was:

$$R_E = (b + b_1 WT)\left[\exp\left(b_2\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)\right)\right](s + VGA) \qquad (6.3)$$

In Equation 6.3, T_{ref} was set at 283.15 K and T_0 at 227.13 according to Lloyd and Taylor (1994). T_0 is the temperature minimum at which the respiration reaches zero. Air temperature (T) is given in degrees K. R_{TOT} model parameters for sample plots in WT drawdown and flooding sites are given in Table 6.2. Model parameters for sample plots in control site can be found from Table 4.3.

Table 6.2. Estimated parameter values and goodness of fit (R^2) for ecosystem respiration (R_E) model for sample plots in WT drawdown and flooding sites. Standard errors of the estimates are given in brackets.

	b	b_1	b_2 (K)	s	R^2
HU3	0.05 (0.01)	-0.001 (0.000)	212.14 (20.56)	2.32 (0.59)	0.71
HU4	0.12 (0.02)	-0.002 (0.001)	177.45 (20.12)	0.72 (0.16)	0.71
HU5	0.002 (0.003)	-0.002 (0.001)	237.44 (20.41)	3.69 (1.94)	0.76
HL1	0.04 (0.01)	-0.001 (0.000)	244.33 (16.68)	1.86 (0.38)	0.83
HL3	0.03 (0.01)	-0.004 (0.001)	227.15 (19.91)	1.68 (0.37)	0.85
HL5	0.09 (0.01)	-0.0002 (0.001)	200.93 (25.35)	0.80 (0.19)	0.72
LL1	0.09 (0.02)	-0.001 (0.000)	224.87 (25.00)	0.67 (0.15)	0.70
LL3	0.06 (0.01)	-0.006 (0.001)	244.45 (26.79)	0.68 (0.14)	0.84
LL6	0.02 (0.01)	-0.001 (0.000)	234.69 (32.70)	1.58 (0.67)	0.63

6.3.4.2 CH_4 fluxes

CH_4 fluxes were related to T_{20} and WT using exponential and linear sub-models, respectively. VGA was not included in the model since it correlated strongly with T_{20}. The model was parameterised separately for each sample plot and the same models were used for the whole study period. The models took the form:

$$CH_4 = (a + bWT)(\exp(cT_{20})) \tag{6.4}$$

The type of model, model parameters and R^2 for each sample plot are given in Table 6.3. SPSS 12.0.1 for Windows statistical package (SPSS, Inc.) was used in flux modelling.

Table 6.3 Estimated parameter values and goodness of fit (R^2) for CH_4 flux model for each sample plot. Standard errors of the estimates are given in brackets.

SP	*a*	*b*	*c*	R^2
HU1	3.78 (2.30)	0.06 (0.08)	0.10 (0.04)	0.22
HU2	2.62 (1.72)	0.10 (0.07)	0.19 (0.05)	0.50
HU3	0.21 (0.20)	0.01 (0.01)	0.26 (0.06)	0.50
HU4	0.10 (0.14)	0.004 (0.005)	0.42 (0.09)	0.66
HU5	1.33 (1.68)	0.05 (0.07)	0.22 (0.09)	0.47
HL1	0.74 (0.69)	0.03 (0.03)	0.29 (0.06)	0.71
HL2	0.44 (0.39)	0.01 (0.01)	0.30 (0.06)	0.71
HL3	0.21 (0.12)	0.002 (0.002)	0.37 (0.03)	0.80
HL4	0.01 (0.02)	0.0004 (0.001)	0.51 (0.12)	0.65
HL5	0.25 (0.27)	0.003 (0.004)	0.36 (0.08)	0.77
LL1	0.15 (0.18)	0.006 (0.007)	0.39 (0.08)	0.67
LL3	0.13 (0.12)	-0.004 (0.004)	0.41 (0.06)	0.80
LL4	0.06 (0.13)	0.001 (0.002)	0.63 (0.13)	0.50
LL5	3.59 (3.69)	0.20 (0.21)	0.18 (0.07)	0.33
LL6	0.75 (0.93)	0.02 (0.03)	0.22 (0.09)	0.37

6.3.5 Reconstructing annual fluxes

Equations (6.1) – (6.4) that were individually parameterised for each sample plot and in case of P_G for calibration and experiemental years, were used to calculate hourly P_G, R_E and CH_4 fluxes for each sample plot. Fluxes were reconstructed for the time period 1st October 2003 – 30th September 2005 using the continuous time serious of environmental variables described in Section 6.3.3. The period from 1st October 2003 to 30th September 2004 is regarded as the calibration year, while the period from 1st October 2004 to 30th September 2005 is regarded as the experimental year.

6.4 Results

6.4.1 Environmental conditions

Weather conditions were similar during the years. The average T_{AIR} was 10.4 and 10.6 °C and the average T_{20} was 10.9 and 11.3 °C in the calibration and experimental years, respectively. Precipitation was 2420 and 2440 mm in the calibration and experimental year, respectively.

Water level (WT) followed the same pattern in all sample plots during the calibration and experimental years (Fig. 6.2). During the calibration year WT was on average -14, -5 and -1 cm below the soil surface in HU, HL and LL, respectively. In the control site, the difference in mean WT between the calibration and experimental years was negligible. WT drawdown lowered WT by 10 cm in sample plots HU4, HL1 and LL1 and by 7 cm in sample plots HU5, HL5 and LL6 compared to calibration year. The flooding experiment increased WT by 6 cm in HU3, HL3 and LL3.

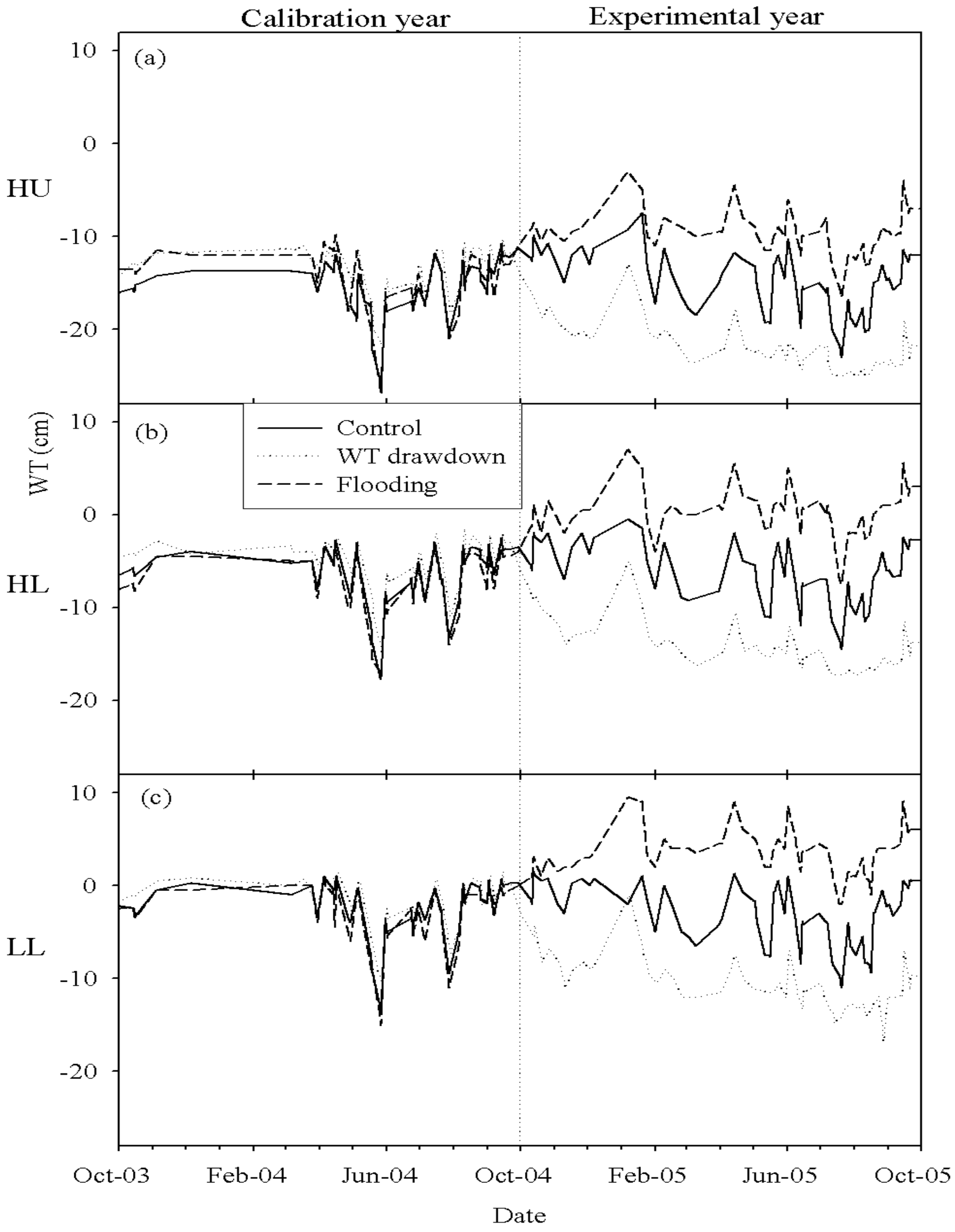

Figure 6.2. Variation in water level (WT) in (a) hummocks, (b) high lawns and (c) in low lawns in control, WT drawdown and flooding experimental sites during calibration and experimental years.

6.4.2 Changes in vegetation

The maximum vascular green area (VGA) was highest in HL and lowest in LL (Table 6.4). Between the years the VGA varied little, generally, VGA was higher in the experimental year than in the calibration year. The increase in VGA was highest in the WT drawdown site (Table 6.4). The only sample plot where VGA decreased was HU3 in the flooded conditions. The moss cover did not change significantly during the study period.

Table 6.4 The maximum vascular green area (VGA, $m^2\ m^{-2}$) (standard error in parentheses) in hummocks, high lawns and low lawns of control, water level (WT) drawdown and flooding experimental sites in 2004 (calibration year) and 2005 (experimental year).

	Control		**WT drawdown**		**Flooding**	
	2004	2005	2004	2005	2004	2005
Hummock	1.5 (0.6)	1.5 (0.6)	0.9 (0.3)	1.0 (0.4)	0.9	0.8
High lawn	1.5 (0.3)	1.8 (0.1)	1.4 (0.3)	1.9 (0.4)	1.3	1.4
Low lawn	1.0 (0.1)	0.9 (0.0)	0.7 (0.1)	0.9 (0.2)	0.8	0.9

6.4.3 Changes in gross photosynthesis (P_G)

In the calibration year the P_G flux varied between vegetation communities in order HU > HL > LL (Fig. 6.3). The average annual P_G in the calibration year was 467 (32), 376 (21), and 167 (20) g C m^{-2} (n = 5, SE in brackets) in HU, HL and LL, respectively. PPFD was the most important controller of P_G fluxes (Fig. 6.3), explaining from 20 to 70 % of the variation in summertime fluxes (June-September) in different vegetation communities.

In the control site, the response of summertime P_G to PPFD varied little between the calibration and experimental years (Fig. 6.3a, d, g). The maximum P_G in the experimental year was 93, 95 and 69 % of the calibration year flux in HU, HL and LL, respectively. The average annual P_G in the experimental year was 505 (61), 434 (15) and 171 (11) g C m^{-2} (n = 2, SE in brackets) in HU, HL and LL, respectively.

The integrated weekly P_G of the vegetation communities was at a similar level in the WT drawdown and control sites during the calibration year (Fig. 6.4). In the WT drawdown site the maximum P_G during the experimental year was 86, 78 and 67 % of the calibration year flux in HU, HL and LL, respectively (Fig. 6.3 b, e, h). This reduction in P_G is more than that observed between the two years in the control site, which indicates a decrease in flux due to WT drawdown. Also, the weekly flux rates decreased noticeably in HU and LL, whereas in HL the decrease was small (Fig. 6.4).

The decrease in P_G was most noticeable during summertime, while during winter fluxes were similar in both sites. The average annual P_G in the WT drawdown plots during the experimental year was 286 (110), 333 (71) and 119 (54) g C m^{-2} (n = 2, SE in brackets) in HU, HL and LL, respectively. The sample plots responded individually to the WT drawdown (Fig. 6.5a).

The annual flux decreased strongly in HU5. HU4 and HL1 were not affected by the WT drawdown and the absolute decrease was moderate in HL5, LL1 and LL6. Proportionally the change was most noticeable in LL6 that had the smallest flux rate. A paired t-test was performed between the calibration and experimental years for the WT drawdown and control sites. The between year differences in P_G were significant in neither site ($p = 0.065$ and $p = 0.02$ for WT drawdown and control, respectively), but in the WT drawdown site the flux was lower and in the control site higher in experimental year.

The weekly P_G was similar in the control and flooding sites during the calibration year (Fig. 6.4). In the flooding site the maximum P_G in the experimental year was 103, 85 and 112 % of the calibration year flux in HU, HL and LL, respectively. Compared to the change in the control site, the flooding increased P_G in HU and LL, but decreased P_G in HL (Fig. 6.3c, f, i). Flooding decreased the weekly P_G in HU and HL (Fig. 6.4a and b). In HL the flux was lower throughout the experimental year (Fig. 6.4b), while in HU the change was more noticeable during summer (Fig. 6.4a). In LL the weekly flux rates increased due to flooding after mid July when VGA reached its maximum (Fig. 6.4c). Flooding decreased the annual P_G in HU and HL but did not affect it in LL (Fig 6.5a). The average annual P_G in the experimental year was 249, 213 and 218 g C m^{-2} (n = 1) in HU, HL and LL, respectively.

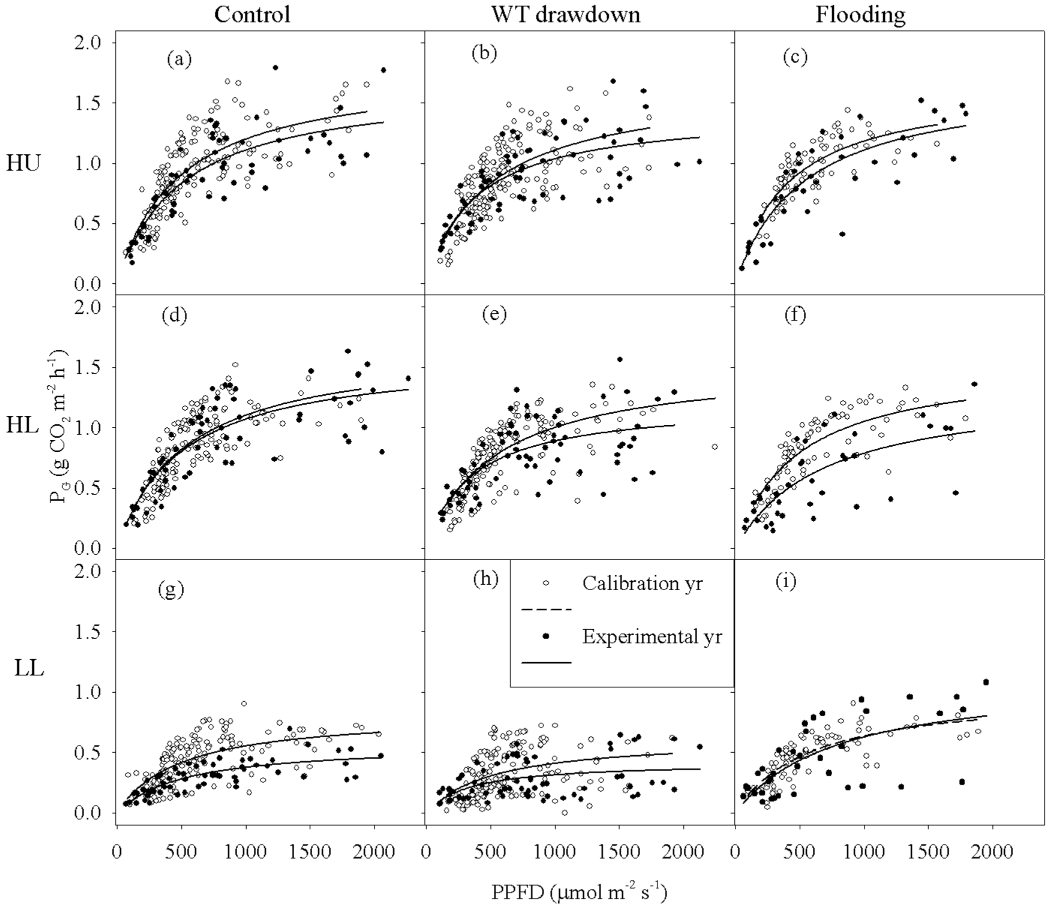

Figure 6.3 Relationship between summertime (May-September) gross photosynthesis (P_G) and photosynthetic photon flux density (PPFD) in hummocks (HU) of (a) control, (b) WT drawdown and (c) flooding experiment sites during the calibration and experimental years. Relationship in high lawns (HL) of (d) control, (e) WT drawdown and (f) flooding experiment sites during the calibration and experimental years. Relationship in low lawns (LL) of (g) control, (h) WT drawdown and (i) flooding experiment sites during the calibration and experimental years.

