

The short-term effect of altered water level on carbon dioxide and methane fluxes in a blanket bog

Vedenpinnan muutoksen lyhytaikaiset vaikutukset hiilidioksidi- ja metaanipäästöihin peittosuolla

Anna M. Laine, Kenneth A. Byrne, Gerard Kiely, Eeva-Stiina Tuittila

Anna M. Laine, Department of Civil and Environmental Engineering, University College Cork, Cork, Ireland, Department of Biology, University of Oulu, Oulu, Finland, P.O.Box 3000, 90014 University of Oulu; telephone: +358 8 5531521; email: anna.laine@oulu.fi

Kenneth A. Byrne, Department of Life Sciences, University of Limerick, Limerick, Ireland.

Gerard Kiely, Department of Civil and Environmental Engineering, University College Cork, Cork, Ireland.

Eeva-Stiina Tuittila, Peatland Ecology Group, Department of Forest Ecology, University of Helsinki, Helsinki, Finland

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 inhibits 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 (CO₂) and methane (CH₄) fluxes from vegetation communities ranging from hummocks to low lawns in a blanket bog. After a one-year calibration period the water level was both lowered and raised experimentally and the changes in vegetation composition and gas fluxes were monitored during a further year. In all vegetation communities the water level drawdown increased the respiration rate and decreased methane emission; rising water level decreased respiration and increased methane emissions. The effect of altered water level on photosynthesis depended on species composition. Water level drawdown decreased photosynthesis in most communities; rising water level decreased the photosynthesis of hummocks species, and increased the photosynthesis of *Rhynchospora alba*.

Keywords: ecohydrology, drainage, flooding, methane, peatland, photosynthesis, respiration, *Racomitrium*, *Rhynchospora alba*, *Sphagnum*

Introduction

Globally peatlands cover circa 4 million km² (Lappalainen, 1996). Since the last ice age north-

ern peatlands have accumulated 270 to 450 Pg of C in peat (Gorham, 1991; Turunen et al., 2002). This represents ~ 1/3 of the global soil carbon pool (Gorham, 1991). Peatlands play an impor-

tant role in atmospheric C gas concentrations; on one hand they remove carbon dioxide (CO₂) in photosynthesis and on the other hand produce CO₂ and methane (CH₄) in decomposition processes. Although peatlands have acted as long-term C sinks, the C gas dynamics are sensitive to interannual variation 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 & Tallis, 2000). These changes in climate have, however, been modest compared to the changes currently projected (Petit et al., 1999).

The predicted changes for Ireland include (1) warmer temperatures, especially during summers, (2) higher winter and lower summer precipitation and (3) increased occurrence of extreme weather events (storms, drought) (McGrath & Lynch, 2008). While the predictions are comparable to those for northern Europe (Christensen et al., 2007), some delays can be expected due to buffering by the Atlantic Ocean (Sweeney et al., 2002). The changes are expected to be stronger in the midlands and mildest on the west coast (McElwain & Sweeney, 2007).

Blanket bogs are sensitive ecosystems, supported by a high precipitation and water level. Their distribution is restricted to humid regions with cool summers and mild winters (Lindsay et al., 1988). Any change in moisture conditions, whether natural or anthropogenic, may disturb their functioning (Bragg & Tallis, 2001). The C gas fluxes of maritime peatlands, and especially blanket bogs, have received relatively little attention compared to northern continental peatlands. The degree of climate change in the main region of blanket bogs may not be as severe as in continental areas, and due to the increasing rainfall (McElwain & Sweeney, 2007) the water level may even rise. Blanket bogs have developed in very particular climatic conditions; 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, as a result of increased evaporation and decreased summer precipitation (Gorham, 1991). Water level drawdown increases aerobic respiration (Silvola et al., 1996; Bubier et al., 2003b) and decreases CH₄ emission (Roulet et al., 1992; Moore & Dalva, 1993). 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). As concluded by Alm et al., (1999), the increased frequency of dry growing seasons may threaten the C sink function of peatlands. In western Ireland, where the winter precipitation is projected to increase by 10 %, with minor changes in temperature (Sweeney & 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). It has been shown that the vegetation communities respond differently to changing water level conditions (Belyea & Malmer, 2004; Strack & Waddington, 2007). In order to assess the response of peatlands to climate change it is necessary to study the changes at the vegetation community level.

We aim to experimentally study how a moderate change in ecohydrology — water level drawdown and flooding — affects the carbon gas fluxes (CO₂ and CH₄) of different vegetation communities in a blanket bog over a short time period. In the wettest peatland microhabitats water level is typically at the soil surface. At that position even a small change in water level creates an ecologically different situation: flooding or exposing the surface peat to oxygen. We therefore expect the plant communities with water level at the soil surface to respond most readily to water level alterations. We monitored vegetation and C flux components for one year before and one year after the water level experiments were carried out and used regression modelling to integrate the chamber flux measurements over the study period.

Material and methods

Site description

The study site was located in an extensive low-land 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 described in detail by Sottocornola et al. (2009). The study site was established in June 2003 when 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 CO₂ and CH₄ 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.

Following a calibration period from June 2003 to September 2004, the water level (WL) experiments were initiated. Sample plots HU4, HU5, HL1, HL5, LL1 and LL6 were surrounded by a narrow drainage ditch in order to decrease the WL (Fig. 1). These six plots form the WL drawdown experiment. The excess water was directed to flow towards the lower lying plots HU3, HU6, HL3, HL6, LL2 and LL3 (Fig. 1). A dam was constructed below these sample plots in order to retain the runoff and raise the water level. Due to the proximity of the drainage ditch, the WL did not rise in plots HU6, HL6 and LL2 and they were excluded from the data analysis, this left only three sample plots for the flooding experiment. The remaining six sample plots formed the control site (Fig. 1).

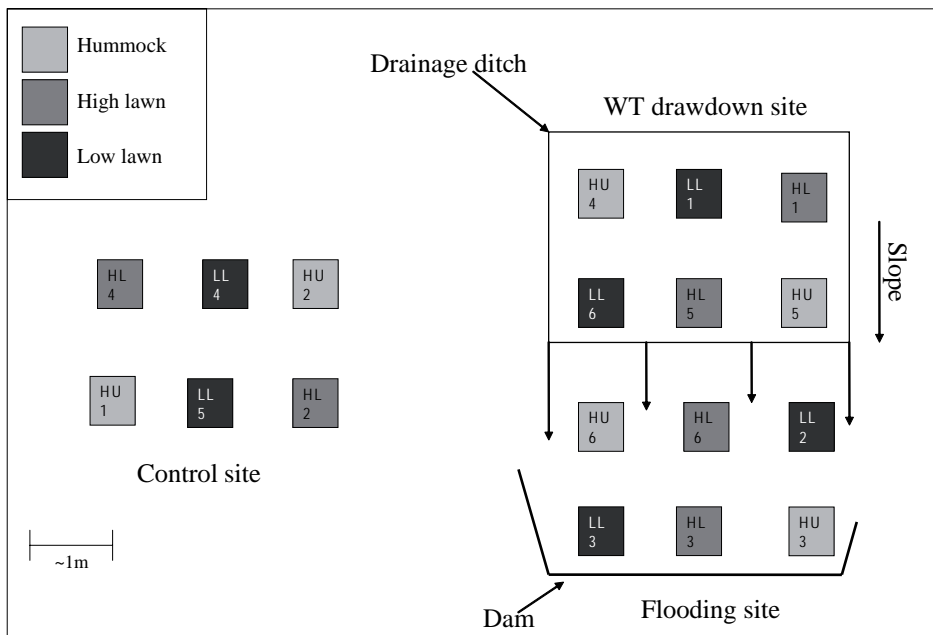


Figure 1. Experimental design used to study the short term effect of altered water level on carbon gas fluxes of different microforms in a blanket bog. The downward direction of the slope is shown by an arrow. Water level drawdown treatment was achieved by digging a ditch around the site, the flooding treatment by leading the water from the ditch to the flooding site that was located downwards along the slope and surrounded by a dam. Treatments were applied after a calibration year.

Kuva 1. Koejärjestely vedenpinnan muutoksen lyhytaikaisten vaikutusten tutkimiseksi peittosuon eri pienmuodoilta. Rinteen laskusuunta on esitetty nuolella. Vedenpinta alennettiin kaivamalla matala oja koealaan kuuluvien näytealojen ympärille. Tulvituskoalan vedenpintaa nostettiin johtamalla ojien vesi alajuoksulla olevalle koealalle, näytealojen alapuolelle rakennettiin pato. Vedenpinnankäsittelykoe toteutettiin kalibrointivuoden jälkeen.

