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Influence of Vegetation Removal and Altering Water Levels on CO2 Flux Rates of a Northern Bog

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INFLUENCE OF VEGETATION REMOVAL AND ALTERING WATER LEVELS
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By

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Abstract

Boreal peatlands contain approximately one third of the global soil carbon and are considered net sinks of atmospheric CO_2. Water level position is one of the main regulators of CO_2 fluxes in northern peatlands because it controls both the thickness of the aerobic layer in peat and plant communities. However, little is known about the role of different plant functional groups and their possible interaction with changing water level in boreal peatlands with regard to CO_2 cycling. Climate change may also accelerate changes in hydrological conditions, changing both aerobic conditions and plant communities. To help answer these questions, this study was conducted at a mesocosm facility in Northern Michigan where the aim was to experimentally study the effects of water levels, plant functional groups (sedges, shrubs and mosses) and the possible interaction of these on the CO_2 cycle of a boreal peatland ecosystem.

The results indicate that Ericaceous shrubs are important in the boreal peatland CO_2 cycle. The removal of these plants decreased ecosystem respiration, gross ecosystem production and net ecosystem exchange rates, whereas removing sedges did not show any significant differences in the flux rates. The water level did not significantly affect the flux rates. The amount of aboveground sedge biomass was higher in the low water level sedge treatment plots compared to the high water level sedge plots, possibly because the lowered water level and the removal of *Ericaceae* released nutrients for sedges to use up.

Key words: peatland, CO$_2$ flux, sedge, shrub, water level

Introduction

Peatlands store an estimated one third of the Earth's soil organic carbon (Moore *et al.* 1998), which is more than half of the amount of carbon in the atmosphere (Gorham 1991). The carbon stocks of peatlands are large because over the long-term plant production is greater than the loss of carbon from decomposition, fires, and dissolved organic carbon (Brown 1998; Moore *et al.* 1998). Peatlands are, therefore, long-term net sinks for atmospheric CO_2 (Moore *et al.* 1998; Dorrepaal *et al.* 2009), which is a greenhouse gas in the atmosphere (Wuebbles and Hayhoe 2002).

Plants take up CO_2 during photosynthesis and release it during respiration (Lambers *et al.* 2008), which occurs both in aboveground and belowground parts of the plants. The belowground respiration occurs in the roots and rhizosphere (Le Mer and Rogers 2001), which are in the anaerobic peat layer, or catotelm (Brown 1998). Carbon dioxide is produced also when plant biomass decomposes. Most decomposition occurs in the acrotelm, or the uppermost aerobic layer of peat (Brown 1998).

Changing climate has been predicted to increase precipitation in the northern boreal and temperate areas (Lemke *et al.* 2007) where most of the peatlands are located (Rydin and Jeglum 2006). In the northernmost regions this, together with the predicted rise in the air temperature (Trenberth *et al.* 2007), could cause thawing of permafrost peatlands (Frolking *et al.* 2011). Permafrost thawing is patchy and results in thermokarst terrain with an uneven surface topography (Lemke *et al.* 2007). This has been reported to raise the water tables in arctic areas (Hinzman *et al.* 2005; Oksanen and Väliranta 2006). On the other hand the rising temperatures further south may lead to higher evapotranspiration rates and lower the water table levels of peatlands (Gorham 1991; Frolking *et al.* 2011).

The position of the water table is an important regulator of peatland CO_2 cycling (Davidson and Janssens 2006). Peatlands with low water levels tend to have

higher CO_2 emissions peatlands with high water level, because their aerobic peat layer is thicker (Moore and Knowles 1989; Silvola *et al.* 1996; Goulden and Crill 1997; Komulainen *et al.* 1999; Whalen 2005; Chivers *et al.* 2009). Decreasing water levels could stimulate aerobic heterotrophic respiration so that ecosystem respiration exceeds photosynthesis rates, making peatlands a source of CO_2 (Moore *et al.* 1998; Davidson and Janssens 2006). Lower water levels may also lead to higher photosynthesis rates and plant growth through increased soil temperature and oxygen supply to plant roots, as well as higher availability of nutrients (Shaver *et al.* 1992). In order for photosynthesis rates in a peatland to increase more than decomposition rates in warmer and drier conditions, increased nutrient mineralization is usually required because most northern peatlands are nutrient limited (Shaver *et al.* 1992).

Changes in water table levels can also cause changes in vegetation communities (Lemke *et al.* 2007). For instance, several studies, including peatland restoration studies, have shown that increasing water levels can change plant communities (Moore and Knowles 1989; Komulainen *et al.* 1999). Drier conditions can also change peatland communities, such as from a sedge-dominated to shrub-dominated on a relatively short time-scale (Bubier *et al.* 2003).

Different plant species have different structures and photosynthesis rates (e.g. Lambers *et al.* 2008), so the net exchange, respiration and gross production rates of an ecosystem can change with changes in plant communities. For instance, woody plant tissue has a carbon: nitrogen (C:N) ratio of approximately 200:1, whereas herbaceous plant tissue C:N ratio is about 100:1. This ratio describes how efficiently a plant can use available nitrogen in order to store carbon (Shaver *et al.* 1992). *Ericaceae*-dominated bogs have, however, lower photosynthesis rates relative to respiration than sedge-dominated fens, which means that sedge-dominated fens have the potential to sequester more CO_2 (Bellisario *et al.* 1998). Sedges can tolerate waterlogged conditions better than shrubs because of their aerenchyma cells but they are not drought tolerant like shrubs (Bubier *et al.* 2003). However, in the absence of shrubs, sedge production was found to

increase when water tables decreased (Strack *et al.* 2006). This was explained by the ability of sedges to acquire deep water as their roots were found to extend deeper in the dry peat (Strack *et al.* 2006). Woody plants have higher rates of CO_2 exchange in drier conditions compared to wet conditions, whereas for sedges only respiration rates increased in dry conditions (Bubier *et al.* 2003). Peatlands rich in woody plant vegetation might be able to balance out the loss of CO_2 through increased respiration caused by lowered water table and warmer temperature (Bubier *et al.* 2003).

Despite their abundance, information of the role of *Ericaceae* in the CO_2 cycle of northern peatland ecosystems is still scarce. Many of the sedge and moss related peatland studies have also concentrated more on the methane (CH_4) cycle, (e.g. (Bubier 1995; Waddington *et al.* 1996; Raghoebarsing *et al.* 2005; Treat *et al.* 2007; Larmola *et al.* 2010), rather than the CO_2 cycle. Yet, these plant groups are very abundant on boreal peatlands (e.g.Roulet *et al.* 1992; Shannon and White 1994; Bellisario *et al.* 1998; Bubier *et al.* 2003), which may be facing hydrological changes caused by the climate change (Frolking *et al.* 2011; Lemke *et al.* 2007). Therefore, the objective of this study was to experimentally test how ecosystem CO_2 cycling is influenced in peatlands by the interactive effects of: 1) changing water table levels, and 2) different plant functional groups (moss, sedge and Ericaceae).

Methods

Site Description and Experimental Design

The study was conducted at a mesocosm facility (PEATCOSM) at the US Forest Service, Northern Research Station in Houghton (47°7′2″N 88°33′45″W), Michigan. The facility consists of 24 1m x 1m x 1m teflon coated stainless steel bins of intact peat. The bins are open from above with a tunnel below the bins that has a controlled climate and access to and below-ground visibility of the bins.

The peat cubes were collected from a bog site near Meadowlands, Minnesota and transferred to Houghton in May 2010. Once in Houghton, each bin was individually monitored and water table levels controlled by either removing or adding water (Potvin *et al.* unpublished data). In the beginning of the field season 2011 minirhizotron tubes, environmental sensors and the water control system were installed. The first CO_2 gas exchange measurements were performed once a month in July, August and September 2010 and the first full field season of CO_2 measurements started in May 2011. The experimental plant treatments were established in June 2011. The plant treatments consisted of 1) *Ericaceae* (shrubs) were removed from one third of the bins, 2) *Carex* (sedges) from one third of the bins and 3) the remaining eight bins were left as control plots. The plants were removed by gently pulling them up with their roots. The bins were checked every week to see if additional plant removal was necessary. In addition to the plant treatment, we also established two water table treatments: 1) high water and 2) low water. Long-term precipitation and water table depth data from Marcell Experimental Forest was used to determine the high and low water levels. The high water level is imitating a high minimum water table year with a typical low variability in water table depth over the season. The low water level imitates a low minimum water table year with a high variability in water table depth over the season. This design gave us 6 treatments: 1) high water level with sedges removed (HE), 2) high water level with *Ericaceae* removed (HS), 3) low water level with sedges removed (LE), 4) low water level with *Ericaceae* removed (LS), and 5) control plots with high water level (HC) and 6) control plots with low water level (LC).

Problems occurred after the vegetation removal, as the mosses started drying out and dying in the bins from which *Ericaceae* had been removed. Therefore, the water levels had to be raised in order to keep the vegetation alive, so the data from year 2011 is not consistent when it comes to water levels. However, in the field season of 2012 the water levels were successfully set to high and low. Additions of artificial

rainwater were used to increase the water tables and rainout shelters were employed during rain events to exceed water from bins where water tables would have become too high. If water tables needed to be lowered water was removed from the bins through drainage ports set 10-15 cm below the peat surface.

Environmental Parameters

Peat temperature sensors (Temperature Probes 107, Campbell Scientific Inc., Logan, UT, USA) were installed in winter 2011. The temperature is monitored at five different depths in each bin: 5 cm, 10 cm, 20 cm, 40 cm and 80 cm, and at 2 locations (one in the center and one 10 cm away from the edge of the bin) and recorded hourly. Air temperature (HMP50-L, Vaisala Oyj, Finland) is measured hourly at four locations, one by bins number 6 and 14 and two by bin 18. There are also similar sensors in the fence surrounding the mesocosms, on the top, in the middle and on the bottom. Daily rainfall has been measured (385-L, Met One Instruments, Inc., Grants Pass, OR, USA) since early 2011 and wind speed (2 D Windsonic-4 L, Gill Instruments Ltd., Lymington, Hampshire, UK) and PAR (photosynthetically active radiation) since late 2010 (LI 190s B-L Quantum Sensor, LI-COR Biosciences, Lincoln, NE, USA) at the meteorological station. The water level measurements started in 2010 but the data for the first sampling dates in May in 2011 is missing. The water levels are measured hourly and recorded with a CR 1000 Datalogger (Campbell Scientific Inc., Logan, UT, USA). Daily means from temperature and water level parameters were used in the calculations.