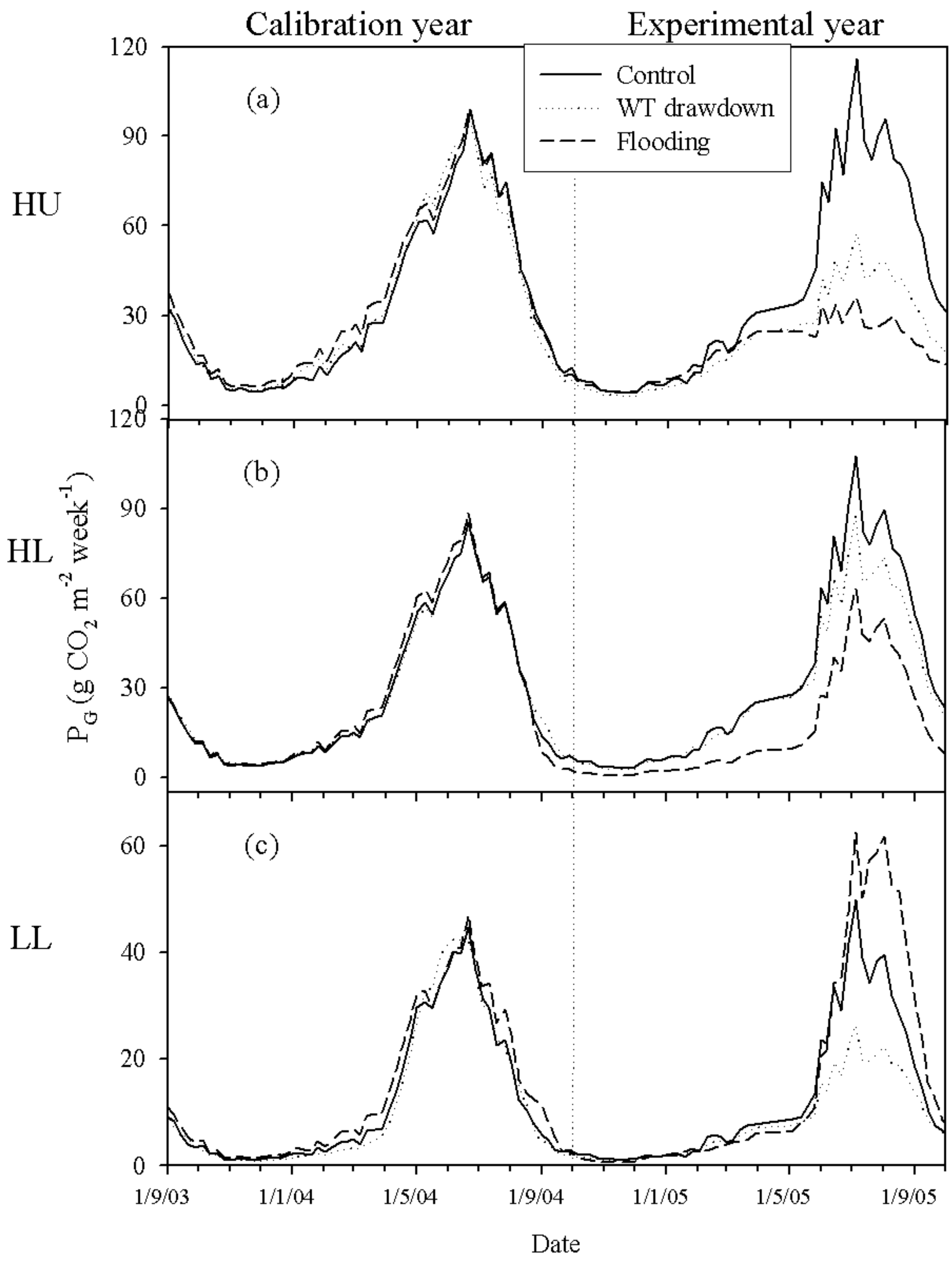

Figure 6.4 Weekly, modelled gross photosynthesis (P_G) in (a) hummocks, (b) high lawns and (c) low lawns in control, WT drawdown and flooding experimental sites during calibration and experimental year.

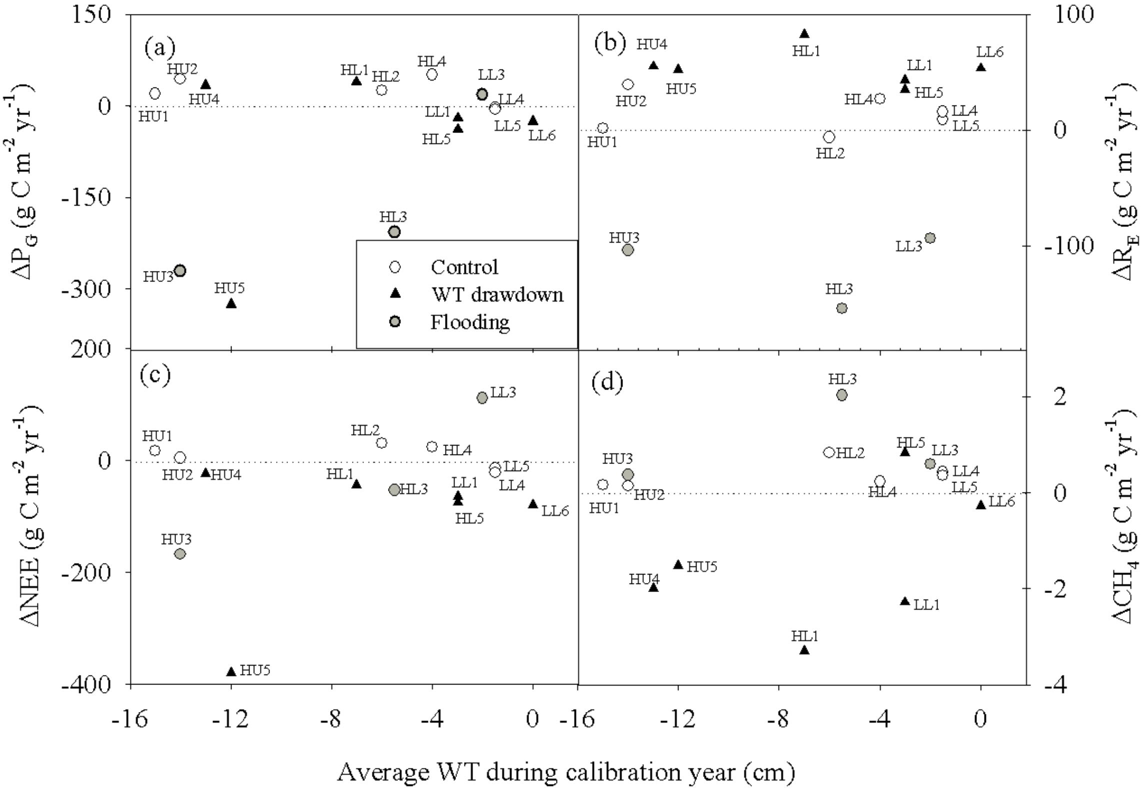

Figure 6.5 The change in the annual (a) gross photosynthesis (P_G), (b) ecosystem respiration (R_E), (c) net ecosystem CO_2 exchange (NEE) and d) CH_4 flux between the calibration and experimental years relative to the average WT of the sample plots in the calibration year. Zero line indicates no change, positive values indicate an increase and negative values a decrease in flux rates between calibration and experimental year. Plots HU1, HU2, HL2, HL4, LL4 and LL5 belong to the control site; plots HU4, HU5, HL1, HL5, LL1 and LL6 belong to the WT drawdown experiment; plots HU3, HL3 and LL3 belong to flooding experiment.

6.4.3 Changes in ecosystem respiration (R_E)

R_E was highest in HU and lowest in LL (Fig. 6.6), the average annual R_E in the calibration year was 373 (22), 308 (19) and 179 (20) g C m^{-2} (n = 5, SE in brackets) in HU, HL and LL, respectively. R_E was most strongly related to air temperature (T_{AIR}) (Fig. 6.6), which explained 40 to 63 % of the variation.

In the control site the R_E at 20 °C in the experimental year was 81, 82 and 63 % of the calibration year flux in HU, HL and LL, respectively (Fig 6.6a, d, g). The annual fluxes in each sample plot were, however, slightly higher in the experimental year (Fig. 6.5b), with the average flux being 410 (74), 320 (33) and 210 (4.8) g C m^{-2} yr^{-1} (n = 2, SE in brackets) in HU, HL and LL, respectively.

During the calibration year the level of weekly R_E was similar in the control and WT drawdown sites, except in LL, where the WT drawdown site had originally lower fluxes than the control site (Fig. 6.7). In the WT drawdown site, the R_E at 20 °C in the experimental year was 90, 92 and 83 % of the calibration year flux in HU, HL and LL, respectively (Fig 6.6b, e, h). This is more than that observed between the two years in the control site and indicates an increased rate of R_E in all vegetation communities due to WT drawdown. The increase in the integrated weekly flux was modest and in LL the control site had higher fluxes still in the experimental year (Fig. 6.7). The effects of WT drawdown on the annual R_E flux were similar throughout the WT gradient from driest hummocks to wettest low lawns (Fig. 6.5b). Proportionally the change was, however, largest in the wettest sample plot LL6. The average annual R_E in the WT drawdown site during the experimental year was 423 (33), 358 (52) and 200 (48) g C m^{-2} (n = 2, SE in brackets) in HU, HL and LL, respectively. Annual R_E was significantly higher in the WT drawdown site in the experimental year (Paired t-test, $p < 0.001$). The increase was less significant in the control sites ($p = 0.09$).

During the calibration year the integrated weekly fluxes were similar in the control and flooding sites (Fig. 6.7). During the experimental year the flooding clearly decreased the weekly R_E in all vegetation communities (Fig. 6.7). Flooding decreased R_E especially in HL and LL (Fig. 6f and i), in the flooding site the R_E at 20 °C in the experimental year was 72, 53 and 54 % of the calibration year flux in HU, HL and LL, respectively (Fig 6.6b, e, h), which is less than in the control site. The effects of flooding on annual R_E flux were similar throughout the WT gradient from the driest HU to wettest LL (Fig. 6.5b), proportionally the change was largest in the wettest sample plot where fluxes were small. The average annual R_E in the experimental year was 243, 168 and 100 g C m^{-2} (n = 1) in HU, HL and LL, respectively.

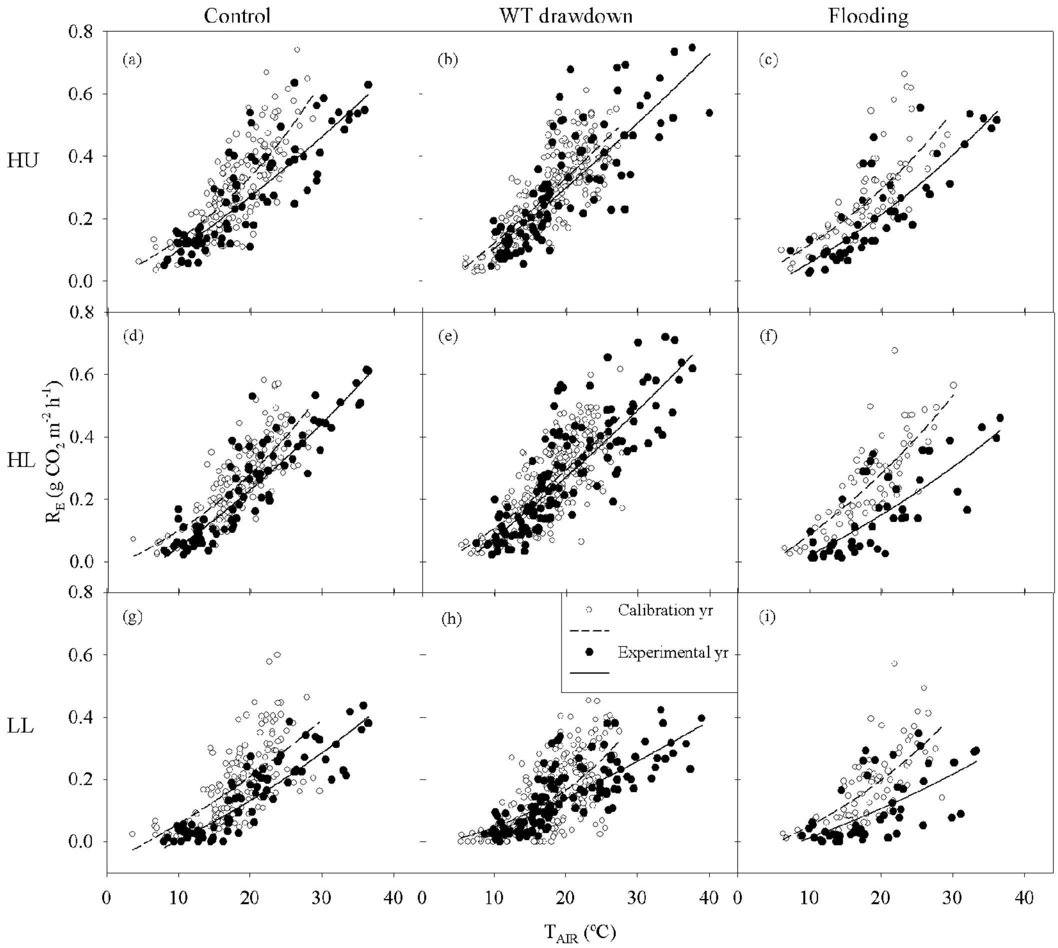

Figure 6.6 Relationship between ecosystem respiration (R_E) and air temperature (T_{AIR}) in hummocks (HU) of (a) control, (b) WT drawdown and (c) flooding experiment sites during the calibration and experimental years. Relationship in high lawns (HL) of (d) control, (e) WT drawdown and (f) flooding experiment sites during the calibration and experimental years. Relationship in low lawns (LL) of (g) control, (h) WT drawdown and (i) flooding experiment sites during the calibration and experimental years.

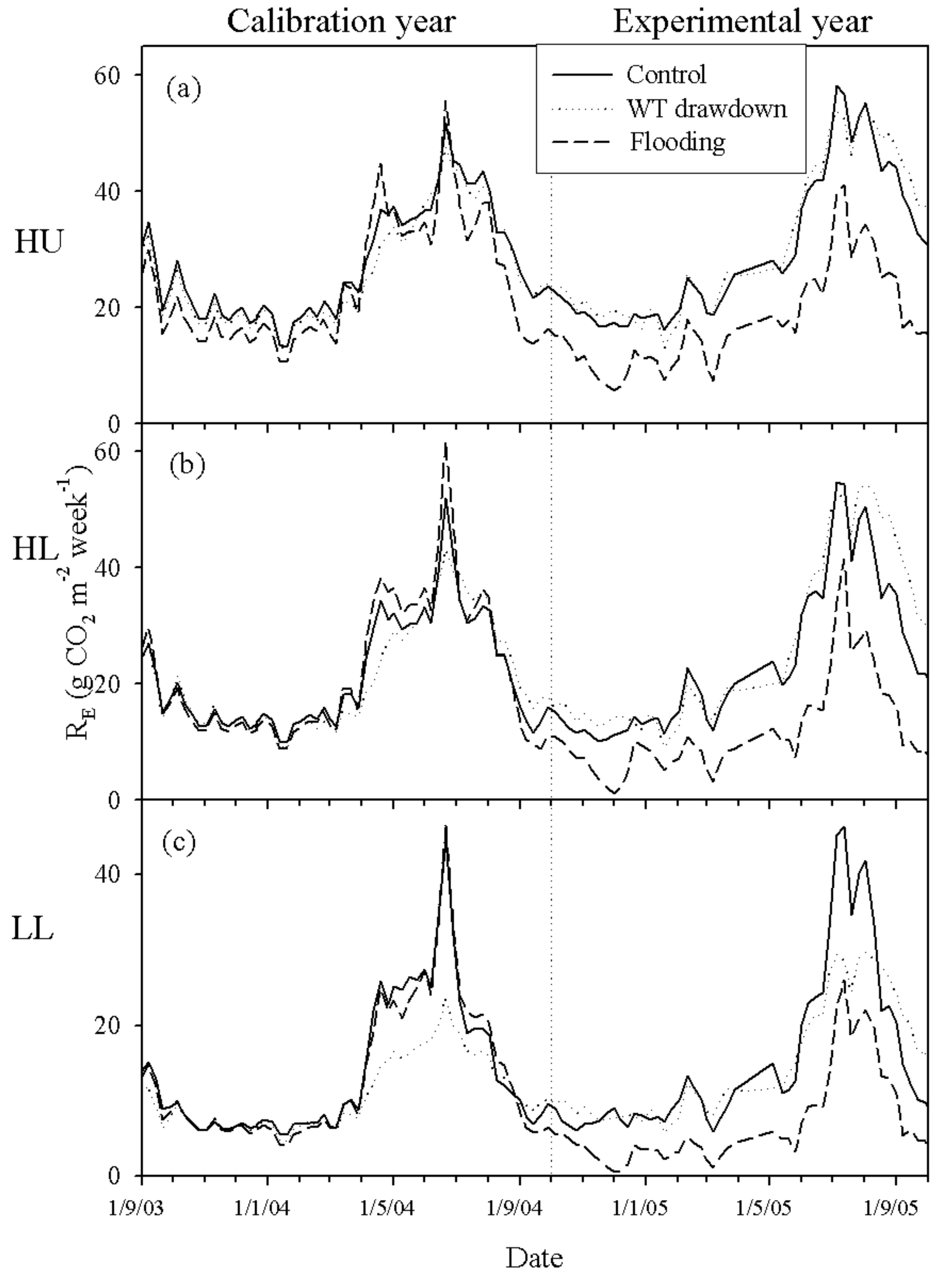

Figure 6.7 Weekly, modelled ecosystem respiration (R_E) in (a) hummocks, (b) high lawns and (c) in low lawns in control, WT drawdown and flooding experiment sites during calibration and experimental years.