Gas flux measurements

CO₂ exchange measurements

Carbon dioxide exchange measurements were carried out at weekly intervals from July 2003 until September 2005. Measurements were made using a closed transparent plexiglass chamber ($0.6 \times 0.6 \times 0.33$ m). The chamber was vented and included a cooling system (Alm et al., 1997). The CO₂ concentration inside the chamber was monitored with a portable infrared gas analyser (EGM-4, PP Systems, UK). 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). For a detailed description of the method see Laine et al. (2006).

CH₄ flux measurements

Methane measurements were carried out at bi-weekly to monthly intervals during the period August 2003 to September 2005 using a closed chamber method (Saarnio et al., 1997). Four air samples were taken 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. Flux rate ($\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) was calculated as a linear rate of change in gas concentration with time. For a detailed description of the method see Laine et al. (2007b).

Environmental measurements

To relate the gas fluxes to prevailing environmental conditions, the photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{ s}^{-1}$) was recorded simultaneously with NEE readings using a quantum sensor (PAR-1, PP-Systems, UK). Air temperature inside the chamber was recorded simultaneously with CO₂ and CH₄ flux measurements. Water level 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, was estimated at biweekly to monthly intervals. We counted the number of leaves of each species from five subplots within sample plots, and measured the species specific leaf size from marked individuals outside the sample plots following the method described in Wilson et al. (2007). 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 models see Laine et al. (2006). Plant species composition was determined for each sample plot in July of 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 variables (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 WL measurements made during gas flux measurements was used to derive a continuous time series of daily WL for each sample plot. Daily VGA was estimated for each sample plot using the GA models of each species (see Laine et al., 2006).

Modelling of gas fluxes

CO₂ exchange components

We constructed CO₂ 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) and Laine et al. (2007a). Gross photosynthesis 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 WL, which represented the major difference between the years, was not included in the models. Ecosystem respiration (R_E) consists of soil and plant respiration, which are both affected by temperature and WL. We related R_E to air temperature (T_{AIR}) using an exponential relationship described by Lloyd and Taylor (1994). In our study the WL fluctuation remained modest, and we therefore observed a linear relationship between R_E and WL. 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. For a description of the model see Laine et al. (2007a).

CH₄ fluxes

CH_4 fluxes were related to soil temperature at 20 cm depth (T_{20}) and WL using exponential and linear sub-models, respectively. Vascular green area (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 both the calibration and experimental years. For a description of the model see Laine et al. (2007b). All flux modelling was carried out using SPSS 12.0.1 for Windows statistical package (SPSS, Inc.).

Reconstructing annual fluxes

The models — individually parameterised for each sample plot and in the case of P_G for the calibration and experimental years separately — 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 series of environmental variables described above. 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.

Results

Environmental conditions

Average T_{AIR} was 10.4 and 10.6 °C and 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 (WL) followed the same pattern in all sample plots during the calibration and experimental years (Fig. 2). During the calibration year, WL was on average –14, –5 and –1 cm below the soil surface in hummocks, high lawns and low lawns, respectively. In the control site, the difference in mean WL between the calibration and experimental years was negligible. The WL drawdown experiment lowered WL 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 WL by 6 cm in HU3, HL3 and LL3.

Changes in vegetation

The maximum VGA was highest in high lawns and lowest in low lawns (Table 1). 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 WL drawdown site (Table 1). The moss cover did not change significantly during the study period.

Changes in gross photosynthesis (P_G)

The average annual P_G in the calibration year was 467 (32), 376 (21), and 167 (20) g CO₂-C m⁻² (n = 5, SE in brackets) in hummocks, high lawns and low lawns, respectively. In the experimental year the average annual P_G was 505 (61), 434 (15) and 171 (11) g CO₂-C m⁻² (n = 2, SE in brackets) in the control site hummocks, high lawns and low lawns, respectively.

Gross photosynthesis (P_G) of the vegetation communities was at a similar level in the WL drawdown and control sites during the calibra-

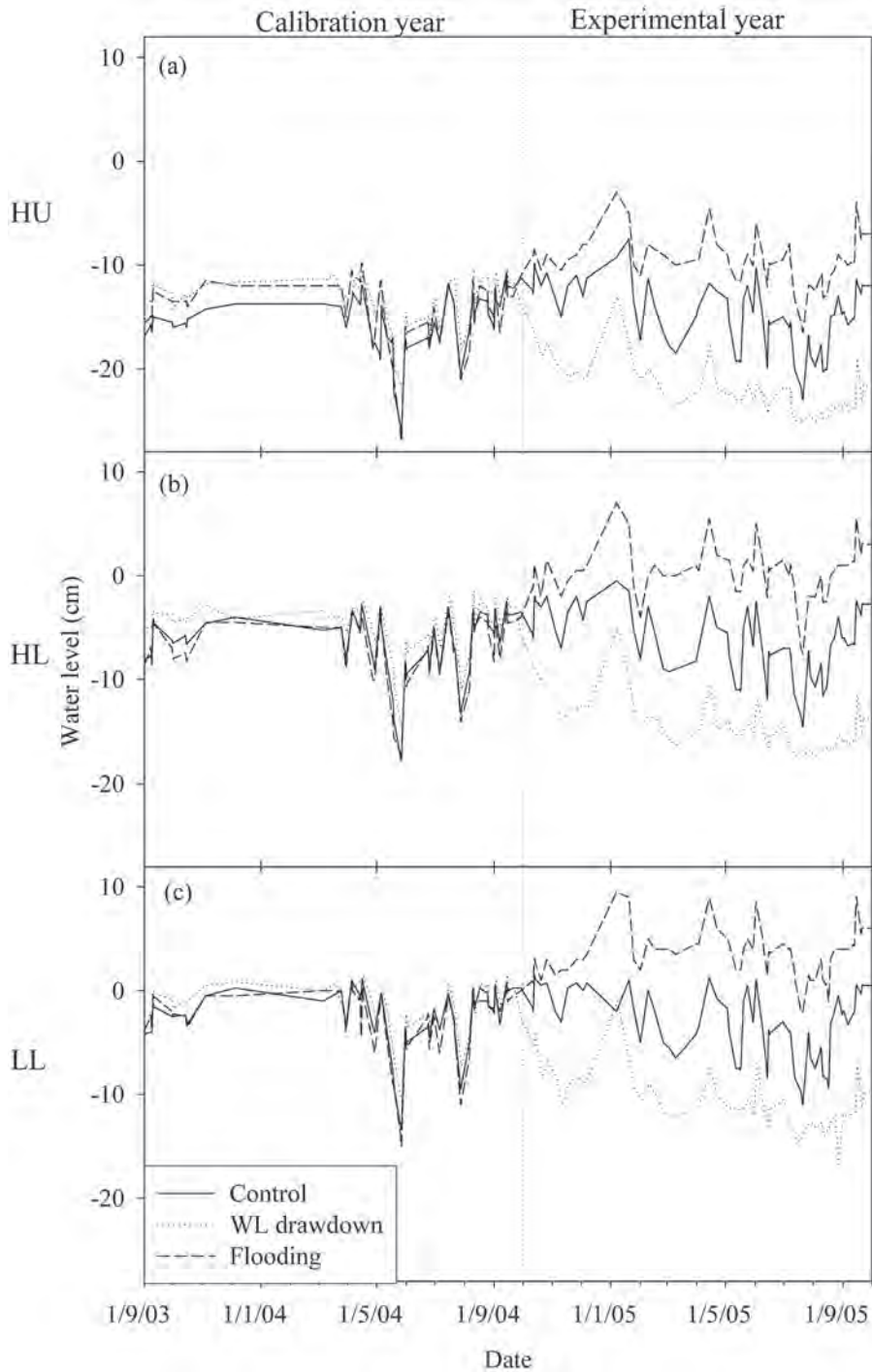


Figure 2. Variation in water level (WL) in (a) hummocks, (b) high lawns and (c) in low lawns in the control, WL draw-down and flooding experimental sites during the calibration and experimental years.

Kuva 2. Vedenpinnan (WL) vaihtelu (a) mäntäillä (HU), (b) korkeilla välipinnoilla (HL) ja (c) matalilla välipinnoilla (LL) kontrolli-, vedenpinnan lasku- ja tulvituskoelaitoilla kalibrointi- ja koevuoden aikana.

tion year (Figures 3 and 4). The WL drawdown decreased the weekly flux rates noticeably in hummocks and low lawns, whereas in high lawns the decrease was small (Fig. 4). The decrease in P_G was most noticeable during summertime, while during winter the fluxes were similar in both sites. The average annual P_G in the WL drawdown sites during the experimental year was 286 (110), 333 (71) and 119 (54) g CO₂-C m⁻² (n = 2, SE in brackets) in HU, HL and LL, respectively. The sample plots responded individually to the WL drawdown (Fig. 5a). The annual flux decreased strongly in HU5, while HU4 and HL1 were not affected by the WL drawdown and the absolute decrease was moderate also in HL5, LL1 and LL6. Proportionally the change was, however, most noticeable in LL6 that had initially the smallest flux rate (Fig. 5a).

