

**Comparison of the annual exchange of carbon dioxide between treed and open  
portions of a temperate bog peatland and the atmosphere**

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## Abstract

An examination of carbon dioxide (CO<sub>2</sub>) exchange at treed bog and open bog portions of the Mer Bleue Peatland Complex near Ottawa, Ontario was carried out. Tower derived eddy covariance net ecosystem exchange of CO<sub>2</sub> (NEE) and chamber derived species-level net primary productivity were collected for the 2006/07 study year and growing season, respectively. The goal was to compare the CO<sub>2</sub> exchange processes between these two peatlands with the hypothesis that peatlands are relatively conservative ecosystems and differences in species composition may lead to only minimal differences in CO<sub>2</sub> exchange. As such, these peatlands might be considered to be the same surface type for modelling purposes. However, growing season differences in NEE resulted in the open bog sequestering substantially more CO<sub>2</sub> (NEE = -104.1 g C m<sup>-2</sup> y<sup>-1</sup>) than the treed bog (NEE = -71.8 g C m<sup>-2</sup> y<sup>-1</sup>). Dissimilar structure and functioning, due to differing vegetation characteristics and microclimate influence, are responsible for the disparity in NEE between the sites. Differences in CO<sub>2</sub> exchange are small when compared to either other ecosystem types or interannual variability within a given peatland ecosystem.

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## List of Symbols

Term/ Symbol	Unit	Definition
$\alpha$	mol CO <sub>2</sub> mol <sup>-1</sup> photons	describes sensitivity of C uptake to change in light
BP	kPa	barometric pressure
CH <sub>4</sub>	ppm	methane
CO <sub>2</sub>	ppm	carbon dioxide
d	d	day
DOC	g C m <sup>-2</sup> y <sup>-1</sup>	dissolved organic carbon
EC	N/A	eddy covariance
ER	$\mu\text{mol m}^{-2} \text{s}^{-1}$ or g C m <sup>-2</sup> y <sup>-1</sup> or g C m <sup>-2</sup> d <sup>-1</sup>	ecosystem respiration (R <sub>a</sub> + R <sub>h</sub> )
GEP	$\mu\text{mol m}^{-2} \text{s}^{-1}$ or g C m <sup>-2</sup> y <sup>-1</sup> or g C m <sup>-2</sup> d <sup>-1</sup>	gross ecosystem productivity (GEP = NEP + ER)
H <sub>2</sub> O	ppm or mmol mol <sup>-1</sup>	water vapour
IRGA	N/A	infrared gas analyser
LAI	m <sup>-2</sup> m <sup>-2</sup>	leaf area index
MAT <sub>a</sub>	°C	mean annual air temperature
min	m	minute
NEE	$\mu\text{mol m}^{-2} \text{s}^{-1}$ or g C m <sup>-2</sup> y <sup>-1</sup> or g C m <sup>-2</sup> d <sup>-1</sup>	net ecosystem exchange (NEE = ER - GEP)
NEP	$\mu\text{mol m}^{-2} \text{s}^{-1}$	net ecosystem productivity (NEP = GEP - ER)
NPP	$\mu\text{mol m}^{-2} \text{s}^{-1}$	net primary productivity (NPP = GEP - R <sub>a</sub> )
PAR	W m <sup>-2</sup>	photosynthetically active radiation
P <sub>max</sub>	$\mu\text{mol m}^{-2} \text{s}^{-1}$	maximum rate of NEE at light saturation
PPFD	$\mu\text{mol m}^{-2} \text{s}^{-1}$	photosynthetic photon flux density
PPFD <sub>d</sub>	$\mu\text{mol m}^{-2} \text{s}^{-1}$ or mol m <sup>-2</sup>	downwelling PPFD
PPFD <sub>u</sub>	$\mu\text{mol m}^{-2} \text{s}^{-1}$	upwelling PPFD

