AGRICULTURAL DRAINAGE IMPACTS ON THE PHOTOSYNTHETIC CAPACITY AND WATER USE EFFICIENCY OF BOREAL PEATLANDS

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A Thesis submitted to the

school of Graduate Studies in partial fulfillment of the

requirements for the degree of

Master of Science in Environmental Science

Memorial University of Newfoundland

February 2018

St. John's, Newfoundland and Labrador

Abstract

Even though boreal peatlands cover a relatively small area of the Earth's surface compared to forested areas, they are known to contain approximately a quarter of the total organic carbon in the soil. As a globally important store of carbon and terrestrial surface water, natural peatland ecosystems are known as a sink for atmospheric carbon dioxide (CO_2) since the rate of carbon accumulation through photosynthesis exceeds the rate of decomposition. The slow decomposition rate and the subsequent accumulation of carbon under the anoxic condition are mainly due to the high water table depth (WTD) in peatland ecosystems. However, peatlands have been drained for agricultural purposes.

Peatland drainage for agricultural purposes helps to improve soil aeration condition by deepening the water table depth. This keeps the soil dry and improves plant growth and development. Since plants control their stomata in order to optimize the trade-off between the amount of carbon absorbed and the amount of water loss, I anticipated that the improved plant growth and development through drainage could also impact on the evapotranspiration rate (ET) (a critical component in the water balance of terrestrial ecosystems) and hence, the water use efficiency (WUE) of peatland ecosystems. Therefore, this study was aimed to investigate the effects of peatland drainage for agriculture on the photosynthetic capacity (represented as gross primary productivity (GPP)) and the WUE of boreal peatlands, on a plot and site scale. Here, a comparison

was made between agriculturally drained and a natural peatland during the 2016 growing season.

GPP was found to be significantly higher among the subplots affected by drainage compared to the hummock and hollow subplots at the natural site. Site average showed that, during the 2016 growing season, GPP ($mgCO_2/m^2/s$) was significantly higher at the drained site (0.468 ± 0.04) compared to the natural site (0.093 ± 0.01) (p < 0.001). The seasonal pattern of GPP was linked to WTD. WTD variation and its effect on the physical and hydrothermal properties of the peat (e.g., electrical conductivity (EC) and peat temperature at 5cm depth (T_5)), was seen to account for most of the variation in GPP at the drained subplots and site relative to the natural site. Respectively, a decrease in soil moisture (SM), EC, and increase in T_5, significantly explained ~ 44%, 49% and 27% of variation in GPP at the drained site. The combined effect of EC and T_5 accounted for approximately 61% of the variation in GPP at the drained site. Growth in the hollow subplot was also seen to be at its peak when the WTD was at its deepest point. However, the deepest WTD seen at the hummock subplot did not lead to any production increase. This was attributed in part to the extremely lower water table depth at the hummock and its effect on water availability for plant growth and development, and the inability of the peat makeup to hold on to water during the summer when the water level dropped.

In spite of statistically similar ET rate between the hummock and hollow subplots, the results showed a higher WUE (i.e., the ratio of GPP to ET) when GPP is high. However, when comparing the drained and natural sites, higher ET

rate at the drained site still resulted in a higher WUE due to its significantly higher GPP rate, making GPP the primary controller of WUE. WUE ($mgCO_2/mgH_2O$) was significantly higher (0.047 ± 0.01) at the drained site relative to the natural site (0.005 ± 0.00). Between the hummock and hollow subplots, WUE ($mgCO_2/mgH_2O$) was significantly higher at the hollow subplot (0.010 ± 0.001) compared to the hummock subplot (0.005 ± 0.001). No significant difference in WUE was found among the plant functional types (PFTs) as GPP was statistically the same for the sedge, shrub and the grass subplots at the drained site. This study suggests that land use changes, microforms and PFTs would be significant in regulating the carbon and hydrological cycle in peatland ecosystems, and thus land use practices, microforms and PFTs need to be explicitly parameterized in modeling the carbon and hydrological cycle in peatland ecosystems.

Acknowledgement

Above all, my profound gratitude goes to the almighty God, who in his wisdom has granted me the strength, knowledge and wisdom since the inception of this work.

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List of abbreviations and symbols

ABS	Acrylonitrile butadiene styrene
ANOVA	Analysis of variance
CH_4	Methane
CO_2	Carbon dioxide
DOC	Dissolved organic carbon
DOY	Day of year
EC	Electrical conductivity
ER	Ecosystem respiration
ET	Evapotranspiration
GHG	Greenhouse gas
GPP	Gross primary production
GtC	Gigatons of carbon
H_2O	Water (water vapour)
MLR	Multiple linear regression
NEE	Net ecosystem carbon dioxide exchange
PAR	Photosynthetically active radiation
PFT	Plant functional type
SM	Soil moisture
PVC	Polyvinyl chloride
SE	Standard error
T_5	Soil temperature at 5cm depth

TN	Total nitrogen
WTD	Water table depth
WUE	Water use efficiency

1. Introduction

1.1 Background

Boreal peatlands are known to contain roughly 25% of the total organic soil carbon while covering only 3% of the earth's land surface (Wu, 2012; Turunen et al., 2002; Gorham, 1991). The total carbon pool in northern peatlands is estimated to be 547 gigatonnes of carbon (GtC) (Yu et al., 2010) which is about 90% of the global total peatland carbon of 612 GtC accumulated since the last glacial maximum (Yu, 2011). Peatlands interact with the climate system through the long-term accumulation of carbon dioxide (CO_2) from the atmosphere, and release of methane (CH_4) (Frolking and Roulet, 2007). Natural peatlands accumulate atmospheric carbon (i.e. they are a carbon sink) since the rate of biomass production through photosynthesis exceeds the rate of decomposition (Turunen et al., 2002; Armentano and Menges, 1986; Frolking et al., 1998). Therefore, peatlands are an important component of the global carbon cycle (Armentano and Menges, 1986). Slow decomposition rate of organic material under an anoxic condition leads to carbon accumulation. Also, the anoxic condition due to shallow water table depth (WTD) makes the system a source of CH_4 (Drösler et al., 2008). The comparatively long residence time of this carbon pool (organic material) makes it a crucial sink for carbon (Post et al., 1982). However, human disturbance (e.g. peatland drainage for agriculture), via changes in hydrology and vegetation composition, can cause a decrease in soil carbon storage and in some cases, has converted peatlands into a carbon source

(Xing et al., 2016; Roulet, 2000; Armentano and Menges, 1986). According to Charman et al. (2015), future climate change may also increase the carbon sink ability of peatlands or may become a source.

Peatland ecology is strongly influenced by hydrology (Siegel and Glaser, 2006) as hydrology controls most of the biogeochemical and ecological functions of the peatland ecosystem (Vitt, 2006). Although other factors such as climate, chemistry, substrate and vegetation/flora affect how peatlands function (Vitt, 2006), hydrology remains the critical factor in determining peatland ecosystem development and function. Variation in the source and amount of water are critical in determining nutrient and pH levels, and species composition (Chapin et al., 2004; Bridgham et al., 1998). A number of studies (e.g. He et al., 2016; Bragg and Tallis, 2001; Arnold et al., 2005; Evans et al., 1999) have reported the effects of hydrological changes on peatland ecosystems and their role as a carbon sink or source. Laine et al. (1995) have reviewed the ecological effects associated with hydrological change as a result of drainage on the chemical (e.g., the oxidation of organic and inorganic compounds) and physical properties (e.g., initiation of subsidence) of the exposed peat, microbial activity, biodiversity, flora and fauna changes. According to Rydin and Jeglum (2013, p. 148), "*understanding the hydrology of peatlands is fundamental to the subject of peatland habitat, as it is probably the single most important condition influencing peatland ecology, development, functions, and processes*". Bridgham et al. (2008) concluded that different peatlands will either become a sink or source of

carbon following changes in hydrology until an appropriate water-level is reached. This shows the importance of hydrology in peatland ecosystems.

Peatlands are drained to lower the water table to improve soil aeration. This keeps the soil dry and improves plant growth and productivity (Hillman, 1992; Stanek, 1977; Hillman, 1987). However, how peatland drainage for agriculture, and the introduction of pasture, directly affects the photosynthetic capacity of a boreal bog on a plot scale, with different dominant plant functional types (PFTs) is understudied. Several studies (e.g., Lafleur et al., 2003; Strachan et al., 2016; Roulet et al., 2007; Nilsson et al., 2008; Dragoni et al., 2007; Loescher et al., 2003; Schmid et al., 2003) have been conducted to examine ecosystem productivity and the net ecosystem carbon dioxide exchange (NEE), based on eddy covariance measurements. Several plot scale studies using chamber measurements (e.g., Pelletier et al., 2011; Strack and Waddington, 2007; Riutta et al., 2007) have examined natural and managed WTD variation and its effects on productivity, respiration and NEE in peatland ecosystems. Pelletier et al. (2011) reported a variation in photosynthesis and respiration across a gradient of microforms (i.e., high hummock, low hummock, lawn and hollow) with a naturally raised WTD. According to Pelletier et al. (2011), WTD closer to the surface was responsible for the increase in NEE on the high and low hummocks by increasing the maximum photosynthesis rate but reducing the NEE of the hollow microform, by flooding the surface vegetation and reducing the maximum photosynthesis. Riutta et al. (2007) reported an increase in respiration and a decrease in gross primary productivity (GPP), and hence the NEE in their

boreal oligotrophic fen ecosystem, with *Sphagnum* mosses being the most affected by water table drawdown. On the other hand, Strack and Waddington (2007) did not find any significant difference in NEE between their natural and experimental sites in a similar ecosystem (i.e., a poor fen) after lowering the WTD to 20 cm below the peat surface. However, there were differences in response among the microforms (hummock, lawn and hollow), with hollow having an increase in respiration and GPP after water table drawdown. Information on how changes in WTD associated with peatland drainage and the subsequent introduction of pasture in a boreal bog, will affect the photosynthetic capacity of the peatland ecosystem on a plot scale is insufficient.

CO$_2$ uptake through photosynthesis leads to water loss due to its escape into the atmosphere whenever the stomata open for CO$_2$ assimilation (especially in a drier atmosphere). With the trade-off between carbon dioxide uptake and water loss from leaves, and the predicted increase in productivity and growth of vegetation on drained peatlands, water loss through evapotranspiration (ET) can be expected to increase due to the increase in the number of stomata. According to Bramley et al. (2013), water use efficiency (WUE) describes this trade-off between ET (i.e., the water loss into the atmosphere) and the carbon gained during photosynthesis. With WTD being the most important driving force in peatland ecosystem productivity (Murphy and Moore, 2010) and carbon accumulation, WUE, the ratio of carbon gain during CO$_2$ uptake for photosynthesis and water loss via ET is of major importance to a peatland ecosystem. Several ecosystem-level studies (e.g., Brümmer et al., 2012;

Mkhabela et al., 2009; Ponton et al., 2006) have used the eddy covariance technique to compare WUE among forest and/or grassland ecosystems. However, studies of such comparison between a drained and natural boreal peatland on a plot scale are limited despite the differences in vegetation and WTD due to land-use practices and peat management. Brümmer et al. (2012) concluded that the significantly higher WUE recorded at their treed fen site compared to their ombrotrophic bog site was associated with peatland productivity and plant functional type. According to Ponton et al. (2006), different plant species vary in their WUE due to variation in their ET rate, a phenomenon known to influence ecosystem processes and parameters such as soil moisture (SM), plant productivity, ecosystem nutrients and water budget (Wever et al., 2002). Ponton et al. (2006) recorded the highest maximum ET rate for grassland, aspen and Douglas-fir sites in decreasing order, with the grassland site having the lowest average WUE relative to their aspen and Douglas-fir sites in an increasing order. Siddique et al. (2001) also confirmed the assertion that different plant species vary in their WUE due to the differences in their leaf gas exchange characteristics even when grown under similar environmental conditions (Brooks et al., 1997; Smedley et al., 1991).

The hydrological changes through peatland drainage for agriculture, and the introduction of pasture and other dominant species at the drained peatland pasture site is likely to cause some differences in productivity and ET rate between the two sites. While the peat at the natural site is predominantly made up of *Sphagnum* moss, with different microtopography and species dominating

these microforms, the drained site is has no microforms and *sphagnum* moss is less abundant. I therefore hypothesize that there could be a significant difference in the production capacity and hence, the evapotranspiration rate between the drained and the natural site, which could also lead to some differences in their WUE.

Canadian peatlands cover roughly 1.136 million km^2 (64% in the boreal region and 33% in the subarctic region) and contain about 147 Gt of soil carbon, which is about 56% of the organic carbon stored in all Canadian soil (Tarnocai, 2006). Surface heterogeneity such as differences in plant functional types and microforms (e.g., hummock and hollow) are normally ignored in broad ecosystem classification used in characterizing the landscape in many global- and regional-scale ecosystem and climate models (Frolking et al., 1998). Therefore, it is important to parameterize the GPP-PAR (photosynthetically active radiation) function for local/fine-scale ecosystem modelling. According to Glenn et al. (2006), the increase in the net production rate during the growing season will differ among peatland ecosystems, based on the dominant vegetation, suggesting the need to parameterize the GPP-PAR function used in modelling plant productivity in peatland ecosystems based on the dominant PFTs.

Therefore, this thesis sought to investigate, on a plot scale, the impact of drainage on the photosynthetic capacity and WUE of boreal peatlands based on a pair of clear and opaque chamber measurements using a portable greenhouse gas (GHG) analyzer. The idea was to provide some information for carbon modelling based on land use practices, differences in PFTs and microforms.