6.4.4 Changes in net ecosystem CO_2 exchange (NEE)

NEE, i.e. the difference between P_G and R_E, was highest in HU and lowest in LL, with annual fluxes of 94 (23), 68 (22) and –11.6 (5) g C m^{-2} (n = 5, SE in brackets) in HU, HL and LL, respectively in the calibration year. In the control site the rate of NEE was similar during the calibration and experimental years in all sample plots (Fig. 6.5c). The average annual fluxes were 95 (12), 114 (49) and –40 (7) g C m^{-2} (n = 2, SE in brackets) in HU, HL and LL, respectively during the experimental year.

In the calibration year the integrated weekly NEE was at a similar level in the control and WT drawdown sites (Fig 6.8). The WT drawdown decreased the weekly NEE in all vegetation communities and the decrease was more noticeable during summer (Fig. 6.8). The average annual fluxes were –137 (143), -25 (19) and –81 (7) g C m^{-2} (n = 2, SE in brackets) in HU, HL and LL, respectively in the experimental year. The annual NEE was lower in all the sample plots in the experimental year and similarly to P_G the NEE of HU4 was unchanged while the decrease was strong in HU5 (Fig. 6.5c). Proportionally the change was largest in LL sample plots that originally had the lowest flux rates. The between calibration and experimental year differences in annual NEE were significant in neither site (p = 0.1 and p = 0.45 for WT drawdown and control, respectively), but in the WT drawdown site the flux was smaller and in the control site higher in the experimental year.

The integrated NEE was similar in the flooding and control sites during the calibration year (Fig. 6.8). The vegetation communities responded differently to the flooding experiment. The flooding increased the wintertime NEE in HU and LL plots (Fig. 6.8a, c). In summer the flux in HU and HL was smaller in the flooded plots than in the control plots (Fig. 6.8a, b). In LL the flooding greatly increased NEE (Fig. 6.8c). The annual flux rate decreased most in HU (Fig. 6.5c); proportionally the decrease was similar in HU and HL. Conversely, the annual flux in LL increased due to flooding. The average annual fluxes were 6, 45 and 118 g C m^{-2} (n = 1) in HU, HL and LL, respectively at experimental year.

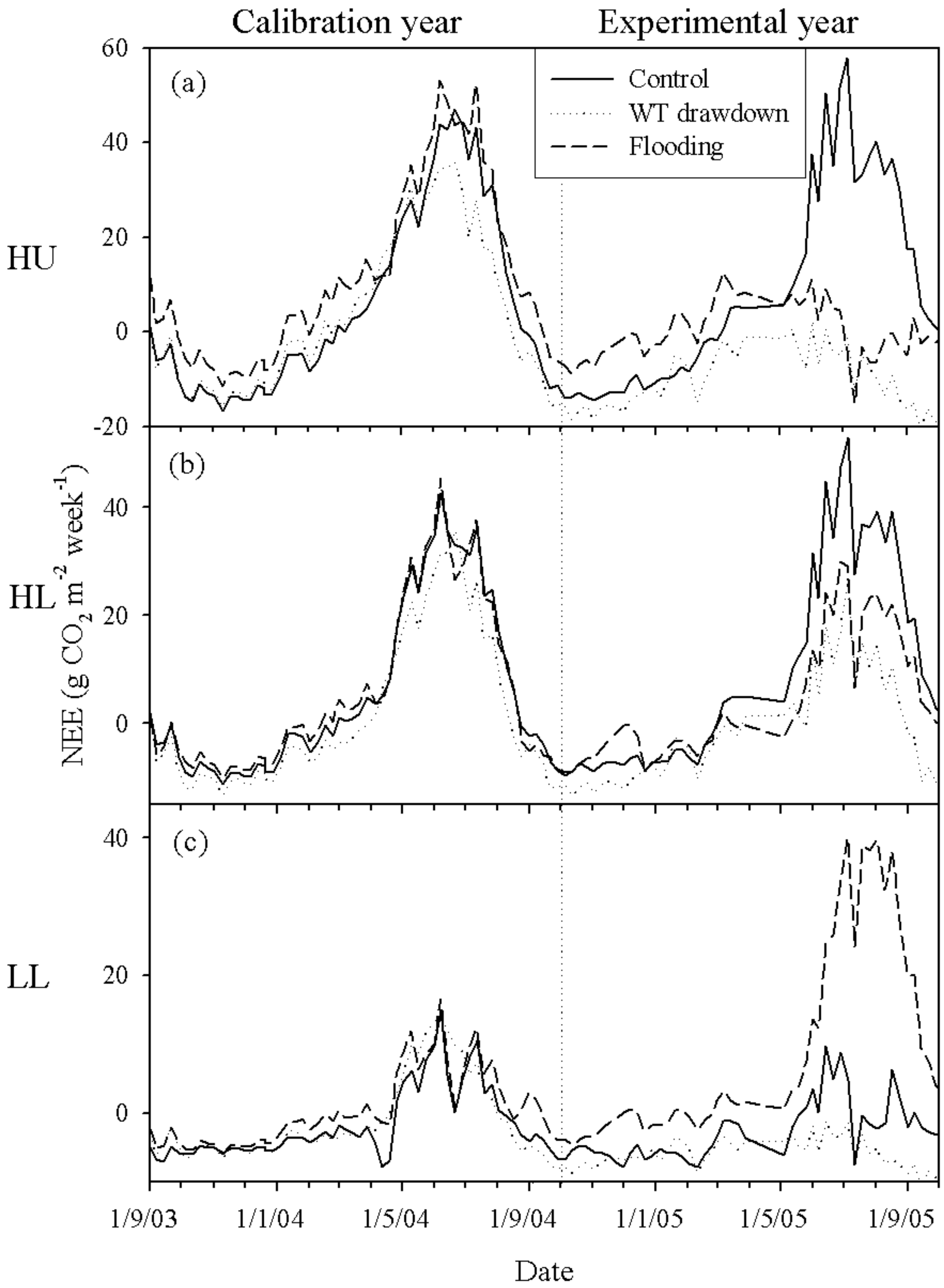

Figure 6.8 Weekly net ecosystem exchange (NEE) in (a) hummocks, (b) high lawns and (c) in low lawns in control, WT drawdown and flooding experiment sites during calibration and experimental years.

6.4.5 Changes in CH_4 flux

The CH_4 flux was highest in LL and lowest in HU (Fig. 6.10), in contrast to CO_2 fluxes (Figs. 6.4, 6.6 and 6.8). The average annual fluxes in the calibration year were 5.0 (1.2), 4.7 (0.9) and 2.4 (0.4) g CH_4 m^{-2} (n = 5, SE in brackets) in LL, HL and HU, respectively. Soil temperature at 20 cm depth (T_{20}) was the strongest controller of CH_4 flux, explaining from 10 to 95 % of the variation.

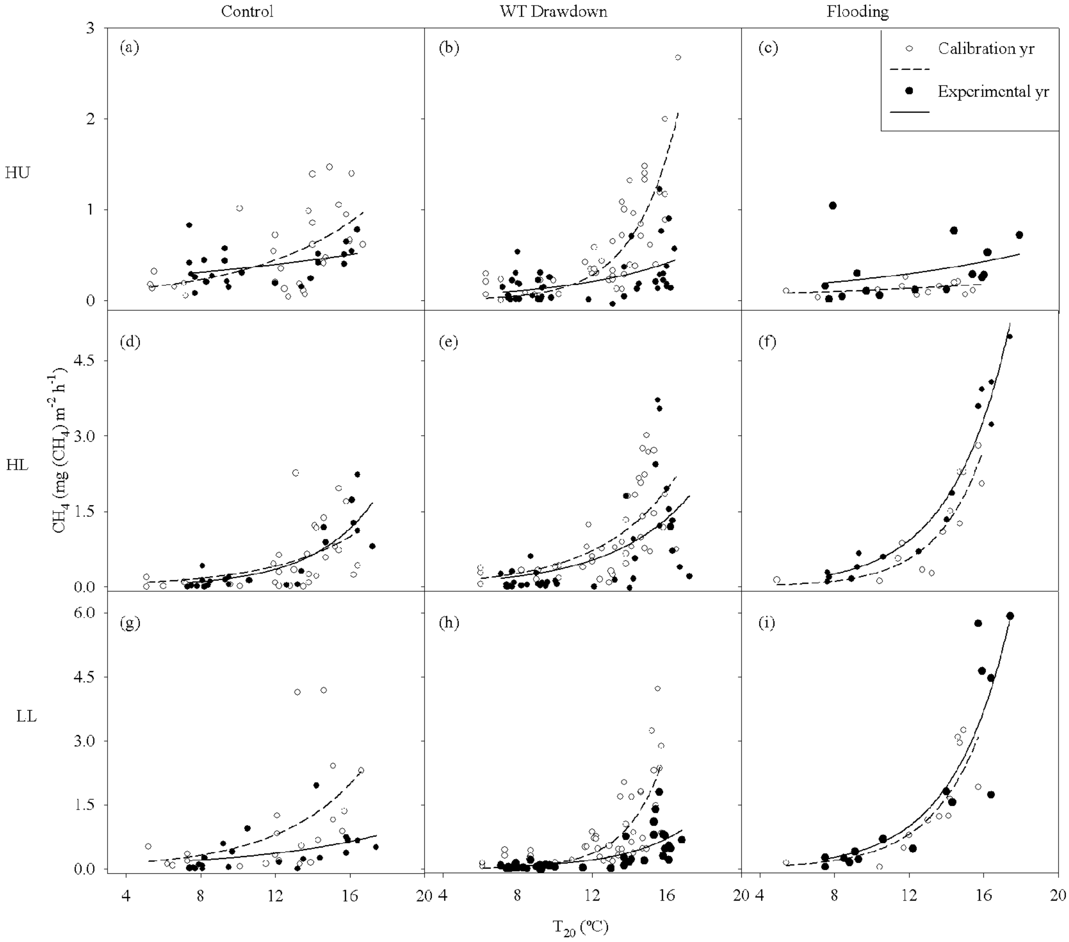

Figure 6.9 Relationship between methane (CH_4) flux and soil temperature at 20 cm depth (T_{20}) in hummocks (HU) of (a) control, (b) WT drawdown and (c) flooding experiment sites during the calibration and experimental years. Relationship in high lawns (HL) of (d) control, (e) WT drawdown and (f) flooding experiment sites during the calibration and experimental years. Relationship in low lawns (LL) of (g) control, (h) WT drawdown and (i) flooding experiment sites during the calibration and experimental years.

In the control site the CH_4 flux at T_{20} = 12 °C in the experimental year was 88, 85 and 46 % of the calibration year flux in HU, HL and LL, respectively (Fig 6.9a, d, g). The annual fluxes were, however, slightly higher in the experimental year in all sample plots (Fig. 6.5d), being 4.8 (2.7), 3.3 (1.8) and 2.9 (0.2) g CH_4 m^{-2} (n = 2, SE in brackets) in LL, HL and HU, respectively.

During the calibration year the WT drawdown site had higher integrated weekly CH_4 flux rates in HU and HL than the control site, while in LL fluxes were at a similar level (Fig. 6.10). In the WT drawdown site the CH_4 flux at 12 °C in the experimental year was 73, 74 and 56 % of the calibration year flux in HU, HL and LL, respectively (Fig 6.9b, e, h). Compared to the differences between the years in the control site, this indicates decreased CH_4 flux in HU and HL and a small increase in LL caused by the WT drawdown. In HU the weekly CH_4 flux decreased strongly after WT drawdown (Fig. 6.10a). In HL the flux was still higher than in the control site, but the difference between the sites was smaller, indicating decreased flux due to the WT drawdown (Fig. 6.10b). In LL fluxes in the control and WT drawdown sites were quite similar (Fig. 6.10c). The WT drawdown experiment caused a similar decrease in the annual fluxes in most of the sample plots (Fig. 6.5d). Exceptions were HL5 and LL6; in HL5 the flux rate increased after WT drawdown (-7 cm), while in LL6 the fluxes were similar in both years. The average annual fluxes in calibration year were 3.0 (0.3), 4.8 (2.8) and 1.1 (0.0) g CH_4 m^{-2} (n = 2, SE in brackets) in LL, HL and HU, respectively. A paired t-test was performed between the years for the WT drawdown and control sites. The between year differences were significant in neither sites ($p = 0.07$ and $p = 0.02$ for WT drawdown and control, respectively), but in the WT drawdown the flux decreased and in the control it increased.

Flooding increased CH_4 fluxes in all vegetation communities; the CH_4 flux at 12 °C in the experimental year was 221, 165 and 123 % of the calibration year flux in HU, HL and LL, respectively (Fig. 6.9c, f, i). The flooded HU had a lower integrated weekly CH_4 flux in the calibration year compared to the control site. In the experimental year the flux in HU increased, but remained lower than the flux in the control site (Fig. 6.10a). In HL and LL the control site had a lower flux in the calibration year than the flooded site, the difference increased during the summer of the experimental year (Fig. 6.10b, c) The flooding increased the annual flux most in HL3, while in HU3 and LL3 the flux remained unaltered (Fig. 6.5d). The percentage increase was, however, largest in HU3 that had a relatively low flux rate during the calibration year. The average annual fluxes in the flooded site in the calibration year were 8.2, 7.9 and 1.2 g CH_4 m^{-2} (n = 1) in LL, HL and HU, respectively.

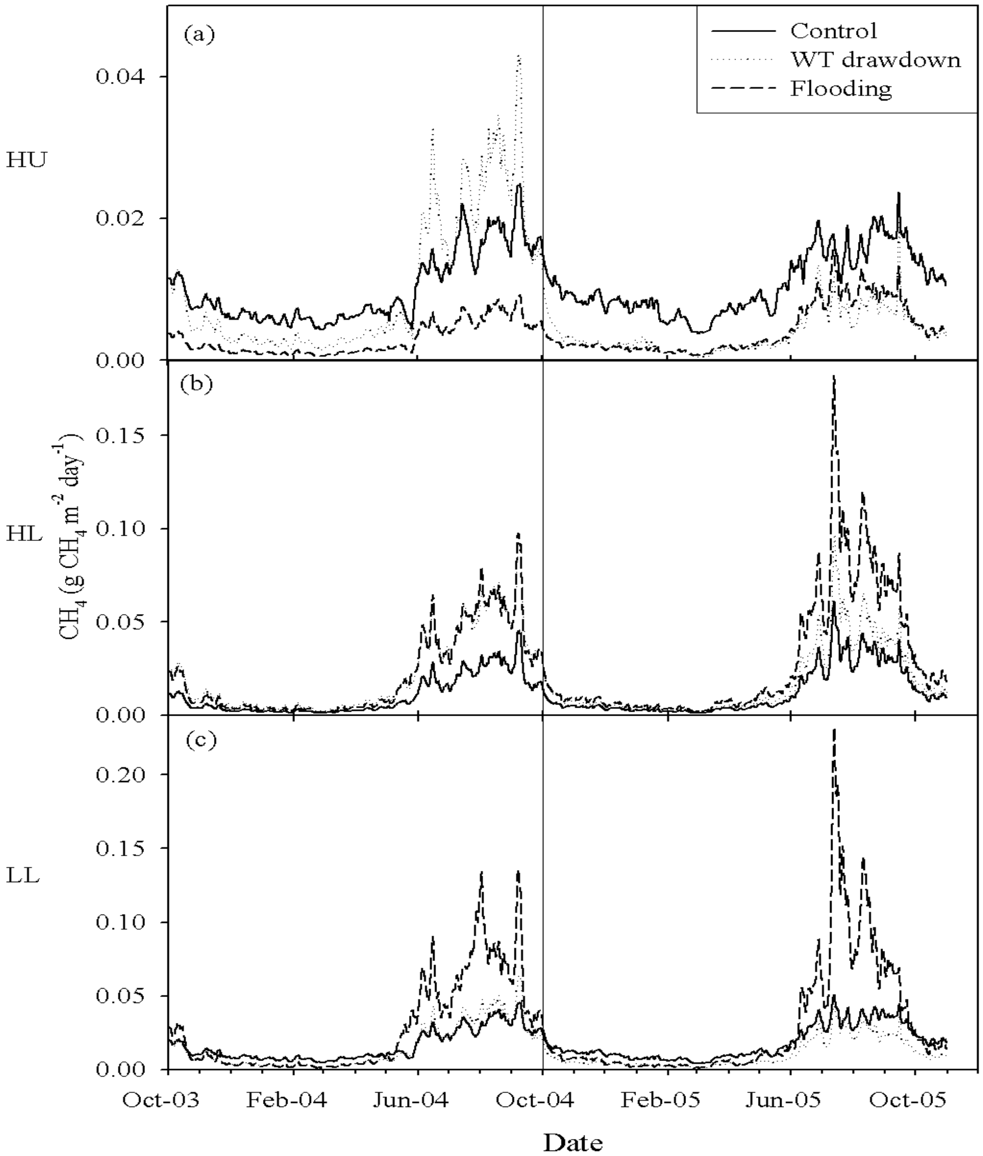

Figure 6.10 Daily modelled methane (CH_4) emission in (a) hummocks, (b) high lawns and (c) in low lawns in control, WT drawdown and flooding experiment sites during calibration and experimental years.