Term/ Symbol	Unit	Definition
R <sub>10</sub>	μmol m <sup>-2</sup> s <sup>-1</sup>	ER at 10 °C (NEE), plant respiration at 10 °C (NPP)
R <sub>a</sub>	μmol m <sup>-2</sup> s <sup>-1</sup> or g C m <sup>-2</sup> y <sup>-1</sup> or g C m <sup>-2</sup> d <sup>-1</sup>	autotrophic respiration
R <sub>h</sub>	μmol m <sup>-2</sup> s <sup>-1</sup> or g C m <sup>-2</sup> y <sup>-1</sup> or g C m <sup>-2</sup> d <sup>-1</sup>	heterotrophic respiration
RH	%	relative humidity
R <sub>n</sub>	W m <sup>-2</sup>	net radiation
s	s	second
SM1	%	soil moisture at 10 cm depth, volumetric water content
SM2	%	soil moisture at 20 cm depth, volumetric water content
t	s, d, y	time
T <sub>a</sub>	°C	air temperature
TP	mm/30 min	total precipitation
T <sub>s</sub>	°C	soil temperature
u <sub>*</sub>	m s <sup>-1</sup>	friction velocity
VP	kPa	vapour pressure
VPD	kPa	vapour pressure deficit
w	m s <sup>-1</sup>	vertical wind velocity
WT	N/A	water table
WTD	cm	water table depth
y	y	year

### Flux Conversion

$$\frac{\mu\text{mol } CO_2}{m^2 s} \times \frac{\text{mol } CO_2}{10^6 \mu\text{mol } CO_2} \times \frac{12 \text{ g C}}{\text{mol } CO_2} \times 1800 s = \frac{\text{g C}}{m^2}$$

# 1. Introduction

## 1.1 Introduction

Peatlands are abundant and widespread within Canada and are significant stores of carbon (C) at both the regional and global scales (Tarnocai *et al.* 2000, Gorham 1991). It is important to understand how these ecosystems will react to current and future climate warming due to the potential for feedback effects on climate through carbon dioxide (CO<sub>2</sub>) uptake or loss (Moore 2002). Peatland ecosystems include a wide range of hydrological, chemical, and biological characteristics but all have accumulated a minimum 40 cm layer of partially decomposed organic material (National Wetlands Working Group 1997). The main differentiation between fens and bogs is the source of water and nutrients. Bogs receive nutrient and water input solely from precipitation while fens also receive mineral-rich groundwater. Vegetation cover varies, with regions dominated by *Sphagnum* moss characterised by a lack of both water flow and nutrients. Bogs, which are on the stagnant water and nutrient poor end of the peatland spectrum, have varying above-ground vegetation including herbs, shrubs, grasses, and trees. Treed peatlands generally have more acidic conditions and less water flow than non-treed ones (Zoltai and Vitt 1995).

All peatlands assimilate CO<sub>2</sub> via photosynthesis which results in short-term C storage in plants. As plants die they accumulate at the surface where decomposition of the organic material results in C loss via respired CO<sub>2</sub> and methane (CH<sub>4</sub>) gases and outflow of dissolved organic carbon (DOC). In the long-term, C is stored in peat which is the result of slow decomposition rates rather than overly productive vegetation.

Investigating how ecosystem structure relates to ecosystem function is pertinent to determining whether peatlands can be treated as one surface cover type in land surface schemes and general circulation models. Model complexity has been increasing in an attempt to improve accuracy and confidence in predictions related to climate change (Sellers *et al.* 1997). These models use specific information about surface types such as CO<sub>2</sub>, water vapour, heat, and radiation fluxes, as well as the physiological parameters that are associated them, as input data and for validation of modelled values.

There is not a large body of literature on unharvested treed peatlands but the importance of vegetation characteristics on net ecosystem exchange of CO<sub>2</sub> (NEE) was noted by Humphreys *et al.* (2006b) and Lafleur *et al.* (1997). In the first study, key ecosystem characteristics such as surface conductance were shown to be influenced by vegetation composition with woody plants reducing transpiration more under large atmospheric vapour deficit conditions than *Sphagnum* mosses. The authors' conclusion was that while NEE may be similar, vascular plant biomass and moss cover play a large role in peatland CO<sub>2</sub> and H<sub>2</sub>O fluxes due to their influence on ecosystem functioning (Humphreys *et al.* 2006b). Lafleur *et al.* (1997) also reported that vegetation affects ecosystem functioning with an increase in solar albedo and switch from CO<sub>2</sub> source to sink occurring during the growing season as vascular vegetation leafs out. CO<sub>2</sub> flux by treed peatlands has been described as both similar to (Humphreys *et al.* 2006b) and a larger net C sink than (Syed *et al.* 2006) bogs and fens without trees. Trees add an upper-canopy layer that accompanies the lower-canopy shrub layer and moss ground layer. As