1.2 Objectives

The main objective was to find out if peatland drainage for agriculture, differences in PFTs, and microtopography have any significant impact on the GPP and WUE of boreal peatland bogs. To achieve this, the following specific objectives were set:

- To measure the NEE and ecosystem respiration (ER) at plot level and use them to estimate both the plot- and site-scale GPP.
- To fit the GPP and PAR data to the GPP-PAR relation in order to parameterize the model for the drained and natural sites.
- To estimate the ET, and hence WUE at both plot- and site-scale.
- To verify if there is any significant difference in GPP and WUE at both plot- and site-scale.

2. Materials and methods

2.1 Site description

The study was conducted on an area of ombrotrophic boreal bog, within the Robinsons pasture in western Newfoundland, about 90 km southwest of Corner Brook, Newfoundland and Labrador (48° 15.842'N, 58° 39.913' W). The site is located within an oceanic climate, receiving an annual rainfall of about 995 mm (Environment Canada, 2011). Mean annual temperature is 5 °C, with monthly lowest and highest average temperature of -11 and 21°C in February and August, respectively, based on Canadian climate normals data from 1981 to 2010 for the nearest weather station in Stephenville (Environment Canada, 2011). The site is located in a peatland complex made up of an abandoned pasture with active drainage ditches and natural peatlands (Figure 1).
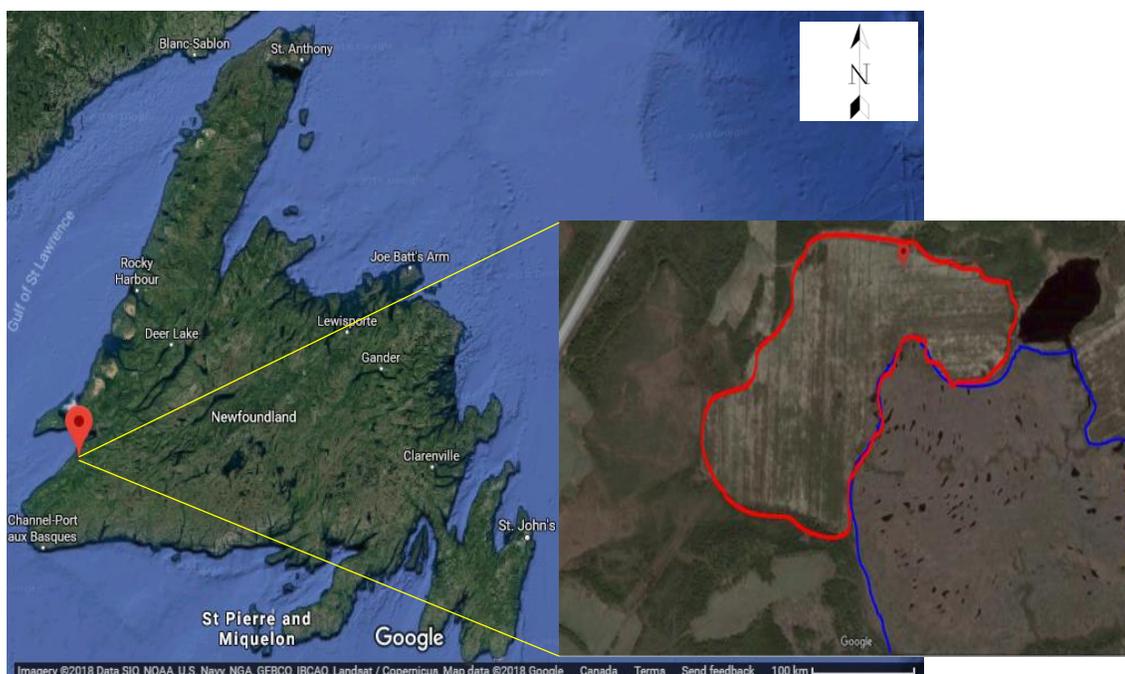
Figure 1. Satellite image showing the drained and natural peatland sites used for this research, and where it's located in Newfoundland. The area demarcated with red ink represents the drained peatland while the area demarcated with blue ink is the natural site.

The abandoned pasture was converted from drained peatland 35 years ago with the introduction of pasture grasses, and was abandoned after 10 years of active use (Luan and Wu, 2014). The effect of drainage on GPP and WUE relative to a control, the natural peatland site, was evaluated. The abandoned pasture is composed of patches of various dominant species, including reed canary grass (*Phalaris arundinacea*) dominated patches, various lower herbaceous and graminoid species (*Carex* spp., *Ranunculus acris*, *Ranunculus repens*, *Hieracium* sp.) dominated patches, and clumps of low shrubs overtopped by tall shrub, including sweet gale (*Myrica gale),* labrador tea (*Rhododendron groenlandicum*), mountain fly honeysuckle *(Lonicera villosa)*,

rhodora (*Rhododendron canadense*), and chokeberry (*Photinia* sp.). Additionally, *Sphagnum* moss is less abundant in the pasture compared to the natural peatlands. Unlike the drained peatland pasture site, the natural peatlands are wetter due to shallow WTD, with some depressions and peatland pools, containing about 40 – 60 cm deep water. Microtopography (hummocks and hollows) exists in the natural peatlands but disappeared in the discontinued pasture site. Pools also disappeared at the discontinued pasture site. The substrate in the natural peatlands is predominantly made up of *Sphagnum* species (e.g., *S. capillifolium, S. warnstorfii*), and covered partly with several species of lichens (*Cladina* spp.). Parcels of low ericaceous shrubs such as huckleberries (*Gaylussacia* spp.) are interspersed with a variety of other shrubs (*R. groenlandicum*) and herbs (*Trichophorum cespitosum*) typical of this type of peatland ecosystem on the island of Newfoundland (Luan and Wu, 2014). The hollows are dominated by sedge while the dry hummocks are dominated by shrubs. I expected some variations in leaf gas exchange and hence the WUE due to the differences in WTD and vegetation dominating each of the patches and microforms.

2.2 Experimental design

Measurements were conducted at the natural peatland and the discontinued pasture peatland throughout the growing season (May – September) of 2016. A simplified plot layout in both sites is shown in Figure 2. At

the discontinued pasture, three plots representing three replicates of the measurements were established. Within each of the three plots, four subplots were set up to cover the drainage ditch, and 3 dominant plant communities (i.e., sedge, shrub, and grass) (Figure 2, top row). At the natural peatland site, three plots were set up, and in each plot, two subplots were set up to cover one hummock and one hollow (Figure 2, bottom row). The pools at the natural site were not considered due to the absence of standing vegetation. The location of subplots within a particular plot at both sites did not have any specific pattern for the sedge, shrub, grass, hummock and hollow. This is because the subplots were laid out to cover certain dominant species and microforms. Hence the location of the sedge, shrub and grass subplots depended on the location of the patches of shrub, sedge and grass within a plot. However, a minimum distance of 2 m was allowed between subplots. Only one ditch was involved and hence, all the three replicates of the ditch subplots were located along a ditch. A distance of about 200 m was allowed between the plot layout at the drained site and that of the natural site.

Abiotic conditions, including soil temperature at 5 cm depth (T_5), soil electrical conductivity (EC) and soil moisture (SM), PAR and WTD were also recorded manually during the flux measurement. Soil pore water samples at 5-10 cm depth were also extracted using the MacroRhizon soil water samplers (http://www.rhizosphere.com/macrorhizons) installed at 10 cm depth beside each collar during the gas sampling. The Shimadzu TOC-LCPH/TN analyzer was used

to analyze the soil pore water samples to obtain the dissolved organic carbon (DOC) and total nitrogen (TN) concentrations.

Drained site

Plot 1			Plot 2			Plot 3		
	sedge			shrub			grass	
shrub		ditch	sedge		ditch	shrub		ditch
	grass			grass			sedge	

Natural site

Plot 1		Plot 2		Plot 3	
	hummock		hummock		hummock
	hollow		hollow		hollow
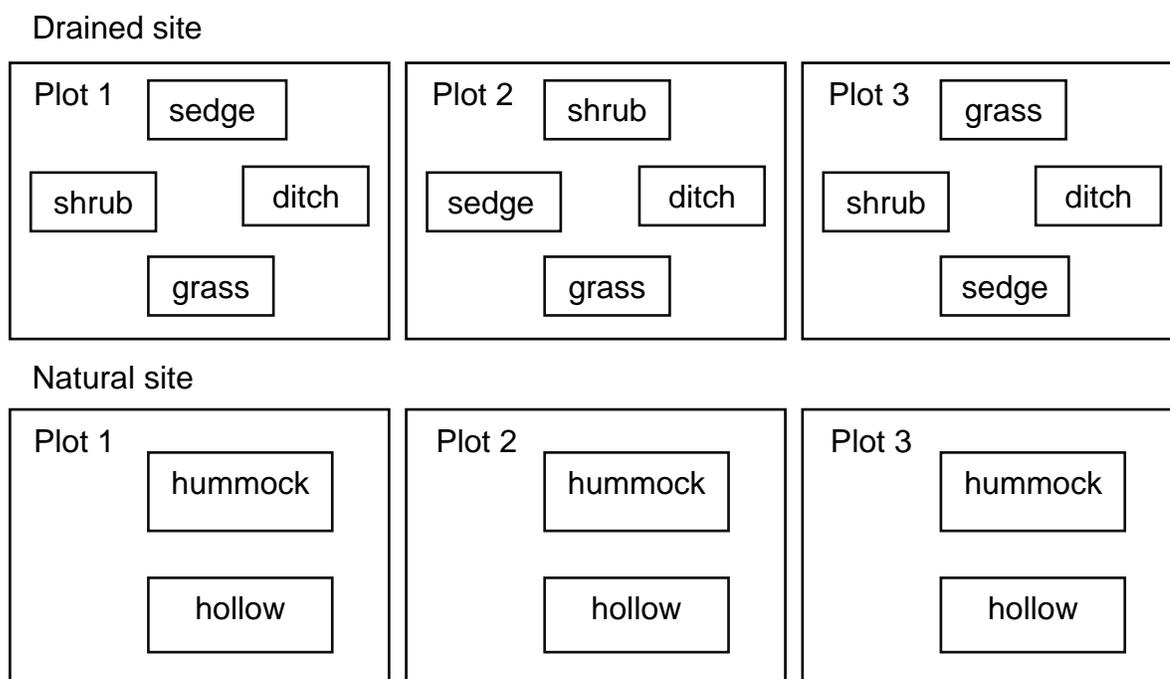
Figure 3. Experimental design of both the drained and natural sites. Note: figure is not drawn to scale.

2.3 Measurement of NEE, ER and ET

Boardwalks were constructed around the sampling plots to minimize damage to the vegetation and compression of the surrounding peat, which could cause peat gas emission during regular visits to the site. This study used the same subplots that were established in early May 2013 for the measurement of greenhouse gas (GHG) emissions (Luan and Wu, 2014; Luan and Wu, 2015). In each of the subplots, a 26 cm diameter gas sampling base ring (collar), made of a polyvinyl chloride polymer (PVC) was permanently inserted into the peat to a

depth of 10 cm in early May 2013. The collar had a moat/groove which served as water seal during the gas sampling. Next to each collar, perforated acrylonitrile butadiene styrene (ABS) pipes with sealed bottom were inserted into the peat to help measure the WTD with a ruler. The sedge, shrub and grass subplots, however, shared the same ABS pipe. Here, the plots had similar elevation.

The chamber measurement technique as recommended by Holland et al. (1999) has been widely used to study the dynamics of carbon dioxide and other GHGs due to its simplicity and relatively inexpensive nature (e.g., Järveoja et al., 2016; Karki et al., 2016; Strack and Zuback, 2013; Altor and Mitsch, 2008; Wang et al., 2013; Davidson et al., 2008) despite notable artificial effects of both opaque and clear chamber on flux measurement as a result of long covering period (Morrissey et al., 1993; Davidson et al., 2002; Livingston and Hutchinson, 1995). The portable GHG analyzer employed here allowed for a shorter covering period (three minutes, with a response rate of 1 Hz.) (Luan and Wu, 2014; Luan and Wu, 2015), compared to 30 mins for manual gas sampling and gas chromatography method.

Gas measurements were done biweekly, from May to September 2016 between the hours of 10:00 – 16:00. Measurements of NEE, ER and water vapour (representing ET) were made over 180 second intervals for each subplot. The NEE and water vapour concentrations of each subplot were measured using a clear chamber (90% light transmission), with diameter and height of 26.3 cm and 50 cm, respectively. Water vapour and CO_2 concentrations from the chamber were measured with an Ultra-Portable GHG Analyzer (Los Gatos Research, CA,

USA), connected to the chamber lid by a 4 m tubing, with an internal diameter of 3 mm. The air from the chamber after covering, passes through the tube to the analytical box where the concentrations of NEE and ET (in the form of water vapour) are measured and recorded. Simultaneously, concentrations of methane (CH_4), water vapour, and CO_2, as well as air temperature in the chamber, were recorded every second for a period of 180 seconds. A battery operated fan circulated air in the chamber headspace measurements. Equivalent atmospheric pressure was retained inside the chamber during sampling, with a capillary tube installed in the chamber lid. ER (i.e., soil and plant dark respiration) was also determined from CO_2 concentrations measured by using an opaque chamber. One to two minutes was allowed between successive measurements to clear the chamber and allow it to equilibrate to ambient CO_2 concentration and temperature. All fluxes were adjusted for field sampling temperature, headspace volume, and chamber area (Holland et al., 1999), and estimated using linear regression of all time points sampled according to the model:

$$\text{flux } (f) = C_{rate}/A \times V \qquad\qquad (1),$$

where $C_{rate} = dC/dt$ = change in gas concentration over time of enclosure, A = the soil area covered by the chamber, and V = the internal volume of the chamber.