The weekly P_G was similar in the control and flooding sites during the calibration year (Fig. 4). Flooding decreased the weekly P_G in hummocks and high lawns (Fig. 4a and b). In high lawns the flux was lower throughout the experimental year (Fig. 4b), while in hummocks the change was more noticeable during summer (Fig. 4a). In low lawns the flux rates increased due to flooding after mid July (Figs. 3c and 4c) when the VGA reached its maximum. Flooding decreased the annual P_G in hummocks and high lawns but did not affect it in low lawns (Fig. 5a). The average annual P_G in the experimental year was 249, 213 and 218 g CO₂-C m⁻² (n = 1) in HU, HL and LL, respectively.

Changes in ecosystem respiration (R_E)

The average annual R_E in the calibration year was -373 (22), -308 (19) and -179 (20) g CO₂-C m⁻² (n = 5, SE in brackets) in hummocks, high lawns and low lawns, respectively. In the experimental year the annual fluxes were slightly higher, with the average fluxes being -410 (74), -320 (33) and -210 (4.8) g CO₂-C m⁻² yr⁻¹ (n = 2, SE in brackets) in the control site hummocks, high lawns and low lawns, respectively.

During the calibration year the level of R_E was similar in the control and WL drawdown sites, except in low lawns, where the WL drawdown site had originally lower fluxes than the control site (Figs. 3 and 4). The increase in the integrated weekly flux in the WL drawdown site was modest, and the low lawns in the control site retained higher fluxes still in the experimental year (Fig. 4). The effects of WL drawdown on the annual R_E flux were similar in all vegetation communities (Fig. 5b). Proportionally the change was, however, largest in the wettest sample plot LL6. The average annual R_E in the WL drawdown site during the experimental year was -423 (33), -358 (52) and -200 (48) g CO₂-C m⁻² (n = 2, SE in brackets) in hummocks, high lawns and low lawns, respectively.

During the calibration year the integrated weekly fluxes were similar in the control and flooding sites (Figs. 3 and 4). During the experimental year the flooding clearly decreased the weekly R_E in all vegetation communities (Fig. 4). The effects of flooding on annual R_E flux

Table 1. The maximum vascular green area (VGA) (standard error in parentheses) in hummocks, high lawns and low lawns of control, water level (WL) drawdown and flooding experimental sites in summer of 2004 (calibration year) and 2005 (experimental year).

Taulukko 1. Putkilokasvien maksimilehtiala (VGA) (suluissa estimaatin keskivirhe) määrittäällä (HU), korkeilla välipinnoilla (HL) ja matalilla välipinnoilla (LL) kontrolli-, vedenpinnan lasku- ja tulvituskoelaitteilla kesällä 2004 (kalibraatiovuosi) ja kesällä 2005 (koevuosi).

	Control		WL 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

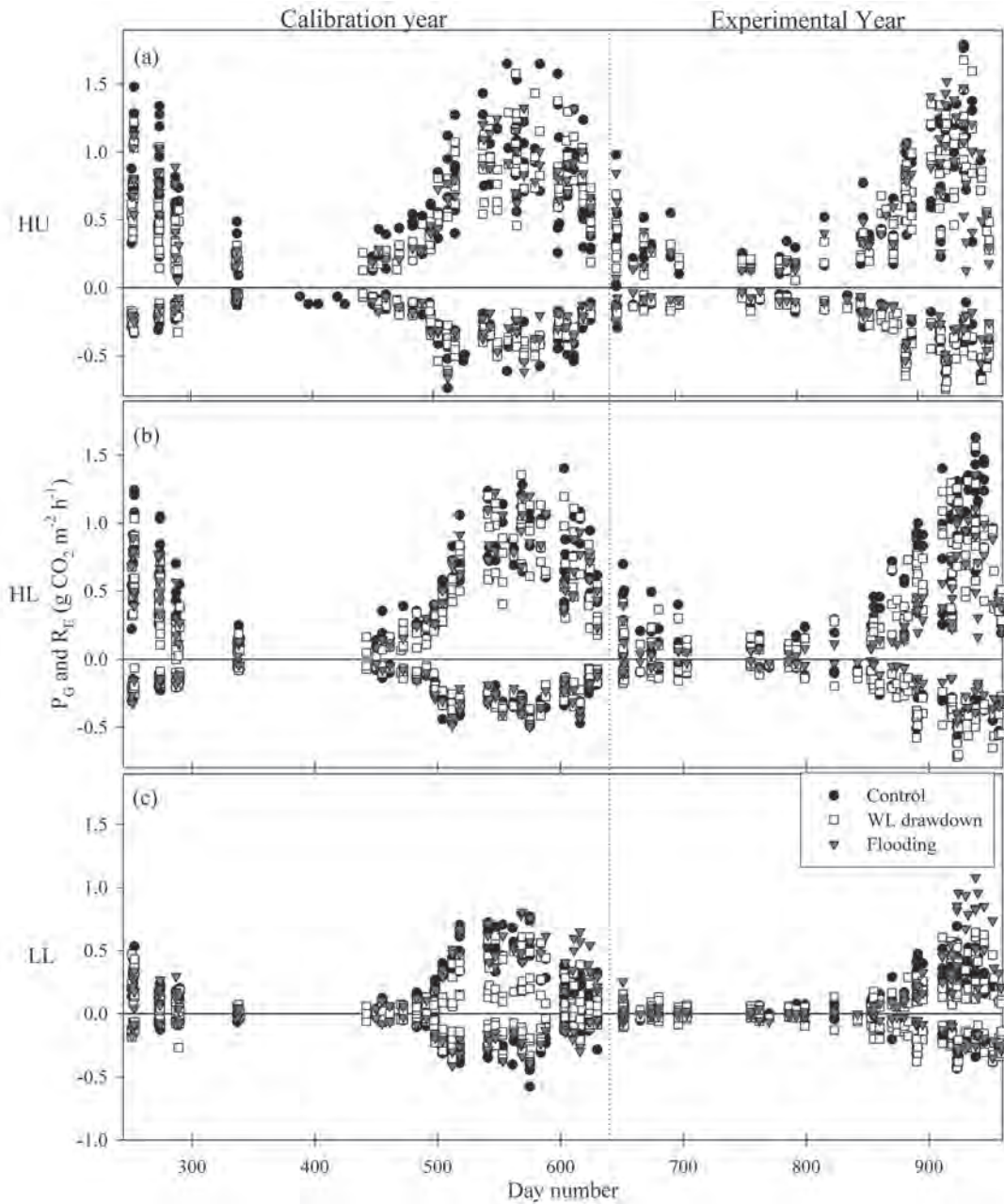


Figure 3. Measured gross photosynthesis (P_G) and ecosystem respiration (R_E) fluxes in (a) hummocks, (b) high lawns and (c) low lawns in the control, WL drawdown and flooding experimental sites during the calibration and experimental years. Measurements started at September 2003 (day number 244) and were continued until October 2005. Positive values indicate a flux from atmosphere to ecosystem.

Kuva 3. Mitatut bruttofotosynteesi- (P_G) ja ekosysteemirespiraatiovuot (R_E) (a) mättäillä (HU), (b) korkeilla välipinnoilla (HL) ja (c) matalilla välipinnoilla (LL) kontrolli-, vedenpinnan lasku- ja tulvituskoealoilla kalibrointi- ja koevuoden aikana. Mittaukset alkoivat syyskuussa 2003 (päivänumero 244) ja jatkuivat lokakuuhun 2005 asti. Positiiviset arvot tarkoittavat kaasuvuota ilmakehästä ekosysteemiin.