such, the additional vegetation should increase C sequestration with the extent of the increase depending upon the productivity of trees in saturated and acidic conditions.

The atmospheric exchange of CO<sub>2</sub> has been monitored since 1998 using the eddy covariance technique (EC) within an open portion of an ombrotrophic bog at the Mer Bleue Peatland Complex (MBPC) near Ottawa, Ontario. Over a 6 year period, this ecosystem sequestered an average of approximately  $21.5 \pm 39 \text{ g C m}^{-2} \text{ y}^{-1}$ , approximately the same rate of C uptake determined for the past 3000 years (Roulet *et al.* 2007). The C sequestered by the ecosystem is the net difference between CO<sub>2</sub> uptake via photosynthesis and CO<sub>2</sub> release via aerobic respiration and oxidation, CH<sub>4</sub> release by anaerobic respiration, and DOC export via waterways. This bog is part of a larger peatland complex that also includes treed bog areas, a poor fen, and cattail marshes. A study reported the cattail marsh to be a substantially greater net C sink ( $264 \text{ g C m}^{-2}$ ) than the open bog (Bonneville *et al.* 2008). The marsh is a mineral wetland with dramatically different structure and function than the open bog. The MBPC is an ideal complex to study the role that trees play in peatland ecosystem C exchange as open and treed bog areas are in close proximity and experience the same weather and long-term climate conditions. I hypothesize that short-term NEE at open and treed bog sites should be similar because long-term data indicates that peatlands are conservative ecosystems that accumulate  $20\text{-}30 \text{ g C m}^{-2} \text{ y}^{-1}$  regardless of type (Gorham 1991). This suggests that peatlands can only sustain a certain amount of net C sequestration regardless of differences in plant species composition. This research will contribute to the growing

body of treed peatland NEE work in the literature and assist in the development of future models.

Ecosystem-level and plant-level CO<sub>2</sub> measurements for the 01 November 2006 to 31 October 2007 C-year were carried out at treed and open portions of MBPC to investigate how CO<sub>2</sub> fluxes at these sites compare. The objectives of this research project are to 1) quantify the annual net ecosystem exchange of CO<sub>2</sub> (NEE) of these ecosystems and 2) investigate the role that trees play in peatland functioning. Due to the similar weather conditions at these sites, dissimilarities in CO<sub>2</sub> fluxes may be attributed to differences in structural characteristics related to species composition and/or differences in microclimate. CO<sub>2</sub> exchange is examined at different scales with continuous EC measurements of NEE representing the largest spatial scale – an area of approximately 10,000 m<sup>2</sup> (Baldocchi 2003). Periodic chamber measurements of net primary productivity (NPP) from above-ground portions of individual plants are used to investigate the contributions of various plant species to ecosystem-level NEE. Year-round measurements of weather and soil microclimate variables allow for the relationships and influences of environmental variables on NEE and NPP to be explored.