6.5 Discussion

6.5.1 CO_2 fluxes in blanket bog

Knowledge of CO_2 fluxes in blanket bogs is limited. Of the few existing studies, Chapman and Thurlow (1996) measured respiration rates ranging from 0.03 to 0.3 g m^{-2} h^{-1}, while Fowler et al. (1995) measured an average summertime rate of 0.04 g m^{-2} h^{-1} in Scotland. These estimates are in the low range of R_E measured in this study that averaged 0.2 g m^{-2} h^{-1} over the study period. Also the average summertime NEE measured by Fowler et al. (1995) (0.06 g m^{-2} h^{-1}) is lower than was measured in this study or by Laine et al. (2006) and Sottocornola and Kiely (2005) using both chamber and EC techniques, respectively. In the current study, the annual NEE of the sample plots in the calibration year ranged from -91 to 641 g CO_2 m^{-2} being lowest in LL and highest in HU. Sottocornola and Kiely (2005) and Laine et al. (2006) estimated similar areal NEE for the same bog (181 – 242 g CO_2 m^{-2} yr^{-1}).

Many studies have measured CO_2 fluxes in boreal and continental peatland ecosystems. Frequently, a unimodal relationship has been observed between P_G and WT, with higher P_G in lawns than in hummocks and the lowest fluxes in hollows (Alm et al., 1999b; Alm et al., 1997). However, similar to our study Waddington and Roulet (1996; 2000) working in a Swedish raised bog found higher P_G from the driest vegetation communities. In our study the HU were small and had a relatively high WT compared to other studies. In agreement with our finding, R_E is commonly higher in communities with deep WT (Alm, 1997; Waddington and Roulet, 1996).

6.5.2 CH_4 fluxes in blanket bog

Research on CH_4 fluxes in blanket bogs is limited to a few studies carried out in Scotland. Our estimates for different vegetation communities are similar to those measured by MacDonald, et al. (1998). Other studies have also measured comparable fluxes: Chapman and Thurlow (1996) measured fluxes from undetectable in winter to 33.6 mg m^{-2} day^{-1} in late summer, while Fowler et al. (1995) estimated summertime mean fluxes of 13.6 mg m^{-2} day^{-1}. The existing estimates of annual CH_4 flux (4.9 g m^{-2} (Chapman and Thurlow, 1996) and 6.9 g CH_4 m^{-2} yr^{-1} (Hargreaves and Fowler, 1998)) are similar to our estimates ranging from 0.8 to 7.6 g CH_4 m^{-2} yr^{-1} for different vegetation communities.

The fluxes were within the range of estimates for continental raised bogs (Bubier et al., 1993; Granberg et al., 1997), but lower than has been measured in boreal and arctic fens (Christensen et al., 2000; Heikkinen et al., 2002b; Saarnio et al., 1997).

6.5.3 General impacts of water level experiments

According to Gorham (1991) the principal impacts of climate change on northern peatlands will be derived from the water level drawdown. Roulet et al. (1992) estimated that according to the 2 × CO_2 scenario, the water level in a boreal fen would drawdown approximately 14 cm even when considering the increasing precipitation rate. Since in Ireland the warming is projected to be milder than in the continental regions we aimed at more moderate WT drawdown of ~ 10 cm (Fig. 6.2). The flooding experiment was carried out in order to simulate the case in which the WT in a maritime bog is raised due to increasing precipitation. WT was raised by an expected 6 cm (Fig 6.2). The changes in vegetation and gas fluxes are likely to be caused by changes in WT, since the weather conditions (precipitation, air temperature, PPFD) were otherwise similar during the calibration and experimental years.

6.5.4 Changes in vegetation

Plant species in peatlands adapt differently to the high WT. Of vascular species, sedges with aerenchymatic tissue (Armstrong, 1964) are able to grow even in inundated conditions, while shrubs need aerobic peat layer for roots and are therefore more constrained to hummocks. Shrubs are xeromorphic and therefore tolerant for dry conditions (Small, 1972), while most sedges suffer when soil moisture is reduced (Busch and Losch, 1999). Mosses have species specific and some times very restricted niches along the WT gradient (Rydin and McDonald, 1985).

The one-year time period was too short for the vegetation to change significantly. The maximum VGA was similar or higher in all sample plots except in the flooded hummock (Table 6.4). The shrubs suffered from the flooding in all communities; this had a crucial effect on the VGA of the flooded hummock.

6.5.5 Effect of changing WT on CO_2 fluxes

WT drawdown decreased NEE in all vegetation communities, with the strongest decrease in HU and LL (Fig. 6.8). Generally, the changes in NEE have been linked with increased R_E due to lower WT position (Bubier et al., 2003a; Bubier et al., 2003b; Strack et al., 2006a) and WT drawdown of 14-22 cm has increase respiration rates by 50-100 % (Bubier et al., 2003b; Silvola et al., 1996). In our study the WT drawdown of 7 to 10 cm increased R_E by 10 to 50 % (Fig. 6.6).

The effect of WT drawdown on photosynthesis is complex, since different vegetation communities respond differently to changes (Bubier et al., 2003a; Strack et al., 2006b). Especially in HU, but also in LL the decrease in NEE after WT drawdown was affected more by decreased P_G rather than increased R_E (Fig. 6.4 and 6.7). In HL the decrease in NEE (Fig. 6.8) was caused by a moderate decrease in P_G (Fig. 6.4) and a small increase in R_E (Fig. 6.7). These findings contrast somewhat with Bubier, et al. (2003a) who found no difference in P_G of sedge communities between wet and dry years, while shrub communities experienced increased P_G rates. In other studies the dry conditions have, however, decreased photosynthesis (Alm et al., 1999b; Griffis et al., 2000b) or as in the current study affected both P_G and R_E fluxes (Lafleur et al., 2003).

Within the vegetation communities the plots, with different species composition, had somewhat individualistic responses to WT drawdown. The P_G of the two HU plots had the most contrasting response to WT drawdown. In HU4, which experienced more severe drainage (-10 cm), P_G was similar in both years, while in

HU5 P_G decreased strongly (Fig. 6.5a). The reasons are bound to differences in vegetation. The VGA of HU5 was higher and did not differ between the years even if the cover of herbs/grasses namely *Molinia caerulea* and *Narthecium ossifragum* decreased more after drainage than in HU4. More significant may have been the differences in moss species composition; HU4 had *Racomitrium lanuginosum* and HU5 *Sphagnum rubellum* as dominant species. *S. rubellum* is associated with low hummocks with maximum abundance at WT of 10 to 20 cm below the surface (Rydin and McDonald, 1985) while *R. lanuginosum* occurs across a wide range of WT depths (2 to 60 cm) and is often associated with the highest hummocks in blanket bogs (Ratcliffe and Walker, 1958), as was the case in this study site. *R. lanuginosum* is known as a desiccation-tolerant species and rapidly recovers photosynthesis after remoistening (Proctor and Smirnoff, 2000). It shows long-term survival at low water contents (Proctor, 2000). This may explain why photosynthesis of HU4 did not decrease after drainage. The increase in R_E was similar in both sample plots (Fig. 6.5b). Also, the P_G of the two HL plots responded differently to WT drawdown. There was no change in HL1, while in HL5 P_G decreased noticeably (Fig. 6.5a). In both years VGA and also the cover of *R. lanuginosum* was higher in HL1. Apparently, the individualistic responses of plant species to WT drawdown have fundamental impact on the rate of photosynthesis.

Conversely to WT drawdown, flooding decreased R_E in all vegetation communities (Fig. 6.5b); proportionally the change was largest in LL that initially had the lowest flux rates. Flux rates are clearly reduced when WT is located above the surface (Chimner and Cooper, 2003), as was the case in HL and LL (Fig. 6.2). As an example, R_E decreased after rewetting in a bog drained previously for forestry (Komulainen et al., 1999). In HU and HL the NEE decreased due to decreased P_G (Fig. 6.4a, b), in HU the declined VGA after flooding decreased P_G. The reduced P_G affected NEE in summer, while in winter NEE was high compared to the control site (Fig. 6.8a) due to decreased R_E. The decrease in summer was more significant on an annual basis, since NEE was smaller in the experimental year. The change in NEE was small in HL where both P_G and R_E were a little lower in the flooded site than in the control site (Fig. 6.8b). NEE of LL was higher in the flooded plot throughout the year than in the control site (Fig. 6.8c). In winter the flux was higher due to decreased R_E and in summer the high P_G added to the increase. Correspondingly, the VGA in the LL was 14 % higher during the experimental year than during the calibration year. Similarly, in restored peatlands drained previously for forestry the response of P_G to rewetting depended on vegetation. Shrubs (*Calluna vulgaris*) suffered and sedges (*Eriophorum vaginatum*) benefitted from rewetting (Komulainen et al., 1999).

6.5.6 Impact of WT change on CH_4 emissions

Methane flux is strongly related to WT and the higher the WT the higher the flux (Bubier et al., 1993). In addition, the vegetation (abundance and species composition) affects strongly the flux rate (Christensen, 1993; Ström et al., 2003). Abundance of sedges, for example, is a sign of high CH_4 fluxes.

As expected and observed in other studies (Moore and Dalva, 1993; Roulet et al., 1992) the WT drawdown decreased CH_4 emission. The decrease was from 9 to 60 % depending on vegetation community. The only exception was HL5 where the flux rates were similar in both years (Fig. 6.5d), corresponding with the relatively small decrease in sedge cover and increased VGA. In a poor fen in Canada a 20 cm drop in WT reduced the CH_4 flux on average by 55 % (Strack et al., 2004). According to Freeman et al. (2002) the decrease in flux rate is more due to reduced production caused by the changing vegetation community that alters the substrate flux to the anoxic layer, than increased oxidation of CH_4. WT drawdown does, however, increase the layer over which CH_4 oxidation can take place (Roulet et al., 1993). In our study the VGA was higher during the experimental year and was not able to explain the decreased CH_4 flux rates in WT drawdown site, therefore it is likely that the reduction was solely caused by the WT drawdown.

The flooding increased flux rates in all vegetation communities (Fig. 6.5d). In HU where the VGA declined the higher flux rate is likely due to decreased oxidation of CH_4. In HL and LL in addition to the direct effect of higher WT, the higher VGA may have increased CH_4 production by enhancing the substrate supply and also the amount of plant mediated CH_4 transport. Increased CH_4 fluxes were observed also after rewetting of cut-away peatland (Tuittila et al., 2000).

6.5.7 Carbon gas flux balance

In the calibration year hummocks had the most positive C gas balance (NEE - CH_4 flux), while in low lawns the C balance was negative. After WT drawdown the C balance was negative in all communities and the decrease was largest in hummocks and least in high lawns. Also the flooding decreased the C balance more in hummocks than in high lawns, while in low lawns the flooding increase the balance. This implies that hummocks are adjusted to the prevailing conditions and a change into drier or wetter conditions may be detrimental for their C balance. High lawns are the most resilient community for changes since the vegetation is a combination of hummock and hollow dwelling species, adapted to opposite WT conditions. Vegetation of low lawns is sparse and dominated by *R. alba*, therefore the wet conditions, suitable for this species, trigger highest C balance.

6.5.8 Implications for climate change

Our study gives an insight into how the present vegetation communities would react to changes in water level over a short time scale. Climate change, on the other hand, is likely to affect the water level gradually over a longer time period that would allow a widespread vegetation succession. R_E and CH_4 fluxes are more directly linked with WT than P_G; therefore this study gives an indication regarding the long-term future changes in these fluxes. P_G, however, is closely coupled with vegetation structure. We observed decreased rates of P_G in communities suffering from water stress, caused either by WT drawdown or flooding. In the long-term the direction of the vegetation succession after the change in WT will define the P_G and C balance.

Since the bog vegetation is a combination of species adapted to hummocks and hollow conditions, the response to WT drawdown is likely to be an increasing proportion of hummock species and conversely the rising WT would increase the proportion of hollow species.

Belyea and Malmer (2004) estimated that the shifts in surface structure towards both wet and dry, decreases C accumulation, due to decreased production and increased decomposition, respectively. Similarly, Waddington, et al. (1998) emphasized the importance of changing surface structure but estimate that drying would increase C accumulation, since hummocks were the most efficient C sinks. We tested both hypothesis and according to the present C gas balance the increased proportion of hummocks and high lawns would likely increase the C accumulation rate. On the other hand, the WT drawdown had a detrimental effect on the C balance of hummocks that presently cover 6 % of the study sites surface (Laine et al., 2006). Based on the negative C balance of low lawns, the increased proportion of this vegetation type, due to rising WT would decrease C uptake considerably. The existing low lawns however benefitted the flooding, shown as the increased P_G in *R. alba* community. This increase must be limited by high enough WT, since permanently inundated hollows are known to have low productivity and high CH_4 fluxes (Waddington and Roulet, 1996).

6.6 Conclusions

The carbon balance in the pristine hydrological conditions was highest in hummocks and negative in low lawns. A moderate WT drawdown decreased the C balance most in hummocks and least in high lawns. Also flooding decreased the C balance most in hummocks, while in low lawns the uptake of C increased greatly after flooding. In a climate change scenario with water level drawdown the increased proportion of dry microforms, hummocks and high lawn would increase C uptake, even though the drying hummocks would turn into C sources. The scenario of wetter climate and rising water level would increase proportion of low lawns and hollows that currently have low or negative C balance. The significance of the increased productivity in the current low lawns may be irrelevant in long-term, since generally, the wettest vegetation communities have a sparse vascular plant cover and low productivity.

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7 Estimating net ecosystem exchange in a patterned ecosystem: an example from a blanket bog

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7.1 Abstract

Net ecosystem exchange (NEE) was measured in a patterned peatland with eddy covariance (EC) and chamber methods during a 12-month period. The peatland surface was composed of microforms characterized by a difference in water level and vegetation composition. The distribution of microforms varied spatially within the peatland. To achieve correspondent half-hourly EC and chamber NEE estimates, we modelled microform level chamber fluxes, estimated them at each instance of weather recordings and integrated them over the year. We then scaled the fluxes up to the EC footprint. On a half-hourly time scale the correlation coefficient (R) of the NEE between the methods was 0.80 and the slope of regression 0.91. Measurements made in summer and during daylight were more highly correlated than measurements made in winter and during darkness. When integrated on a monthly time scale the methods agreed better, with R of 0.98 and slope of regression 1.00. The annual NEE for the EC and chamber methods were 206 and 242 g(CO_2) m^{-2}, respectively. The study confirmed that the surface pattern of the EC footprint in the blanket bog was sufficiently homogeneous, that the changing wind direction did not influence the half-hourly NEE. However, the chamber estimates found that the annual NEE of the driest area within the footprint was 130 % larger than the wettest area, indicating that large spatial variation can be found in NEE.

7.2 Introduction

Blanket bogs are ombrotrophic peatlands receiving water and nutrients from precipitation and atmospheric deposition. They are usually located in flat to moderately sloping terrain. The surface pattern of these bogs is typically a mosaic of undulating microforms namely, hummocks, lawns and hollows (Lindsay, 1995). Microforms differ from each other in terms of water table level, plant composition (Doyle, 1990) and peat pH (Doyle, 1982) and their distribution within a bog varies spatially (Lindsay, 1995). In blanket bogs this structural and functional differentiation is reflected in the spatial variation in carbon (C) accumulation rate (Tallis and Livett, 1994) and methane (CH_4) emissions (MacDonald et al., 1998). Studies in raised bogs (Alm et al., 1999b; Waddington and Roulet, 2000) have found similar spatial variation in carbon dioxide (CO_2) dynamics.

Net ecosystem exchange (NEE) is the difference between CO_2 uptake through photosynthesis and loss via respiration. The two main methods used to measure NEE are chamber (Alm et al., 1997; Bubier et al., 1998) and eddy covariance (EC) (Aurela et al., 1998; Lafleur et al., 2003). Both have advantages and disadvantages when used to assess the NEE of an area over specific time periods. The chamber method enables measurement of a homogenous miniature ecosystem (~ metre scale). Measurements at this scale allow observation of small-scale variation within the ecosystem, e.g. variation between microforms (Griffis et al., 2000b). Furthermore, the chamber method enables the development of environmental response functions (Tuittila et al., 2004). It permits investigation of the functions of the ecosystem at process level and also allows measurements in conditions when the flux rates are small, i.e. winter time (Alm et al., 1999a). However, difficulties are encountered when integrating the measurements over longer time periods and in scaling them up to ecosystem level (~ 1 km scale). The EC method allows non-intrusive, direct and continuous ecosystem scale measurement of NEE (Baldocchi, 2003) of fairly homogenous areas over a range of time scales varying from days to years (Baldocchi et al., 2001). In the EC method the source area of the measured CO_2 exchange, called the footprint, moves with the wind direction. The upwind spatial distribution of the corresponding surface emission (or deposition) flux was called footprint by Schuepp et al. (1990). The footprint is the relative weight given to each elemental emission or uptake flux (Horst and Weil, 1992). In order to estimate the footprint, Schuepp et al. (1990) developed a simple analytical model, which was then further developed by Horst and Weil (1992; 1994). Yet, discussions about the feasibility and reliability of analytical and Lagrangian stochastic models are ongoing (Schmid, 2002). Hsieh et al. (2000) combined similarity theory and a Lagrangian stochastic dispersion model into an easy-to-use analytical model that describes the relationship between footprint, atmospheric stability, observation height and surface roughness. Given that in a patterned peatland, CO_2 fluxes differ between microforms (1999b; Alm et al., 1997) and that the microform distribution within a bog varies (Lindsay, 1995), different instantaneous footprints might show dissimilar CO_2 fluxes. If this were the case, the consequent EC measurements would not constitute a single time series, but a different time series for each different footprint. As a consequence the EC method would not operate in a homogeneous ecosystem as is generally assumed.