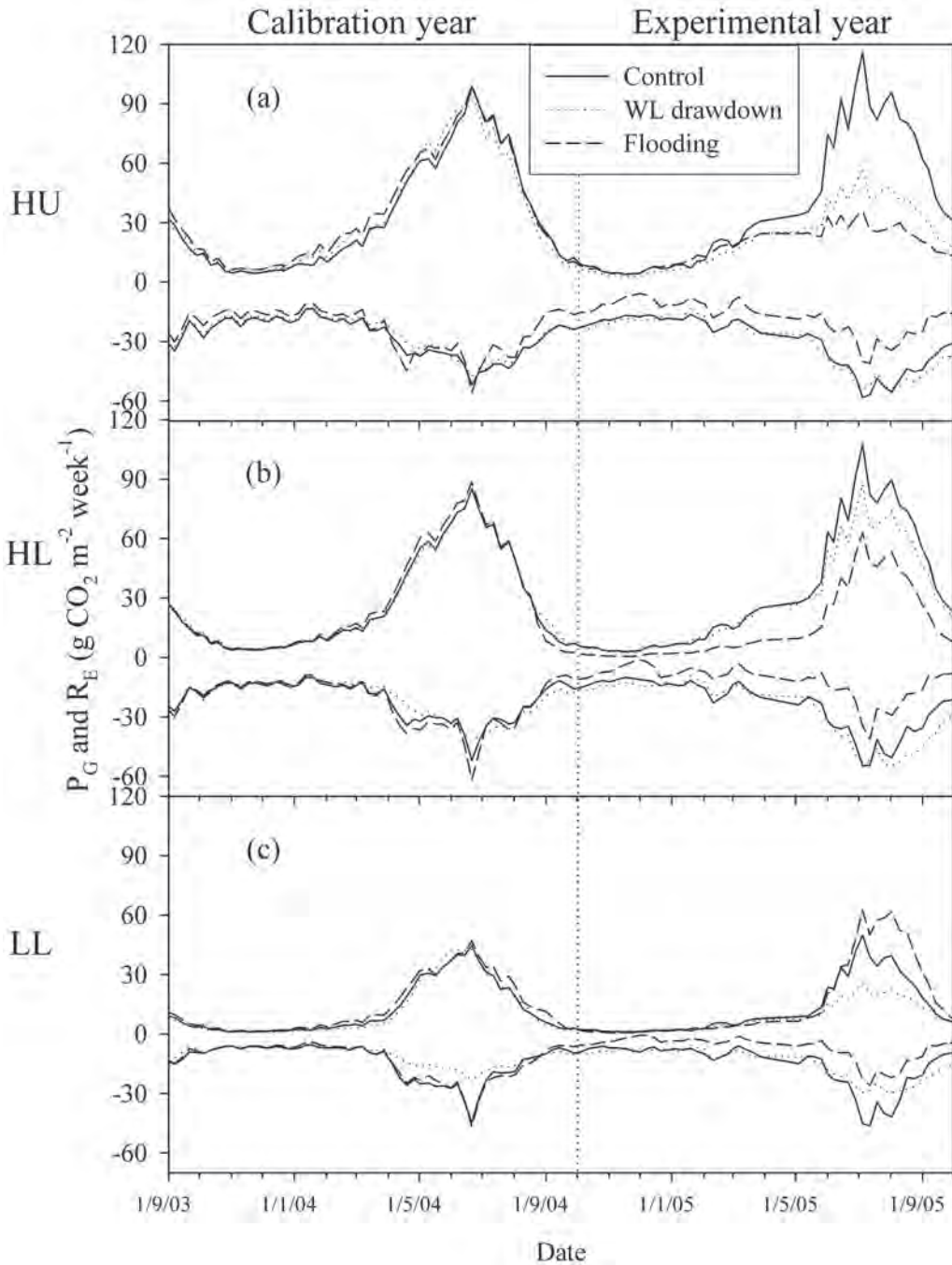


Figure 4. Weekly, modelled gross photosynthesis (P_G) and ecosystem respiration (R_E) in (a) hummocks, (b) high lawns and (c) low lawns in the control, WL drawdown and flooding experimental sites during the calibration and experimental years

Kuva 4. Viikoittainen, mallinnettu bruttofotosynteesi (P_G) ja ekosysteemirespiraatio (R_E) (a) mäntäillä (HU), (b) korkeilla välipinnoilla (HL) ja (c) matalilla välipinnoilla (LL) kontrolli-, vedenpinnan lasku- ja tulvituskoaloilla kalibrointi- ja koevuoden aikana.

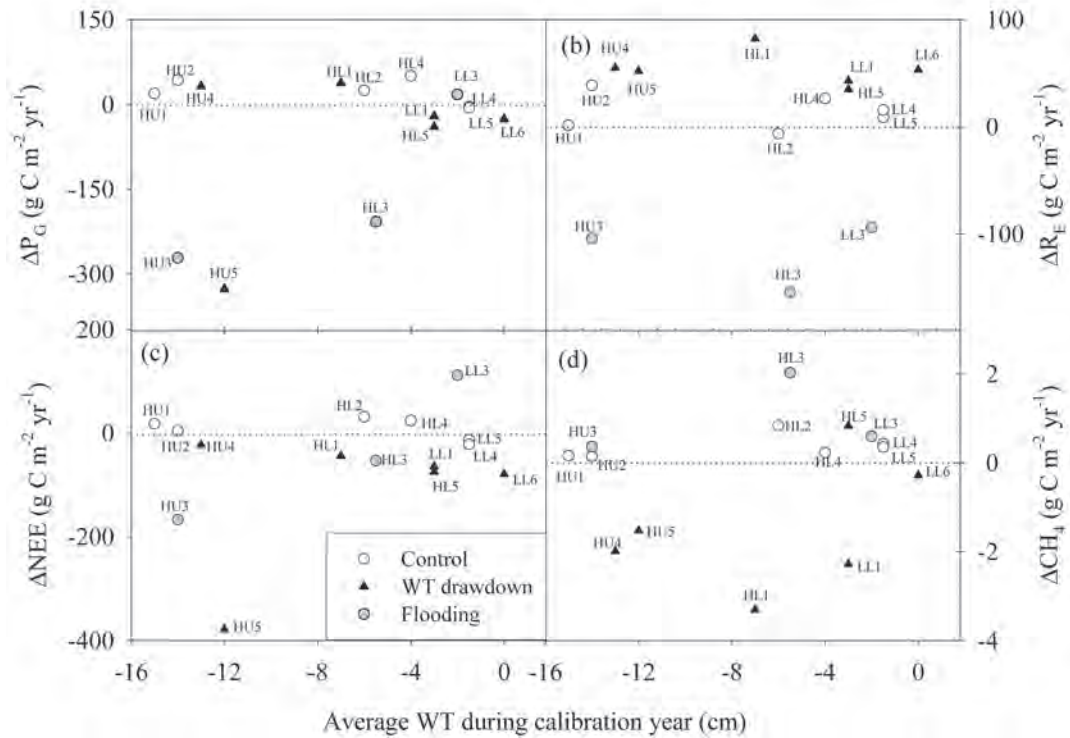


Figure 5. The change in the annual (a) gross photosynthesis (P_G), (b) ecosystem respiration (R_E), (c) net ecosystem CO_2 exchange (NEE) and (d) CH_4 flux between the calibration and experimental years relative to the average WL of the sample plots in the calibration year. The zero line indicates no change, positive values indicate an increase and negative values a decrease in flux rates between the calibration and experimental years. Plots HU1, HU2, HL2, HL4, LL4 and LL5 belong to the control site; plots HU4, HU5, HL1, HL5, LL1 and LL6 belong to the WL drawdown experiment; plots HU3, HL3 and LL3 belong to flooding experiment.

Kuva 5. Muutos vuosittaisessa (a) bruttofotosynteesissä (P_G), (b) ekosysteemi-irespiraatiassa (R_E), (c) ekosysteemin CO_2 :n nettovaihdossa (NEE) ja (d) CH_4 vuossa kalibraatio- ja koevuoden välillä suhteutettuna kunkin näytealan kalibraatiovuoden keskivedenpintaan. Nollataso tarkoittaa 'ei muutosta', positiivinen arvo tarkoittaa kaasuvuon kasvua ja negatiivinen arvo tarkoittaa kaasuvuon pienentymistä vuosien välillä. Näytealat HU1, HU2, HL2, HL4, LL4 ja LL5 kuuluvat kontrollialaan; näytealat HU4, HU5, HL1, HL5, LL1 ja LL6 kuuluvat vedenpinnanlaskukoealaan; näytealat HU3, HL3 ja LL3 kuuluvat tulvituskoeealaan.

were similar in all vegetation communities (Fig. 5b), proportionally the change was largest in the wettest sample plots where fluxes were originally small. The average annual R_E in the experimental year was -243 , -168 and -100 $\text{g CO}_2\text{-C m}^{-2}$ ($n = 1$) in hummocks, high lawns and low lawns, respectively.