A temperature probe was used to measure the soil temperature at a depth of 5 cm for each subplot during gas sampling. EC and SM at 5 cm depth were measured at each subplot during gas sampling, using a ProCheck reader (Decagon Devices, USA) connected to a three-pin probe. The WTD was also

measured from the installed perforated pipes using a ruler. PAR was measured during the clear chamber gas sampling with a quantum sensor (LI-190R, LI-COR, USA) in conjunction with a light meter (LI-250A, LI-COR, USA).

2.4 Gross primary productivity and water use efficiency estimation

Gross photosynthesis rate, represented by GPP, was estimated as the sum of NEE and ER. CO_2 uptake by photosynthesis represented a deduction from the system and hence had a negative value. ER added CO_2 to the system and hence had a positive value. Therefore, a negative NEE value indicated CO_2 uptake from the atmosphere and hence, a sink of CO_2. GPP was estimated for each subplot, by subtracting the overall ER from the NEE values

$$\text{i.e., GPP = NEE} - \text{ER} \qquad\qquad (2)$$

Luan and Wu (2015) estimated the percentage area coverage by each subplot. The site scale GPP, ER and NEE were therefore estimated as a weighted average across the different land forms within a given land-use type. In this study the GPP and ER were reported as positive values.

The WUE of each subplot was calculated using equation (3).

$$\text{WUE = GPP/ET} \qquad\qquad (3)$$

Site scale WUE was estimated by using the weighted site scale values of GPP and ET. The ditch was excluded when the site average of SM, WTD, EC and T_5 was considered. This was to avoid any bias due to its significant

difference when it comes to these variables. The site average of abiotic factors such as SM, WTD, EC and T_5 were also estimated as a weighted average based on spatially weighted measurements across the different subplots within a site.

2.5 Data analysis

Independent t-test was used to compare the differences in seasonal mean values of the environmental variables between the hummock and hollow subplots of the natural site. One-way analysis of variance (ANOVA) was used to compare the seasonal mean values of the environmental variables among the four subplots of the drained site. Two-way ANOVA was conducted to compare the seasonal mean WUE, ET and GPP among the four subplots at the drained sites, and to examine the main effect of PFT, duration (day of year) and their interaction effect on WUE, ET and GPP. Similar analyses were conducted at the natural site to compare the mean WUE, ET and GPP rate between the hummock and the hollow subplots and to examine the main effect of each subplot, duration and their interaction effect on WUE, ET and GPP. Pearson's correlation analysis was conducted to examine the correlation between WUE, ET, GPP and the environmental variables. Correlation between SM, EC and WTD was examined in a similar way. A stepwise multiple linear regression (MLR) analysis was conducted to investigate the relative importance of the environmental variables in explaining the variation in GPP and WUE at both plot and site level. In the stepwise MLR, a variable was entered into the model if it made a significant

contribution to the model. Here, the set criteria for inclusion was based on the significance of the p-value (i.e., the probability of the F-statistics to enter the model was $p \leq 0.05$).

To estimate the site average values of WUE, all the fluxes and the abiotic factors, the percentage coverage area (spatial weightings) (Table 1) estimated by Luan and Wu (2015) for the different landforms in the site, were respectively applied to each of the different subplots as follows

$$\bar{x} = \sum f_i x_i \, / \sum f_i \qquad\qquad (4),$$

where X_i is the flux for a given subplot, and f_i is the percentage of coverage for the respective subplots or landforms. The overall weighted site average was then compared.

GPP as a function of PAR (represented by a rectangular hyperbolic function) (Frolking et al., 1998) was examined for each of the subplots and also for the two sites using:

$$GPP = (\alpha * PAR * GPP_{max}) * (\alpha * PAR + GPP_{max})^{-1} \qquad\qquad (5)$$

This was done by fitting the above equation to my data: where α ($\mu molCO_2/\mu mol$ PAR) and GPP_{max} ($\mu molCO_2/m^2/s$) are parameters representing the initial slope of the GPP-PAR curve and maximum gross photosynthesis rate respectively. Because GPP_{max} assumes an infinite limit relative to PAR, and most plant species will saturate at PAR levels greater than 1000 $\mu mol/m^2/s$, the mean maximum gross primary photosynthesis rate (represented in this study as

Photo$_{max}$) was estimated using all GPP rates with PAR value greater than 1000

µmol/m^2/s (Bubier et al., 2003a). Data were analyzed using IBM SPSS 23.

3. Results

3.1 Temporal and spatial variability in environmental factors

The seasonal pattern of WTD for all the subplots (both at the drained and

natural peatland sites) are shown in Figure 3. It should be noted that the

reference surface for measuring the WTD in the ditch subplots was from the

bottom of the ditch where the plants were growing and where the other

environmental variables such as EC and soil temperature were measured. Water

level in the soil dropped from the beginning of the sampling in early June (day of

year (DOY) = 163) until the middle of August (DOY = 219), when the deepest

WTD was reached. The WTD in all the subplots followed similar seasonal

pattern. The sedge, shrub and grass subplots maintained identical WTD

throughout the season because they shared the same well with the same surface

reference. The ditch had the shallowest WTD at the beginning of the sampling at

approximately 3 cm above the bottom of the ditch, followed by the hollow, the

other subplots at the drained site and the hummock in increasing depth relative to

the peat surface. The greatest drawdown of WTD (from 13 ± 0.37 cm to 37 ± 2.40

cm below the peat surface) was recorded among the sedge, shrub and grass

subplots from the beginning of sampling to the middle of August (DOY =219). The

hummock recorded the deepest WTD compare to the hollow subplot. On

average, the WTD was significantly higher at the hollow subplots (-15.1 ± 1.70 cm) than the hummocks (-33.8 ± 2.05) (t(34) = -7.02, p < 0.001) (Table 1). Among the drained subplots the ditch had the shallowest average WTD relative to the bottom of the ditch while the other three subplots had their reference from the peat surface. On average, WTD was significantly higher at the ditch subplot (-3.5 ± 0.95 cm) compared to the average WTD for the sedge, shrub and grass subplots (-23.7 ± 2.09 cm) (F(3, 40.8) = 52.0, p < 0.001) (Figure 3 and Table 1).
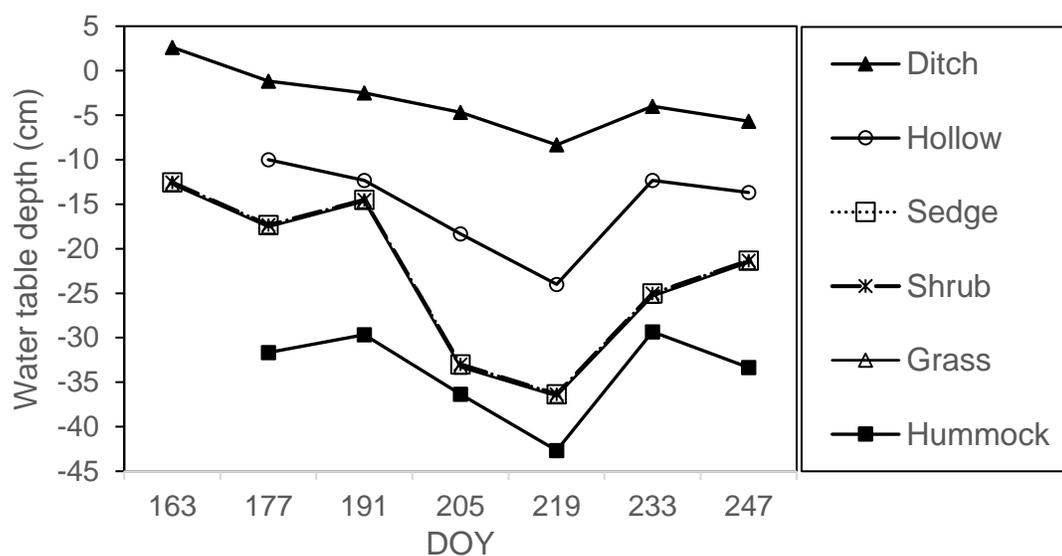
Figure 3. The seasonal pattern of water table depth of the different subplots in the both the natural and drained peatland pasture sites. Negative water table depth represents water level below the peat surface while positive value represents flooding. The actual date for the Julian day, 163 was June 11.

The seasonal mean SM, WTD, EC and T_5 of the subplots in both sites are shown in Table 1. Spatially weighted measurements were averaged across all the subplots within a site. The percentage coverage as indicated by Luan and Wu (2015) for each of the subplots is shown in Table 1. One-way ANOVA revealed a

significant difference among all the drained subplots as far as these

environmental variables are concerned (p < 0.01) (Table 1). The mean SM, WTD,

and T_5 of the ditch subplot were found to be significantly different from the rest of

the subplots at the drained site (Table 1). The mean SM and EC of the grass

subplot were significantly different among the four subplots. Results of post hoc

comparisons to evaluate the pairwise differences (multiple comparisons) among

the drained subplots is presented in Table 1. Here, significant difference and no

significant difference were denoted by different lower case letters and similar

letters for a given pair of variables respectively.

      Independent t-test results between the hummock and hollow subplots are

also shown in Table 1. The hollow subplot recorded a significantly higher WTD,

SM, and hence higher EC relative to the hummock (p < 0.001, Table 1).

However, no significant differences were found between their mean soil

temperature (t(34) = -0.24, p > 0.05) (Table 1).

Table 1. One way ANOVA and t-test results of seasonal mean soil moisture, water table depth, electrical conductivity and peat temperature at 5 cm depth among the drained subplots and between the hummock and hollow subplots at the natural site, with their percentage area coverage.

Plots	Area weighted (%)	Mean SM (%)	Mean WTD (cm)	Mean EC (mS/m)	Mean T_5 (^{O}C)
Drained site					
Sedge	23.8	58.2 ± 1.83 [a]	-23.1 ± 2.09 [a]	0.089 ± 0.00 [a]	16.2 ± 0.48 [a]
Shrub	23.8	54.8 ± 1.84 [a]	-23.1 ± 2.09 [a]	0.080 ± 0.00 [a]	15.1 ± 0.51 [b]
Ditch	5.0	80.5 ± 1.92 [b]	-3.5 ± 0.95 [b]	0.076 ± 0.00 [a]	13.5 ± 0.48 [c]
Grass	47.5	38.5 ± 2.66 [c]	-23.1 ± 2.09 [a]	0.057 ± 0.00 [b]	15.2 ± 0.47 [b]
N		84	81	84	84
df		(3, 80)	(3, 40.8)	(3, 44.2)	(3, 80)
F		68.29	52.02	12.20	5.24
P		< 0.001	< 0.001	< 0.001	< 0.01
Natural site					
Hummock	35.0	31.5 ± 2.23	-33.8 ± 2.05	0.029 ± 0.00	16.4 ± 0.39
Hollow	35.0	65.3 ± 2.48	-15.1 ± 1.70	0.072 ± 0.00	16.5 ± 0.46
N		36	36	36	36
df		34	34	34	34
t		-10.13	-7.02	-9.84	-0.24
p		< 0.001	< 0.001	< 0.001	= 0.41

p-value represents the significance level of one-way ANOVA among the subplots (in the case of the drained site) and that of t-test between the hummock and hollow subplots at the natural site. Similar lower case letters denotes no significant difference while different letters denotes significant difference between or among subplots at each site.

Significant differences were observed between the SM, WTD, EC and T_5 of the drained and natural sites (p > 0.05) (Table 2). Results of the test statistics, degree of freedom and significant levels are also presented in Table 2.

Table 2. Seasonal mean soil moisture, water table depth, electrical conductivity and peat soil temperature at 5 cm depth of the drained and natural sites.

Plots	Mean SM (%)	Mean WTD (cm)	Mean EC (mS/m)	Mean T_5 (^{O}C)
Drained site	45.1 ± 1.90	-21.9 ± 1.98	0.067 ± 0.00	14.6 ± 0.44
Natural site	33.9 ± 1.57	-17.1 ± 1.28	0.035 ± 0.00	11.5 ± 0.29
N	39	39	39	39
df	37	33.3	31.2	33.3
t	4.47	-2.02	9.52	5.91
p	< 0.001	< 0.05	< 0.001	< 0.001

p-value represent the significance level of an independent t-test between the two sites.