We measured the NEE with EC and chamber methods in an Atlantic blanket bog, which has a characteristically patterned surface structure, over a one-year time period.

The objectives of this study were:

1. To investigate the variation in NEE between microforms
2. To compare the EC and chamber estimates of NEE over short (half-hour, day) and long (month, year) time periods
3. To investigate the effect of different environmental conditions on the reliability of the two methods
4. To investigate how the patterned microform structure and shifting footprint affects the performance of the EC method

7.3 Materials and Methods

7.3.1 Site Description

The study was conducted at an Atlantic blanket bog situated at 150 m asl. in Glencar, County Kerry, Ireland, (51°55´N, 9°55´W). The average temperatures of the warmest month (July) and the coldest month (February) were 14.8 and 6.6 ºC, respectively, over the past 30 years at the Valentia weather station (30 km west of the site) (http://www.meteireann.ie/climate/valentia.asp). The annual precipitation in the study site was 2510 and 2356 mm in years 2003 and 2004, respectively.

The surface of the study site is a mosaic of microforms, which were divided into four classes: hummocks (HU), high lawns (HL), low lawns (LL) and hollows (HO). They differ from each other in terms of relative altitude, water level (Fig. 7.1) and vegetation composition. Hummocks were covered by bryophytes (*Sphagnum* spp., *Racomitrium lanuginosum*) and had *Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea* as dominant vascular plant species. Lawn level vegetation ranged from a dense cover of *M. caerulea* and *Schoenus nigricans* in drier areas, to wet areas dominated by *Rhynchospora alba*. Moss cover was sparse in lawns. Hollows supported bryophytes (*Sphagnum cuspidatum*, *Sphagnum auriculatum*) and a scattered vegetation of *Eriophorum angustifolium*, *R. alba* and *S. nigricans*. Two classes were used for lawns, as the vegetation of LL was both shorter and less dense in comparison to HL vegetation. The diameter of hummocks varied from 50 to 100 cm and they were relatively round in form. The shape and size of hollows varied greatly, with length being 50 - 300 cm. Lawns were flat areas between the previously noted microforms.

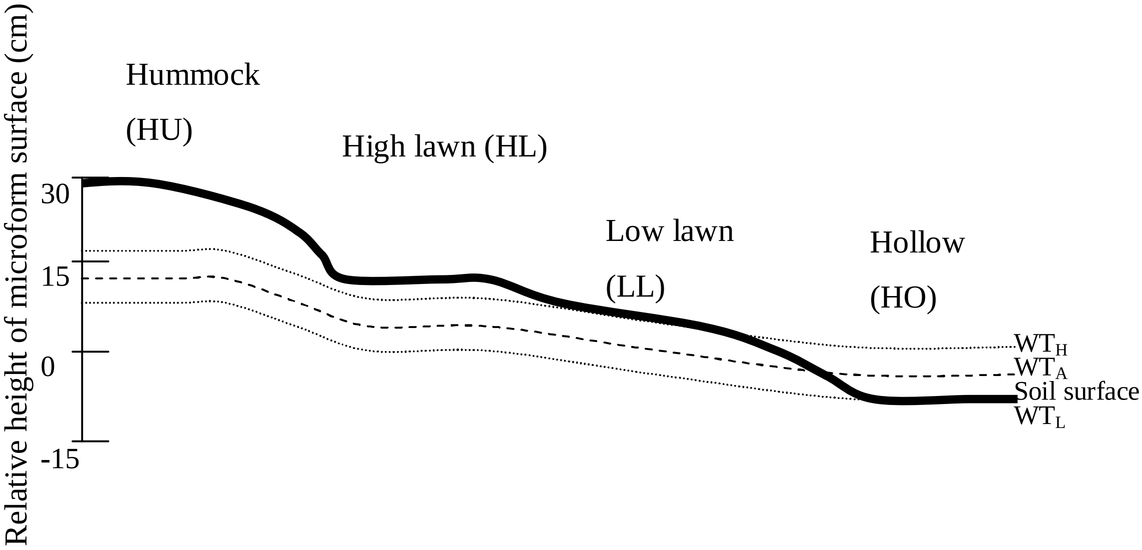

Figure 7.1 Schematic representation of microforms and associated water level (WT) parameters: highest WT (WT_H), average WT (WT_A) and lowest WT (WT_L).

7.3.2 Microform distribution within the EC footprint

In order to compare the chamber and EC methods it is necessary to use the same spatial scale for both. We achieved this by scaling the chamber measurements up to the EC footprint area. To facilitate this, the microform distribution around the EC tower was surveyed along 16 radial transects extending from the tower at 22.5° intervals (Fig. 7.2). At each transect starting 10 m away from the tower, the proportion of each microform was assessed at five meter intervals along a two meter line, perpendicular to the transect. The transect length was 300 m, except in directions NE, E and ENE, where the extent of pristine bog ecosystem was met between 235 and 270 m from the EC tower. An X^2 test was carried out to distinguish which of the transects differed significantly from the average and from the prevailing wind direction (SW) in terms of microform composition.

7.3.3 Eddy covariance (EC) measurements

The EC system consisted of a three dimensional sonic anemometer (Model 81000, R.M. Young Company, Traverse City, Michigan, USA) and an open-path CO_2/H_2O gas analyser (LI-7500, LI-COR Biosciences, Lincoln, NE, USA) mounted on a tower 3 m above the peatland surface. Data were recorded on a CR23X data logger (Campbell Scientific Ltd. Loughborough, UK) at a frequency of 10 Hz and fluxes were Reynolds-averaged every 30 minutes (Reynolds, 1895). The EC system was set up in a moderately flat section of the bog.

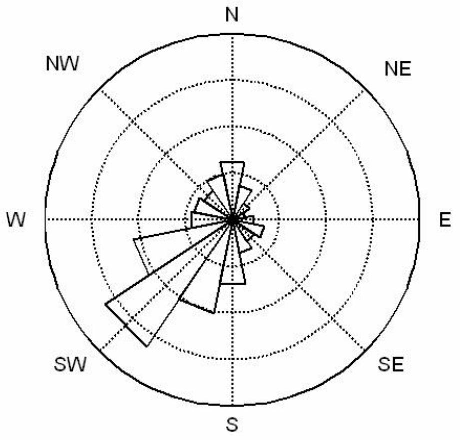

Figure 7.2 Wind rose around the EC tower, illustrating the distribution of the wind directions over the study period. The prevailing wind direction is from the South West. Microform distribution was surveyed along 16 radial transects starting at the EC tower.

7.3.3.1 Environmental measurements

Micrometeorological equipment included a net radiometer (CNR 1, Kipp & Zonen, Delft, the Netherlands) and a photosynthetic photon flux density (PPFD) sensor (PAR Lite, Kipp & Zonen, Delft, the Netherlands). Air temperature (T_{AIR}) and relative humidity were measured at 2 m height with a temperature and relative humidity sensor (HMP45C, Vaisala, Vantaa, Finland), while soil temperature was recorded at 20 cm depth (T_{20}) (107, Campbell Scientific Ltd. Loughborough, UK) below HL vegetation. Precipitation was measured with two tipping bucket rain gauges (ARG100, Environmental Measurements Ltd., Sunderland, UK and Obsermet OMC-200, Observator BV, Ridderkerk, The Netherlands). The averaging time for EC and meteorological data was 30 minutes and data were transferred from the tower to the office at weekly intervals via telemetry.

7.3.3.2 EC Data handling

Raw EC flux data were double rotated, so that mean horizontal wind speed was rotated into the mean wind direction and vertical wind velocity was set to zero. The vertical rotation was based on the averaged 30-minute angle between the horizontal and vertical axes. The CO_2 fluxes were then corrected for variations in air density due to fluctuation in water vapour and heat fluxes (Webb et al., 1980). The dataset was divided into day and night files using short-wave incoming radiation of 10 W m^{-2} as the threshold between day and night. 46 % of all the data were daytime data.

Filters were used to remove bad flux values. Records collected during rainy half hours, and up to one h after rain events, were rejected because of the poor performance of the open path gas analyser in wet weather. In low wind speed conditions the computation of the vertical angle used for the vertical rotation can give unrealistic outputs; therefore, fluxes that were rotated for angles $< -2°$ or $> 10°$ were rejected. In order to assess the existence of adequate turbulence required by the EC system for good performance, the night-time fluxes are usually examined in different friction velocity (u_*) conditions and a lower u_* threshold established (Gu et al., 2005). In our study, no clear correlation was found between dry night CO_2 fluxes and u_*. Consequently, the night u_* filter was not applied. Nighttime uptake values were, however, rejected. Flux records were divided into bimonthly data sets for both day and night and filtered for unrealistic low or high values.

The gaps in CO_2 fluxes were filled with gap filling equations defined using the Curve Fitting Function of MATLAB 6.5 (The MathWorks, Inc., USA). Separate non-linear regression equations were used for daytime and nighttime gap filling. Daytime gaps were filled using rational functions of polynomials in one variable of different powers between good NEE values and PPFD or air temperature for bimonthly or monthly periods. The functions used for October 2003 and September 2004 were defined with a bimonthly data analysis together with September 2003 and October 2004, respectively. For nighttime a single Q_{10} relationship between good NEE values and soil temperature at 20 cm depth was used for the 12-month study period computed from the full data set collected in the biennium 2003-2004 (Sottocornola and Kiely, 2005).

7.3.4 Chamber measurements

Six stainless steel collars (0.6 × 0.6 × 0.15 m) were inserted into the peat in HU, HL and LL, respectively in June 2003. In March 2004 three more sample plots were established in microform HO. Each collar had a water channel at the top to allow water sealing during gas sampling. Boardwalks were constructed around the sample plots to minimize disturbance. The sample plots, with microforms similar to those within the EC footprint, were located 300-350 m northwest of the EC tower.

CO_2 exchange measurements were made at weekly to biweekly intervals using a closed transparent plastic chamber (0.6 × 0.6 × 0.33 m). The square chamber was vented and included a cooling system (Alm et al., 1997). The CO_2 concentration (ppm) inside the chamber was monitored with a portable infrared gas analyser (EGM-4, PP Systems, Hitchin, Hertfordshire, UK). Instantaneous net CO_2 exchange (P_N, this term is used to distinguish it from the ecosystem scale NEE) was first measured under a stable ambient illumination at 15-second intervals over a 60-240 second period. This was then repeated with the chamber covered with an opaque canvas cover, in order to obtain P_N in the dark, which is used here as an estimate of the instantaneous ecosystem respiration rate (R_E). For a description of the method see Alm et al. (1997) and Tuittila et al. (1999). Measurements were carried out between 9:00 am and 7:00 pm.

In order to relate the gas fluxes to prevailing environmental conditions, PPFD and air temperature inside the chamber (T_{AIR}) were recorded simultaneously with P_N measurements. At the same time, soil temperature at 20 cm depth (T_{20}) and water level (WT), relative to the sample plot surface, were measured. The PPFD was measured with a quantum sensor in μmol m^{-2} s^{-1} (PAR-1, PP-Systems, Hitchin, Hertfordshire, UK).

Vascular Green Area (VGA), which describes the area of green vascular plant material, was measured according to Wilson et al. (in Press) in order to simulate the phenological changes of the vegetation communities during the study period and to incorporate these changes into the CO_2 flux models. VGA was measured by counting the leaves of each vascular plant species within the sample plot and multiplying the number by the leaf area, which was measured concurrently. Measurements were made at biweekly to monthly intervals throughout the study period. Non-linear regression analysis was used in interpolating data between measurements to describe the seasonal changes in phenology.

7.3.5 Response functions for chamber CO_2 fluxes (P_G, R_E)

Instantaneous CO_2 flux rates P_N and R_E were calculated from the linear rate of change in CO_2 concentration inside the chamber headspace.Instead of directly modelling the P_N flux, we computed the separate components of gross photosynthesis (P_G) and ecosystem respiration (R_E). This was made in order to describe the direct environmental controls on fluxes and decrease the overlap of effects. P_G was calculated as a sum of P_N and R_E. We developed regression models for each microform (Tables 1 and 2) following the ecological interpretation of Tuittila et al. (2004). We used a multiplicative model format for P_G and based the model construction on the Michaelis-Menten relationship between PPFD and photosynthesis (Stryer, 1988). VGA was used to describe the seasonal changes in P_G. For microforms HU, HL and LL, P_G was also dependent on the temperature of the active soil layer (T_A), which was calculated as the average of T_{AIR} and T_{20} measured simultaneously with chamber measurements. For HO, P_G was dependent on water level (WT). The model for HU, HL and LL had the following form:

$$P_G = P_{MAX}\left(\frac{Q_P}{k+Q_P}\right)(a_1+V)\exp\left(-0.5\left(\frac{T_A-a_2}{a_3}\right)^2\right) \quad (7.1)$$

The model for HO had the following form:

$$P_G = \left(\frac{Q_P}{k+Q_P}\right)(b+b_1W)\left(\frac{V}{b_2+V}\right) \quad (7.2)$$

where Q_P is the photosynthetic photon flux density, V vascular green area, T_A the temperature of the active soil layer and W is water level. P_{MAX} is the maximum light saturated photosynthesis rate, k is half saturation constant and a_1, a_2, a_3, b, b_1, b_2 are parameters.

For R_E we used an additive model format. R_E had a positive exponential relationship to T_A and the response to WT and VGA was linear in all microforms, except in HO, where VGA did not have explanatory power. The R_E model for HU, HL and LL had the following form:

$$\mathrm{R_E} = a\exp(bT_A) + (b_1W) + (b_2V) + (b_3WT_A) \tag{7.3}$$

The R_E model for HO had the following form:

$$R_E = a\exp(bT_A) + (b_1W) + (b_3WT_A) \tag{7.4}$$

where T_A is temperature of the active soil layer, V vascular green area, W water level and a, b, b_1, b_2, b_3 are parameters. The R_E model for HU underestimated and gave negative flux rates in low temperatures (< 3.9 ºC). Given that such temperatures occurred rarely (50 h annum^{-1}), the effect was ignored.

Table 7.1 Estimated parameter values (with standard error in parenthesis) and coefficient of determination (R^2) for gross photosynthesis (P_G) models for microforms: hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO)

	HU	HL	LL	HO
Q	0.66 (0.04)	0.64 (0.04)	0.82 (0.06)	
k	322.7 (27.03)	346.6 (29.70)	306.3 (45.56	612.8 (239.51)
a_1	1.49 (0.11)	1.25 (0.12)	0.28 (0.05)	
a_2	19.11 (0.24)	19.58 (0.26)	21.06 (0.83)	
a_3	7.35 (0.33)	6.96 (0.34)	8.44 (1.25)	
b				0.29 (0.05)
b_1				-0.02 (0.01)
b_2				0.003 (0.00)
R^2	0.81	0.81	0.70	0.51

Table 7.2 Estimated parameter values (with standard error in parenthesis) and coefficient of determination (R^2) for ecosystem respiration (R_E) models for microforms: hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO)

	HU	HL	LL	HO
a	0.02 (0.02)	0.04 (0.01)	0.01 (0.00)	0.01 (0.00)
b	0.01 (0.00)	0.09 (0.13)	0.12 (0.03)	0.09 (0.02)
b_1	0.01 (0.00)	0.02 (0.00)	0.01 (0.01)	0.00 (0.00)
b_2	0.08 (0.01)	0.04 (0.01)	0.14 (0.01)	
b_3	-0.00 (0.00)	-0.00 (0.00)	-0.0 (0.00)	-0.01 (0.00)
R^2	0.76	0.80	0.78	0.51

Using the models of (7.1) - (7.4) and environmental data, P_G and R_E were calculated at half hourly intervals for each microform over the hydrological year 1 October 2003 - 30 September 2004. The PPFD and T_{AC} data used in the reconstructions were obtained from half hourly meteorological data at the EC tower. Daily WT for each sample plot was interpolated from WT measurements made during chamber measurement campaigns. Microform WT was calculated by averaging the WT of sample plots representing each microform. Average daily VGA was estimated for each microform using the VGA models. There were no WT or VGA measurements of HO during the period from October 1st 2003 to April 5th 2004. Therefore, the daily water table level was estimated from LL values using the difference in the relative altitude between microforms LL and HO. To estimate the average daily VGA of the HO for this period, the VGA models based on data from 2004 were used. P_N was calculated half-hourly for each microform using the following equation:

$$P_N = P_G - R_E \qquad (7.5)$$

7.3.6 Scaling chamber fluxes up to ecosystem level

In order to compare the chamber and EC methods it was necessary to scale the chamber P_N estimates up to ecosystem level to obtain the chamber net ecosystem exchange (NEE) estimate. Hereafter the acronym CHA is used for scaled up chamber fluxes. Three scaling up approaches were performed.