Changes in net ecosystem CO_2 exchange (NEE)

Net ecosystem exchange, i.e. the difference between P_G and R_E , was highest in hummocks

and lowest in low lawns, with annual fluxes of 94 (23), 68 (22) and -11.6 (5) $\text{g CO}_2\text{-C m}^{-2}$ ($n = 5$, SE in brackets) in hummocks, high lawns and low lawns, respectively in the calibration year. In the control site the rate of NEE was quite similar during the calibration and experimental years in all sample plots. During the experimental year the average annual fluxes in the control site were 95 (12), 114 (49) and -40 (7) $\text{g CO}_2\text{-C m}^{-2}$ ($n = 2$, SE in brackets) in hummocks, high lawns and low lawns, respectively. We use the ecological sign convention, in which the positive NEE value

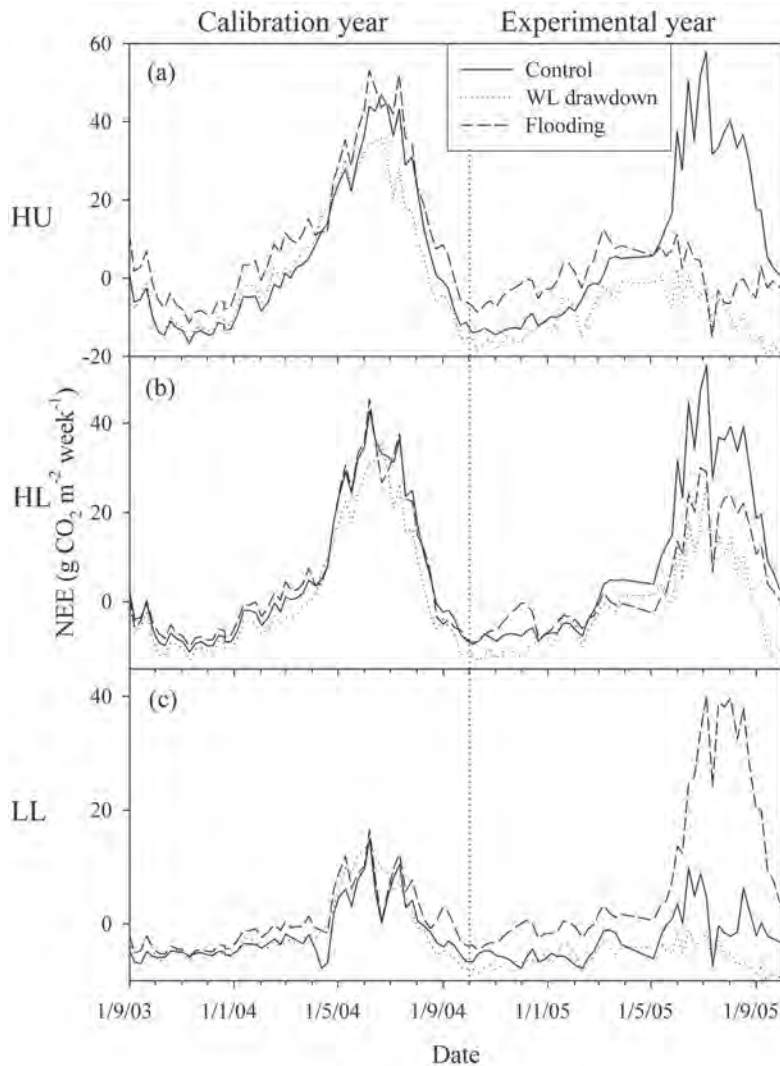


Figure 6. Weekly net ecosystem exchange (NEE) in (a) hummocks, (b) high lawns and (c) in low lawns in the control, WL drawdown and flooding experimental sites during the calibration and experimental years.

Kuva 6. Viikoittainen ekosysteemi nettovaihto (NEE) (a) mäntäillä (HU), (b) korkeilla välipinnoilla (HL) ja (c) matalilla välipinnoilla (LL) kontrolli-, vedenpinnan lasku- ja tulvituskoeloilla kalibrointi- ja koevuoden aikana.

indicates a flux from atmosphere to ecosystem (i.e. ecosystem being a sink of CO_2)

During the calibration year the integrated weekly NEE was at a similar level in the control and WL drawdown sites (Fig. 6). The WL drawdown decreased NEE in all vegetation communities, and the decrease was most noticeable during summer (Fig. 6). After water level drawdown all

vegetation communities were sources of CO_2 to atmosphere with the average annual fluxes of -137 (143), -25 (19) and -81 (7) $\text{g CO}_2\text{-C m}^{-2}$ ($n = 2$, SE in brackets) in hummocks, high lawns and low lawns, respectively in the experimental year. The annual NEE was lower in most sample plots during the experimental year; similarly to P_G the NEE of HU4 was unchanged while the

decrease was strong in HU5 (Fig. 5c). Proportionally the change was largest in low lawn plots that initially had the lowest flux rates and acted as sources of CO₂.

The integrated NEE was similar in the flooding and control sites during the calibration year (Fig. 6). The vegetation communities responded differently to the flooding experiment. The flooding increased the wintertime NEE in hummock and low lawn plots (Fig. 6a, c). During summer the hummocks and high lawns were smaller CO₂ sinks in the flooded plots than in the control plots (Fig. 6a, b). In low lawns, flooding greatly increased the summertime NEE (Fig. 6c) shifting them to CO₂ sinks. The annual flux rate decreased most in the hummocks (Fig. 5c); proportionally the decrease was similar in hummocks and high lawns. The average annual fluxes during the experimental year were 6, 45 and 118 g CO₂-C m⁻² (n = 1) in hummock, high lawn and low lawn, respectively.

Changes in CH₄ flux

The average annual CH₄ fluxes in the calibration year were -5.0 (1.2), -4.7 (0.9) and -2.4 (0.4) g CH₄-C m⁻² (n = 5, SE in brackets) in low lawns, high lawns and hummocks, respectively. The annual fluxes in the control site during the experimental year were on average -4.8 (2.7), -3.3 (1.8) and -2.9 (0.2) g CH₄-C m⁻² (n = 2, SE in brackets) in low lawns, high lawns and hummocks, respectively. Negative values indicate a flux from ecosystem to atmosphere.

During the calibration year the WL drawdown site had higher CH₄ efflux rates in hummocks and high lawns than the control site, while in low lawns the fluxes were at a similar level (Figs. 7 and 8). In hummocks the weekly CH₄ flux decreased strongly after WL drawdown (Figs. 7a and 8a). In high lawns the flux was still higher than in the control site, but the difference between the sites was smaller, indicating decreased flux due to the WL drawdown (Fig. 8b). In low lawns the fluxes in the control and WL drawdown sites remained quite similar also during the experimental year (Fig. 8c). The WL drawdown experiment caused a similar decrease in the annual fluxes in most of the sample plots (Fig. 5d). Exceptions were

HL5 and LL6; in HL5 the flux rate increased after WL drawdown (-7 cm), while in LL6 the fluxes were similar in both years. The average annual fluxes in the experimental year were -3.0 (0.3), -4.8 (2.8) and -1.1 (0.0) g CH₄-C m⁻² (n = 2, SE in brackets) in low lawns, high lawns and hummocks, respectively.

Flooding increased CH₄ fluxes in all vegetation communities. The flooded hummock had lower CH₄ fluxes in the calibration year compared to the control site (Fig. 7a). In the experimental year the flux in the flooded hummock increased, but remained lower than the flux in the control site hummocks (Figs. 7a and 8a). The high and low lawns of the control site had a lower flux in the calibration year than those in the flooded site, this difference increased during the experimental year (Fig. 8b, c). The average annual fluxes in the flooded site during the experimental year were -8.2, -7.9 and -1.2 g CH₄-C m⁻² (n = 1) in low lawn, high lawn and hummock, respectively. The flooding increased the annual flux most in HL3, while in HU3 and LL3 the flux remained quite unaltered (Fig. 5d). The percentage increase was, however, largest in HU3 that had a relatively low flux rate during the calibration year.