The seasonal pattern of SM, EC and T_5 for the subplots and the two sites are shown in Figure 4. The mean values were seen to follow a pattern similar to that of the WTD. SM decreased at all the subplots as well as at both sites during the interval of water table drawdown (Figure 3 and Figure 4). SM started increasing after the middle of August (similarly to EC) when the WTD started rising. The lowest SM content was recorded at the hummock and hence the lowest EC (Figure 4). This coincided with the lowest WTD recorded at the hummock (Figure 4). On the other hand, T_5 increased during the interval of water table drawdown at the various subplots and the two sites (Figure 4).
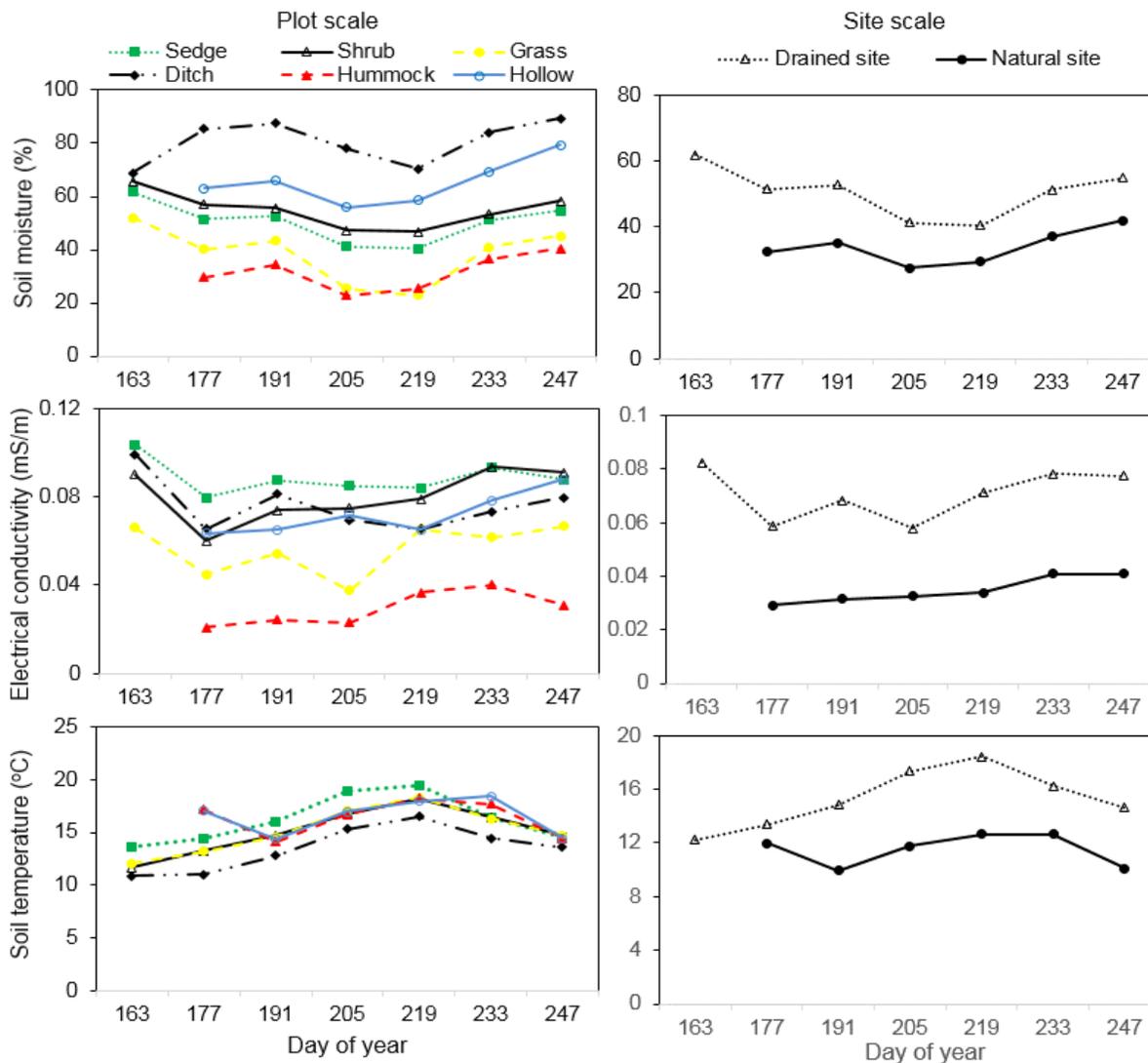
Figure 4. Seasonal pattern of soil moisture, electrical conductivity and peat temperature at 5 cm depth for all the subplots and for the two sites.

3.2 Temporal and spatial variability in ET, GPP and WUE

ET rate saw a sharp increase at the beginning of the growing season until a peak was reached in DOY = 177, and thereafter declined. From the beginning of August 2016, ET rate began to increase again (this time, to a peak not so high as the previous peak) until mid August 2016, when it again declined until the end

of sampling. The seasonal pattern of ET rate followed a similar pattern in all the subplots (both at the drained and natural sites) (Figure 5(a)). A similar trend can also be seen at the site level (Figure 5(b)).
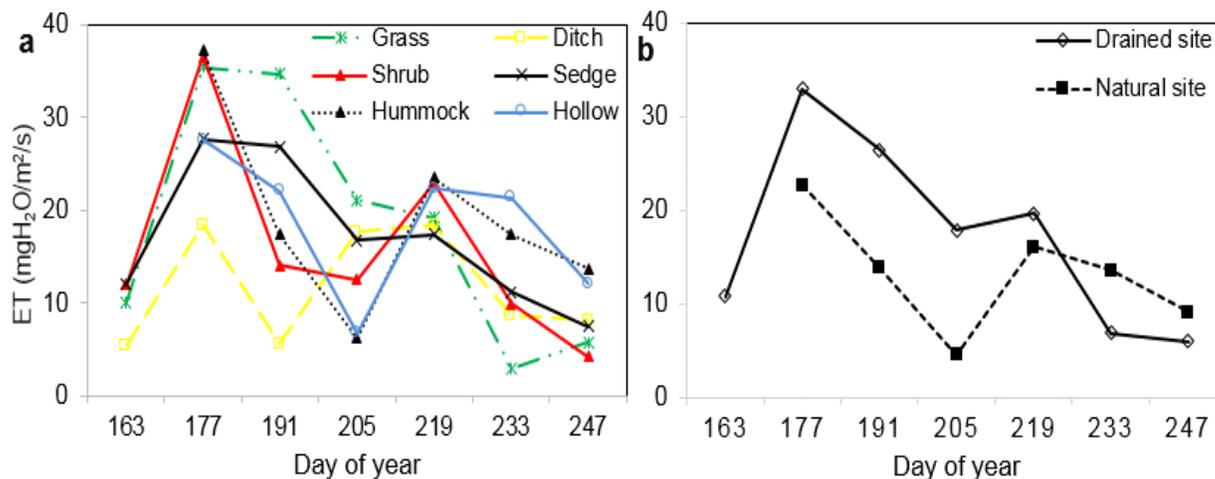
Figure 5. Seasonal pattern of evapotranspiration rate at (a) plot scale and at (b) site scale.

Different PFTs and microtopography might affect WUE, GPP and ET rate. However, this effect might differ across the growing season or sampling date (DOY). Hence, two-way ANOVA was conducted to examine the main effect of PFTs, microforms and sampling date, and their interaction effect on GPP, WUE and ET across the 2016 growing season (May – September). GPP increased from the beginning of the growing season until a peak was reached in August 2016, and thereafter declined (Figure 6). The mean GPP of the subplots at the drained pasture site was greater than that of the natural site, with the maximum mean GPP (0.168 ± 0.02 $mgCO_2/m^2/s$ from the hollow subplot) being far less

than the minimum mean GPP among the subplots at the drained pastures site (i.e., 0.380 ± 0.05 mgCO$_2$/m^2/s from the ditch subplot) (Table 3). The shrub subplot recorded the highest mean GPP among the drained subplots (Table 3). There was a significant main effect of plot differences (PFT) on GPP at the drained site ($F_{(3, 56)}$ = 3.30, $p < 0.05$). This significant main effect is likely to reflect the drop in GPP at the ditch relative to that of the shrub subplot (Table 3). DOY also had a highly significant effect on GPP among the drained subplots ($F_{(6, 56)}$ = 17.63, $p < 0.001$). This means that overall, when plot differences or PFT is ignored, variation within the DOY will influence the GPP among the drained subplot. No significant interaction effect between DOY and plot differences was observed ($F_{(18, 56)}$ = 1.46, $p > 0.05$). This means that the effect of sampling date on GPP is the same among the subplots (Figure 6(a)). Thus, the GPP rate for all the subplots increased from the beginning of the growing season until a peak was reached, and then declined towards senescence. When the ditch subplot was excluded, no significant main effect of plant functional type was observed on GPP ($F_{(2, 42)}$ = 2.14, $p > 0.05$). However, there was a significant main effect of DOY on GPP ($F_{(6, 24)}$ = 23.38, $p < 0.001$), with a significant interaction effect on GPP between PFTs and DOY ($F_{(12, 42)}$ = 3.20, $p < 0.01$). This means that the effect of DOY on GPP was different for the different PFTs when data from the ditch subplot was excluded. Respectively, the grass, shrub, sedge and the ditch subplots contributed 46%, 26.4%, 23.5% and 4.1% of the overall GPP at the drained site based on their percentage coverage area (spatial weightings) (Table 3).

There was a significant main effect of microform on GPP ($F_{(1, 24)}$ = 12.93, P < 0.01). Pairwise comparison revealed a significantly greater GPP at the hollow (0.168 ± 0.02 mgCO_2/m^2/s) compared to the hummock (0.098 ± 0.01 mgCO_2/m^2/s) (p < 0.01) (Table 3). DOY also had a significant main effect on GPP ($F_{(5, 24)}$ = 3.912, p < 0.05). There was a non-significant interaction between microtopography and DOY on GPP ($F_{(5, 24)}$ = 1.59, p > 0.05). Both the hummock and hollow subplots covered 35% of the area but respectively contributed 36.8% and 63.2% of the overall GPP at the natural site.

There was a significant main effect of site (being it natural or drained) on GPP rate ($F_{(1, 26)}$ = 691.29, p < 0.001). This significant effect is likely to reflect the drop in GPP at the natural site. On average, the GPP of PFTs affected by agricultural drainage was found to be significantly greater (0.468 ± 0.04 mgCO_2/m^2/s) than that of the natural site (0.093, ± 0.01 mgCO_2/m^2/s), p < 0.001 (Table 3). DOY had a significant effect on GPP ($F_{(6, 26)}$ = 31.65, p < 0.001). GPP at the beginning of the growing season and towards the end of the season are statistically the same and significantly lower than GPP rate at the middle of the growing season. There was a significant interaction effect of DOY and site differences on GPP rate ($F_{(5, 26)}$ = 19.78, p <0.001). This means that, the effect of DOY on GPP rate is different for the drained site than it is for the natural site.

Although ER (mgCO_2/m^2/s) at the drained site was much greater (0.275 ± 0.03) than that of the natural site (0.048 ± 0.01; $F_{(1, 26)}$ = 201.42, p < 0.001) as far as the main effect of site is concerned, the NEE (mgCO_2/m^2/s) of the drained site was also found to be significantly greater (-0.188 ± 0.02) than that of the

natural site (-0.050 ± 0.01) ($F_{(1, 26)}$ = 166.40, $p < 0.001$) (Table 3). This makes the drained site more of a carbon sink relative to the natural site. There was a significant effect of DOY on NEE ($F_{(6, 26)}$ = 12.27, $p = 0.001$). The interaction effect of DOY and site differences on NEE was also significant ($F_{(5, 26)}$ = 4.85, $p < 0.01$).
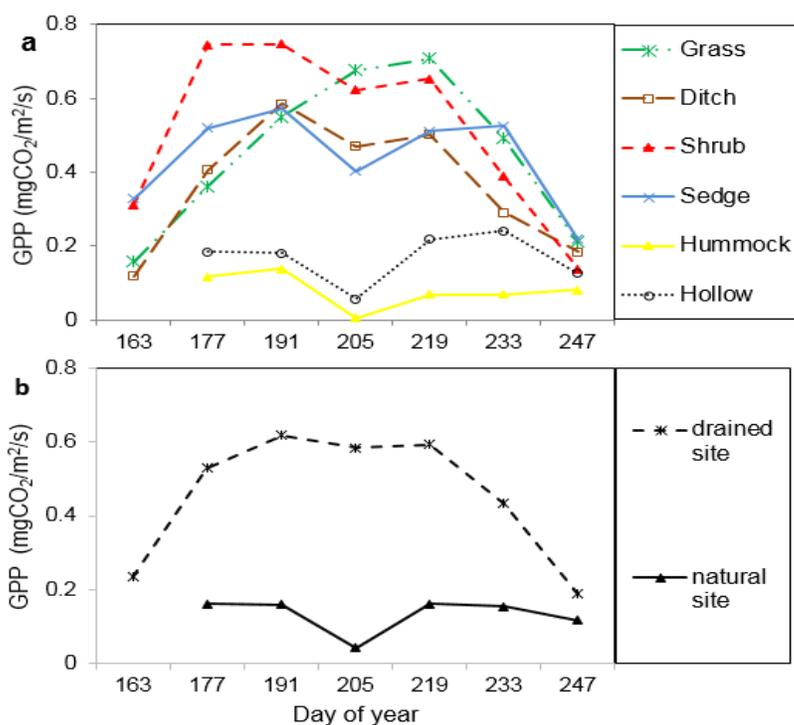
Figure 6. Seasonal pattern of gross primary productivity rate for (a) the different subplots and (b) the two sites.

Table 3. Summary of the mean gross primary productivity rate of each subplot and site, mean ecosystem respiration, and the net ecosystem carbon dioxide exchange for each site and their respective standard error.

		Drained pasture site		Natural site	
				Mean site value	Mean plot GPP
	Contribution	Mean site value	Mean plot GPP		
Item	(%)	$(mgCO_2/m^2/s)$	$(mgCO_2/m^2/s)$	$(mgCO_2/m^2/s)$	$(mgCO_2/m^2/s)$
GPP		0.486 ± 0.04 [a]		0.093 ± 0.01 [b]	
NEE		-0.188 ± 0.02 [e]		-0.050 ± 0.01 [f]	
ER		0.275 ± 0.03 [g]		0.048 ± 0.01 [h]	
Sedge	23.5		0.463 ± 0.03 [a]		
Shrub	26.4		0.521 ± 0.06 [a, b]		
Grass	46.0		0.453 ± 0.05 [a,]		
Ditch	4.1		0.380 ± 0.05 [a, c]		
Hummock	36.8				0.098 ± 0.01
Hollow	63.2				0.168 ± 0.02

Similar lower case letter denotes no significant difference while the different letters denotes significant difference between the site or subplot averages. Negative NEE represents carbon sink.