CO_2 measurements

CO$_2$ fluxes were measured from each bin approximately once a week during the summer and biweekly in the fall of 2011 and in 2012. Monthly measurements were conducted in 2010 when the experiment was being set up. Carbon dioxide flux rates were measured using a custom built clear PVC chamber (100 cm x 100 cm x 40 cm) with small fans in conjunction with an EGM-4 Environmental Gas Monitor (PP-Systems, Amesbury, MA, USA). Clear chamber techniques have been used previously in several studies to measure CO$_2$ exchange (Vourlitis *et al.* 1993; Chivers *et al.* 2009; Chimner *et al.* 2010). Photosynthetically Active Radiation (PAR) was measured simultaneously by using the standard EGM-4 TRP-1 probe inserted into the clear chamber. The lid was put on for each measurement and taken off between them to let the air inside the chamber mix with the ambient air (Vourlitis *et al.* 1993). Each measurement was running for 120 seconds with the EGM-4 logging the results from measuring the difference between the CO$_2$ concentration of the air going in and the air coming out. Directly after doing a light measurement for net ecosystem exchange (NEE), which is the net exchange of CO$_2$ between an ecosystem and the atmosphere (Wofsy *et al.* 1993), a dark measurement for ecosystem respiration (ER) was conducted for every bin by using a non-transparent dark cloth that was put on the chamber (Vourlitis *et al.* 1993). Ecosystem respiration is plant and soil respiration together (Moore *et al.* 1998). The sampling was performed similarly as the NEE measurement. Gross ecosystem production (GEP), which is the total amount of CO$_2$ assimilated by an ecosystem (Wofsy *et al.* 1993), was calculated by subtracting ER from NEE. In this study ER is referred to with negative numbers and NEE and GEP with positive numbers. The unit used for CO$_2$ flux rates is μmol m^{-2} s^{-1}. The values, where R^2 between the CO$_2$ concentration (ppm) and time was lower than 0.8, were excluded from the calculations.

Vegetation measurements

A vegetation survey for each bin was conducted annually in the late summer by using a point intercept method. A one meter tall metal frame structure with 8 x 8 grid was set on top of a bin. A removable beam with 8 holes drilled in it, 10 cm away from each other, was used so that there were 64 holes and data points altogether. Laser pens were put in each hole of the frame. Each species as well as the plant organ (dead or alive) the laser touched and how many hits the laser caught in each data point were recorded. The percentage cover of each species was calculated based on these surveys (Potvin et al. unpublished).

The ground layer of the original vegetation in the bins consists mostly of *Sphagnum* species: *S. rubellum*, *S.magellanicum* and *S. fuscum* with some *Polytrichum strictum*. *Vaccinium oxycoccos* is also present in the ground layer. The field layer is composed of *Chamaedaphne calyculata*, *Carex oligosperma*, *Kalmia polifolia*, and some *Ledum groenlandicum* and *Andromeda glaucophylla*.

The aboveground biomass calculation was done based on the three most abundant species of the field layer: *C. calyculata*, *C. oligosperma* and *K. polifolia*. Aboveground biomass of the bins was measured and calculated in 2012. Each bin was divided in six sections with fiber glass rods that were taped into the foam edges of the bin. Digital calipers were used to measure the diameter of the main stem of each *K. polifolia* and *C. calyculata.* This was done separately for each section. Aboveground biomass was calculated by using the diameters in an allometric equation that was developed at the original site in Meadowlands (Potvin et al. unpublished data). The aboveground biomass of *C. oligosperma* was determined by counting the number of living and dead stems and using an allometric equation developed at Nestoria, Michigan (Potvin *et al.* unpublished data).

Statistical Analysis

The statistical analysis was performed by using SPSS Statistics 20 (IBM SPSS, 2011). Repeated measures analysis by year with water level (high or low) and vegetation treatment as independent, between measures, variables was performed for all NEE, ER and GEP. Bonferroni post hoc analysis was used for pairwise comparison if statistically significant differences were found between different factors. Separate repeated measures analyses were conducted for different vegetation treatments if statistically significant differences were found in the between-measures effects or if significant interactions between different main effects were detected. Stepwise multiple regression with air temperature, water level (cm below peat surface) and peat temperatures as independent variables were used to see if there are interrelationships between the environmental parameters and NEE, ER and GEP values. Regressions were run for each six treatment combinations separately for years 2011 and 2012. Pearson correlations were used in the tests to see if the environmental parameters correlated with each other. One-way ANOVAs were run to see if the NEE, ER and GEP were similar from all the bins in 2010 and 2011 before the treatments. Two-way ANOVAs with water level and vegetation treatment as independent variables were performed for 2012 NEE, ER and GEP data to compare the means of different treatments. Tukey's post hoc test was used for pairwise comparisons in case statistically significant differences were found between independent variables. Simple linear regressions were also done to see how the control plot CO_2 fluxes correlated with air temperature and water level (cm below surface) in 2011 after starting the treatments and 2012.

Results

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Environmental Parameters

The mean daily air temperatures of the days when CO_2 was measured were slightly lower in 2011 (16.7 ± 1.4°C) than in 2012 (17.7 ± 1.6 °C) (mean ± standard error). Between the first and the last measurement day of field seasons 2011 and 2012 there were 55 and 50 days with rainfall, respectively. The sum of rainfall during this time was 146 mm in 2011 and 151.9 mm in 2012. Four of the sampling days in 2011 received rainfall, two sampling days in 2012. In all rainy days except for the first one in 2011(15.7 mm) rainfall was small, between approximately 0.9 and 1.4 mm per day. The average wind speed in the sampling days was 1.08 ± 0.10 m/s in 2011 and 1.03 ± 0.05 m/s in 2012. Averaged PAR rate in 2011 sampling days was 1622 ± 60.8 µmol m^{-2} s^{-1} and 1658 ± 78.0 µmol m^{-2} s^{-1} in 2012.

The average water table (average of the sampling dates) for high water level and low water level bins were at approximately 21.9 ± 6.0 and 19.3 ± 3.4 cm below surface, respectively, in 2010 when the treatments were not started yet. In 2011 high water level bins had the water level on average 9.5 ± 0.64 cm below surface and low water level bins 11.4 ± 0.95cm below surface. In 2012 the two different water levels were more clearly differentiated from each other (Figure 1). The high water level bins had a water table approximately 8.4 ± 1.0 cm below surface and low water level bins 15.0 ± 1.0 cm below surface. A more detailed look at the water level data from 2012 shows the water table in high water level bins varied between 2.4 cm and 15.0 cm below surface and between 6.5 and 29.7 cm below surface in low water level bins. The water tables were at their lowest between July and October in both the high and low water level bins. The data for 2011 shows clearly the point in the beginning of August when the water levels were elevated in order to improve the condition of the mosses in the bins.

The differences in average peat temperature between treatments were small (Figure 2). In 2012, the peat temperatures at 80 and 10 cm below surface, respectively,

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were on average the coldest ones. Peat was warmest at 20 cm below surface for other treatments except for high water level sedge treatment where the peat at 40 cm below surface was slightly warmer. The temperature difference between the three warmest depths (20, 40 and 5 cm below surface) was, however, very small for all the treatments. In 2011 the peat temperatures were consistently warmer in the upper peat layer and cooled down towards the deeper layers.

Stepwise multiple regressions showed that in all the treatment combinations air temperature correlated with peat temperatures ($p \leq 0.05$, Table 1).

Vegetation Dynamics

Vegetation was similar in 2010 before the treatments were started (Table 2). The survey of 2011 was conducted after starting the treatments, but there were still some shrubs left in the sedge bins and some sedges in the *Ericaceae* bins on that year. In 2010 the average overall sedge coverage in the bins was 33%, shrub coverage was 172 % and moss coverage was 118 %. In 2012 the sedge coverage in the control bins had dropped by to 21 % (58 % decrease). The shrub and moss coverage in the control bins in 2012 were 98 % (43 % decrease) and 117 % (no change), respectively. Although the overall moss coverage of the control plots did not change, species composition did change. *S. rubellum* continued to be the most dominant moss species in 2012 and its coverage increased by 8 % from 2010. The coverage of *S. fuscum* increased by 6 %, and the coverage of *S. magellanicum* by 33 %, whereas the coverage of *P. strictum* decreased by 99 % compared to 2010.All the shrubs in the control plots decreased between 2010 and 2012, *C.calyculata* by 41 %, *K. polifolia* by 49 % and *V. oxycoccos* by 100%. In 2012 the coverage of *C. oligosperma* in sedge plots had decreased by 78 % compared to 2010 control plots. All the mosses in the sedge plots increased their coverage from 2010. *P.strictum* covered 38 % more, *S. fuscum* 15 % more, *S. magellanicum* 0.15 % more and

S. rubellum 10 % more of the area in sedge plots in 2012 than in the control plots in 2010. Removing sedges decreased the area covered by *P.strictum* in 2012 by 61 % compared to 2010 control plots. All the *Sphagnum* species increased their coverage in *Ericaceae* treatment bins, especially *S. magellanicum* with almost 40 % and *S. fuscum* with approximately 30 % compared to pre-treatment situation. The shrub coverage decreased in *Ericaceae* treatment plots compared to the pre-treatment situation. The biggest change occurred with *V. oxycoccos*, whose coverage was 64 % lower in 2012 compared to 2010. *C.calyculata* coverage decreased by 6 % and *K. polifolia* by 55 %, when comparing 2012 to pre-treatment situation. *L. groenlandicum* decreased by over 300 %, but its coverage stayed under 1 % both in 2012 and 2010.