Discussion

Impacts of water level drawdown

In this study the WL drawdown decreased NEE in all vegetation communities, with the strongest decrease in hummocks and low lawns. The changes in NEE have been linked with increased R_E due to thicker aerobic peat layer (Bubier et al., 2003a; Bubier et al., 2003b; Strack et al., 2006a). In our study the WL drawdown of 7 to 10 cm increased R_E by 10 to 50 %. The effect of WL drawdown on photosynthesis appeared to be more complex, different vegetation communities responding differently as also noted by Bubier et al., (2003a) and Strack et al. (2006b). Similarly to Strack and Waddington (2007) we found community specific responses of P_G on WL drawdown. In hummocks and low lawns the decrease in NEE after WL drawdown was caused by decreased P_G rather than increased R_E. In high lawns the

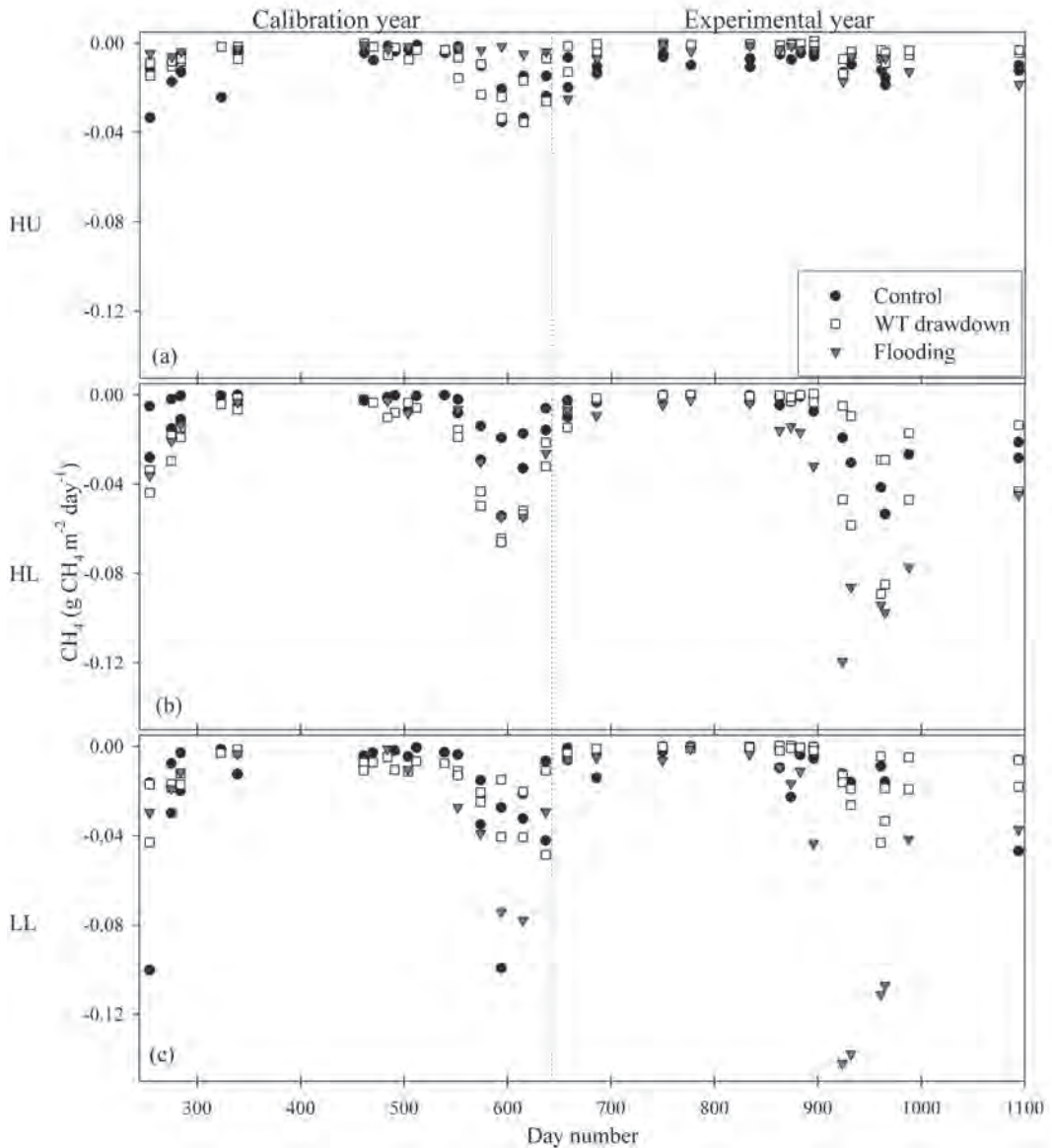


Figure 7. Measured methane (CH_4) flux in (a) hummocks, (b) high lawns and (c) in low lawns in the control, WL drawdown and flooding experimental sites during the calibration and experimental years. Negative values indicate flux from ecosystem to atmosphere.

Kuva 7. Mitatut metaani (CH_4) vuot (a) mätävillä (HU), (b) korkeilla välipinnoilla (HL) ja (c) matalilla välipinnoilla (LL) kontrolli-, vedenpinnan lasku- ja tulvituskoeloilla kalibrointi- ja koevuoden aikana. Negatiiviset arvot tarkoittavat kaasuvuota ekosysteemistä ilmakehään.

decrease in NEE was caused equally by a moderate decrease in P_G and a small increase in R_E . As the moss species composition varied within the vegetation communities, the plots had somewhat

individualistic responses to WL drawdown. The most contrasting was the response of P_G to WL drawdown in the two hummock plots. Plot HU4, which is dominated by *Racomitrium lanugino-*

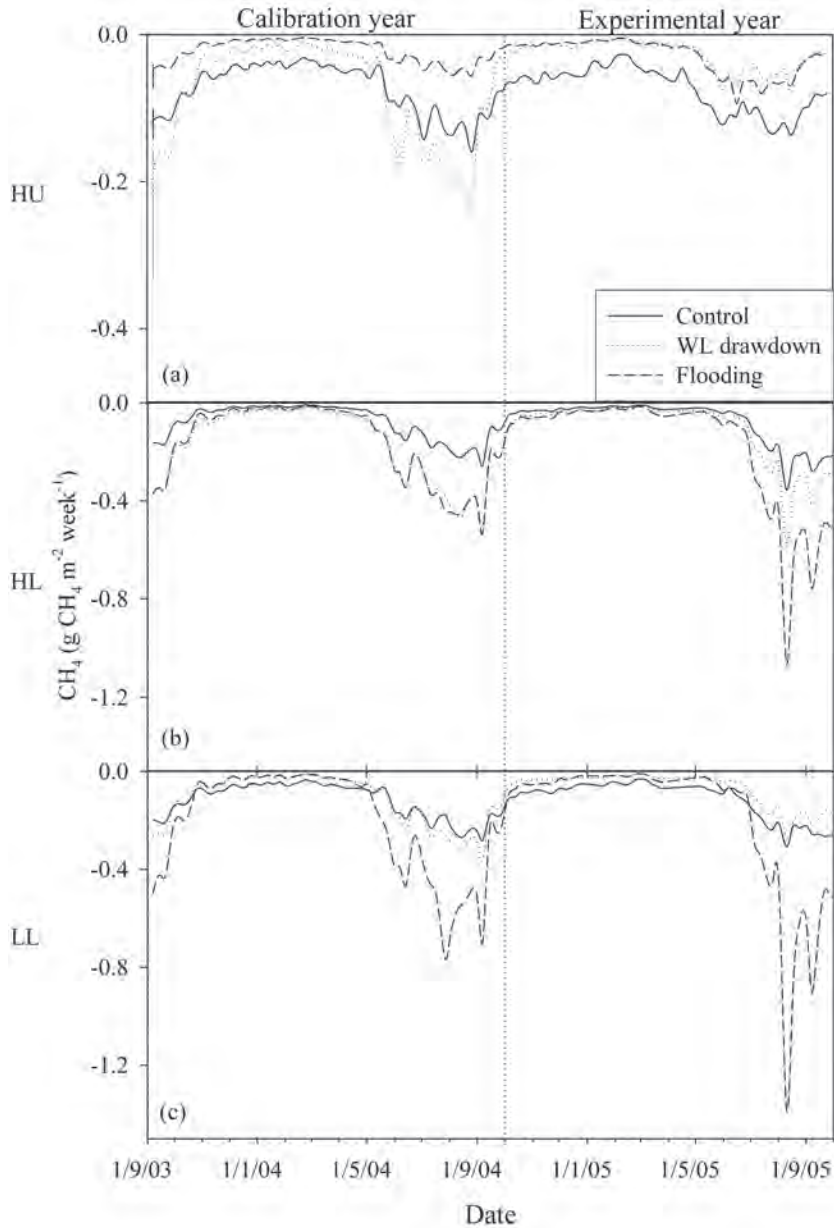


Figure 8. Weekly modelled methane (CH_4) emission in (a) hummocks, (b) high lawns and (c) in low lawns in the control, WL drawdown and flooding experimental sites during the calibration and experimental years.