The first approach considered the changes in the footprint at half-hourly intervals. The footprint length changes depending on the fluctuating atmospheric conditions and momentum flux. Consequently, the span of the transect to be considered in the scaling up process also changes. Hsieh et al. (2000) described the half hourly EC footprint as a positive skew distribution curve. Using this curve we described the area, which contributed the maximum to the flux. We considered this area to be located between the points where 1 and 67 % of the contributing area to the footprint occurred. The positive skew distribution curve is asymmetric with a steep slope before the peak and a long tail after the peak. By setting the end of the considered source area at 67%, we eliminate the long tail and reduce the impact of areas with a low flux contribution to the considered footprint span. For each half hour measurement, the microform distribution of the defined transect span was averaged along the existing wind direction. However, when the 67 % end point occurred at a distance further than the length of the transect in that wind direction, or when the computation of the footprint boundary failed (3047 out of 17568 instances), the average microform distribution of the full transect was used. The half hourly P_N of the different microforms (HU, HL, LL, HO) were then weighted by the proportion of the microform within the estimated transect span. Finally the area weighted P_N for each microform were summed up to an ecosystem NEE, hereafter referred to as wind direction scaled NEE (CHA_{WD} NEE). Monthly and annual NEE during the study period were calculated from the half-hourly CHA_{WD} estimates.

The second scaling up approach did not consider the changing footprint but was simply based on the average microform distribution around the EC tower, covering a more or less circular area of ~300 m radius; hereafter this NEE is referred to as CHA_{AV} NEE.

Finally, chamber fluxes were scaled up according to the average microform distribution of each of the 16 transects (Fig. 7.3) and integrated over the study period to produce a separate annual NEE estimate for each transect. This was made in order to distinguish the spatial variation of NEE within the EC footprint.

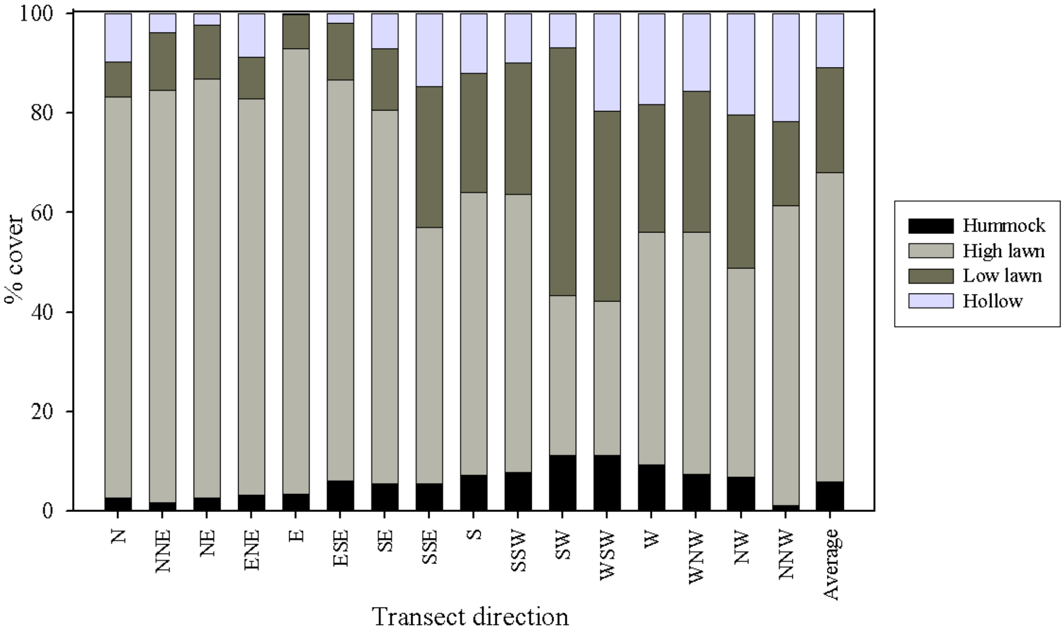

Figure 7.3 Percentage cover of microforms along the 16 transects around the eddy covariance (EC) tower. The dominant microform in the prevailing wind direction (SW) is low lawn (LL); while on average high lawn (HL) dominates.

7.3.7 Variability of microform level P_N fluxes

In order to test whether the microforms supported different P_N fluxes, a simple model describing the relationship between P_N and PPFD (Q_P) was parameterised for each of the 21 chamber measurement sample plots. The model took the form:

$$P_N = P_{MAX} \frac{Q_P}{(k + Q_P)} - R \qquad (7.6)$$

where parameter P_{MAX} is the maximum photosynthesis, k the half saturation constant and R is the constant. To obtain the corresponding flux rate for each sample plot we calculated $P_{N(1000)}$ using a PPFD of 1000 µmol m^{-2} s^{-1}. One-way analysis of variance (ANOVA) was used to test if $P_{N(1000)}$ differed between the microforms. Following this the Tukey test was used as a post hoc test, to find out which microforms differed significantly from each other, in terms of $P_{N(1000)}$.

7.3.8 Comparison between the chamber and EC methods

Linear regressions were performed between the chamber and EC estimates of NEE in order to quantify the similarity of the methods under different conditions. Firstly, all half-hour measurements during the study period were used to compare the EC measurements with the two scaling up methods CHA_{WD} and $CHA_{AV.}$ Secondly, the EC NEE estimates were compared with the CHA_{WD} NEE during winter (Nov – Feb) and summer (Jun – Sept) in order to investigate if the performance of the methods varied between seasons. Finally, the data set was divided into separate groups according to the tower data quality and environmental conditions (radiation, temperature and wind properties), which could affect the performance of the EC and chamber method (Table 7.3). Linear regression was performed for each of these groups. SPSS 12.0.1 for windows statistical package (SPSS, Inc.) was used in statistical analysis and chamber flux modelling.

Table 7.3 The year's data set was divided into groups according to environmental variables and eddy covariance (EC) data quality in order to investigate the performance of the methods in different conditions. Correlation coefficient (R), n and the slope of the regression between the wind direction scaled up chamber (CHA_{WD}) and EC method are provided for each group.

Group	n	R	Slope
PPFD (µmol m^{-2} s^{-1}):			
<20	9222	0.51	0.68
20-1000	7413	0.68	0.82
>1000	930	0.55	0.58
Temperature ˚C:			
<5	1808	0.58	1.18
5-10	6373	0.64	1.06
10-15	7071	0.83	0.97
>15	2312	0.76	0.74
Wind property:			
$\bar{u}$			
<1	1812	0.84	0.88
>1	15590	0.79	0.91
u_*			
<0.1	1697	0.84	0.89
>0.1	15724	0.79	0.91
EC data quality:			
Good	8750	0.75	0.87
Gap filled	8816	0.92	0.96

7.4 Results

7.4.1 Microform distribution of the EC footprint

The average microform distribution around the EC tower was 6 %, 62 %, 21 % and 11 % for HU, HL, LL and HO, respectively (Fig. 7.3), while between transects their cover varied within 1 - 11 % (HU), 31 - 90 % (HL), 7 - 50 % (LL) and 0 - 22 % (HO). Microforms are relatively small (~100 cm diameter) formations and their spatial variation is large. Each of the microform types can be found within an area of e.g. 2 m diameter. Drier microforms (HU and HL) dominated most transects showing the highest occurrence (93 %) in transect E (Fig. 7.3). Only three transects were dominated by wetter microforms (LL and HO), with WSW being the wettest direction (58 % cover of LL and HO). HU was the least common of all microforms (Fig. 7.3). Statistical differences were found when the microform frequency of the 16 transects was compared against the footprint average microform frequency of the study area (X^2-test, p-value <0.05) only transects ESE, SE, S and SSW were not different from the average. The comparison with the main wind direction (SW) showed even stronger differences, while only transect SSE did not have significantly different microform composition (p-value >0.05) in compared to that observed in the prevailing wind direction.

7.4.2 Eddy Covariance NEE

The average daytime flux was 0.18 g(CO_2) m^{-2} h^{-1} and when PPFD > 500 μmol m^{-2} s^{-1} the average flux was 0.27 g(CO_2) m^{-2} h^{-1}. The average nighttime flux was –0.11 g(CO_2) m^{-2} h^{-1}. From the daytime and nighttime flux data, 31 % and 66 %, respectively, were considered bad and needed to be gap filled. Between the seasons the proportion of bad data was 70 % in wintertime (Nov-Feb) and 35 % in summertime (Jun-Sep). The coefficient of determination (R^2) of the daytime gap filling functions ranged between 0.17 (Nov-Dec 2003) and 0.52 (Jul-Aug 2004). The nighttime Q_{10} gap filling function had R^2 of 0.16. The combined estimate of systematic and random error for the EC measurements was approximately 35 and 30 % for 2003 and 2004 respectively (Sottocornola and Kiely, 2005).

7.4.3 Chamber CO_2 exchange

The observed maximum and average P_N fluxes, in conditions with PPFD > 500 µmol m^{-2} s^{-1} were as follows: HU, 1.7 and 0.69; HL, 1.16 and 0.61; and LL, 0.83 and 0.23; and HO, 0.33 and 0.11 g(CO_2) m^{-2} h^{-1}. The maximum and average R_E fluxes were as follows: HU, -0.74 and -0.30; HL, -0.67 and -0.27; and LL, -0.75 and -0.17; and HO, -0.22 and -0.05 g(CO_2) m^{-2} h^{-1}. P_N and R_E showed similar seasonal variation in all microforms with highest uptake and release in mid-summer and lowest fluxes during winter months (Fig. 7.4). A significant difference was found between the P_N of microforms, when PPFD was set to value 1000 µmol m^{-2} s^{-1} (ANOVA (F (3, 17) = 32.1, $p < 0.001$). According to the Tukey test the microforms could be divided into dry (HU and HL) and wet (LL and HO) groups, whose P_N differed significantly from each other ($p < 0.001$).

The regression models of microform P_G and R_E, which were used to integrate the chamber fluxes over the study period, explained 51 to 81 % of the variation in P_G (Table 7.1) and 51 to 80 % in R_E (Table 7.2). The poorer performance of the models for HO can be explained by the smaller number of data points and the lower flux rates. The narrow range of observed CO_2 fluxes, compared to the other microforms, made the development of robust ecological response functions difficult. The standard error estimates of the P_G models varied from 0.16 g m^{-2} h^{-1} for hummocks to 0.11 g m^{-2} h^{-1} for hollows. The standard error estimates of the R_{TOT} models varied from 0.07 g m^{-2} h^{-1} for hummocks to 0.04 g m^{-2} h^{-1} for hollows.

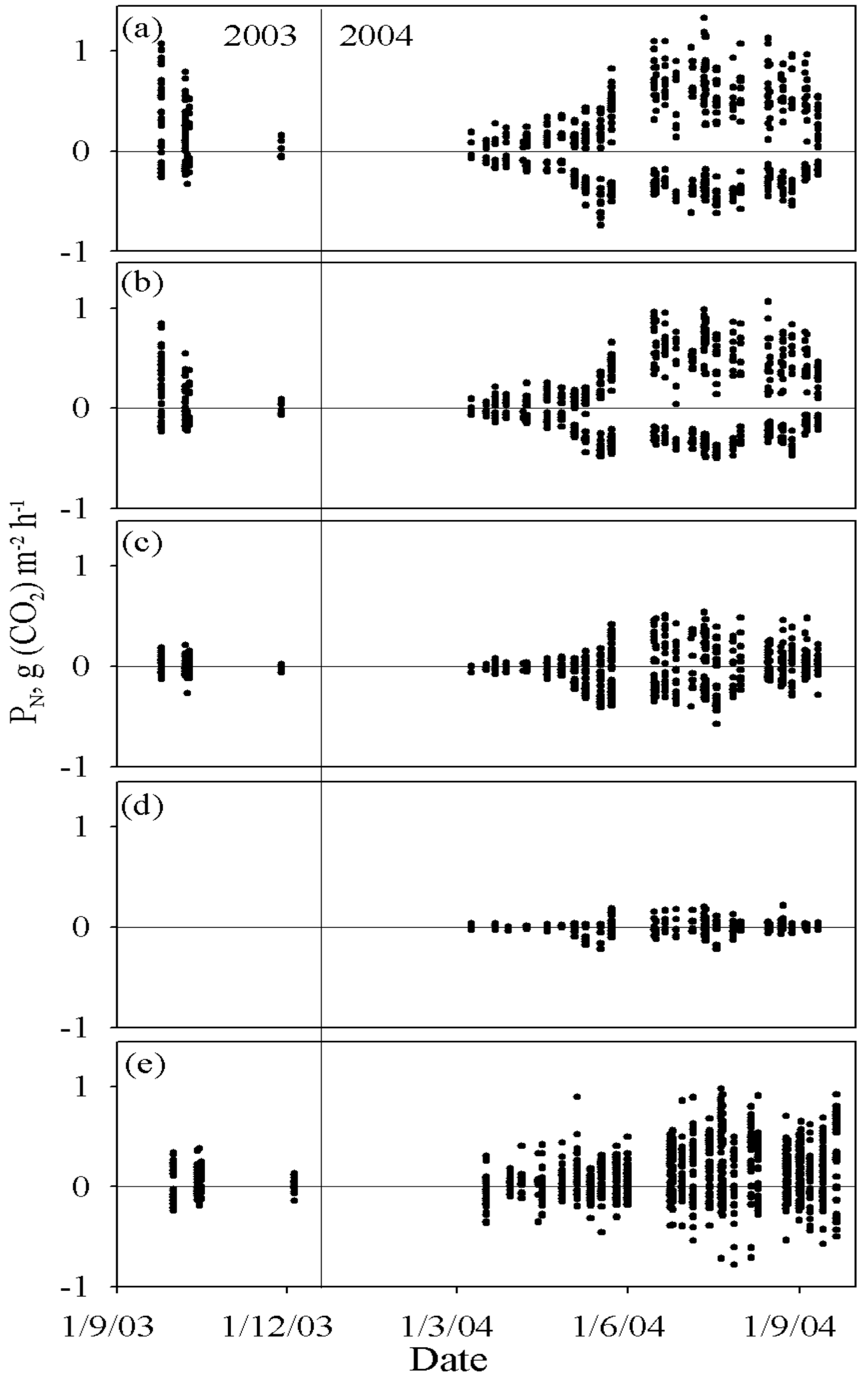

Figure 7.4 Net photosynthesis (P_N) of individual microforms (a) hummock (HU), (b) High lawn (HL), (c) low lawn (LL) and (d) hollow (HO) measured with the chamber method. Different values during the same day within each microform represent P_N measured from different sample plots under different environmental conditions. (e) Net ecosystem exchange (NEE) measured by eddy covariance tower during the same dates when chamber measurement campaigns were carried out.

7.4.4 Comparison of short-term EC and chamber NEE

The detailed wind direction scaled ($\mathrm{CHA_{WD}}$) NEE estimates were used to compare the instantaneous performance of the chamber and EC methods. Daily NEE determined by the two methods followed a similar seasonal pattern (Fig. 7.5). NEE was highest during the growing season (summer) and lowest during the winter period. Throughout the year the daily EC measurements were more variable than the modelled chamber estimates, but no systematic difference could be observed between the methods (Fig. 7.5). The correlation coefficient (R) between the half-hourly NEE estimates obtained by the two methods was 0.80 and the slope of regression 0.91 (Fig. 7.6a). The methods agreed better in summer than in winter. Correlation coefficients were 0.67 in winter (Fig. 7.6b) and 0.83 in summer (Fig. 7.6c). In winter the slope of regression (1.69) indicated departure from a 1:1 relationship (Fig 7.6b).

The effect of environmental variables and EC data quality on the performance of the methods was investigated by comparing data groups collected in different conditions (Table 7.3). The two methods agreed best in normal daylight (PPFD 20 - 1000 μmol m^{-2} s^{-1}), while the correlation between NEE measurements made in darkness (PPFD < 20 μmol m^{-2} s^{-1}) or under high irradiation (PPFD > 1000 μmol m^{-2} s^{-1}) was poorer (Table 7.3). Similarly, the two methods showed highest agreement in intermediate temperatures (T_{AIR} 10 - 15 °C), while agreement decreased towards the extreme ends of the temperature range. The wind properties, friction velocity (u_*) and horizontal wind speed ($\bar{u}$) did not affect the agreement of the two methods, since the correlation coefficient and slope were similar in all groups (Table 7.3). The gap-filled (i.e. modelled) EC NEE correlated better with chamber estimates (modelled) than the measured EC NEE (Table 7.3).