At the plot level, WUE values ranged from 0.005 to 0.061 $mgCO_2/mgH_2O$, with the hummock and shrub subplots recording the lowest and the highest values of WUE respectively (Table 4). ET rate varied from 11.75 to 19.26 $mgH_2O/m^2/s$ with the highest ET value recorded at the hummock followed by the hollow. The lowest ET value was recorded at the grass subplot (Table 4). Two-way ANOVA revealed a significant effect of plot differences on ET at the drained site ($F_{(3, 56)} = 3.24$, $p < 0.05$). This significant difference is likely to reflect the drop in ET at grass subplot relative to the ditch subplot (Table 4). Without the ditch subplot, there was non-significant effect of PFT on ET ($F_{(2, 42)} = 0.53$, $p > 0.05$). There was a highly significant main effect of DOY on ET ($F_{(6, 56)} = 14.87$, $p < 0.001$). The interaction effect of DOY and PFTs also had a

significant effect on ET ($F(18, 56) = 2.07$, $p < 0.05$). Between the hummock and hollow subplots, a non-significant effect of microform on ET was observed ($F(1, 24) = 0.13$, $p > 0.05$). However, DOY had a highly significant effect on ET ($F(5, 24) = 22.40$, $p < 0.001$). No significant interaction effect between microform and DOY on WUE was observed. Significant effect on ET was observed between the drained and natural sites ($F(1, 26) = 12.19$, $p < 0.01$). There was a significant effect of DOY on ET ($F(6, 26) = 16.93$, $p < 0.001$). The interaction effect between DOY and site differences on ET was also significant ($F(5, 26) = 5.87$, $p < 0.01$). In a two-way ANOVA, non-significant effect of PFTs on WUE was observed (Table 4; $F(3, 56) = 0.53$, $p > 0.05$). However, DOY had a significant effect on WUE ($F(6, 56) = 2.75$, $p < 0.02$). Non-significant interaction effect on WUE was observed between DOY and PFTs ($F(18, 56) = 0.77$, $p > 0.05$. On the other hand, microforms had a significant effect on WUE ($F(1, 24) = 25.29$, $p < 0.001$). However, there was non-significant effect of DOY and its interaction with microform on WUE ($F(5, 24) = 1.78$, $p > 0.05$). Between the drained and natural sites, the results show a significant effect on WUE ($F(1, 26) = 28.51$, $p < 0.001$). DOY also had a significant effect on WUE ($F(6, 26) = 4.86$, $p < 0.01$). There was a significant interaction effect between DOY and site differences on WUE ($F(5, 26) = 4.93$, $p < 0.01$).

Table 4. Summary of the mean evapotranspiration and water use efficiency rate of each subplot and site with their respective standard error.

Item	Mean site ET $(mgH_2O/m^2/s)$	Mean site WUE $mgCO_2/mgH_2O$	Mean plot ET $(mgH_2O/m^2/s)$	Mean plot WUE $mgCO_2/mgH_2O$
Drained site	17.225 ± 2.32 [a]	0.047 ± 0.01 [c]		
Sedge			17.06 ± 2.44 [a]	0.037 ± 0.01 [a]
Shrub			16.05 ± 2.58 [a]	0.061 ± 0.03 [a]
Grass			11.75 ± 1.72 [a, b]	0.037 ± 0.01 [a]
Ditch			18.47 ± 2.84 [a, c]	0.046 ± 0.02 [a]
Natural site	13.291 ± 1.45 [b]	0.005 ± 0.00 [d]		
Hummock			19.26 ± 2.40 [g]	0.005 ± 0.00 [e]
Hollow			18.71 ± 2.03 [g]	0.010 ± 0.00 [f]

Similar lower case letter denotes no significant difference while the different letters denotes significant difference between the site or subplot averages.

3.3 GPP-PAR relationship

The GPP-PAR relationship assessed by fitting the rectangular hyperbola model (

$$GPP = (\alpha * PAR * GPPmax) * (\alpha * PAR + GPPmax)^{-1})$$ to the data is shown in Figure 7. GPP increased with PAR and explained 93 to 99% of the variation in GPP at the subplots and at the site level based on the rectangular hyperbola model (Figure 7 and Table 5).

The parameters (α and GPP_{max}) of the rectangular hyperbola relationship showed variation among the PFTs at the drained site and between the microforms at the natural peatland site. GPP_{max} among the PFTs varied from 0.90 $mgCO_2/m^2/s$ at the sedge subplot to 86.17 $mgCO_2/m^2/s$ at the ditch subplot

(Table 5). The hollow and hummock subplots recorded a GPP_{max}($mgCO_2/m^2/s$) of 0.22 and 0.10 respectively. At the site scale, the drained site recorded the highest GPP_{max} (2.68 $mgCO_2/m^2/s$) compared to 0.13 $mgCO_2/m^2/s$ at the natural site (Table 5). α varied from 2.8 x 10^{-4} to 7.8 x 10^{-4} $mgCO_2/\mu mol$ among the PFTs at the drained peatland pasture site. The hummock recorded the highest α-value (approximately 1 $mgCO_2/\mu mol$) compared to 5.9 x 10^{-4} $mgCO_2/\mu mol$ at the hollow. On a site scale, the natural site recorded the highest α (4.41 x 10^{-2} $mgCO_2/\mu mol$) compared to 4.6 x 10^{-4} $mgCO_2/\mu mol$ at the drained site (Table 5).

Photo_max (i.e., GPP at PAR greater than 1000 $\mu mol/m^2/s$) also varied significantly among the subplots and between the two sites (Table 5). The seasonal mean Photo_max ($mgCO_2/m^2/s$) was significantly higher at the hollow (0.17 ± 0.01) compared to the hummock (0.10 ± 0.00) ($t(14) = -43.59$ $p < 0.001$). One-way ANOVA revealed a significant difference in the mean Photo_max among the drained subplots ($F(3, 30.84) = 11.64$, $p < 0.001$). Between the natural and drained sites, Photo_max ($mgCO_2/m^2/s$) was significantly higher at the drained site (0.52 ± 0.02) compared to the natural site (0.13 ± 0.00) ($t(16) = 16.59$, $p < 0.001$). To realistically compare the GPP results of the GPP-PAR function among the subplots and between the two sites, statistical analysis was performed on only the GPP rates with PAR greater than 1000 $\mu mol/m^2/s$ (Photo_max). The results (Table 5) revealed that, at optimum condition (i.e., PAR greater than 1000 $\mu mol/m^2/s$), the mean GPP (Photo_max) varies spatially among the plant functional types, between the microforms, and between the drained and natural peatland sites.

Table 5. Parameters (α and GPP$_{max}$) of the rectangular hyperbola function (GPP-PAR relationship), Photo_max (mean GPP at PAR greater than 1000 µmol/m^2/s), and the results of a one-way ANOVA comparing the mean Photo_max among the drained subplots and that of a t-test comparing the mean Photo_max between the hummock and hollow, as well as between the natural and drained site.

Plot/Site	Alpha (α) (mgCO$_2$/µmol)	GPP$_{max}$ (mgCO$_2$/m^2/s)	Photo_max (mgCO$_2$/m^2/s)	r^2
Drained site	0.00046	2.68	0.52 ± 0.02 [d]	0.99
Natural site	0.04407	0.13	0.13 ± 0.00 [e]	0.94
Sedge	0.00078	0.90	0.50 ± 0.01 [a]	0.99
Shrub	0.00049	3.86	0.59 ± 0.03 [b]	0.98
Grass	0.00056	1.15	0.47 ± 0.01 [a, c]	0.99
Ditch	0.00028	86.17	0.42 ± 0.02 [c]	0.93
Hummock	0.99932	0.10	0.10 ± 0.00 [f]	0.95
Hollow	0.00059	0.22	0.17 ± 0.01 [g]	0.95

d and e, f and g, represents independent t-tests which were significantly different. Similar letters among the subplots at the drained site represent no statistical difference.
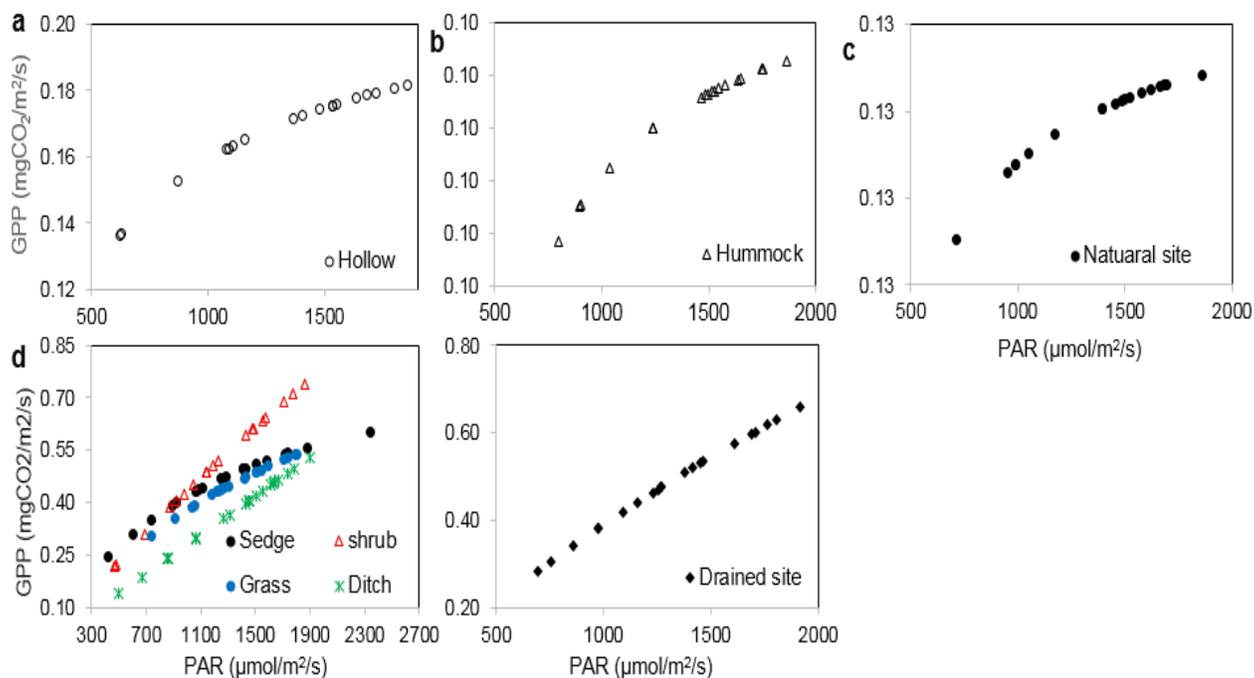
Figure 7. Relationship between photosynthetically active radiation and gross primary productivity at the subplots and sites fitted with the rectangular hyperbola model.

3.4 Factors controlling ET, GPP and WUE

Correlation analysis conducted between ET and environmental variables, such as SM, WTD, PAR, EC and T_5, revealed a significant positive relationship between ET and PAR at the drained site ($p < 0.001$, Figure 8(a)). On the other hand a significantly negative correlation was observed between ET and EC ($p < 0.05$, Figure 8(b)). In a stepwise MLR analysis, PAR alone explained ~68 % of the variation in ET at the drained site ($F(1, 19) = 40.04$, $p < 0.001$). Similar analyses at the natural site did not show any significant correlation between ET and the environmental variables.
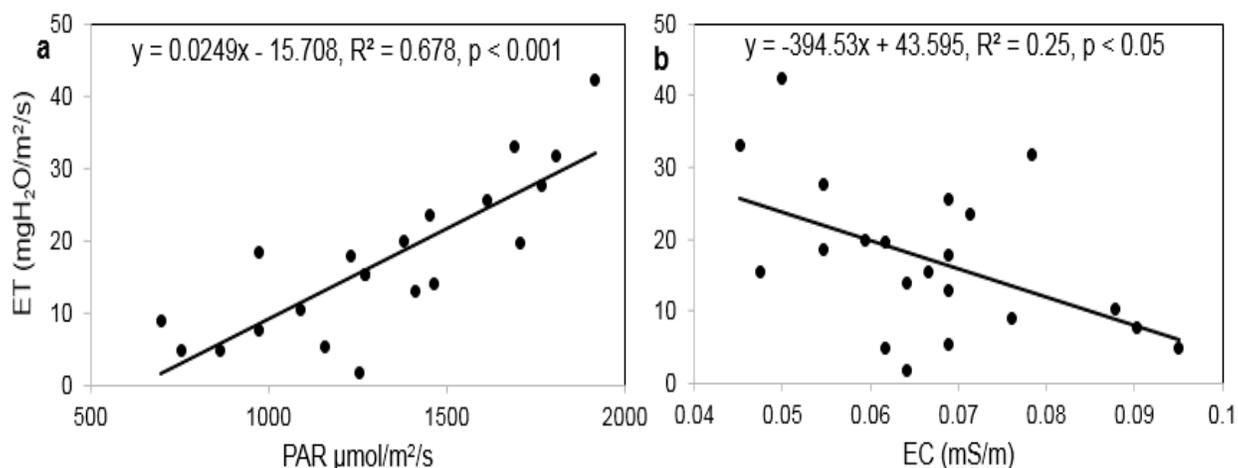
Figure 8. Correlation between (a) evapotranspiration rate, (b) electrical conductivity and photosynthetically active radiation at the drained site.