The aboveground biomass of living and senesced plants varied between vegetation treatments (Table 3). Some of the sedge treatment bins had more dead than living sedge biomass in them, which was not observed for the control bins. There was also variation between different bins within each vegetation treatments. For example the sedge total biomasses (living + dead) in sedge treatment plots ranged between 0.5 and 33.2 g/m^2. The low water level sedge treatment plots had a larger total sedge biomass than the high water level plots (163.3 and 96.9 g/m^2, respectively) and the same occurred with high water level versus low water level total sedge biomass in control bins (52.3 and 68.7 g/m^2, respectively). No senesced *Ericaceae* were found in the bins. The *Ericaceae* biomass in high water level *Ericaceae*/shrub treatment plots was 501.3 g/m^2 and in low water level *Ericaceae* plots 513.7 g/m^2. In high water level control plots the *Ericaceae* biomass was 493.2 g/m^2 and in low water level control plots 449.1 g/m^2.

Net ecosystem exchange

The NEE results from each sampling day within each year can be seen in Figure 6. There were only three sampling days in the year 2010. The effect of the

vegetation removal can clearly be seen in the 2011 graph as the drop of the NEE from sedge plots in the end of June. In 2012 these plots still have lower NEE than the others do.

The mean NEE rates for all the plots for years 2010 and 2011 before the treatments were started were 5.29 ± 0.13 and $4.55 \pm 0.35 \mu mol\ m^{-2}\ s^{-1}$, respectively. The one-way ANOVA for control bins in 2010 and 2011 pre-treatments confirmed that the NEE rates between the plots were not significantly different before starting the treatments ($p=0.566$ in 2010, $p=0.810$ in early 2011). The mean NEE rates for control bins in 2011 after starting the treatments were $6.54 \pm 1.11\ \mu mol\ m^{-2}\ s^{-1}$ for high water level and $6.06 \pm 1.22\ \mu mol\ m^{-2}\ s^{-1}$ for low water level. There was no significant difference ($p>0.05$) in 2012 between the control high and low water level treatments ($6.63 \pm 1.27\ \mu mol\ m^{-2}\ s^{-1}$ and $6.09 \pm 0.80\ \mu mol\ m^{-2}\ s^{-1}$, respectively) (Figure 3 and 4).

There were significant differences in NEE between vegetation treatments in 2012 (Figure 3 and 4) ($p<0.001$). The sedge treatment differed significantly from *Ericaceae* treatment (mean difference $-2.00\ \mu mol\ m^{-2}\ s^{-1}$, $p=0.002$) and control plots (mean difference $-2.50\ \mu mol\ m^{-2}\ s^{-1}$, $p<0.001$) in 2012. The NEE rates of sedge plots were lower than NEE rates of shrub and control plots (by 34 % and 39 %, respectively). The NEE rates were 12 % lower in the high water level sedge treatment compared to low water level sedge treatment. The NEE rates of high water level sedge treatment were also 45 % lower compared to NEE rates of high water level control plots. The low water level sedge plots had NEE rates 33 % lower than low water level control plots. The NEE of *Ericaceae* plots were about 8 % smaller compared to control plots. The high water level *Ericaceae* plots had 13 % higher NEE rates than low water level *Ericaceae* plots and 6 % lower NEE rates compared to high water level control plots. The NEE rates for low water level *Ericaceae* treatment were 10 % smaller in comparison with low water level control plots. The high water level control plot NEE rates were about 9 % higher than low water level control plot NEE rates.

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The mean NEE rates from control plots on different water levels from the late season of 2011 and 2012 were similar (Figure 5). In both years the high water level showed slightly greater NEE rates than low water level, but the differences were relatively small and not significant. Simple regression analysis were also performed to the control plots to see if there are correlations between CO_2 fluxes and air temperature or water level (cm below surface). Data from 2012 and 2011 after the treatments were started were used for these analyses. These NEE rates did not significantly correlate with either of the environmental parameters (Table 4).

A statistically significant interaction was found between time (year) and vegetation treatment (p=0.02) (Table 5). NEE rates from different vegetation treatments differed significantly from one another (p=0.024) (Table 6) with sedge plots being different from *Ericaceae* plots (mean difference -1.23 µmol m^{-2} s^{-1}, p=0.046). The difference between sedge and control plots was also nearly statistically different (mean difference -1.18, p=0.057). Neither the different water levels nor the combinations of water level and vegetation treatments showed any statistically significant difference between one another over the years. Additional repeated measures analysis showed NEE from sedge plots differed significantly between years 2010 and 2011 (mean difference 2.67 µmol m^{-2} s^{-1}, p=0.03). Control plots differed significantly between years 2011 and 2012 (mean difference -0.93 µmol m^{-2} s^{-1}, p=0.03).

Stepwise multiple regressions found no correlation between the environmental parameters and high water level sedge plots in 2011 and 2012. For high water level *Ericaceae* plots in 2011 peat temperature at 40 cm seemed to best explain NEE values (model R^2 =59, p=0.006) as well as for 2012 (model R^2 =0.59, p=0.005). Peat temperatures explained high water level control plot NEE values in both 2011 and 2012: in 2011 the temperature at 40 cm was the best correlated (model R^2 =0.78, p<0.001) and in 2012 the temperature at 10 cm (model R^2=0.61, p=0.005). Low water level sedge plot NEE values in 2011 correlated with water level (model R^2=0.67, p=0.002), whereas in 2012 no correlations between NEE and environmental parameters

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were found. No correlations were found between environmental parameters and low water level *Ericaceae* plots in either of the years. In 2011 low water level control plots did not correlate with the environmental parameters, but in 2012 peat temperature at 40 cm explained NEE values the best (model R^2=0.44, p=0.026).

Ecosystem respiration

The pattern of ER in each year can be seen in Figure 7. The ER values from 2010 are from the end of the summer, but they are within similar range than the values of 2012. The difference of 2011 compared to 2010 and 2012 can clearly be seen from the figure.

The mean ER flux rates for all the plots in 2010 were -4.86 ± 0.13 µmol m^{-2} s^{-1} and in 2011 before the treatments were initiated they were -2.24 ± 0.23 µmol m^{-2} s^{-1}. No differences between the plots were found before the treatments were started (p=0.512 for 2010 and p= 0.572 for 2011). The mean ER rates for control bins in 2011 after starting the treatments were -2.48 ± 0.49 µmol m^{-2} s^{-1} for high water level plots and -2.90 ± 0.54 µmol m^{-2} s^{-1} for low water level plots. In 2012 the rates were -4.12 ± 0.58 µmol m^{-2} s^{-1} and -4.29 ± 0.57 µmol m^{-2} s^{-1}, respectively. No significant effects of different water levels on the ER rates were found in 2012 (Figure 3 and 4) and there was also no interaction between water level and vegetation treatments. The vegetation treatments affected ER (p= 0.008), and sedge plots differed from both *Ericaceae* and control plots (mean difference 0.58 and 0.60 49 µmol m^{-2} s^{-1}, p=0.018 and p=0.014, respectively). The sedge plot ER rates were about 14 % lower than those of *Ericaceae* and control plots. The ER of *Ericaceae* plots was 0.5 % smaller compared to control plots. The high water level sedge plots had ER rates approximately 12 % lower than the low water level sedge plots and 18 % lower than high water level control plots. The low water level sedge plots had ER rates 11 % lower than low water level control plots. High water level *Ericaceae*

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plots had 2 % lower ER rates than low water level and for control plots high water level ER rates were 4 % lower than for low water level.

Control plots had higher ER rates in 2012 than in 2011 (Figure 5). The low water level ER rates were higher on both years. The regression analysis on the control plot ER rates and environmental parameters showed that ER correlated with air temperature and water level on both high and low water level plots in 2011 (after starting the treatments), but only with air temperature in 2012 (Table 4).

Statistically significant differences could be found in ER rates over time (year) (Table 5). Years 2010 and 2011 differed from each other (mean difference -2.52 μmol m^{-2} s^{-1}, p<0.001) as well as years 2010 and 2012 (mean difference -0.87 μmol m^{-2} s^{-1}, p=0.026) and 2011 and 2012 (mean difference 1.65 μmol m^{-2} s^{-1}, p<0.001). No statistically significant interactions were found in the between-subjects factors (Table 6). Neither the vegetation treatments nor different water levels, or the combinations of these seemed to have any statistically significant effect on the ER rates over the years. Plots with *Ericaceae* removed had lowest ER rates in 2011 and 2012 and in general the ER rates were highest in 2010, followed by 2012 and being lowest in 2011.

Stepwise multiple regression analysis showed no correlations between environmental parameters and ER values in 2011 for high water level sedge plots. In 2012 peat temperatures at 20 and 5 cm explained ER values the best (model R^2=0.93, p<0.001). Peat temperature at 5 cm and 20 cm explained the high water level *Ericaceae* plot ER values in 2011 and 2012, respectively (model R^2=0.84, p<0.001 in 2011 and model R^2=0.74, p=0.001 in 2012). The same pattern occurred with high water level control plots in 2011 and 2012 (model R^2=0.70, p=0.001 in 2011, model R^2=0.69, p=0.002 in 2012). Low water level sedge plot ER rates from 2011 did not correlate with the environmental parameters, but in 2012 peat temperature at 20 cm explained the rates the best (model R^2=0.64, p=0.003). Ecosystem respiration rates from low water level *Ericaceae* plots correlated the best with peat temperature at 5 cm in 2011 (model

$R^2=0.72$, p=0.001), and in 2012 air temperature explained the rates the best (model $R^2=0.76$, p<0.001). The same pattern occurred with low water level control plots (model $R^2=0.86$, p<0.001 in 2011, model $R^2=0.80$, p<0.001 in 2012).