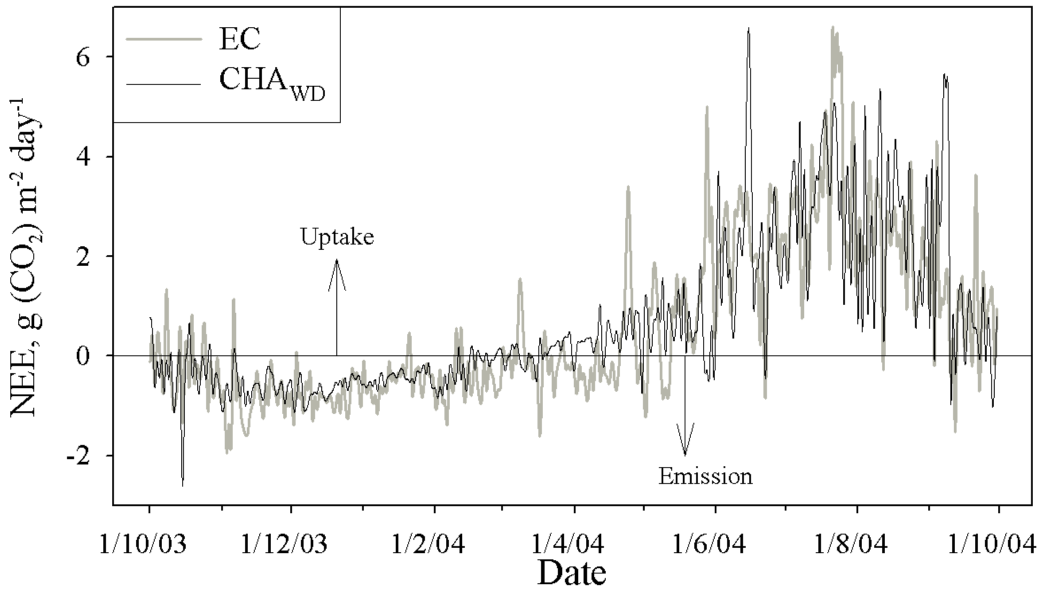

Figure 7.5 Daily sum of net ecosystem exchange (NEE) derived from wind direction scaled up chamber measurements ($CHA_{WD}NEE$) (black line) and from eddy covariance measurements EC NEE (grey line).

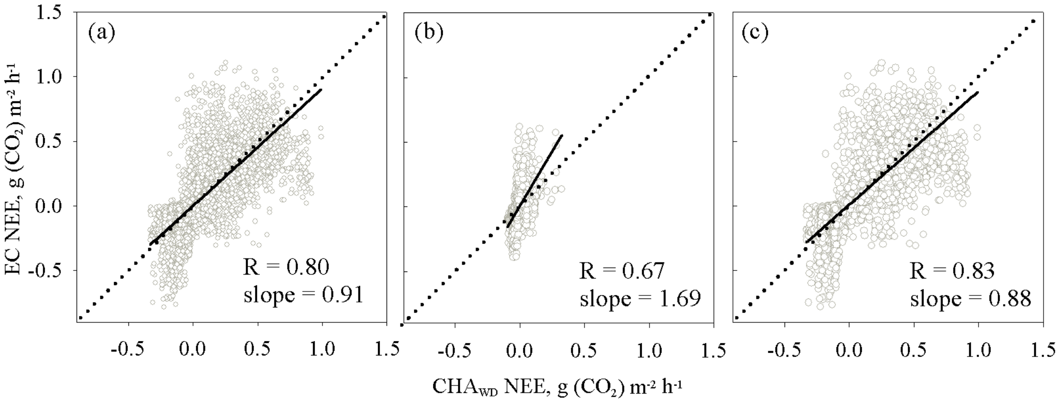

Figure 7.6 Regression of half hourly net ecosystem exchange (NEE) fluxes between eddy covariance (EC) and chamber (CHA_{WD}) estimates a) over the 12-months time period, b) in winter (November 2003 – February 2004) and c) in summer (June 2004 – September 2004). The dotted line represents a 1:1 relationship.

7.4.5 Comparison of long-term EC and chamber NEE

The agreement between the results from the two methods increased when the time period was extended. The regression between the 12 monthly EC and Chamber (CHA_{WD}) NEE estimates had high correlation (R = 0.98) and the slope of the regression (1.00) was equal to one to one line (Fig. 7.7). The annual (Oct 2003 – Sep 2004) NEE estimated by the EC and chamber (CHA_{WD}) methods were 206 and 242 $g(CO_2)\ m^{-2}$, respectively.

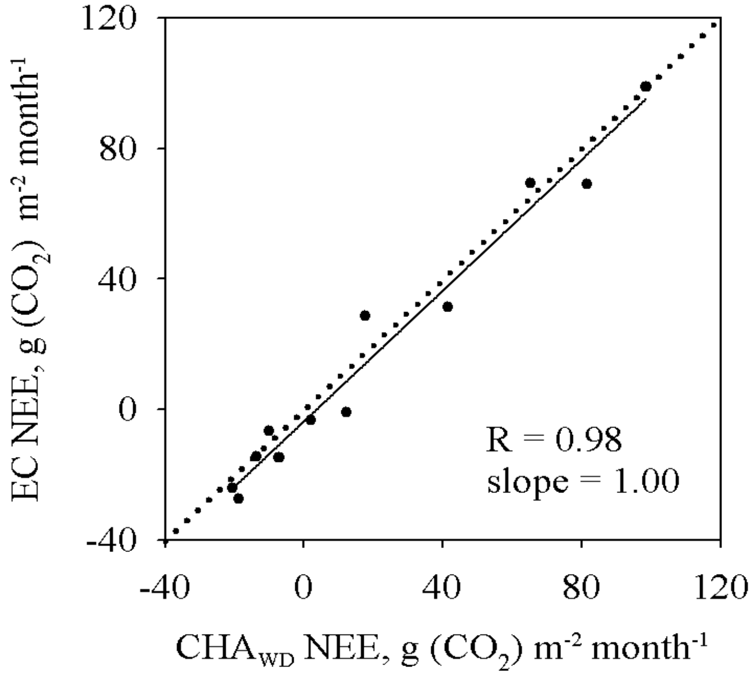

Figure 7.7 Regression of monthly net ecosystem exchange (NEE) estimated by wind direction scaled up chamber (CHA_{WD}) and eddy covariance (EC) methods. The dotted line represents a 1:1 relationship.

7.4.6 Heterogeneity of the footprint

We postulate that if the footprint had a homogeneous distribution of microforms, the microform distribution, which changes with the wind direction, would not affect the performance of chamber or EC methods. If this were the case the half-hourly chamber NEE estimates scaled up by the average microform distribution of the footprint (CHA_{AV}) should be correlated with the EC NEE measurements in a way similar to the CHA_{WD} NEE estimates. The linear regression between EC and CHA_{AV} NEE estimates had R of 0.82 and slope of 0.86. This correlation was nearly identical with the correlation between EC and CHA_{WD} NEE estimates (R = 0.80 and slope = 0.91) (Fig. 7.6a).

We found a large variation in annual cumulative NEE when we scaled the chamber estimates individually up for each of the 16 radial transects around the EC tower (Fig. 7.8). The annual NEE of the driest transect (E) was 130 % larger than NEE of the transect in the prevailing wind direction (SW).

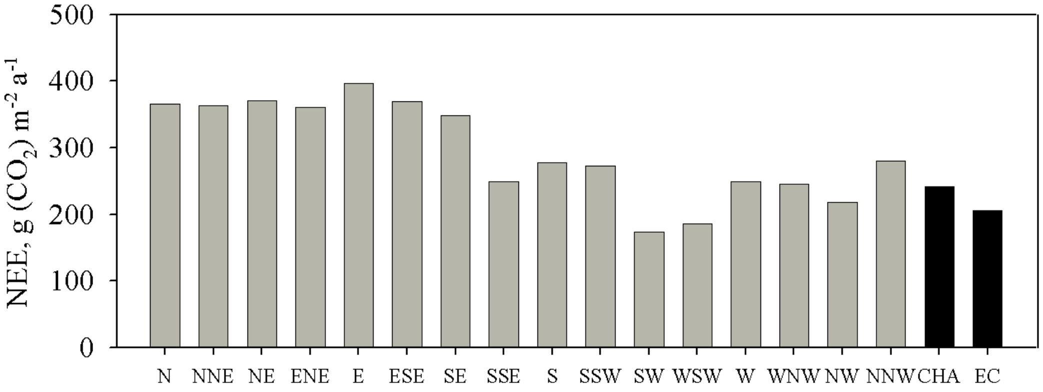

Figure 7.8 Annual net ecosystem exchange (NEE) in different transects around eddy covariance (EC) tower, modelled chamber flux is weighted by the microform distribution of each transect (grey bars). Black bars represent annual NEE of whole EC footprint with CHA being the wind direction scaled up chamber estimate and EC the eddy covariance estimate.

7.5 Discussion

7.5.1 Spatial and temporal variation in CO_2 exchange

As has been reported for raised bogs (Alm et al., 1999b; Bubier et al., 1998) and fens (Alm et al., 1997; Heikkinen et al., 2002b), microforms in blanket bogs supported different CO_2 dynamics (P_N and R_E fluxes) (Fig. 7.4). Statistically the microforms could be divided into wet (LL and HO) and dry (HU and HL) groups, which support similar net CO_2 fluxes. Similar to the findings of Waddington and Roulet (2000) we found that the drier microforms were more effective CO_2 sinks even if their respiration was higher than that of wet microforms. The flux differences between the microforms are primarily due to differences in water level, since it controls both gross photosynthesis and respiration (Alm et al., 1997; Bubier et al., 1999; Tuittila et al., 2004; Waddington and Roulet, 2000).

Both chamber and EC methods found similar seasonality in NEE, although the chamber method estimated the onset of daily net CO_2 uptake to occur earlier in spring than the EC method (Fig. 7.5). NEE was highest at the middle of the summer and lowest during mid-winter (Fig. 7.5). The seasonal dynamics are controlled by the changes in photosynthesising leaf area of vascular plants (Tuittila et al., 1999), the intensity of photosynthetic photon flux density (Bubier et al., 1998) and soil temperature, which is one of the key factors determining the respiration rate (Bridgham and Richardson, 1992; Lloyd and Taylor, 1994).

7.5.2 Comparison of chamber and EC methods

The net flux rates (both release and uptake) measured by the EC method were within the range of the observed chamber fluxes from dry and wet microforms (Fig. 7.4). Therefore, it can be said that on average the measurements of both methods are in agreement with each other, which supports the results of Frolking et al. (1998) and Heikkinen et al. (2002b) and is in contrast to Griffis et al. (2000b) who found that the chamber method overestimated respiration or underestimated photosynthesis.

More detailed analysis showed, however, that over short time periods (half hour, day) the methods were less in agreement. We made the modelled half hourly chamber NEE estimates correspond to half hourly EC NEE by weighting them according to the microform distribution of the current wind direction (CHA_{WD}). In this way the microform composition of the flux source area should be similar for both methods at all times. Similarly to a study by Lavigne et al. (1997) we found that EC measurements were noisy, which caused relatively low correlation ($R = 0.80$) between the instantaneous measurements made by the two methods (Fig. 7.6a). However, the slope of regression ($\beta = 0.91$) shows EC measurements to be 9 % smaller than chamber estimates. The correlation in our study is higher and the difference between the methods smaller than that reported by Lavigne et al. (1997) who compared nighttime respiration measurements in coniferous forest sites. However, if we consider only measurements made in darkness (PPFD < 20 μmol m^{-2} s^{-1}, generally the nighttime conditions), the correlation was similar to that observed by Lavigne et al. (1997) (Table 7.3). Since the EC system encounters problems especially during nighttime (Baldocchi, 2003; Goulden et al., 1996), this type of difference between correlations made for daytime and nighttime measurements is expected.

The methods showed less agreement in wintertime compared to summertime (Fig. 7.6b and c). Aurela et al. (2002) explained a similar large scatter in half-hourly flux rates in winter by the relatively low flux rates, which cause a low signal-to-noise ratio, compared to summer. The less favourable weather conditions in winter were reflected in the higher percentage of bad data that needed gap filling, compared to summertime. Since a large quantity of EC data required gap filling in winter, the procedure and functions used influenced the EC result. As the gap filled data correlated strongly ($R = 0.92$ and slope 0.96) with the chamber estimates (Table 7.3) we can expect the EC gap filling procedure to obey the same rules as chamber estimates with respect to the environmental controls. However, the daytime gap filling functions for summer months were more reliable, since they had a higher R^2 value than the functions for winter months. This can explain part of the difference between summer and wintertime correlations.

Distinguishing environmental conditions when the methods agreed best was difficult, since the conditions were strongly correlated with each other. However, correlation between EC and CHA_{WD} NEE was high during daytime and in warm temperatures (Table 7.3). Such conditions commonly occur together in summertime when the photosynthesising leaf area is large. These are optimal conditions for photosynthesis and as a result the CO_2 fluxes are high. Therefore, it can be generalised that the detection of NEE is more accurate in summer days than in winter nights. Fewer data points can explain the low correlation in the highest PPFD and temperature groups (Table 7.3). Wind properties (u^*, $\bar{u}$) did not have an effect on the correlation between the EC and chamber methods (Table 7.3). This observation is in line with the lack of a clear relationship between night EC NEE and u^*, which prevented the use of a night u^* filter.

In contrast to the short-term comparison we found a strong correlation between the methods when estimating NEE on a monthly and annual basis. When fluxes were integrated over longer time periods, the random variation in EC data was reduced and correspondence between the methods increased. The monthly (Fig. 7.7) and annual estimates of NEE were closely consistent between the two methods. This suggests that the difference between the methods was due more to random variation than systematic error. Consequently, the longer sampling period gave more reliable estimates both in time and space as found by Amiro (1998).

7.5.3 Heterogeneity in the landscape and in the footprint

In grassland the spatial heterogeneity of the source area has been found to cause large wind direction related variation in N_2O EC fluxes (Laville et al., 1999). Our aim was to investigate if the studied EC footprint was homogeneous enough to fulfil the assumption that the EC method operates in a homogeneous ecosystem and all measurements compose a single time series. The landscape of an Atlantic blanket bog is derived from the underlying terrain and the peat depth within the bog varies considerably (Belyea and Lancaster, 2002; Tallis, 1998). The landscape is often formed by convex and concave regions, which are water-shedding and water-collecting, respectively (Tallis, 1994). The distribution of microforms inside these areas differ: a hummock-hollow pattern is more distinctive in the wet depressions, while the more homogenous lawn vegetation dominates the drier areas (Lindsay, 1995; Tallis, 1998). The high occurrence of lawn vegetation, especially HL, was characteristic for the whole study area but we found that even over a small area around the EC tower there were significant differences in microform distribution between angular directions (Fig. 7.3). Importantly, the microform composition of the prevailing SW wind direction differed significantly from other directions, except from SSE. Due to the variable surface pattern the study site is ideal for testing the performance of the EC system in a patterned ecosystem.

The comparison of correlations between EC NEE and chamber NEE weighted with either wind direction determined microform distribution (CHA_{WD}) or average microform distribution (CHA_{AV}) gave similar results and therefore showed no difference between the scaling up methods. This suggests that more detailed knowledge of the footprint surface structure did not increase the agreement between the methods and therefore the footprint can be considered homogeneous. However, the annual NEE, based on chamber measurements and scaled up according to microform distribution of each transect, differed between the transects (Fig. 7.8) and followed the division of wet and dry microforms (Fig. 7.3). Transects with high cover of high lawns (HL) were the largest CO_2 sinks; for example the NEE of the driest transect E was 130 % larger than that of SW, which was the wettest transect, having the highest cover of low lawns. This variation between the transects shows that since the landscape of blanket bogs is often a combination of wetter and drier areas, the location of the EC tower might be a significant factor when determining areal CO_2 balances. If the aim is to obtain an estimate for whole bog area it is important to place the tower in a location, which is representative of the whole landscape. Knowledge of the footprint helps to identify and include the desired parts of the landscape and also to define the number of sample points (EC towers) required to cover the desired landscape unit for reliable flux estimates (Amiro, 1998).

It has been stated that scaling chamber measurements up to landscape level is problematic, since each sample plot represents such a small part of the landscape (Aurela et al., 1998) and that differences can occur if the chamber sample plots are not located within the EC footprint (Heikkinen et al., 2002b). In our study the chamber sample plots were not within the EC footprint, but approximately 300 m away from the EC tower; however the sample plots were chosen to represent the microforms in the footprint. The study shows that with a reasonable knowledge of the spatial variation in the flux sources (e.g. microform distribution in peatland) within the studied ecosystem it is possible to achieve similar monthly and annual C budget with chamber and EC methods.

7.6 Concluding remarks

Measurements of NEE are needed to quantify the contribution of land use and land use changes to global warming and climate change. Measurements at both large (landscape level) and small scale (homogeneous miniature ecosystems) are necessary in order to understand NEE and its relationship to environmental and climatic variables. Closed chambers and eddy covariance are the most widely used methods to estimate NEE. We demonstrated that, despite, disagreement over the short term (half-hour, day), both methods give similar estimates of monthly and annual NEE. This is an important result, as it strengthens trust in the accuracy of both methods. When planning a study of NEE the choice of method should be based upon the purpose of the study. If the aim is to achieve long-term C budgets over a landscape unit, the EC method is a more direct and straightforward method for the purpose. However, it may be more beneficial to use a closed path gas analyser rather than an open path, due to the wet environment. On the other hand, if the aim is to study direct responses of the ecosystem to environmental variables or changes in these variables, the chamber method is appropriate. The surface pattern of the studied bog was composed of microforms, which supported dissimilar net CO_2 fluxes. The distribution of microforms varied within the studied area and this resulted in spatial variation in NEE. Dry and wet regions showed significantly different annual NEE. Therefore it is necessary to carefully consider the location of the EC tower if the landscape of patterned peatland is not homogeneous. Similarly, if chamber fluxes are scaled up to landscape level, the microform distribution of the area should be well known and the sample plots should well represent the chosen microform classes.