Kuva 8. Viikoittainen, mallinnettu metaanivuo (CH_4) (a) mättäillä (HU), (b) korkeilla välipinnoilla (HL) ja (c) matalilla välipinnoilla (LL) kontrolli-, vedenpinnan lasku- ja tulvituskoealoilla kalibrointi- ja koevuoden aikana.

sum, had similar P_G before and after the drainage, while in the *Sphagnum rubellum* dominated plot HU5 the P_G strongly decreased. *R. lanuginosum*

occurs across a wide range of WL depths (2 to 60 cm below surface) and is often associated with the highest hummocks in blanket bogs (Ratcliffe &

Walker, 1958), it is also known as a desiccation-tolerant species and rapidly recovers photosynthesis after remoistening (Proctor & Smirnov, 2000). In addition, it shows long-term survival at low water contents (Proctor, 2000). The buffering role of *R. lanuginosum* was evident in the two high lawn plots, as well. The moss cover was higher in HL1, whose P_G suffered less from the WL drawdown. Apparently, the individualistic responses of plant species to WL drawdown have fundamental impact on the rate of photosynthesis in changing hydrological conditions. Water level drawdown affected the CO_2 exchange only during the growing season, while during winter, cool and wet conditions retained the fluxes in equally low levels in all sites.

Water level drawdown decreased CH_4 emissions from 9 to 60% depending on vegetation community in all but one sample plot. Similar decrease has been observed in other studies (Roulet et al., 1992; Moore & Dalva, 1993). According to Freeman et al. (2002) the decrease in flux rate is more due to reduced CH_4 production caused by the vegetation change that alters the substrate flux to the anoxic layer, than increased oxidation of CH_4 . WL 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; in addition, there was no drastic change in plant community composition able to explain the decreased CH_4 flux rates in WL drawdown site. Therefore, our result supports the hypothesis of increased oxidation of CH_4 due to a thicker oxic peat layer rather than reduced CH_4 production due to changes in vegetation.

During the calibration year the C gas budget ($NEE - CH_4$ flux) was negative (source of C) only in the low lawns. After WL drawdown the budget became negative in all communities, the decrease was largest in hummocks and least in high lawns. The observed changes in gas fluxes are likely to be caused by WL drawdown, since the weather conditions (precipitation, air temperature, PPF) were otherwise similar during the calibration and experimental years. In addition, the fluxes in the control site did not change in similar manner between the years.

Impacts of flooding

Our experiment raised the water level by 6 cm, which meant regular inundation for lawn plots. Flooding decreased R_E in all vegetation communities. Respiration rates are clearly reduced when water level is located above the surface (Chimner & Cooper, 2003), as was the case in the flooded high and low lawns. In hummock the decrease in P_G after flooding was large enough to decrease NEE, despite the decrease the hummock still remained a weak CO_2 sink. The decrease in P_G can be explained with the declined VGA after flooding; the ericoid shrubs, typical of hummocks, suffered severely from the flooding. In high lawn the decrease in NEE was smaller since the changes in P_G and R_E counter balanced each other. In low lawns NEE increased after the flooding; in winter NEE was higher due to the decreased R_E and in summer the high P_G further increased the flux. Therefore, low lawn shifted to a CO_2 sink. Correspondingly, the VGA in low lawn was 14% higher during the experimental year than during the calibration year. Similarly, in restored peatlands previously drained for forestry, the response of P_G to rewetting depended on vegetation. Shrubs (*Calluna vulgaris*) suffered and sedges (*Eriophorum vaginatum*) benefited from rewetting (Komulainen et al., 1999).

The flooding increased CH_4 efflux rates in all vegetation communities. Impacts of in situ flooding on CH_4 emissions have been studied very little, but our findings are in line with those of Turetsky et al. (2008). In the hummock where the VGA declined after flooding the higher flux rate is likely due to decreased oxidation of CH_4 . In the lawns, in addition to the direct effect of higher WL, the higher VGA of sedges may have increased CH_4 production by enhancing the substrate supply and also the amount of plant mediated CH_4 transport. Increased CH_4 efflux was observed also after rewetting of a cut-away peatland; similarly the increase was accelerated by sedges (Tuittila et al., 2000). While hummocks and high lawns remained C sinks after flooding, the decrease in the C gas budget was larger in hummocks than in high lawns. While the control low lawns were sources of C, the flooding increase their C-budget, turning them into C sinks.

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. Since R_E and CH_4 fluxes are more directly linked with WL than P_G , this study gives quite adequate prediction regarding the long-term changes in these effluxes. Changes in vegetation structure are likely to affect R_E and CH_4 fluxes, in terms of substrate supply and transport pathway, P_G , however, is more directly coupled with vegetation structure. We observed decreased rates of P_G in communities suffering from water stress, caused either by WL drawdown or flooding. In the long-term the direction of the vegetation succession after the change in WL will define the P_G and concurrently C budget. Since the bog vegetation is a mosaic of species adapted to hummocks and hollow conditions, the response to WL drawdown is likely to be an increasing proportion of hummock species and conversely the rising WL would increase the proportion of hollow species.

Belyea and Malmer (2004) and Laine et al. (2007a) estimated that the shifts in surface structure towards both wet and dry, would decrease C accumulation, due to decreased production and increased decomposition, respectively. Similarly, Waddington, et al. (1998) emphasized the importance of changing surface structure but estimated that drying would increase C accumulation, since hummocks were the most efficient C sinks. Our experiment implies that the increased proportion of low hummocks and high lawns would likely increase the C accumulation rate. On the other hand, the WL drawdown would have a detrimental effect on the C budget of present day hummocks. Hummocks appeared to be adjusted to the prevailing conditions and a change into drier or wetter conditions to be detrimental for their C budget. High lawns are the most resilient communities for changes since the vegetation is a combination of hummock and hollow dwelling species, adapted to opposite WL conditions. Based on the negative C budget of low lawns, the increased proportion of this vegetation type, due to rising WL, would

decrease C uptake considerably. The existing low lawns, however, benefited from the flooding, shown as the increased P_G in *R. alba* community. This increase must be limited by high enough WL, since permanently inundated hollows are known to have low productivity and high CH_4 fluxes (Waddington & Roulet, 1996). As we hypothesised, the low lawns where even a small change in water level leads to an ecologically different situation responded readily to water level alterations. However, the hummocks were at least equally sensitive to changes in water level.

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References

- Alm, J. 1997. CO₂ and CH₄ fluxes and carbon balance in the atmospheric interaction of boreal peatlands. PhD thesis, Joensuu, University of Joensuu.
- Alm, J., Sculman, L., Walden, J., Nykänen, H., Martikainen, P.J. & Silvola, J. 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology* 80: 161–174.
- Alm, J., Talanov, A. & Saarnio, S. 1997. Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia* 110: 423–431.
- Belyea, L.R. & Malmer, N. 2004. Carbon sequestration in peatland: patterns and mechanisms

- of response to climate change. *Global Change Biology* 10: 1043–1052.
- Bragg, O.M. & Tallis, J.H. 2001. The sensitivity of peat-covered upland landscapes. *Catena* 42: 345–360.
- Bubier, J.L., Bhatia, G., Moore, T.R., Roulet, N.T. & Lafleur, P.M. 2003a. Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems* 6: 353–367.
- Bubier, J.L., Crill, P.M., Mosedale, A., Frolking, S. & Linder, E. 2003b. Peatland responses to varying interannual moisture conditions as measured by automatic CO₂ chambers. *Global Biogeochemical Cycles* 17.
- Chimner, R.A., Cooper, D.J. 2003. Influence of water table levels on CO₂ emissions in a Colorado subalpine fen: an in situ microcosm study. *Soil Biology & Biochemistry* 35: 345–351.
- Christensen, J.H., Hewitson, B. & Busuioc, A. 2007. Regional climate projections. In: Solomon, S., Qin, D. & Manning, M. (eds.). *Climate Change 2007: The physical science basis. Contribution of working group I to the Fourth assessment report of the Intergovernmental Panel on Climate Change*: Cambridge, UK, Cambridge University Press, p. 847–940.
- Ellis, C.J. & Tallis, J.H. 2000. Climatic control of blanket mire development at Kentra Moss, north-west Scotland. *Journal of Ecology* 88: 869–889.
- Freeman, C., Nevison, G.B., Kang, H., Hughes, S., Reynolds, B. & Hudson, J.A. 2002. Contrasted effects of simulated drought on the production and oxidation of methane in a mid-Wales wetland. *Soil Biology & Biochemistry* 34: 61–67.
- Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1: 182–195.
- Komulainen, V.-M., Tuittila, E.-S., Vasander, H. & Laine, J. 1999. Restoration of drained peatlands in southern Finland: initial effects on vegetation change and CO₂ balance. *Journal of Applied Ecology* 36: 634–648.
- Lafleur, P.M., Roulet, N.T., Bubier, J.L., Frolking, S. & Moore, T.R. 2003. Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles*, 17, doi:10.1029/2002GB001983.
- Laine, A., Byrne, K.A., Kiely, G. & Tuittila, E.-S. 2007a. Patterns in vegetation and CO₂ dynamics along a water level gradient in a lowland blanket bog. *Ecosystems* 10: 890–905.
- Laine, A., Sottocornola, M., Kiely, G., Byrne, K.A., Wilson, D. & Tuittila, E.-S. 2006. Estimating net ecosystem exchange in a patterned ecosystem: example from blanket bog. *Agricultural and Forest Meteorology* 138: 231–243.
- Laine, A., Wilson, D., Kiely, G. & Byrne, K.A. 2007b. Methane flux dynamics in an Irish lowland blanket bog. *Plant and Soil* 299: 181–193.
- Laine, J., Vasander, H. & Laiho, R. 1995. Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *Journal of Applied Ecology* 32: 785–802.
- Lappalainen, E. 1996. *Global Peat Resources: Jyskä, International Peat Society and Geological Survey of Finland*.
- Lindsay, R.A., Charman, D.J., Everingham, F., O'Reilly, R.M., Palmer, M.A., Rowell, T.A. & Stroud, D.A. 1988. *The flow country: The peatlands of Caithness and Sutherland*: Peterborough, Nature Conservation Council.
- Lloyd, D. & Taylor, J.A. 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8: 315–323.
- McElwain, L. & Sweeney, J. 2007. *Key Meteorological Indicators of Climate Change in Ireland*. Wexford, Environmental Protection Agency 31.
- McGrath, R. & Lynch, P. 2008. Ireland in a warmer world. Scientific predictions of the Irish climate in the twenty-first century, Community Climate Change Consortium for Ireland (C41), p. 109.
- Moore, T.R. & Dalva, M. 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *Journal of Soil Science* 44: 651–664.