Gross ecosystem production

The different years and their sampling days can be seen in Figure 8. Vegetation removal took place in the end of June 2011 and the effects of it to the GEP can be seen in graph b. The mean total GEP rates in 2010 and early 2011 (pre-treatments) were 9.93 ± 0.19 and 6.75 ± 0.53 µmol m^{-2} s^{-1}, respectively. No statistically significant differences were found between the plots before the treatments were started (p=0.259 for 2010 and P=0.902 for early 2011). After starting the treatments the mean GEP rates for control plots were 8.93 ± 1.34 and 9.06 ± 1.25 µmol m^{-2} s^{-1} for high and low water level in 2011. In 2012 the rates were 10.75 ± 1.50 and 10.38 ± 1.10 µmol m^{-2} s^{-1} for high and low water level. Water level did not have a significant effect on GEP rates in 2012 (Figure 3 and 4) and there was also no significant interaction between water level and vegetation treatments. The vegetation treatments caused difference in GEP rates (p<0.001). The sedge plots differed from both *Ericaceae* plots (mean difference -2.58 µmol m^{-2} s^{-1}, p=0.001) and control plots (mean difference -3.10 µmol m^{-2} s^{-1}, p<0.001). The GEP rates of sedge plots were about 26 % lower than of *Ericaceae* plots and 29 % lower than of control plots. The GEP rates of *Ericaceae* plots were 5 % lower than of control plots. The high water level sedge plot GEP rates were about 12 % lower than the rates of low water level sedge plots and 35 % lower than the rates of high water level control plots. The low water level sedge plots had GEP 24 % lower than low water level control plots. The high water level *Ericaceae* plots had GEP rates about 7 % higher than low water level *Ericaceae* plots and high water level control plots had rates about 4 % higher than low water level control plots.

The analysis of control plots showed that GEP rates in 2011, after starting the treatments, were slightly higher on low water level plots (Figure 5). In 2012 this was reversed, as the high water level plots had higher GEP rates. The difference between these two water levels was also more clearly seen than in 2011. The simple linear regression analysis showed GEP rates from high water level plots correlated with air temperature and water level in 2011 (Table 4). In 2012 both high and low water level control plot GEP rates correlated with air temperature.

Gross ecosystem production differed significantly between different years (p<0.001): year 2010 differed from 2011 (mean difference 3.00 µmol m^{-2} s^{-1}, p<0.001) and year 2011 differed from 2012 (mean difference -2.43 µmol m^{-2} s^{-1}, p<0.001). Time (year) interacted significantly with vegetation treatment (p<0.001) (Table 5). Vegetation treatments differed significantly from each other (p=0.001), but no other treatment effects were detected (Table 6). Gross ecosystem production from sedge plots differed from *Ericaceae* plots (mean difference -1.45 µmol m^{-2} s^{-1}, p=0.049). Separate repeated analysis on different treatments showed that all vegetation treatments differed over time (Figure 3). Sedge plots differed between years 2010 and 2011 (mean difference 5.67 µmol m^{-2} s^{-1}, p<0.001) and between 2011 and 2012 (mean difference -2.32 µmol m^{-2} s^{-1}, p=0.008). *Ericaceae* plots had significant differences between 2010 and 2011 (mean difference 2.11 µmol m^{-2} s^{-1}, p=0.011) as well as 2011 and 2012 (mean difference -2.24 µmol m^{-2} s^{-1}, p=0.007). Control plots differed significantly between 2011 and 2012 (mean difference -2.71 µmol m^{-2} s^{-1}, p=0.001).

According to stepwise multiple regressions GEP rates from high water level sedge plots did not correlate with the environmental parameters in 2011 and 2012. High water level *Ericaceae* plot GEP from 2011 were explained by air temperature (model R^2=0.72, p=0.001) and in 2012 by peat temperature at 20 cm (model R^2=0.85, p<0.001). The high water level control plot GEP rates were best correlated with peat temperature at 20 cm in both 2011 and 2012 (model R^2=0.78, p<0.001 in 2011, model R^2=0.83, p<0.001 in 2012). Low water level sedge plots from 2011 correlated the most

with water level (model R^2=0.64, p=0.003) and from 2012 with peat temperature at 20 cm (model R^2=0.41, p=0.035). The low water level Ericaceae plot GEP rates correlated the most with peat temperature at 5 cm in 2011 (model R^2=0.51, p=0.014) and with air temperature in 2012 (model R^2=0.85, p<0.001 in 2012). Low water level control bins in 2011 were best explained by peat temperature at 40 cm (model R^2=0.46, p=0.022) and in 2012 by peat temperature at 20 cm (model R^2=0.79, p<0.001).

Discussion

Differences in NEE, ER and GEP between treatments and over time

Our ER rates are within the same range as ER rates measured in similar systems. A study using experimental temperature and water level manipulations in a rich fen in Alaska (Chivers *et al.* 2009) reported ER rates varying approximately between -3.5 and -4 µmol m^{-2} s^{-1} depending on the treatment. The NEE rates of the same study were low compared to ours (approximately between -0.5 to 2 µmol m^{-2} s^{-1}) but GEP was close to ours with rates of approximately between 4 and 8 µmol m^{-2} s^{-1}. The vegetation and nutrient status of the peatland in the study of (Chivers *et al.* 2009) was different than in our study, however. The site on the study by (Treat *et al.* 2007), a poor fen, had similar vegetation to our site. The seasonal NEE rates varied between 5 and 7 µmol m^{-2} s^{-1}, ER rates between -4.8 and -7.5 µmol m^{-2} s^{-1} and GEP rates between 10.5 and 15 µmol m^{-2} s^{-1}, which again are within similar rage to our results. The study by Turetsky *et al.* (2002) reported lower ER rates than ours.

The GEP rates at a poor sedge-dominated fen have been reported to be higher in the drained conditions than at natural conditions (Strack *et al.* 2006), thus our results from sedge treatment plots support this. In general, the results from examining the

relationship of GEP and water level position vary. In some studies, GEP rates have been found to increase with lower water level (e.g. Laiho 2006; Ballantyne et al. unpublished). However, if the water level drops too low the plants may suffer from drought stress and their production decreases (Weltzin *et al.* 2000). The ER rates were all lower from high water level compared to low water level. The biggest difference between high and low water level ER rates was found in sedge plots, though none of these differences were statistically significant.

Many studies have found that water level is an important regulator of peatland CO_2 dynamics and that high water levels in general reduce CO_2 emissions, whereas low water levels increase them because the aerobic peat layer is thicker (Moore and Knowles 1989; Silvola *et al.* 1996; Goulden and Crill 1997; Komulainen *et al.* 1999; Whalen 2005; Chivers *et al.* 2009). For instance, a study conducted in a subalpine fen in Colorado (Chimner 2003) found the CO_2 emissions doubled when the water table was 0-5 cm below surface compared to a situation where it was 6-10 cm above the surface. A peatland restoration study at drained fen and bog sites in Finland (Komulainen *et al.* 1999) recorded CO_2 emissions from untreated plots to be twice as high as from rewetted plots. The ER rates also decreased from rewetted plots after all the vegetation was removed. In addition a laboratory study focusing on the influences of water levels on peatland CO_2 and CH_4 emissions found dried peatlands to release more CO_2 at least in the short term compared to the ones with high water level (Moore and Knowles 1989). Long-term water table drawdown was found to affect peatland CO_2 fluxes even 80 years after the disturbance in a study of (Ballantyne *et al.* unpublished) conducted on a peatland in Northern Michigan. The ER and GEP rates both decreased when water levels were raised approximately 10 cm and increased on the site where water level was lowered with approximately 15 cm. However, some long-term studies have shown an opposite result. The CO_2 emissions of a peatland, where water levels were lower, have not increased compared to high water level peatlands because of increased photosynthesis rates caused by lower water level (Flanagan and Syed 2011). In Finland, where many peatlands have

been drained for forestry, it has been discovered that many of the drained peatlands have continued to be carbon sinks after drainage due to increased production from the growing trees (Minkkinen *et al.* 2002).

A water manipulation study in an Alaskan bog also found that water table was not significant in predicting CO_2 emissions (Turetsky *et al.* 2002). Substrate quality and the properties of soil were found to be important among with hydrological conditions and temperature in soil respiration rates in a modeling study of C and N mineralization of northern wetlands (Updegraff *et al.* 1995). According to the study local variations in soil properties and wetland type should be taken into consideration when projecting the study results to a larger scale because they could have an effect on the soil respiration that can't be explained with hydrological and temperature conditions.

Vegetation and CO_2 dynamics

Ericaceous shrubs form a symbiosis with mycorrhiza fungi in their roots, which help them to scavenge nutrients from the soil (Largent *et al.* 1980; Andersen *et al.* 2010). Studies suggest that because of the efficient uptake of nutrients, mycorrhiza are strongly competitive and may prevent or at least restrict the saprophytes of the soil from using nutrients. This slows down the decomposition rate of peat (Read *et al.* 2004), which could lead to higher peat accumulation at *Ericaceae*-dominated peatlands compared to sedge-dominated peatlands. *Sphagnum* species, which are capable of living in highly nutrient poor conditions (Clymo 1970) are the primary peat formers in shrub-dominated bogs (Van Breemen 1995). Although some evidence of sedges having mycorrhiza has been found (Miller *et al.* 1999) C.*oligosperma* is not known to have any. The aerenchyma tissue of sedges helps them to bring oxygen from the atmosphere down to the rhizosphere and therefore accelerates the peat decomposition (Laine *et al.* 2000). The previous studies support that sedges are important in peatland CO_2 dynamics, and our results confirmed

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that their aboveground biomass increased in the plots where only sedges were growing. Yet, our results also imply that role of *Ericaceae* is influential because the removal of sedges didn't change any NEE, ER or GEP rates significantly compared to control plots, unlike the shrub removal did.

The *Ericaceae* removal caused NEE, ER and GEP all to decrease compared to sedge removal and control plots, whereas sedge removal plots were not significantly different compared to control plots. The results imply that Ericaceous shrubs may have an important role in CO_2 dynamics in this type of peatland. It is also possible, that the amount of biomass removed in the *Ericaceae* removal is more important than the species themselves. The shrub removal also caused more damage to the soil than the sedge removal. The lowered NEE and GEP rates of sedge treatment compared to the other plots, could be caused by a loss of plant biomass (Potvin et al. unpublished data), which reduces the amount of photosynthesizing plants. Plant biomass is related to the photosynthesis rate of a plant (Lambers *et al.* 2008). However, if we look at the aboveground biomass of *C. oligosperma* in both water levels of sedge plots (Table 6) we see that the biomass of both living and senesced sedges is almost 70 % greater in low water level than high water level. Sedges have been shown to increase their above and belowground biomass and production in low water levels if shrubs are not present (Strack *et al.* 2006). Altogether the sedge biomass, including living and senesced plants, of sedge plots was almost 90 % greater than the sedge biomass of control plots in 2012. The removal of *Ericaceae* may have increased the saprophyte activity of the peat and released nutrients for sedges to use up, which results in their increased aboveground biomass in the sedge plots. As Table 2 shows the percentage cover of *C. oligosperma* was higher on low water level bins compared to high water level. The sedge coverage was, however, largest in the low water level control plots. The aboveground biomasses of *Ericaceae* did not differ as radically between different water levels: the biomass of high water level *Ericaceae* plots was approximately 2 % smaller than low water level *Ericaceae* plots.