GPP significantly correlated with SM, WTD, PAR, EC, and T_5 at the drained pasture site ($p < 0.01$). However, no significant correlation was found between TN concentration, DOC concentration and GPP at the drained site ($p >$

0.05). Figure 9(a) – (g) shows the correlation between GPP and the environmental factors at the drained site. Site differences had a significant main effect on TN ($F_{(1, 26)} = 172.92$, $p < 0.001$). On average, TN concentration of the drained site was significantly higher (1.79 ± 0.06 mg/L) than that of the natural site (0.56 ± 0.02 mg/L) ($p < 0.001$). The higher level of TN accounted for 9.9% of the variation in GPP at the drained site as opposed to 7.2% of the variation in GPP at the natural site (Figure 9(f) and Table 6 respectively). There was a non-significant main effect of DOY on TN concentration ($F_{(6, 26)} = 1.531$, $p > 0.05$). However the interaction effect of DOY and site differences was significant ($F_{(5, 26)} = 3.066$, $p < 0.05$). Likewise, the average DOC concentration of the drained peatland was significantly higher (87.13 ± 2.62 mg/L) than that of the natural site (37.66 ± 2.83 mg/L) ($F_{(1, 26)} = 172.92$, $p < 0.001$). DOY had a significant main effect on DOC ($F_{(6, 26)} = 4.43$, $p < 0.01$). No significant interaction effect between DOY and site differences was found on DOC ($F_{(5, 26)} = 1.88$, $p > 0.05$). DOC also accounted for only 0.7% of the variation in GPP at the drained-peatland pasture site as opposed to 0.04% of the variation in GPP at the natural site (Figure 9(g)) and Table 6. In a stepwise MLR analysis, EC and T_5 combined significantly explained ~61% of the variation in GPP at the drained pastured site ($F_{(2, 18)} = 13.92$, $p < 0.001$. The resulting equation for the stepwise MLR analysis is: GPP = $0.66 - 9.10$ (EC) + 0.03 (T_5).
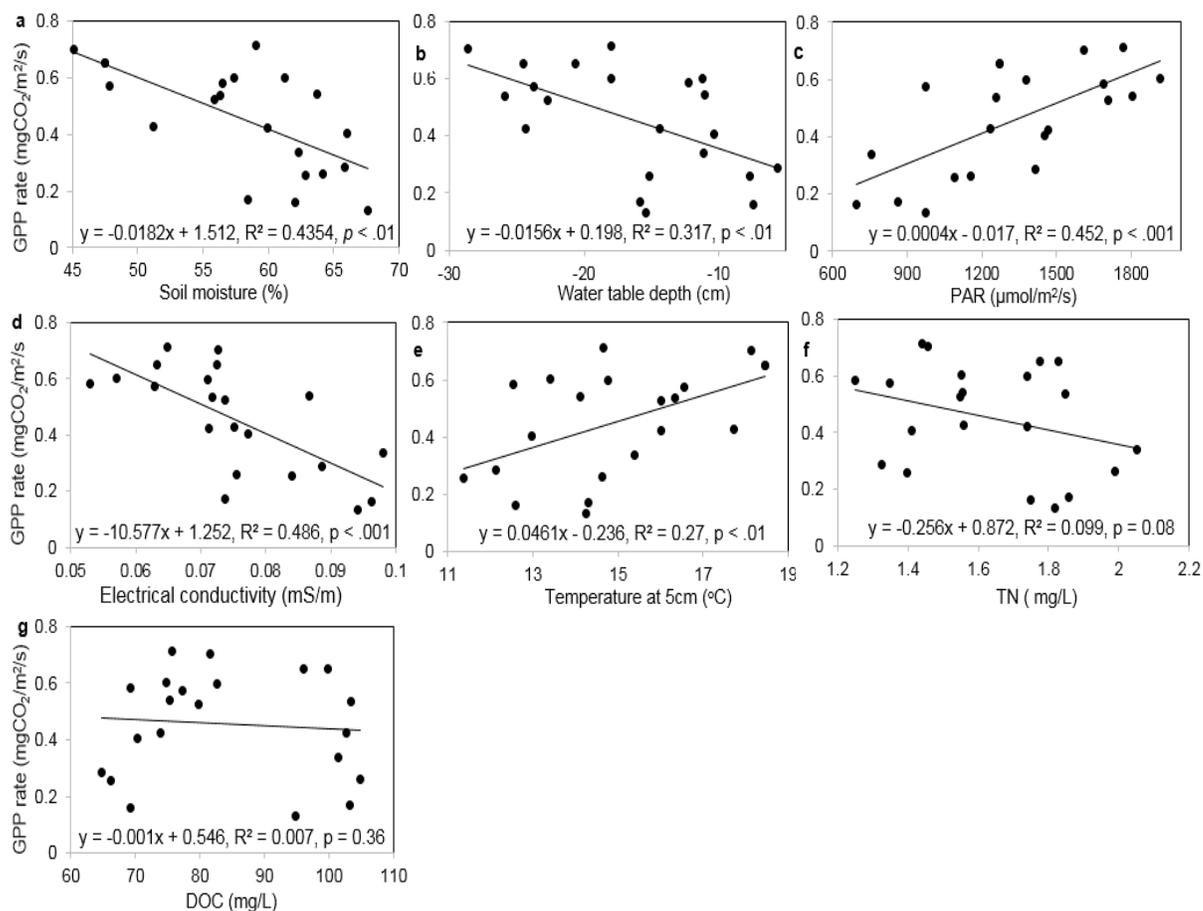
Figure 9. Correlation between different environmental factors and gross primary productivity rate at the drained pasture site (a) – (g).

Due to the significant difference in GPP between the hummock and hollow subplots, correlation analysis was done separately for the two subplots. Results of these analyses are shown in Table 7. At the plot scale, only TN was found to be significant in explaining about 17% (p < 0.04) of the variability in GPP at the hummock subplot. At the hollow subplot, WTD significantly accounted for 18% (p < 0.04), of the dynamics of GPP (Table 7). The rest of the variable-flux relationships were not significant. In a stepwise MLR analysis, no variable or

combination of variables could significantly explain the GPP at either the

hummock or hollow subplots. At a site scale, none of these environmental factors

could significantly account for the GPP rate at the natural site (with Pearson

correlation (r) < 0.30 and a p-value > 0.05) (Table 6).

Table 6. Correlation between soil moisture, water table depth, photosynthetically active radiation, electrical conductivity, temperature at 5 cm depth, total nitrogen, dissolved organic carbon and the gross primary productivity at the natural site.

Factor	r	r^2	P value	n
SM	0.251	0.06	0.16	36
WTD	0.243	0.06	0.17	36
PAR	-0.015	0.00	0.48	36
EC	0.083	0.01	0.37	36
T_5	0.044	0.00	0.43	36
TN	0.269	0.07	0.14	36
DOC	0.019	0.00	0.47	36

Table 7. Correlation between soil moisture, water table depth, photosynthetically active radiation, electrical conductivity, temperature at 5 cm depth, total nitrogen, dissolved organic carbon and the gross primary productivity rate at the hummock and hollow subplots at he natural site.

Factor	Hummock			Hollow			n
	r	r^2	P value	r	r^2	P value	
SM	-0.150	0.02	0.28	0.387	0.15	0.06	18
WTD	-0.235	0.06	0.17	0.423	0.18	0.04	18
PAR	-0.239	0.06	0.17	0.122	0.02	0.32	18
EC	-0.315	0.10	0.10	0.188	0.04	0.23	18
T5	-0.193	0.04	0.22	0.334	0.11	0.09	18
TN	-0.416	0.17	0.04	0.064	0.00	0.40	18
DOC	0.076	0.01	0.38	-0.135	0.02	0.30	18

Correlation analysis between WUE and environmental factors revealed a

significant correlation with WTD, T_5, and SM at the drained peatland pasture site.

Respectively, WTD, T_5, and SM explained 26%, 37% and 19% of the variation in

WUE at the drained site (Figure 10 (a) – (c)). In a similar analysis at the natural

site, only T_5 significantly explained the variation in WUE ($R^2 = 0.25$, $p < 0.05$)

(Figure 10 (e) and Table 8). In a stepwise MLR analysis, the combined effect of

T_5 and ET explained ~54% of the variation in WUE at the drained pasture site

($F_{(2, 16)} = 8.51$, $p < 0.01$). The resulting equation for the stepwise MLR analysis

is: WUE = -0.011 + 0.003(T_5) +0.0004(ET).

Table 8. Correlation between environmental factors and water use efficiency at the natural site.

Factor	r	r^2	P value	n
WTD	-0.19	0.04	0.23	36
T_5	-0.50	0.25	0.02	36
SM	0.07	0.49	0.39	36
ET	-0.25	0.06	0.16	36
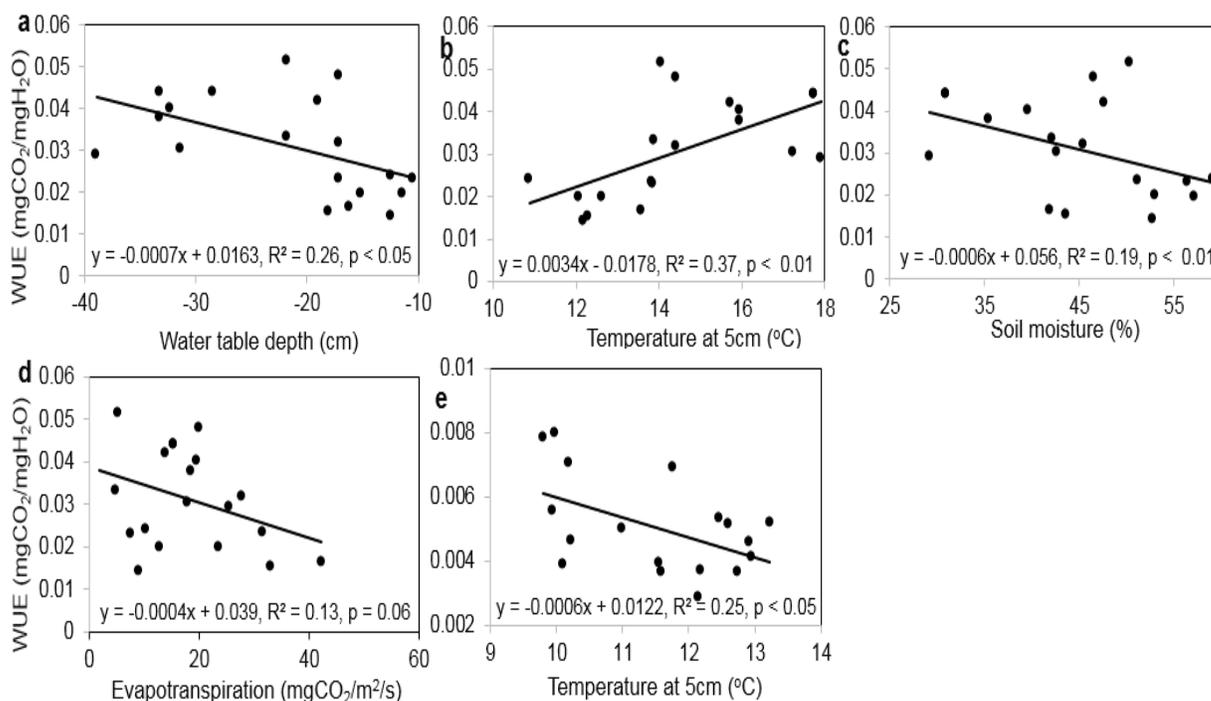
Figure 10. Correlation analysis between water use efficiency and environmental variables (a) – (d) at the drained site, and (e) at the natural site.

Correlation between WTD and environmental factors such as SM and EC at the hummock and hollow subplots of the natural site are shown in (Figure 11). A significantly positive correlation was found between WTD and SM at both the hummock and hollow subplots ($p < 0.01$). Although a positive correlation was found between WTD and EC at both the hummock and hollow subplots, the relationship was not statistically significant ($p > 0.05$; Figure 11).
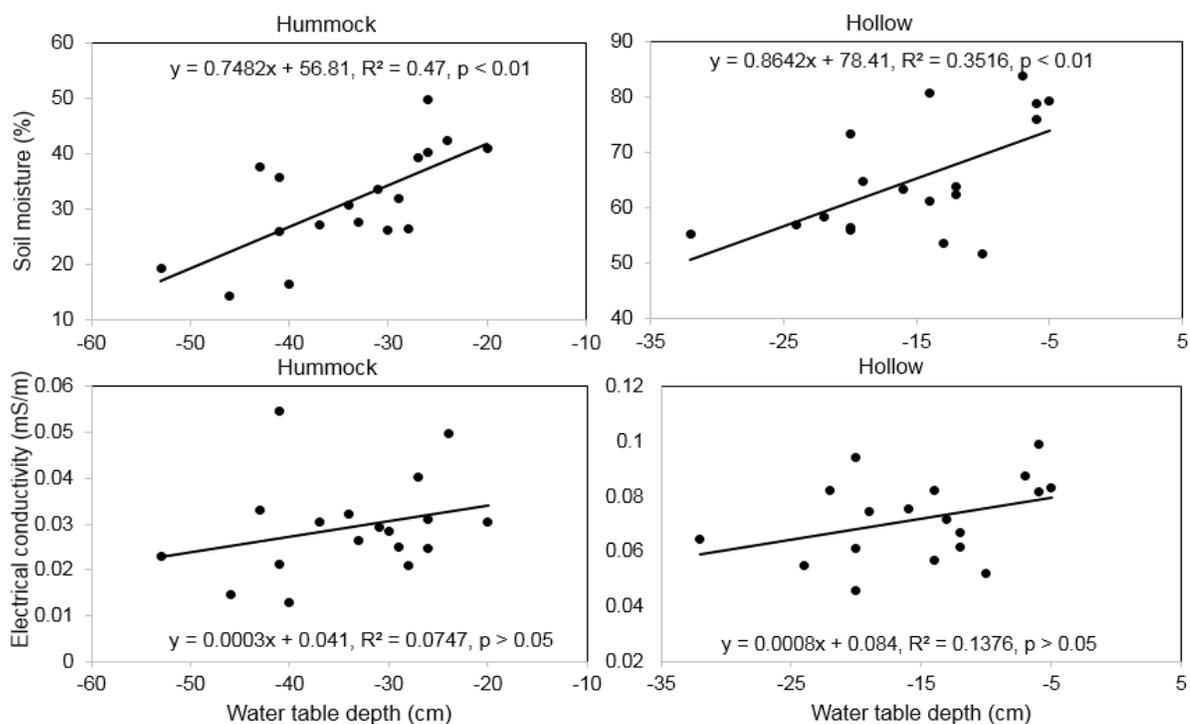
Figure 11. Relationship between soil moisture, electrical conductivity and water table depth at the hummock and hollow subplots.