- Petit, J.R., Jouzel, J. & Raynaud, D. 1999. Climate and atmospheric history of the past 42,000 years from the Vostok ice core, Antarctica. *Nature* 399: 429–436.
- Proctor, M.C.F. 2000. The bryophyte paradox: tolerance of desiccation, evasion of drought. *Plant Ecology* 151: 41–49.
- Proctor, M.C.F. & Smirnov, N. 2000. Rapid recovery of photosystems on rewetting desiccation-tolerant mosses: chlorophyll fluorescence and inhibitor experiments. *Journal of Experimental Botany* 51: 1695–1704.
- Ratcliffe, D.A. & Walker, D. 1958. The Silver Flowe, Galloway, Scotland. *The Journal of Ecology* 46: 407–445.
- Roulet, N.T., Ash, R., Quinton, W. & Moore, T. 1993. Methane flux from drained northern peatlands: effect of a persistent water table lowering on flux. *Global Biogeochemical Cycles* 7: 749–769.
- Roulet, N.T., Moore, T.R., Bubier, J.L. & Lafleur, P.M. 1992. Northern fens: methane flux and climatic change. *Tellus* 44B: 100–105.
- Saarnio S, Alm J, Silvola J, Lohila A, Nykänen H, Martikainen PJ (1997) Seasonal variation in CH₄ emissions and production and oxidation potentials at microsites on an oligotrophic pine fen. *Oecologia*, 110, 414–422.
- Silvola, J., Alm, J., Ahlholm, U., Nykänen, H., Martikainen, P.J. 1996. CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. *Journal of Ecology* 84: 219–228.
- Smith, A.J.E. 1990. *The liverworts of Britain and Ireland*. Cambridge, Cambridge University Press.
- Smith, A.J.E. 2004. *The Moss Flora of Britain and Ireland*. Cambridge, Cambridge University Press, 1012.
- Sottocornola, M., Laine, A., Kiely, G., Byrne, K. & Tuittila, E-S. 2009. Vegetation and environmental variation in an Atlantic blanket bog in South-western Ireland. *Plant Ecology* 203: 69–81, DOI:10.1007/s11258-008-9510-2.
- Stace, C. 1997. *New Flora of the British Isles*. Cambridge, Cambridge University press, 1130.
- Strack, M., Waddington, J.M. 2007. Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment. *Global Biogeochemical Cycles* 21, GB1007: doi:10.1029/2006GB002715.
- Strack, M., Waddington, J.M., Rochefort, L. & Tuittila, E-S. 2006a. Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. *Journal of Geophysical Research* 111: doi:10.1029/2005JG000145.
- Strack, M., Waller, M. & Waddington, J. 2006b. Sedge Succession and Peatland Methane Dynamics: A Potential Feedback to Climate Change. *Ecosystems* 9: 278–287.
- Sweeney, J., Donnelly, A., McElwain, L. & Jones, M. 2002. *Climate Change. Indicators for Ireland*. Wexford, Environmental Protection Agency, 54.
- Sweeney, J. & Fealy, R. 2002. A preliminary investigation of future climate scenarios for Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* 102B: 121–128.
- Tuittila, E-S., Komulainen, V-M., Vasander, H., Nykänen, H., Martikainen, P.J. & Laine, J. 2000. Methane dynamics of a restored cut-away peatland. *Global Change Biology* 6: 569–581.
- Tuittila, E-S., Vasander, H., Laine, J. 2004. Sensitivity of C sequestration in reintroduced Sphagnum to water-level variation in a cutaway peatland. *Restoration Ecology* 12: 483–493.
- Turetsky, M.R., Treat, C.C., Waldrop, M.P., Waddington, J.M., Harden, J.W. & McGuire, A.D. 2008. Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *Journal of Geophysical Research* 113, G00A10: doi:10.1029/2007JG000496.
- Turunen, J., Tomppo, E., Tolonen, K. & Reinikainen, A. 2002. Estimating carbon accumulation rates of undrained mires in Finland — application to boreal and subarctic regions. *The Holocene* 12: 69–80.
- Waddington, J.M., Griffis, T.J. & Rouse, W.R. 1998. Northern Canadian wetlands: Net ecosystem CO₂ exchange and climate change. *Climatic Change* 40: 267–275.
- Waddington, J.M. & Roulet, N.T. 1996. Atmosphere-wetland carbon exchanges: Scale dependency of CO₂ and CH₄ exchange on

- the developmental topography of a peatland. *Global Biogeochemical Cycles* 10: 233–245.
- Weltzin, J.F., Bridgham, S.D., Pastor, J., Chen, J. & Harth, C. 2003. Potential effect of warming and drying on peatland plant community composition. *Global Change Biology* 9: 141–151.
- Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K., Farrell, E. & Tuittila, E-S. 2007. A high resolution green area index for modelling the seasonal dynamics of CO₂ exchange in peatland vascular plant communities. *Plant Ecology* 190: 37–51.

Tiivistelmä: Vedenpinnan muutoksen lyhytaikaiset vaikutukset hiilidioksidi- ja metaanipäästöihin peittosuolla

Soilla on merkittävä rooli globaalissa hiilen (C) kierrossa, sillä ne muodostavat suuren pitkäaikaisen hiilinielun. Hiilinielua ylläpitää korkea vedenpinnan taso, joka hidastaa orgaanisen aineksen hajotusta. Suon hiilikaasudynamiikka onkin herkkä vedenpinnan muutoksille ja ilmastollisesti erilaisina vuosina suo voi muuttua hiilinielusta sen lähteeksi. Mittasimme hiilidioksidi (CO₂) ja metaani (CH₄) virtoja Irlantilaisen peittosuon kasviyhdyskunnista, jotka vaihtelivat mättäistä mataliin välipintoihin. Vuoden mittaisen kalibraatiokauden jälkeen vedenpintaa keinoitekoisesti sekä nostettiin että laskettiin, jonka jälkeen muutoksia kasvillisuudessa ja kaasuvirroissa seurattiin vuoden verran. Kaikkien kasviyhdyskuntien respiraatio kasvoi ja metaaniemissio laski vedenpinnan laskun johdosta; tulvitus osaltaan pienensi respiraatiota ja kasvatti metaaniemissiota. Vedenpinnan muutoksen vaikutus fotosynteesiin riippui kasviyhdyskunnasta. Vedenpinnan lasku pienensi useimpien yhdyskuntien fotosynteesiä; tulvitus taas vähensi mätäslajien fotosynteesiä, mutta lisäsi *Rhynchospora alba* (valkopiirtoheinä) fotosynteesiä.

Avainsanat: ekohydrologia, kuivatus, tulvitus, metaani, turvemaa, fotosynteesi, respiraatio, *Racomitrium*, *Rhynchospora alba*, *Sphagnum*