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There were no radical differences between the control plots and *Ericaceae* treatment either, although the shrub biomass was about 7 % higher in *Ericaceae* treatment plots.

The autotrophic respiration rates of different plant groups were not measured in this study and previous studies have shown the ER rates of mosses can be high. A study on CO_2 exchange of the moss surface conducted in black spruce forest Goulden and Crill (1997) showed the respiration from moss surface can account for 50-90 % of the respiration of the whole forest. In the study feather mosses had higher respiration rates than *Sphagnum*, but this was believed to occur because the feather moss sites had black spruce growing on them and hence received carbon input from the trees, whereas *Sphagnum* mosses were growing on more open areas. By comparing the GEP rates of different vegetation treatments from 2012 it was possible to estimate that mosses accounted for approximately 65.5 %, shrubs 29.3 % and sedges 5.2 % to GEP. In the study of (Goulden and Crill 1997) mosses contributed 10-50 % of whole forest GEP, depending on the growing conditions. The lowest rates were detected from shaded sites. The moss GEP rates have been shown to correlate negatively with the leaf area index (LAI) of vascular plants on the same site (Douma *et al.* 2007).

Environmental parameters and NEE, ER and GEP

Ecosystem respiration has been shown to be dependent on temperature (Updegraff *et al.* 1995; Moore *et al.* 1998). Warming manipulation studies have shown the ER rates to increase along with the warmer temperature (Updegraff *et al.* 1995; Silvola *et al.* 1996). In our study air temperature correlated with ER rates but it was the best possible predictor only for ER and GEP rates of low water level *Ericaceae* plots in 2012 and high water level *Ericaceae* plots in 2011. Peat temperature was correlated with ER rates in all the other treatments except high and low water level sedge plots in 2011, which could not be predicted by any of the environmental parameters. The warmest peat

temperatures are the ones that best explain the ER values in the treatments where correlation was found (Figure 2).

The correlations between peat temperatures and NEE were few and they differed between 2011 and 2012. As Figure 2 shows some of the lower measuring points had higher temperatures than the point closer to the surface in 2012, which was not the case in 2011. The height of water levels in 2012 (Figure 1) could explain why the peat was warmest at 20 cm below surface in most treatments and this temperature correlated so well with the ER rates. During the warmest time of the summer the water levels in both high and low water level bins were at their lowest. The low water level plots had their water level below 20 cm peat depth for quite a long time period, from July until the end of the samplings, except for a couple of days in July when it was at 20 cm. From mid-July until the end of the samplings the lowest water levels for low water level plots were above 20 cm but mostly below 10 cm and at some point even lower than 15 cm. This means that the 20 cm temperature sensor was the highest temperature sensor under water and inside saturated peat during most of the summer. The wet peat reserves heat better than dry peat, because its thermal conductivity is higher than that of dry peat (Kujala *et al.* 2008), so the highest parts of saturated peat were the warmest. The top 5 cm peat layer was the most susceptible to air temperature and therefore it was warmer than the peat at 10 cm below surface, which was at times saturated and at times dry. In 2011 such a pattern with the mean peat temperatures did not occur. The temperatures decreased the deeper they had been measured during the sampling season. This was probably because the water level treatments lasted for such a short time before the water levels were elevated again.

According to our results air and peat temperatures were positively correlated with each other. Other studies have reported similar results (Turetsky *et al.* 2002). Turetsky et al. (2002) found a negative correlation between water table levels and air temperature.

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The mean air temperature in 2012 was 1.0 °C higher than in 2011. Air temperature does not explain the flux rates in most cases, but it has an effect on the peat temperatures. The mean peat temperatures of all treatments together were higher in 2012 at all depths compared to 2011 temperatures expect for the two top measuring points: at 5 cm below surface temperatures were the same in both years and in 10 cm the temperature of 2012 was 0.5 °C lower than it was in 2011.

Both years 2011 and 2012 had approximately same amount of rainy days during the sampling season and the sum of rainfall was similar as well. Sampling during the rain was avoided because the EGM-4 does not hold water. Average wind speeds were almost equal in both years. Windy days were avoided for sampling, because the accuracy of chamber measurements declines due to pressure changes inside the chamber caused by wind turbulence (Davidson 2002). However, there may be small differences between the flux rates from 2011 and 2012 because there were some issues with the sealing of the bins to the chamber in 2011, so small leakages are possible. In the beginning of 2012 the seals were replaced with better, heavy duty cell foam to diminish the possibility of leakages. The average PAR rates for both 2011 and 2012 are similar, though there might be some changes between different days as cloudy days were not completely avoided. However, the sampling days were chosen so that the conditions stayed as similar as possible during the day.

Conclusions

Air temperature affected peat temperature and peat temperature was positively correlated with ER rates, which has been the case in previous studies as well (Turetsky *et al.* 2002). Some correlations were found in between NEE and GEP rates from low water level sedge plots and water level position in 2011, but otherwise the water level treatments had no significant effect on NEE, ER or GEP by year. The

difference caused by vegetation treatments could easily be observed and water level also caused some changes in 2012 though they were not statistically significant. This differs from previous study results, which have reported water level to influence NEE, ER and GEP rates (Komulainen *et al.* 1999; Chimner 2003; Chivers *et al.* 2009). There has been some research on the importance of substrate quality and wetland type, which should be taken into consideration along with hydrology and temperature of the site (Updegraff *et al.* 1995).

Removing *Ericaceae* decreased NEE, ER and GEP rates rather dramatically compared to control plots and those where sedges were removed, although the aboveground biomass of sedges was found to be higher in sedge plots than control plots. It was also higher on low water level compared to high water level, like previous studies conducted in similar conditions have shown (Strack *et al.* 2006). The competition for nutrients between sedges and shrubs in the control plots may hold back the sedge growth. Shading could also be a reason to this as well as the water level: the differences between GEP rates between high and low control plots were relatively small. Removing *Ericaceae* increased sedge growth, but lowering the water level enhanced this effect. The increased growth of sedges in sedge plots could not compensate the loss of plant material resulted from *Ericaceae* removal, which is probably why the gas flux rates of sedge plots were low compared to other treatments. Sedge removal did not have a significant effect on NEE, ER or GEP compared to control plots, which confirms the important role of *Ericaceae* in peatland CO_2 cycle. The data for this study was collected during a 3-year time period, of which the last year is the first one showing the actual effects of the different treatments. This is a relatively short time period, but as a long-term study on a Northern Michigan peatland (Ballantyne *et al.* unpublished) found, the short-term studies may be accurate in predicting the long-term effects.

Tables

Table 1.The correlations between air temperature and peat temperatures on different depths below surface (5, 10, 20, 40 and 80 cm) by treatment in 2011 and 2012. H= high water level, L= low water level, S=*Ericaceae* removed, E=sedges removed, C=control. The p-value is in parentheses.

2011	T5	T10	T20	T40	T80
Air temperature **HS**	0.95 (<0.001)	0.93 (<0.001)	0.91 (<0.001)	0.85 (0.001)	0.79 (0.002)
LS	0.95 (<0.001)	0.93 (<0.001)	0.90 (<0.001)	0.82 (0.001)	0.78 (0.002)
HE	0.93 (<0.001)	0.93 (<0.001)	0.89 (<0.001)	0.78 (0.002)	0.77 (0.003)
LE	0.93 (<0.001)	0.93 (<0.001)	0.90 (<0.001)	0.84 (0.001)	0.79 (0.003)
HC	0.94 (<0.001)	0.92 (<0.001)	0.89 (<0.001)	0.80 (0.002)	0.78 (0.002)
LC	0.93 (<0.001)	0.90 (<0.001)	0.89 (<0.001)	0.80 (0.001)	0.78 (0.002)

2012	T5	T10	T20	T40	T80
Air temperature **HS**	0.88 (<0.001)	0.84 (0.001)	0.87 (<0.001)	0.86 (<0.001)	0.83 (0.001)
LS	0.89 (<0.001)	0.87 (<0.001)	0.88 (<0.001)	0.87 (<0.001)	0.83 (0.001)
HE	0.88 (<0.001)	0.85 (<0.001)	0.85 (<0.001)	0.85 (<0.001)	0.84 (0.001)
LE	0.88 (<0.001)	0.85 (<0.001)	0.87 (<0.001)	0.88 (<0.001)	0.84 (0.001)
HC	0.89 (<0.001)	0.86 (<0.001)	0.88 (<0.001)	0.86 (<0.001)	0.84 (0.001)
LC	0.89 (<0.001)	0.84 (<0.001)	0.88 (<0.001)	0.86 (<0.001)	0.84 (0.001)

Table 2. Mean percentage cover of plant species on different treatments in 2010-2012