4. Discussion

4.1 Agricultural drainage increases the photosynthetic capacity of boreal

peatlands.

In this study, increase in GPP at a drained peatland pasture relative to a

natural bog has been demonstrated. This in part was driven by variation in SM,

EC, WTD and T_5 caused by peatland drainage for agriculture. Significantly higher

GPP rate was found at the drained peatland pasture site as compared to the

natural site (Table 3 and Figure 6 (b)). Correlation analysis (Figure 9 (a) – (e))

indicates that variation in SM, WTD, PAR, EC and T_5 significantly explains the

increased productivity rate at the drained pasture site. However, TN and DOC did

not have any significant correlation with the increase in productivity. Apart from

PAR, all these factors are influenced by water table drawdown. Water table

drawdown via drainage increases the aeration of the surface peat, improves plant

productivity (Karki et al., 2016; Hillman, 1992; Stanek, 1977; Hillman, 1987;

Burke, 1978), and leads to other physiochemical changes in peat (Belyea and

Clymo, 1999; Laine et al., 1995; Minkkinen and Laine, 1998). Minkkinen and

Laine (1998) found a peat surface subsidence and a corresponding increase in

peat soil density as a long-term drainage effect. The removal of water and the

subsequent collapse, compression, and increase in organic matter decomposition

in peat, contribute to soil subsidence (Laine and Minkkinen, 1996), a

phenomenon known to increase the bulk density of surface peat (Burke, 1978;

Laiho and Laine, 1994), decrease hydraulic conductivity and increase the water

holding capacity or water content, and the electrical conductivity (Stadler et al., 2015; Brevik et al., 2006; Boelter, 1964; Päivänen, 1973).

Drained surface peat temperature conditions are also affected by water table drawdown as thermal conductivity and specific heat decreases with the increase in the proportion of air-filled pores (Belyea and Clymo, 1999). Jin et al. (2008) recorded up to 4 $^{\circ}$C soil temperature increase between the months of May and July due to subsurface soil drainage. Correlation analysis (Figure 9) have also shown that water table drawdown, decrease in SM, EC and an increase in peat temperature can result in GPP increase. The decrease in SM, EC, and increase in T_5 significantly explained approximately 44%, 49% and 27%, respectively, of the production variation at the drained peatland pasture site (Figure 9 (a), (d) and (e)). The maximum variability in GPP was explained by a decrease in EC alone. This is consistent with the findings of Singh et al. (2016) and Kitchen et al. (2003) where, in their comparative study, Singh et al. (2016) found that locations with high pH, TN, and EC corresponded with low yield, and where Kitchen et al. (2003) also concluded that EC alone better account for yield variability more than topographic variables.

The results also showed a significant difference in GPP among the subplots at the drained site. GPP rate at the shrub subplot was significantly greater than that of the ditch subplot (Table 3). This significant effect is likely to reflect the drop in GPP rate at the ditch subplot relative to the shrub (Table 3). Environmental factors explaining most of the dynamics of GPP were significantly different among the subplots affected by drainage for agriculture (Table 1). EC (which

accounted for most of the dynamics in GPP at the drained site) was significantly higher at the drained site (0.067 ± 0.00 mS/m) than that of the natural site (0.035 ± 0.002 mS/m) (t(31.08) = 9.53, p < 0.001) (Table 2).

Combining SM, WTD, EC, T_5 and TN in a stepwise MLR analysis, EC and T_5 significantly explained about 61% of variation in GPP at the drained peatland pasture site (p < 0.001). DOC was excluded from the MLR analysis due to its violation of the assumption of multiple linear MLR analysis (e.g., failed to correlate highly enough with the outcome variable r < 0.3). Although EC explains most of the variability in the production rate, agronomically, it only serves as a measure of how water availability is affected, which is the main cause of variation in yield (Kitchen et al., 2003). Brevik et al. (2006) found a positive correlation between soil water content and EC. Here, a change in soil water content (a single variable) was shown to significantly account for over 70% of the variability in EC of 4 out of their 5 soils samples. Results of this study indicate a negative correlation between EC and GPP (Figure 9 (d)). This suggests that peatland drainage, which leads to water table drawdown and the subsequent changes in the physical (e.g., bulk density) and hydrothermal properties (especially EC and T_5) in the surface peat, is responsible for the increase in productivity at the drained peatland pasture site (Figure 6 (b)).

The results show a statistically significant difference in SM, WTD and EC, with no significant effect on T_5 between the hummock and hollow of the natural site. Figure 11 also shows that water table drawdown at both the hummock and hollow subplots will lead to a corresponding decrease in SM and EC of both

subplots. The deepest WTD was found at the hummock subplot with a corresponding highest decrease in SM and EC compared to the hollow subplots (Table 1). These lend statistical support to the fact that water table drawdown significantly affects the SM and hence the EC. The production rate of all the subplots, at both the natural and drained peatland pasture sites, was seen to be at its peak when the WTD was at its deepest point during the summer (Figure 3 and Figure 6 (a)). However, the hummock, which had the deepest WTD during the summer (Figure 3), had the lowest productivity rate compared to the hollow of the natural site and the subplots at the drained peatland pasture site (Table 3). The significantly lower production rate at the hummock might be due to the structure and density of the peat makeup (in this case, live, porous, undecomposed *Sphagnum* moss), which can adversely affect the hydrology and hence the SM and EC (an indicator of plant water availability) during the deepest WTD. At the plot level, a strong and significant positive correlation existed between the WTD and SM of both the hummock ($r = 0.686$, $p < 0.01$) and the hollow ($r = 0.593$, $p < 0.01$) subplots. Despite being not significant ($p > 0.05$), a positive relationship existed between the WTD and EC at both the hummock and hollow subplots. This effect of WTD on the seasonal pattern of SM and EC is shown in Figure 4 and Figure 3 where the pattern of water table drawdown is seen to coincide with the pattern of SM, EC and T_5).

Boelter (1964) found that for the same level of water table drawdown, a loose, porous, undecomposed moss peat will remove more water than a decomposed and herbaceous peat. For this reason, live, undecomposed peat

moss will lose more water, and may not retain enough water within the reach of

plant roots for growth and development (Boelter, 1964). For an undisturbed

natural peatland, the capillary fringe may stretch out to the rooting area of a well-

developed vegetation (Boelter, 1964) (like the sedge) at the low lying (hollow)

areas and will rarely lack water for growth during the period when the WTD was

below 20 cm (Figure 3). According to Murphy and Moore (2010), WTD has a

significant effect on the distribution of biomass to fine roots (< 1 mm), leaves and

stem. With a deeper WTD, Murphy and Moore (2010) recorded a greater

allocation of biomass to stem and fine root production compared to leaf

production by shrubs. This trade-off between leaf and fine root production by

shrubs, due to deeper WTD condition (Murphy et al., 2009), could account for the

lower GPP rate at the hummock which recorded the deepest WTD (Table 1).

With shrubs dominating the subplots on the hummock, where for most of the time

the WTD was below -30 cm depth (Figure 3), it is likely the capillary fringe may

also not be able to extend up to the surface where the fine roots of shrubs were

found to ensure access to water and nutrients for growth and productivity. As

noted by Boelter (1964), a 20 to 30 cm water table drawdown in a live,

undecomposed moss peat (similar to the one seen at the natural peatland site),

may lead to water shortage for shallow rooting depth. I therefore speculate that

water shortage to the shrubs on the hummock subplots may be the cause for the

low productivity. Also, there could be a shift in biomass allocation to roots in

search of water and other resources needed for growth (Shipley and Meziane,

2002), thereby leading to less leaf biomass which can affect photosynthesis. This

is supported by the significantly deeper WTD at the hummock (approximately 18 cm deeper) than that of the hollow subplots with a corresponding lower SM (approximately half of the amount recorded at the hollow) (p < 0.001, Table 1).

The low decomposition rate at the natural site (especially at the heavily dominated *Sphagnum* moss – hummock), and its subsequent effects on the physical and hydrothermal properties of the peat, and its connection to the low productivity, add credence to the speculation that changes in the physical and hydrothermal properties of peat (especially SM, EC and T_5) could account for the increased productivity at the drained peatland pasture site.

The increase in GPP equally across the sedge, shrub and grass subplots could be due to the ability of the well-decomposed peat to hold on to water particles, making water, oxygen and other nutrients, easily accessible to the PFTs as WTD deepens. This could shift the allocation of biomass to the aboveground plant parts (i.e., leaves and stem), leading to an increase in the production rate. This will eventually lead to a greater flux of carbon (in the form of litter) into the soil after senescence.

Nutrient levels at the drained peatland pasture site were found to be significantly higher than that of the natural site. However, the increase in levels of TN and DOC after drainage explained only 9.9% and 0.7% of the increase in productivity rate respectively. According to Rydin and Jeglum (2013), nutrient levels after drainage will increase due to the increase in depth of the oxic layer and the subsequent increase in mineralization and the amount of available nutrients. However, McLaren and Jeglum (1998) concluded that drainage is

efficient at improving growth when accompanied by fertilization - since the amount of nutrient released are most of the time not enough to make any significant improvement to growth. This could perhaps explain the poor performance of TN and DOC as far as the production rate at the drained pasture site is concerned.

Several plot scale studies (e.g., Pelletier et al., 2011; Strack and Waddington, 2007; Bubier et al., 2003a) and site scale studies (e.g., Strachan et al., 2016; Lafleur et al., 2003; Humphreys et al., 2014) have shown the existence of relationship between water table position and peatland ecosystem productivity. This relationship has also been stated to follow a unimodal relationship (Väliranta et al., 2007; Tuittila et al., 2004), where maximum productivity is seen within a specific range of WTD. Hence, a water table position closer or away from the required range will result in a decrease in productivity (Belyea and Clymo, 1999). Pelletier et al. (2011) concluded that an increase in NEE due to the increase in maximum photosynthesis was a result of rising water table position to the surface of their high and low hummock subplots. However, a rise in WTD at their hollow subplots lead to a reduction in maximum photosynthesis and hence NEE at optimum condition of PAR (i.e., PAR greater than 1000 µmol/m^2/s) due to flooding. Although the hollow subplots were not flooded during the 2016 growing season (Figure 3), productivity at the hollow was at its peak when WTD was around its deepest point (Figure 3 and Figure 6 (a)).

Figure 7 shows the rectangular hyperbola shapes of the fitted GPP-PAR relationship for all the subplots and for both sites while Table 5 shows the

estimated parameters (i.e., α and GPP_{max}) of the GPP-PAR relationship. SM

increase (which is normally associated with rising WTD in natural peatlands) was

seen to negatively correlate with maximum gross primary photosynthesis rate

(Photo_max) at the hollow, significantly accounting for 24% of the variability in

Photo_max (r = -0.49, p < 0.05). TN concentration also significantly explained

25% of the variation in Photo_max (r = 0.495, p < 0.05) at the hollow.

Interestingly, when an average PAR (which included PAR values < 1000

$\mu mol/m^2/s$) was considered, TN concentration at the hollow could only explain

~0.4% of the variation in GPP (Table 7). This implies that the ability of available

nutrients to contribute to the photosynthetic capacity is constrained by low light

levels.

In a fen, Strack and Waddington (2007) recorded a variation in respiration

and GPP among their hummock, lawn and hollow microforms, with hollow seeing

an increase in respiration and GPP after water table drawdown. This also

suggests a negative correlation between productivity and WTD position at the

hollow microforms. On the other hand, the hummock subplots recorded the

deepest WTD during the growing season (Figure 3). EC, an indicator of water

availability, also showed a positive correlation with Photo_max at the hummock (r

= 0.05, even though not statistically significant, p > 0.05). This suggests that an

increase in water availability could increase maximum productivity at the

hummock. Bubier et al. (2003a) showed that the rate of CO_2 uptake is lowered

under drier condition among bog hummock and hollow, poor fen and beaver pond

margins. Results showed a significantly higher mean Photo_max at the hollow

(0.17 ± 0.002 mgCO$_2$/m^2/s) compared to the hummock (0.10 ± 0.00 mgCO$_2$/m^2/s, p < 0.001) (Table 5) which had the deepest WTD. This significantly lower maximum productivity could be due to the drop in water table position at the hummock. Riutta et al. (2007) reported an increase in respiration and a decrease in photosynthesis and NEE at their fen site due to water table drawdown. With *Sphagnum* moss dominating the peat on our hummock subplot, and mosses being the most affected due to water table drawdown, I believe that water table drawdown during the peak photosynthetic period of the 2016 growing season at the hollow (Figure 3) may be within a reasonable range and was responsible for the increased Photo_max while the drawdown at the hummock was therefore beyond a reasonable range, causing a decrease in productivity even at optimum PAR level.