Acknowledgements

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8 General discussion

8.1 Study site characteristics

The variation in vegetation composition along the WT gradient is described in Chapter 4. The vegetation in the study site is typical of Irish lowland blanket bogs as has been described, for example, by Doyle (1982). It forms a continuum of communities along a water level gradient ranging from dry hummocks to permanently inundated hollows, a surface pattern typical of blanket bogs (Lindsay, 1995; Tallis, 1998). The vegetation communities are not strictly delineated, but as has been described by Guinan et al. (1998) they overlap each other in such a way that, for example, the species composition of lawns is a combination of species typical of hummocks and hollows. When compared to the vegetation of raised bogs, the moss cover is poorly developed in the study site as is typical for blanket bogs in general (Doyle, 1990; Forrest, 1971; Vasander, 1982). Only the hummocks and some of the hollows have a continuous cover of mosses. This may be crucial for the C accumulation, since the moss genus *Sphagnum*, in particular, plays an important role in C accumulation in peatlands (Clymo and Hayward, 1982). Grasses (e.g. *Molinia caerulea*) and sedges (e.g. *Schoenus nigricans, Rhynchospora alba*) are more abundant in the study site than in continental raised bogs, where the shrubs are the most characteristic component of vegetation. In blanket bogs the constant and high maritime precipitation maintains the WT near the soil surface and also induces a higher pH (Shotyk, 1997) than is typical for raised bogs (Laine et al., 2002). In the study site the pH is on average 4.6 ±0.2. For these reasons blanket bogs resemble fens (O'Connor and Skeffington, 1997; Osvald, 1949) even though for the most part they are ombrotrophic, with atmospheric deposition being the only source of water and chemical elements.

8.2 Carbon dioxide exchange

Chapter 4 also focuses on the spatial and temporal variation in CO_2 fluxes (gross photosynthesis (P_G), ecosystem respiration (R_E) and net ecosystem exchange (NEE)) along the WT and consequent vegetation gradient. A distinct variation is observed in P_G, R_E and NEE fluxes between the vegetation communities. The variation is chiefly controlled by WT, with higher fluxes in dry vegetation communities (HU, HL) and low fluxes in communities with WT near or above the soil surface (LL, HO). Studies in several peatland ecosystems (e.g. Alm, 1997; Bubier et al., 2003a; Heikkinen et al., 2002a; Waddington and Roulet, 1996) have observed a comparable relationship between WT and CO_2 fluxes and have recognised the vegetation communities / microforms as the basic elements of the spatial variation in CO_2 exchange. The second most important controller of spatial variation is the vegetation composition, which in turn is controlled by WT. The leaf area and the number of species are highest in HU and HL communities, which also have the highest P_G, R_E and NEE fluxes.

The P_G and R_E fluxes follow the seasonal variation in temperature and VGA, with the highest fluxes in July / August and the lowest in December / January. The seasonality is more pronounced in P_G than in R_E, since the above zero soil temperatures maintain R_E fluxes throughout the winter. Wintertime respiration constitutes 8 to 33 % of the annual R_E. The CO_2 uptake is at a similar level as has been measured in a continental raised bog (Lafleur et al., 2001) and in a subarctic fen (Griffis et al., 2000a).

In Chapter 7 the NEE estimates derived from chamber based measurements and from EC measurements are compared. In order to adequately compare the areal chamber NEE estimate to the EC estimate, the chamber estimate was calculated by weighting the flux of each vegetation community by its percentage cover within the momentary EC footprint. Over a short time period (hour, day) the agreement between the methods is relatively poor (R = 0.8), being highest during the warm and bright daylight conditions in summertime when NEE flux was high. Over longer time periods (month, year) the random variation in the flux estimates is decreased and there is good agreement between the methods. The corresponding areal estimates of annual NEE from chamber and EC methods are 65 g C m^{-2} and 56 g C m^{-2}, respectively. The results show that the both methods are able to establish similar NEE estimates, however, within the bog the areas with different vegetation community structures may have large differences in flux rates. Therefore care should be taken when selecting the location of the EC tower.

Similarly the chamber measurement sample plots should be selected to represent the vegetation communities within the bog.

8.3 Methane flux

In Chapter 5 we investigate the spatial and temporal variation in CH_4 flux. Similarly to CO_2 fluxes, the spatial variation in CH_4 flux is controlled by WT and in inundated vegetation communities also by the vegetation. The flux rates are lowest in HU. In HL and LL, in contrast to CO_2 fluxes, the CH_4 fluxes are at a similar low level. The flux rate in HO depends on vegetation composition. Communities with *Menyanthes trifoliata* are hotspots of CH_4 emissions, while the HO community without this species has similar flux rates as HU. MacDonald et al. (1998) found the same phenomenon in hollows in a Scottish blanket bog. WT has been identified as the most important controller of CH_4 flux in several studies (Bubier et al., 1993; Moore and Dalva, 1993; Moore and Roulet, 1993; Saarnio et al., 1997). The flux rates we measured are within the range of measurements from blanket bogs (MacDonald et al., 1998) and raised bogs (Bubier et al., 1993; Waddington and Roulet, 1996). Even if the vegetation composition and pH in the study site resembles poor fens the CH_4 flux is lower than in boreal or arctic fens (Heikkinen et al., 2002b; Saarnio et al., 1997). The areal annual CH_4 flux (5.9 g CH_4 m^{-2} yr^{-1}) was at a similar level to that estimated in Scottish blanket bogs (Chapman and Thurlow, 1996; Hargreaves and Fowler, 1998).

All vegetation communities experience similar seasonal trends in CH_4 fluxes that follows the changes in temperature and the development of vegetation. The varying WT causes oscillation around the trend. The effect of WT is, however, difficult to interpret due to hysteresis, as has also been stated by Moore and Roulet (1993).

8.4 Carbon balance

The large variation in CO_2 and CH_4 fluxes between the vegetation communities is reflected in the C balance of the communities (Fig. 8.1). There is a distinctive difference in C balance between dry (HU, HL) and wet (LL, HO) communities. The dry communities are strong C sinks, while the wet communities, especially, LL act as sources of C into the atmosphere (Fig. 8.1). Correspondingly, the GWP of HU and HL are negative (-272 and -125 g CO_2 eq, respectively) i.e. they have a cooling effect on the atmosphere, whereas LL and HO have a positive GWP (178 and 174 g CO_2 eq, respectively) i.e. they have a warming effect on the atmosphere on a 100-year time frame.

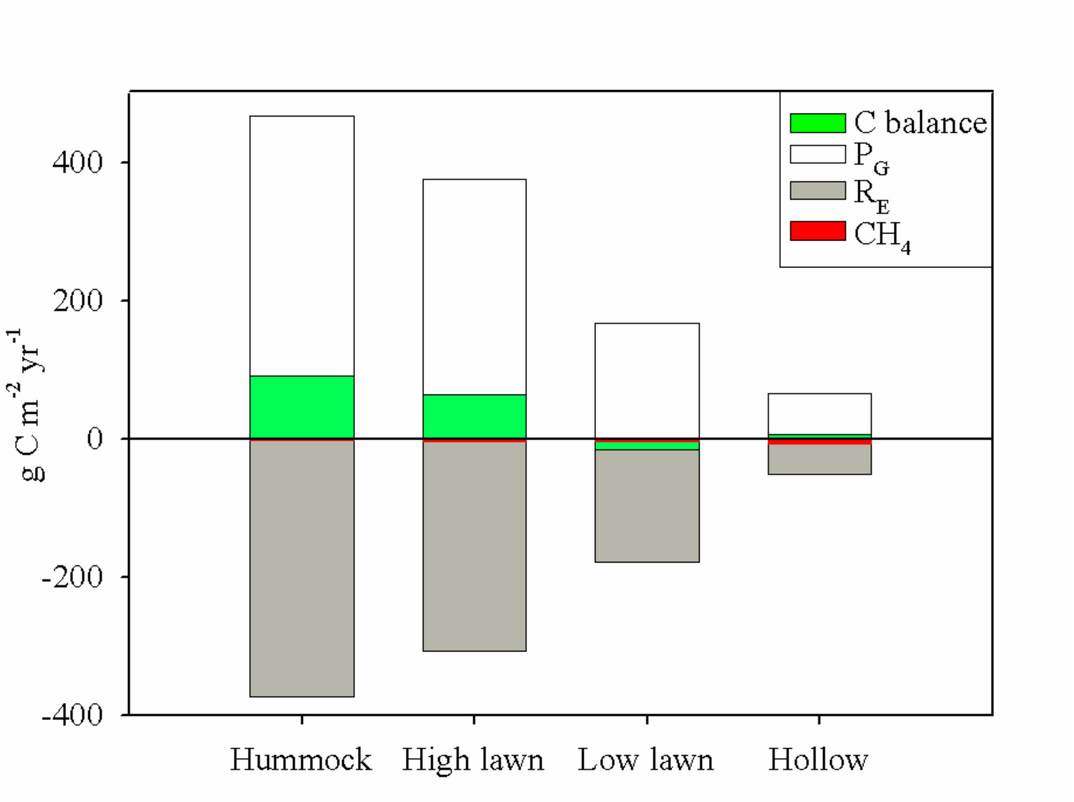

Figure 8.1 The contribution of gross photosynthesis (P_G), ecosystem respiration (R_E) and CH_4 flux to the C balance of each vegetation community. The flux values for each vegetation community are derived from the reconstructed fluxes for the time period October 2003 to September 2004 as described in Chapters 5 and 6.

The areal estimate of the blanket bog C uptake is based on the following surface pattern: hummocks 6%, high lawns 62 %, low lawns 21 % and hollows 11 %. Considering the annual NEE of 80 g C m^{-2} and CH_4 flux of 4.4 g C m^{-2}, the blanket bog is a moderate sink for C. The GWP on a 100-year time frame is –162.9 g CO_2 eq. Compared to the CO_2 flux, the CH_4 flux plays only a small role in the C cycling of a blanket bog. Our estimate includes the gaseous C exchange but excludes the riverine export of dissolved organic carbon (DOC), which is an important component of the peatland C cycle (Moore et al., 1998). In a Scottish peatland catchment the total riverine C export exceeds the NEE (Billett et al., 2004), while in a blanket bog catchment the riverine C export is -37.2 g C m^2yr^{-1}, of which DOC constitutes 9.4 g C m^2yr^{-1} (Worrall et al., 2003). Similar DOC export rates has been measured in Finnish bogs and fens (12.4 and 8 g m^{-2} yr^{-1}, respectively) (Sallantaus, 1992).

8.5 Impacts of changed water level on C fluxes

Since peatlands account for such a large share of global soil C (e.g. Gorham, 1991), any change in their ability to act as sinks for atmospheric CO_2 will play a part in the response of the Earth's system to climate change. The interaction is reciprocal since climate change affects the C uptake in peatlands. The C uptake is most sensitive to changes in water level (Alm et al., 1999b) and for this reason climate change is projected to affect the peatlands via changes in the moisture conditions (Gorham, 1991). In northern peatlands the increase in evapotranspiration is likely to cause a water level drawdown (Roulet et al., 1992). In western Ireland the temperature is projected to increase less, while winter precipitation is projected to increase (Sweeney et al., 2002), therefore the direction of the change in WT is less certain. We simulated the climate change by experimentally raising and lowering the WT of the vegetation communities (HU, HL, LL) in a blanket bog and monitoring C gas exchange for a year (Chapter 6).

The WT drawdown of ~ 10 cm decreases P_G and CH_4 fluxes and increases R_E; consequently the C balance is negative in all vegetation communities (Figure 8.2). The decrease in C uptake is largest in HU, while HL is the community most resilient to the change. The increase in R_E due to WT drawdown has been observed in the field and in the laboratory (Bubier et al., 2003a; Bubier et al., 2003b; Moore and Dalva, 1993; Strack et al., 2006a). Similarly the decrease in CH_4 fluxes due to WT drawdown is well reported (Moore and Dalva, 1993; Roulet et al., 1992; Strack et al., 2004). The impact on P_G has been more complex due to varying responses of vegetation to WT drawdown (Bubier et al., 2003a; Strack et al., 2006b). The GWP on a 100-year time frame was positive after WT drawdown in all vegetation communities (540, 239 and 394 g CO_2 eq in HU, HL and LL, respectively). Our investigation of the effect of changed WT on C fluxes describes the impact on a short (one year) time scale during which the vegetation has not yet adjusted to the changed conditions. On a longer time scale the P_G, in particular, may behave differently: long-term drainage experiments have shown that the productivity of arboreal vegetation reacts positively to WT drawdown (Laiho et al., 2003; Laine et al., 1995) and the C balance may remain positive after drainage (Minkkinen et al., 1999).

The WT rose by ~ 6 cm in all communities due to the flooding treatment. In LL the WT remained above the soil surface throughout the year and also HL was inundated regularly. Flooding decreased P_G and R_E and increased CH_4 flux in all communities (Fig. 8.3). The C balance decreased in HU and HL, but increased in LL. Unlike in the natural conditions, the GWP in 100-year time frame was positive after flooding in HU and HL (15 and 77 g CO_2 eq, respectively) and negative in LL (-184 g CO_2 eq).

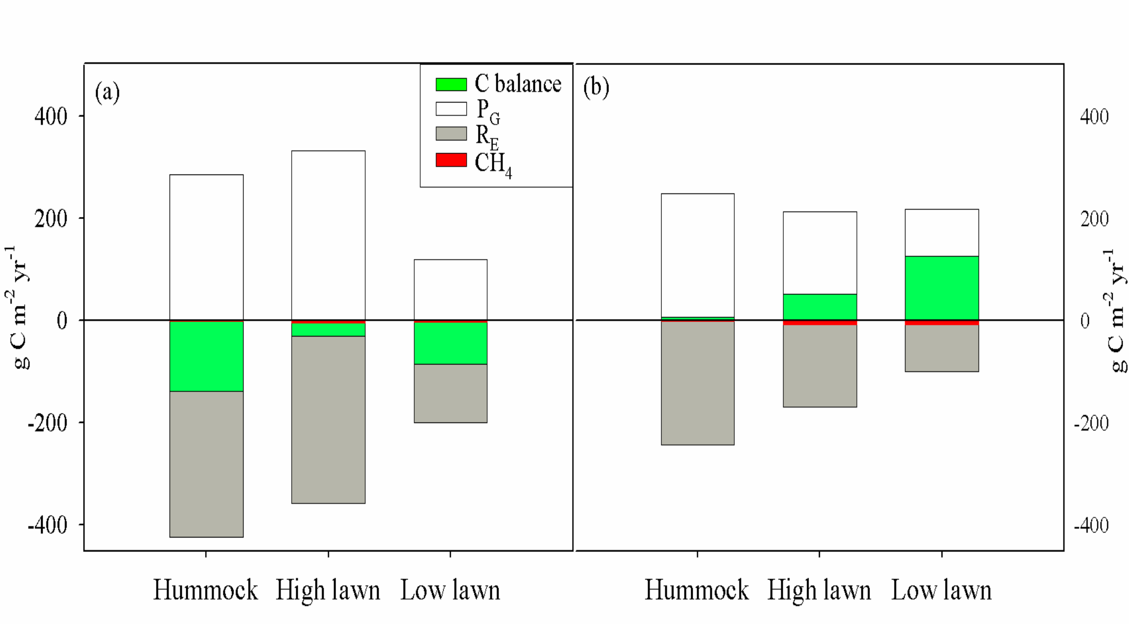

Figure 8.2 The contribution of gross photosynthesis (P_G), ecosystem respiration (R_E) and CH_4 flux to the C balance of each vegetation community after (a) the water level drawdown experiment and (b) the flooding experiment. The flux values for each vegetation community are derived from the reconstructed fluxes for the time period October 2004 to September 2005 as described in Chapter 6.

In pristine peatlands the surface pattern has a strong influence on the C balance, therefore the changing proportion of vegetation communities caused by the WT drawdown or flooding can affect the future C balance. Belyea and Malmer (2004) estimate that the shifts in the surface structure towards both wet and dry, would decrease C accumulation, due to decreased production and increased decomposition, respectively. Similarly, Waddington, et al. (1998) emphasise the importance of changing surface structure but estimate that drying would increase C accumulation, since hummocks are the most efficient C sinks. Our results agree with Waddington, et al. (1998) insofar as in natural conditions the small HU and HL have the highest C uptake and it is likely that an increased cover of these communities will increase the areal C uptake rate. However, the existing hummocks are very sensitive to changes in WT; both WT drawdown and flooding have detrimental effect on their C balance. When considering the C uptake of the present vegetation communities, in accordance with Belyea and Malmer (2004), a decrease in C uptake can be expected if the peatland surface becomes wetter and the cover of LL and HO will increase. However, the flooding increases the C uptake of LL, which in pristine conditions is a source of C. A longer study period and a larger number of sample plots would be needed to comprehend whether the effect is long lasting or if the vegetation composition of inundated LL will change towards the low productivity hollow vegetation. Overall, a long-term study, where the vegetation would have a time to adjust to the changed conditions, would be necessary to understand the long-term effects of changed WT on C fluxes.

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Appendix 1

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