	High water level			Low water level		
2010	**Sedge**	**Ericaceae**	**Control**	**Sedge**	**Ericaceae**	**Control**
Carex oligosperma	32.0%	19.9%	28.5%	48.8%	32.0%	36.7%
Chamaedaphne calyculata	50.0%	42.2%	36.7%	51.2%	39.5%	29.3%
Kalmia polifolia	19.1%	32.0%	29.7%	56.3%	37.1%	41.4%
Ledum groenlandicum	1.2%	0.0%	0.0%	3.5%	0.4%	0.0%
Vaccinium oxycoccos	70.3%	100.8%	84.4%	112.9%	103.1%	91.0%
Andromeda polifolia	0.4%	0.0%	0.0%	0.0%	0.0%	0.8%
Polytrichum strictum	27.7%	21.9%	31.6%	35.5%	23.4%	20.7%
Sphagnum fuscum	23.8%	17.6%	22.7%	9.0%	19.9%	14.1%
Sphagnum magellanicum	12.1%	13.3%	15.2%	10.2%	10.2%	11.7%
Sphagnum rubellum	62.1%	61.7%	54.7%	69.9%	57.8%	60.9%
Sphagnum species	0.4%	0.0%	0.0%	0.4%	0.0%	0.0%
2011						
Carex oligosperma	34.4%	0.4%	14.5%	37.9%	0.4%	18.4%
Chamaedaphne calyculata	1.2%	26.2%	34.0%	0.4%	43.4%	24.2%
Kalmia polifolia	1.6%	28.5%	23.0%	0.0%	32.4%	24.2%
Ledum groenlandicum	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Vaccinium oxycoccos	4.3%	91.0%	47.3%	11.3%	64.8%	49.2%
Andromeda polifolia	0.0%	0.0%	0.0%	0.0%	0.4%	0.0%
Polytrichum strictum	26.6%	15.6%	20.7%	32.8%	26.6%	20.7%
Sphagnum fuscum	33.6%	38.3%	23.8%	18.0%	38.7%	23.8%
Sphagnum magellanicum	8.6%	10.5%	17.2%	7.4%	8.6%	9.0%
Sphagnum rubellum	53.9%	56.6%	60.2%	55.9%	50.8%	65.2%
Sphagnum species	2.0%	0.4%	0.4%	2.7%	0.8%	1.2%
2012						
Carex oligosperma	17.6%	0.0%	14.8%	19.5%	0.0%	27.0%
Chamaedaphne calyculata	0.0%	30.1%	28.5%	0.0%	48.4%	30.5%
Kalmia polifolia	0.0%	16.4%	22.7%	0.0%	30.1%	25.4%
Ledum groenlandicum	0.0%	0.0%	0.0%	0.0%	0.4%	0.0%
Vaccinium oxycoccos	0.0%	45.3%	33.2%	0.0%	69.1%	57.0%
Polytrichum strictum	37.5%	8.2%	10.9%	49.6%	25.0%	16.0%
Sphagnum fuscum	18.4%	18.8%	12.1%	23.8%	33.2%	25.8%
Sphagnum magellanicum	10.9%	21.9%	19.1%	23.0%	17.6%	17.2%
Sphagnum rubellum	78.9%	74.2%	75.8%	56.6%	51.2%	57.4%
Sphagnum species	1.2%	0.0%	0.0%	1.2%	0.4%	0.0%

Table 3. Aboveground biomass (g/m2) living/senesced plants for different plots in 2012. If the value is missing, there were no senesced plants of said species. The water level was high in bins 1, 2, 3, 8, 10, 12, 15, 16, 17, 19, 20 and 21 and low in bins 4, 5, 6, 7, 9, 11, 13, 14, 18, 22, 23 and 24.

S plots:	1	5	7	12	17	18	21	23
C.oligosperma	9.2/5.2	6.3/14.2	33.2/28.3	22.7/11.8	23.5/11.0	51.3/16.7	0.5/13.0	6.7/6.9

E plots:	2	6	10	11	13	16	20	22
C.calyculata	120.8/-	99.1/-	79.5/-	76.5/-	75.1/-	63.0/-	134.6/-	109.1/-
K. Polifolia	15.9/-	26.3/-	19.4/-	34.1/-	20.7/-	38.1/-	30.0/-	72.8/-

C plots:	3	4	8	9	14	15	19	24
C.oligosperma	0.8/0.6	29.8/10.1	20.6/7.2	4.4/2.4	3.7/2.1	0.5/2.4	28.1/4.0	16.2/5.7
C.calyculata	131.1/-	30.2/-	64.2/-	101.7/-	138.7/-	62.8/-	125.0/-	71.6/-
K. Polifolia	23.5/-	34.6/-	18.6/-	17.3/-	28.9/-	40.0/-	28.0/-	26.1/-

Table 4. The correlations of CO_2 flux of the control plots and air temperature and water level for 2011 after starting the treatments and 2012. The p-value is in the parenthesis. Bold values denote p-values below 0.05.

2011		Air temperature	Water level (cm below surface)
High wt	NEE	0.54 (0.059)	0.42 (0.11)
	ER	**0.73 (0.015)**	**0.69 (0.021)**
	GEP	**0.71 (0.017)**	**0.58 (0.048)**
Low wt	NEE	0.022 (0.75)	0.00 (0.99)
	ER	**0.79 (0.007)**	**0.68 (0.022)**
	GEP	0.013 (0.81)	0.036 (0.68)
2012			
High wt	NEE	0.25 (0.12)	0.008 (0.80)
	ER	**0.67 (0.002)**	0.22 (0.14)
	GEP	**0.57 (0.007)**	0.096 (0.35)
Low wt	NEE	0.32 (0.07)	0.067 (0.44)
	ER	**0.80 (<0.001)**	0.16 (0.23)
	GEP	**0.75 (0.001)**	0.15 (0.24)

Table 5. Within-subjects effects of the repeated measures analysis. Greenhouse-Geisser corrected values were used because sphericity could not be assumed with p-value 0.05.

		Type III Sum of Squares	df	Mean Square	F	P-value
NEE						
Year	Greenhouse-Geisser	7.168	1.265	5.668	2.753	.104
Year * Water Table Level	**Greenhouse-Geisser**	.155	1.265	.123	.060	.863
Year * Vegetation treatment	Greenhouse-Geisser	36.669	2.529	14.499	7.041	**.002**
Year * Water Table Level * Vegetation Treatment	**Greenhouse-Geisser**	.709	2.529	.280	.136	.914
ER						
Year	Greenhouse-Geisser	78.673	1.160	67.841	53.353	**<.001**
Year * Water Table Level	**Greenhouse-Geisser**	.272	1.160	.235	.185	.709
Year * Vegetation treatment	Greenhouse-Geisser	4.709	2.319	2.030	1.597	.225
Year * Water Table Level * Vegetation Treatment	**Greenhouse-Geisser**	2.961	2.319	1.277	1.004	.394
GEP						
Year	Greenhouse-Geisser	121.878	1.410	86.461	38.485	**<.001**
Year * Water Table Level	**Greenhouse-Geisser**	.105	1.410	.074	.033	.924
Year * Vegetation treatment	Greenhouse-Geisser	63.166	2.819	22.405	9.973	**<.001**
Year * Water Table Level * Vegetation Treatment	**Greenhouse-Geisser**	2.163	2.819	.767	.342	.784

Table 6. Between-subject effects of the repeated measures analysis.

	Type III Sum of Squares	df	Mean Square	F	P-value
NEE					
Water Table Level	.661	1	.661	.264	.614
Vegetation Treatment	23.163	2	11.582	4.618	**.024**
Water Table Level * Vegetation Treatment	2.650	2	1.325	.528	.599
ER					
Water Table Level	1.032	1	1.032	1.282	.272
Vegetation Treatment	.636	2	.318	.394	.680
Water Table Level * Vegetation Treatment	1.794	2	.897	1.114	.350
GEP					
Water Table Level	.008	1	.008	.002	.964
Vegetation Treatment	31.630	2	15.815	4.391	**.028**
Water Table Level * Vegetation Treatment	5.122	2	2.561	.711	.504