At optimum PAR, significant differences were found among the Photo_max of the sedge, shrub grass and the ditch subplots at the drained peatland pasture site (Table 5). The shrub subplot recorded the highest maximum gross photosynthesis rate (Photo_max) (0.59 ± 0.03 mg/m^2/s) and was significantly different from the Photo_max of the other PFTs affected by peatland drainage. Bubier et al. (2003b) recorded a larger maximum CO$_2$ uptake (30 – 40%) in a drier summer in shrub communities but lower or similar in the case of sedge sites. Here, WTD and temperature were seen as the main regulators of the increase in productivity. Combining SM, WTD, EC, T$_5$, TN and DOC in a stepwise MLR analysis, EC alone significantly accounted for 58% of the variability in maximum gross primary photosynthesis (Photo_max) at the shrub subplot (F(1,

11) = 15.38, p < 0.01). The negative correlation (r = -0.764) between the EC and maximum photosynthesis suggests that the water table drawdown via drainage might be responsible for the increase in maximum productivity at the drained peatland pasture site (since a drop in WTD is known to decrease EC). Significantly, WTD, T_5, TN and DOC respectively explained 36%, 37%, 44% and 30% of variability in the Photo_max at the shrub subplot. Apart from TN and WTD which significantly explained 33% and 21% of the variability in Photo_max at the grass and ditch subplots respectively, none of the other variables were able to significantly account for the variability in the Photo_max at the sedge, grass and ditch subplots. Indeed, plant functional types differ in their maximum CO_2 uptake and photosynthetic capacity (Bubier et al., 2003b).

   All the PFTs affected by drainage had a greater Photo_max than what was recorded by the microforms and the natural site in general (Table 5). Respectively, EC, TN and DOC significantly (p < 0.05) explained 20%, 26% and 27% of the variability in Photo_max at the drained peatland pasture site. In a stepwise MLR analysis, the most important variable in explaining the variability in Photo_max at the drained site was DOC (F(1, 15) = 5.467, p < 0.05). On the other hand, the mean Photo_max at the natural site was primarily linked to changes in WTD as it significantly explained 44% of the variability in Photo_max (F(1, 12) = 9.2, p < 0.01). Adding SM through MLR analysis further increased the coefficient of determination (r^2 = 66%, p < 0.01). The positive correlation between Photo_max and both WTD and SM at the natural site suggests that the drop in WTD during the growing season (Figure 3) could be beyond favorable level for

growth and development at the natural site in general. This suggests that for an

extreme dry case scenario, the maximum gross primary photosynthetic capacity

of the natural peatland site could be reduced especially at the hummocks.

4.2 Differences in gross primary productivity and the primary control of water use efficiency in boreal peatlands.

This study observed a difference in WUE between the drained and natural peatland bog that is primarily controlled by GPP. WUE was higher at the drained peatland pasture site (0.047 ± 0.01 mgCO$_2$/mgH$_2$O) than the natural site (0.005 ± 0.00 mgCO$_2$/mgH$_2$O) ($p < 0.01$) (Table 4). This could be due to the relative increase in GPP at the drained site. Even though the average ET rate was lower at the natural site (13.29 ± 1.45 mgCO$_2$/m^2/s) relative to the drained site (17.22 ± 2.32 mgCO$_2$/m^2/s) (Table 4), the GPP/ET ratio was significantly greater at the drained site than at the natural site. This suggest that increase in GPP is of relative importance when it comes to WUE improvement. The higher ET rate at the drained site may be partly due to the higher surface temperature and SM content compared to the natural site (Table 2 and Figure 4). The increase in ET rate might also be due to the enhanced water loss into the atmosphere through the stomata at the time when most of the PFTs have established and covered most part of the soil. This could limit the amount of radiation transmitted to the peat surface and reduce surface evaporation or unproductive water loss (Brümmer et al., 2012). This loss of water through the stomata (i.e., productive water loss) while reducing surface evaporation, might have contributed to the increased WUE at the drained site. The comparatively lower ET rate at the natural site could be partly due to the deeper WTD recorded at the hummock subplots during the growing season (Figure 3) and the lower productivity (Table

3) thereby increasing surface evaporation with a corresponding decrease in transpiration. This could limit productive water loss to the hollow subplots which were more productive at the time when WTD was at its deepest point. This might have affected the differences in plot ET rate (Table 4 and Figure 5 (a)) and hence the average seasonal pattern of ET rate at the natural site (Figure 5 (b)). This suggests that most of the water loss into the atmosphere at the drained site, after the establishment of most PFTs (i.e., during the period of active growth), was a result of stomata conductance compared to the natural site where for the most part (especially at the hummock subplot) plant growth was limited during the 2016 growing season. On average, this can reduce the WUE of the natural site, as water loss from the exposed peat surface may not be controlled by stomata but by the availability of water as a function of WTD (Brümmer et al., 2012), which was estimated to be shallower at the natural site (-17.13 ± 1.28 cm) compared to the drained site (-21.90 ± 1.98 cm) (Table 2).

At the plot level, distinct differences in WUE and GPP between the hummock and hollow subplots were observed. GPP and WUE were significantly greater at the hollow subplot relative to the hummock subplot (Table 3 and Table 4). However, no significant difference was observed in ET rate between the two subplots. Among the drained subplots where there was no significant difference in their GPP, there was no difference in their WUE even though ET was significantly higher at the ditch subplot relative to the grass subplot. This supports the assertion that GPP is the controlling factor in the GPP/ET ratio even among the subplots. Mkhabela et al. (2009) concluded that sites with comparatively

greater surface evaporation, without carbon uptake through leaves, tend to use water less efficiently compared to sites with whole ecosystem ET. According to Ponton et al. (2006), "*when the effects of soil and surface water evaporation are minimized, variation in WUE is controlled by leaf gas exchange characteristic and environmental factors*". Because plants control stomata in order to optimize the trade-off between the amount of carbon absorbed and the amount of water loss (Cowan and Farquhar, 1977), the significant increase in growth coupled with the corresponding increase in peat surface cover, and stomatal conductance instead of peat surface evaporation, is likely responsible for the increase in WUE at the drained site. Coursolle et al. (2006) have confirmed that differences in the amount of live aboveground biomass among peatland sites can have a significant effect on their gross ecosystem productivity and respiration. GPP and ER were both estimated to be significantly higher at the drained site compared to the natural site ($p < 0.001$, Table 3). The significantly higher ER rate at the drained site could be due to the relatively deeper WTD and the significantly higher peat surface temperature (T_5) ($p < 0.001$, Table 2 and Table 3) since the combined effect of increased peat temperature and lowered WTD promotes the respiration of peat substrates (Hogg et al., 1992).

On the other hand, the reduced WUE at the natural site could be due to the relatively higher proportion of unproductive water loss via surface evaporation (Mkhabela et al., 2009), which is not controlled by stomata conductance but by the availability of water as a function of WTD (Brümmer et al., 2012), especially at the hollow subplot where WTD was relatively high (Table 1). Therefore, if

vegetation growth and the subsequent carbon uptake for photosynthesis are closely related to ET (Brümmer et al., 2012), then the water loss from the natural site was less efficient. This pattern of variation in WUE among the subplots, and between the two sites, where GPP is seen as the primary control, contrasts with the observation made by Ponton et al. (2006), where WUE variation among Douglas fir, aspen and grassland sites was seen to be controlled by differences in ET. However, the pattern of similarity in WUE among the different PFTs is in line with the observations made by Law et al. (2002). Law et al. (2002) found WUE to be similar among different biomes (i.e., forest, crops and grasslands).

Correlation analysis revealed a negative relationship between WTD, SM and WUE at the drained site (Figure 10 (a) and (c)). This means that WUE increased as WTD and SM decrease. The reduction in SM and WTD might have caused a larger proportion of water loss into the atmosphere through the absorption by roots, making water loss more efficient. On the other hand, peat T_5 had a positive correlation with WUE at the drained site (Figure 10 (b)). Several studies have shown that increase in soil temperature leads to a corresponding increase in GPP and respiration among boreal forest species (Pumpanen et al., 2012; Zhang and Dang, 2005; Dang and Cheng, 2004; Peng and Dang, 2003) and within peatlands (Chivers et al., 2009). The results show a higher soil temperature at the drained site (14.6 ± 0.44 °C) compared to the natural site (11.5 ± 0.29 °C) (t(33.3) = 5.91, p < 0.001) (Table 2). This increase in soil temperature accounted for 27% of the variation in GPP at the drained peatland pasture site (Figure 9 (e)). The increase in productivity associated with soil

temperature increase could directly lead to an increase in WUE. Also, plant growth could prevent the direct incident of light on the peat surface, thereby reducing the unproductive water loss through surface evaporation, and limit a larger proportion of water loss to transpiration. Results of similar analyses for the natural site is shown in Table 8. Here, only T_5 was significant in explaining WUE. The negative correlation also shows that WUE decreases as peat surface temperature increases at the natural site. This could be due to increase in surface evaporation, making water loss less efficient. Since plant growth was low at the natural site relative to the drained site (especially at the hummock subplots), increase in soil temperature could lead to increase in surface evaporation with little or no corresponding increase in GPP. This could eventually lead to a relatively low WUE.

5. Conclusion

The significant difference in productivity between the shrub and ditch subplots suggests that community type and land-use practices within a drained peatland pasture site will be a significant factor in GPP modeling. For a natural peatland with different microtopography, the differences in WTD and the subsequent effect on the peat physical and hydrothermal properties, makes them vital when it comes to their production rate. Hence, the difference in productivity between the hummock and hollow subplots as well as the drained and natural sites suggests that large-scale carbon modelling would require information on microforms and disturbance types within large grid cells.

Results of this study support the fact that land-use type and management activities affect productivity of peatlands. The variation in maximum gross primary photosynthesis (Photo_max) at both plot and site scale support the assertion that different plant communities differ in their maximum CO_2 uptake and photosynthetic capacity. Results also show that PFTs at the drained site will differ in productivity just as the microforms at the natural site when the optimum PAR level is considered (especially for the shrubs). This suggests that in ecosystem carbon modelling, the maximum PAR level at which GPP is estimated is critical as it can lead to differences in productivity among plant forms – especially the shrubs.

The results clearly estimated a higher biomass production, with a corresponding increase in peat decomposition due to peatland drainage.

However, the much larger increase in GPP at the drained site compared to the

ER during the 2016 growing season, and the corresponding much greater NEE

(carbon sink) value (-0.188 ± 0.02) at the drained site than that of the natural site

(-0.050 ± 0.01) ($p < 0.001$), suggest a greater net carbon sink ability of the

drained peatland pasture site (Table 3). This is in line with Arnold et al. (2005),

who found their coniferous forest site to be a net carbon sink after drainage, and

Minkkinen and Laine (1998), who recorded an increase in carbon store after 60

years of drainage. The results also confirm the assertion that water table

drawdown will only drain a very small amount of water from a decomposed peat

(Boelter, 1964) thereby making water accessible for plant growth.

Results of this study suggest that hydrological changes via peatland

drainage can affect not only the carbon balance of boreal peatland ecosystem

through photosynthesis, but also the change in the physical and hydrothermal

properties of the peat (especially EC and T_5). I therefore conclude that

differences in microtopography and the corresponding changes in vegetation,

land-use practice (Eickenscheidt et al., 2015) and its effects on peat properties,

and hydrology (WTD in particular), should be taken into account when modeling

the gross primary production in a peatland ecosystem.

No significant difference in WUE was observed among the plant functional

types at the drained peatland pasture site. However, between the hummock and

hollow subplots and between the drained and natural sites, the results show a

significant difference in their WUE. From the results, ET remained statistically the

same between the hummock and hollow subplots. However, GPP was significantly different between the hummock and hollow subplots, resulting in a significant difference in WUE, with the hollow, which had a relatively higher GPP, recording the highest WUE. This makes GPP the only changing factor between the hummock and hollow subplots in the GPP/ET ratio. Although ET was statistically higher at drained site relative to the natural site, the GPP/ET ratio (WUE) was significantly higher at the drained site compared to the natural site. This makes the relative increase in GPP at the drained site, the most important factor in comparing site WUE. Coincidentally, WUE remained statistically the same among the plant functional types affected by drainage. Except between the shrub and the ditch subplots, no significant difference was found as far as their GPP is concerned. Based on the definition of WUE (i.e., the ratio of GPP to ET), I therefore conclude that differences in WUE at the plot level, and between the drained and natural sites are primarily controlled by variation in GPP.

Since ET rate is a critical component in the water balance of terrestrial ecosystem, the significant difference in ET among the drained subplots and between the two sites suggests that land-use type and management activities have a major impact on the water balance and assessment of water resources at a boreal peatland ecosystem. On the other hand, the non-significant difference in ET between the hummock and hollow subplots suggests that differences in microtopography have no major impact on water balance and assessment of water resources at a natural peatland bog.

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