Figures
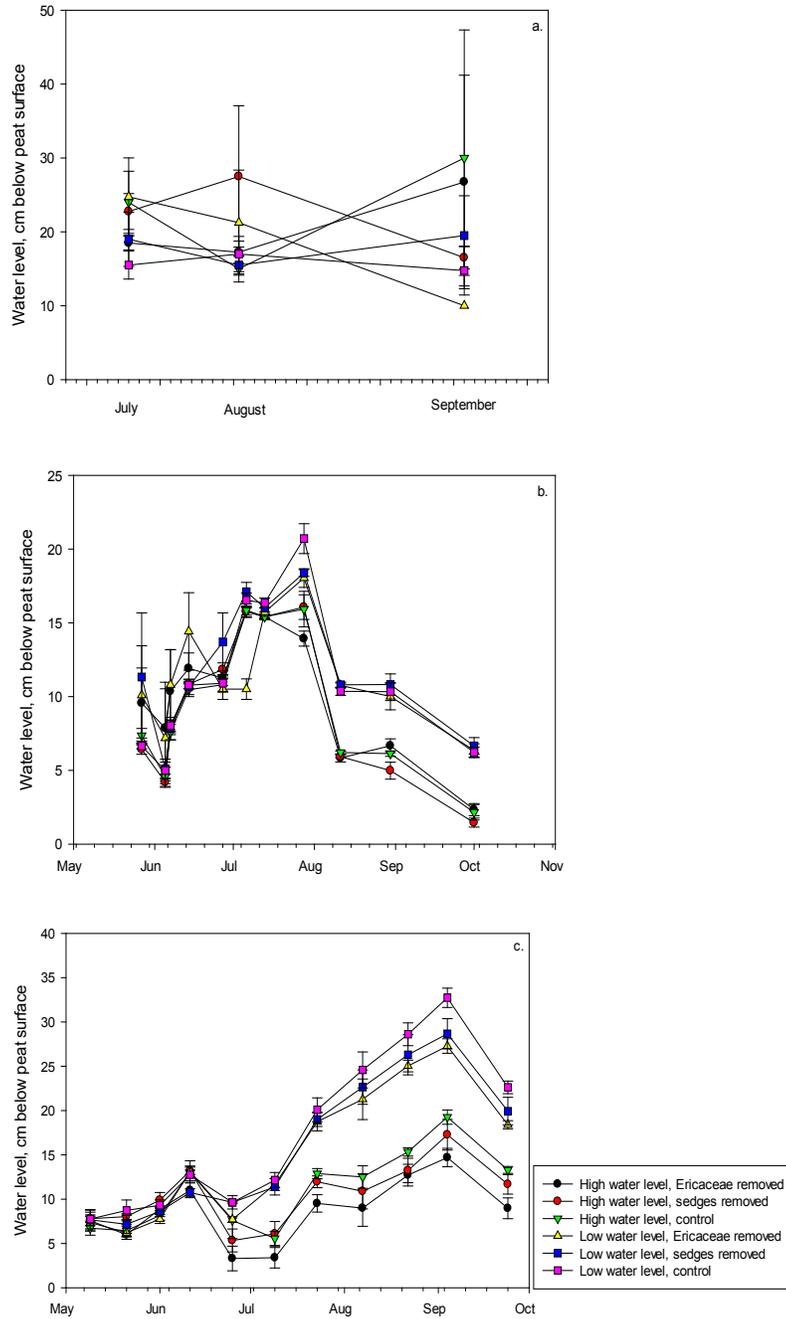
Figure 1. Water levels and treatment combinations in 2010 (a.), 2011(b.) and 2012 (c.).
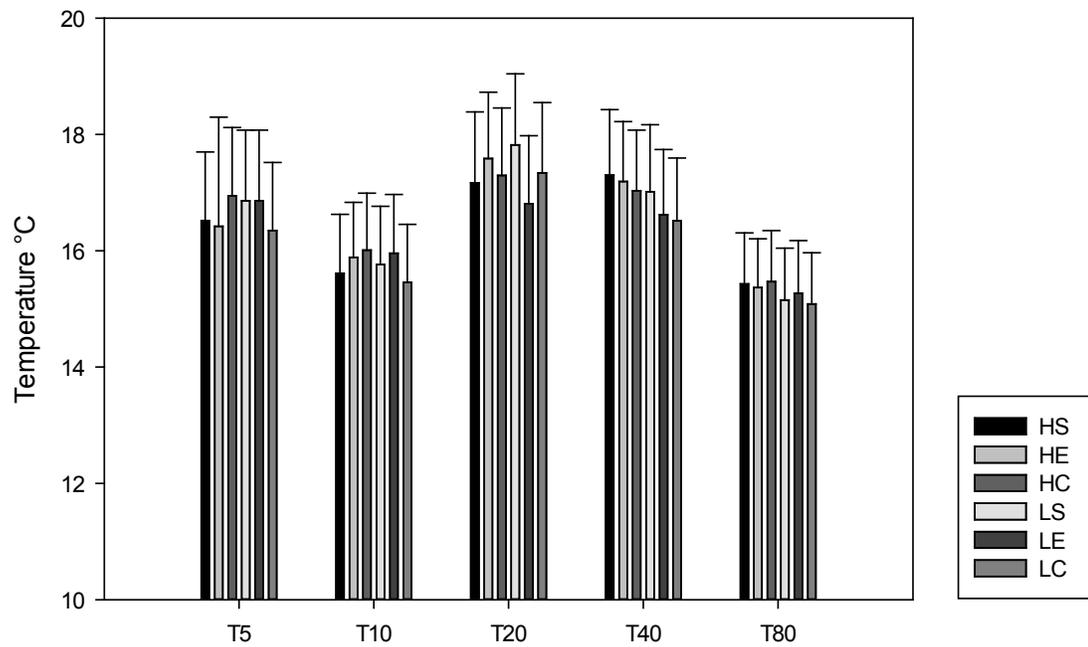
Figure 2. Peat temperatures of different treatments in different depths (5-80 cm below surface). H= high water level, L= low water level, S= Ericaceae removed, E= sedges removed, C= control plots. Mean values based on the days samplings were performed in 2012.
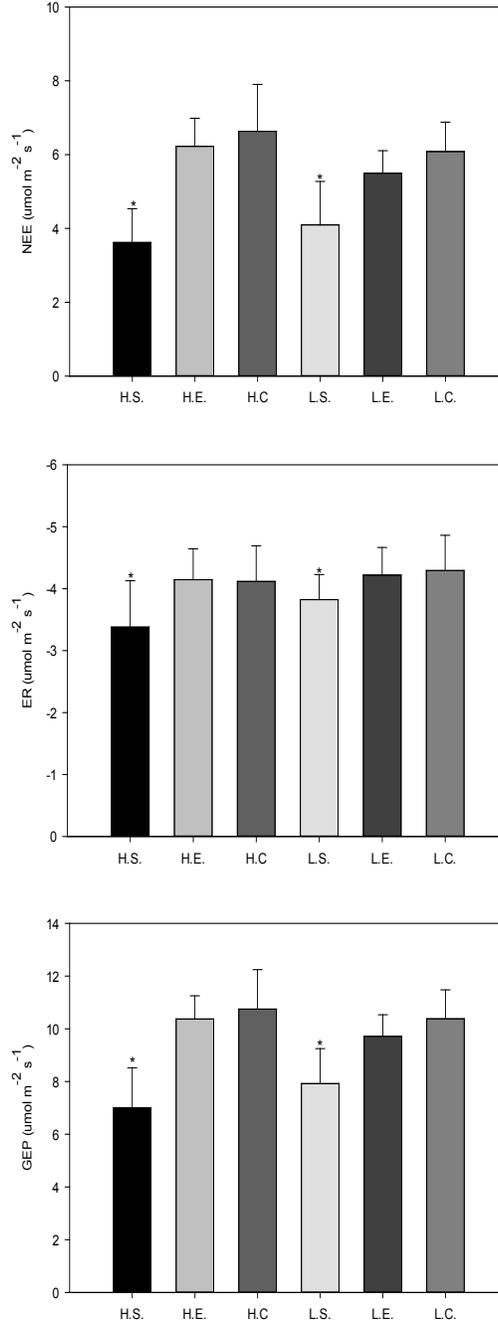
Figure 3. Different treatments and their mean NEE, ER and GEP rates in 2012. H refers to high water level and L to low water level. S is where *Ericaceae* have been removed, E where sedges were removed and C stands for control plots. * denotes sedge treatment is significantly different from *Ericaceae* and control vegetation treatments.
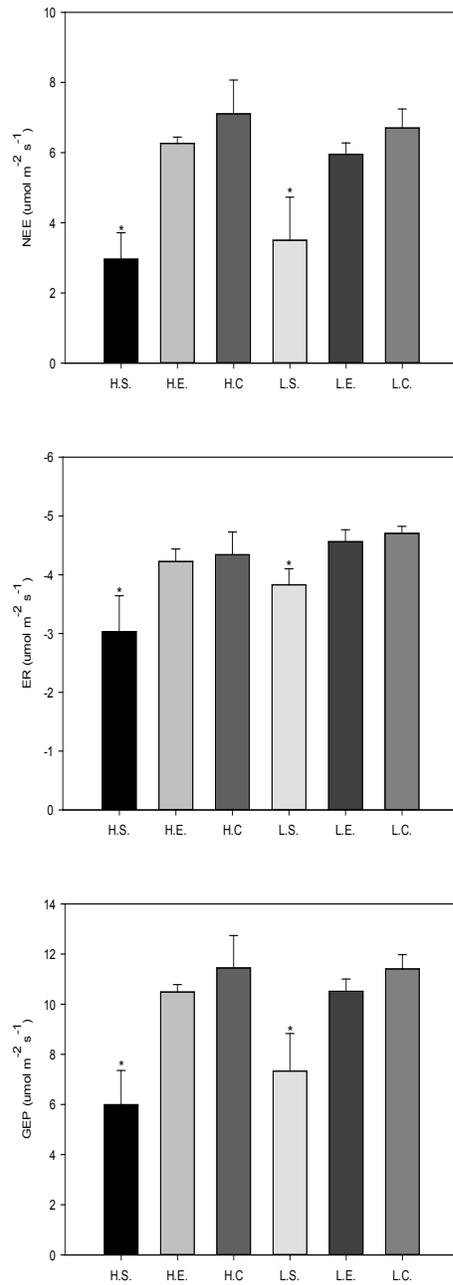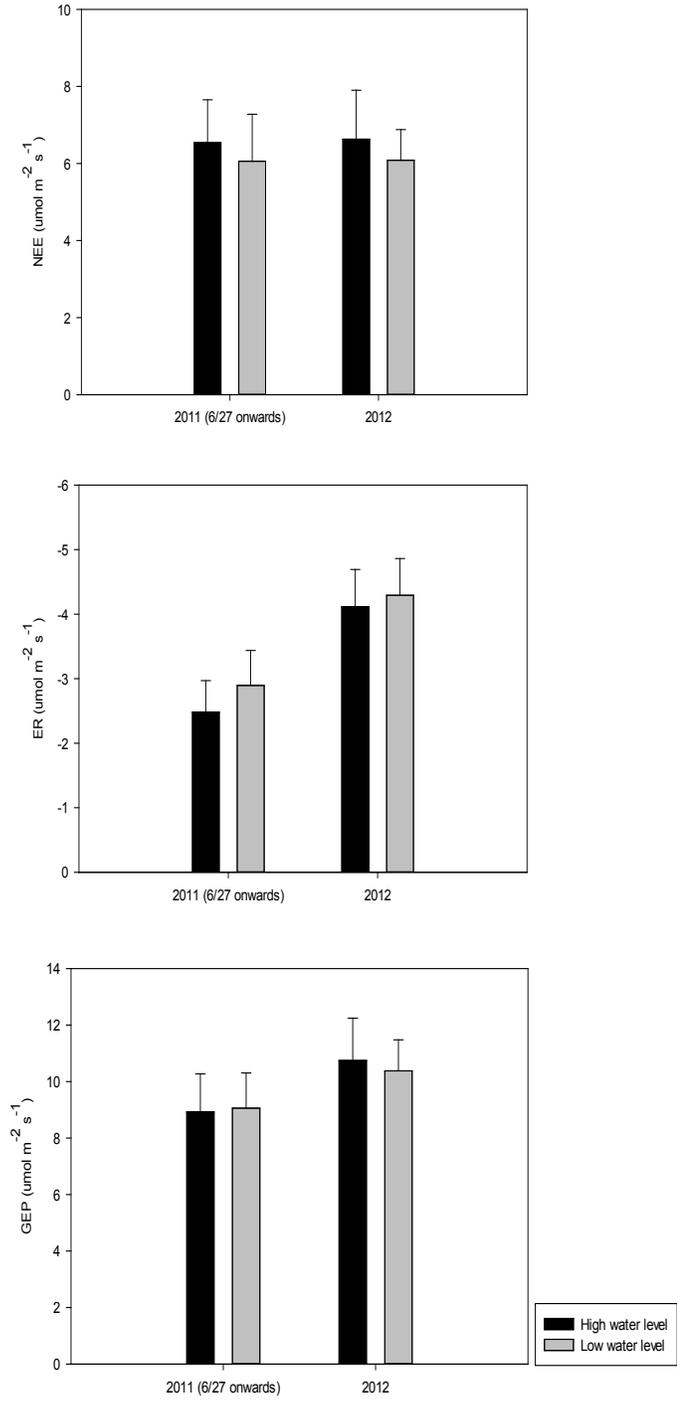
Figure 4. Different treatments and their NEE, ER and GEP rates means of 2012 July, August and September. H refers to high water level and L to low water level. S is where *Ericaceae* have been removed, E where sedges were removed and C stands for control plots. * denotes sedge treatment is significantly different from *Ericaceae* and control vegetation treatments.

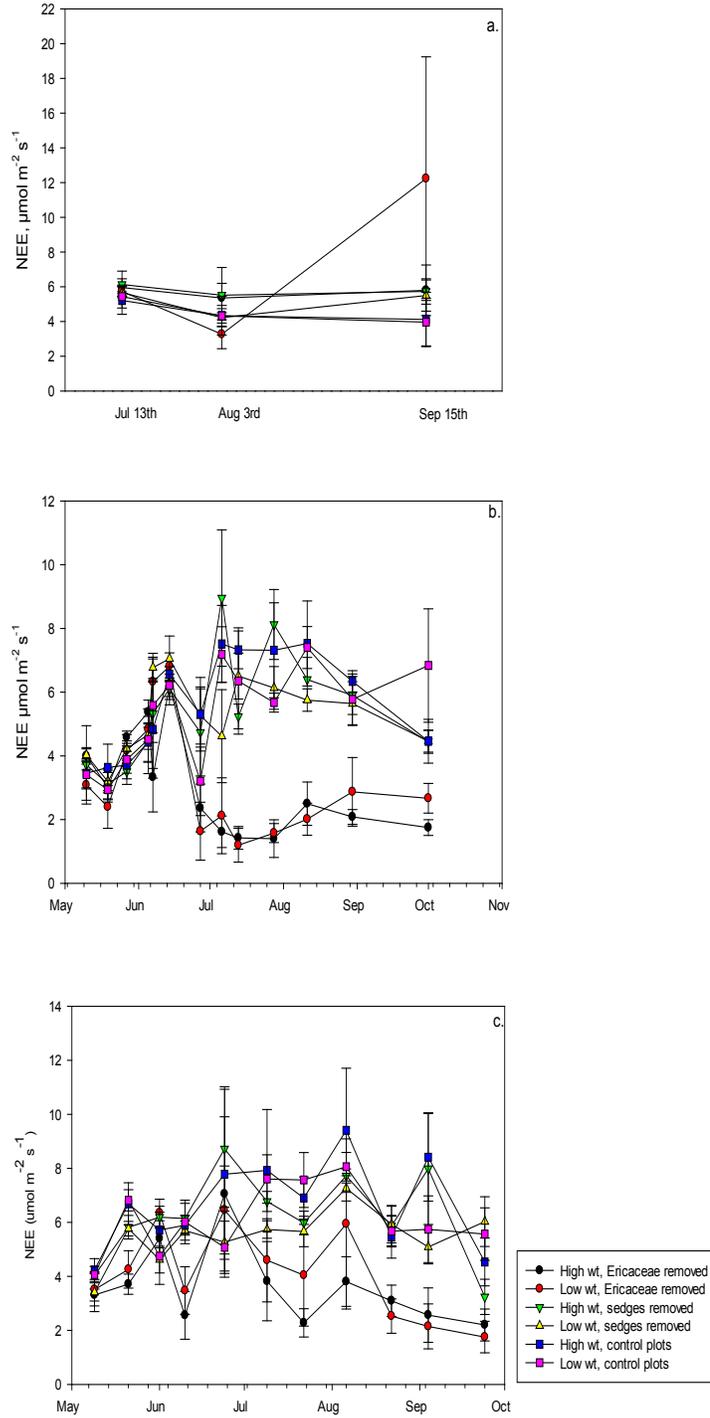Figure 5. The mean NEE, ER and GEP of the control plots in 2011 after starting the treatments and 2012.

Figure 6. NEE of different water level and vegetation treatment combinations on sampling days of 2010 (a.), 2011 (b.) and 2012 (c.).
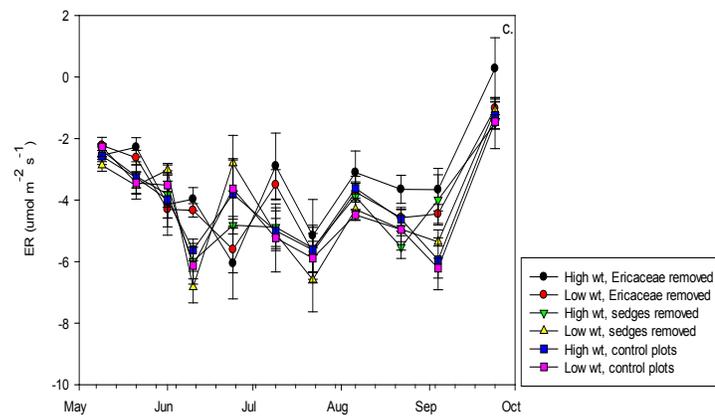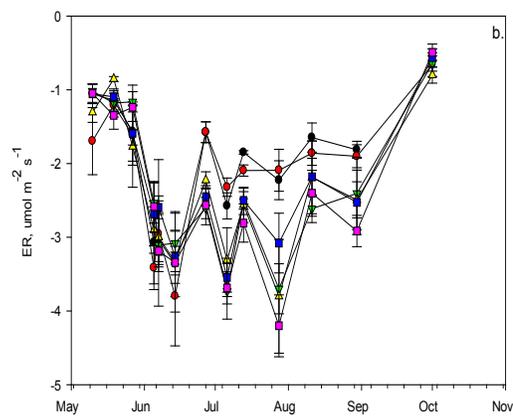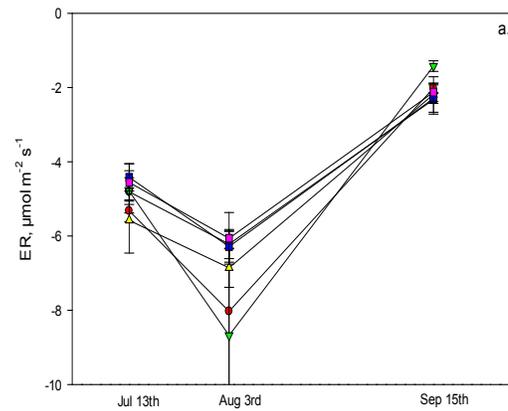
Figure 7. ER of different water level and vegetation treatment combinations on sampling days of 2010 (a.), 2011 (b.) and 2012 (c.).
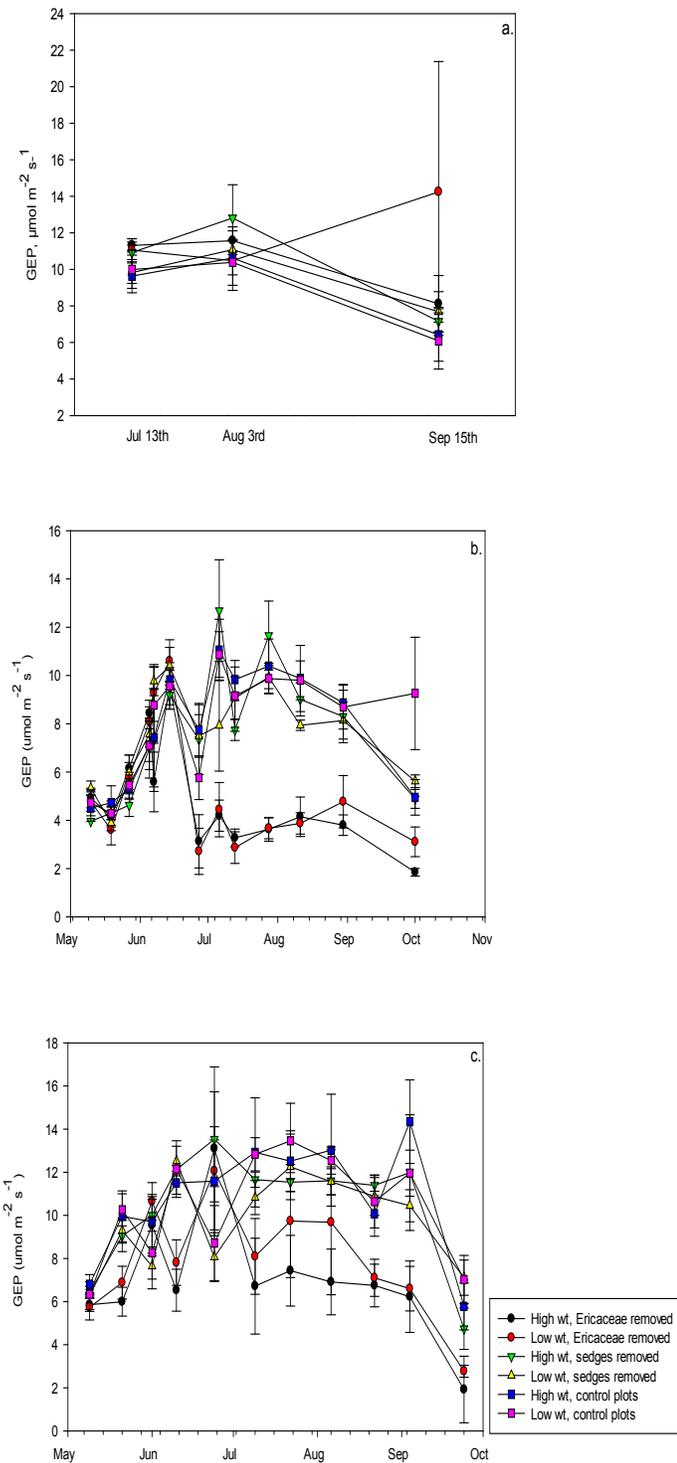
Figure 8. GEP of different water level and vegetation treatment combinations on sampling days of 2010 (a.), 2011 (b.) and 2012 (c.).

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