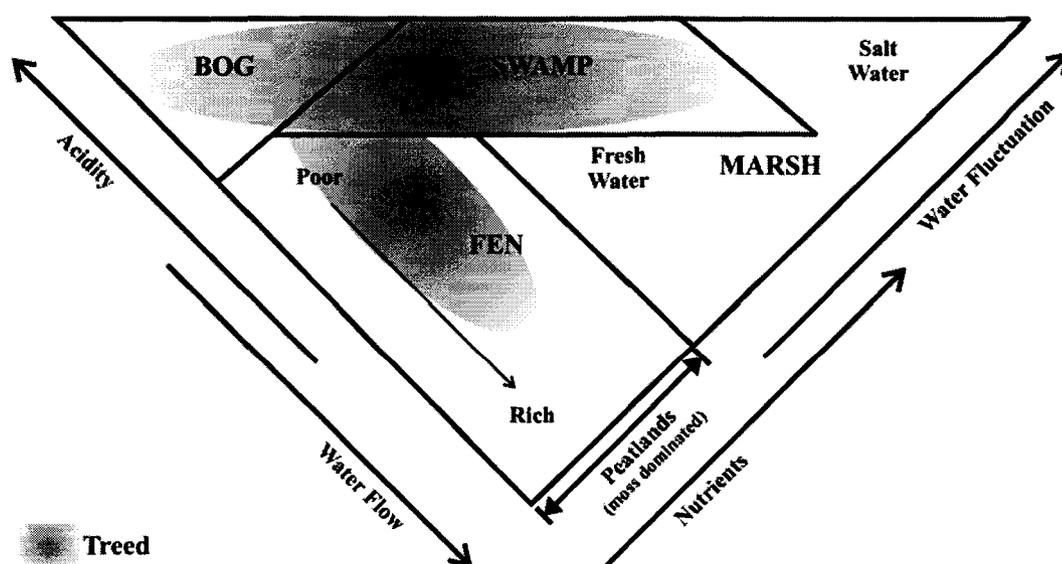
## **1.2 Background**

### *1.2.1 Peatlands*

Land that is saturated with water for a period long enough to promote wetland or aquatic processes is referred to as a wetland (National Wetlands Working Group 1988). Wetlands are associated with poorly drained soils, hydrophytic vegetation, and biological activity which has adapted to a moist environment. The roughly 150 Mha of wetlands

found throughout Canada represent ~24% of global wetlands (National Wetlands Working Group 1986, National Wetlands Working Group 1997). The Canadian Wetland Classification System, 2<sup>nd</sup> Edition (National Wetlands Working Group 1997) contains a hierarchical classification for wetlands. They are separated into two broad categories, namely mineral and organic, depending upon accumulation of organic matter. These categories are further divided into classes based on the origin and nature of a wetland environment, forms related to site specific characteristics, and types based on vegetation characteristics.

Peatlands, also referred to as organic wetlands, contain more than 40 cm of peat, which is composed of poor to moderately decomposed *Sphagnum* mosses, ericaceous shrubs, and cotton grass (*Eriophorum vaginatum*) (National Wetlands Working Group 1997). Although all peatlands by definition contain peat, there is tremendous diversity in peatland hydrological, chemical, and vegetation characteristics (Zoltai and Vitt 1995)



**Figure 1.2:** Schematic diagram of wetland spectrum with areas of tree coverage identified. Based on Figure 2 from Zoltai and Vitt (1995).

(Fig. 1.1). For example, ombrotrophic bogs are nutrient poor peatlands which have *Sphagnum* moss as the dominant ground cover and receive nutrient input solely from precipitation while minerotrophic fens receive additional mineral rich water from underground and surface runoff and have a mixture of graminoid species and brown mosses as the dominant ground cover (National Wetlands Working Group 1997).

Peatlands are estimated to cover 350 Mha worldwide with a majority (86.4%) located in the temperate climate zone (Moore 2002). Within Canada, ~12% of the landmass is covered by peatlands (Tarnocai *et al.* 2000). Peatlands are significant reservoirs of C and constitute about one third of the total global soil C pool. C is sequestered in peatlands as a result of a small imbalance between CO<sub>2</sub> uptake through photosynthesis and CO<sub>2</sub>, CH<sub>4</sub>, and DOC loss associated with decomposition and respiration. This imbalance is likely due to some combination of cold, water-logged, and/or acidic conditions which are often associated with peatlands. C accumulates as peat which is approximately 50% C by weight (Gorham 1991) and represents a long-term C store on the order of 1000's of years. Not all peatlands contain trees, which are above-ground reservoirs of C on short-to-medium time scales.

### *1.2.2 Peatlands and Global Warming*

The C cycle describes the exchange of C between the earth's biogeochemical spheres and links peatlands with the issue of global warming. C is sequestered in peatlands through the uptake of atmospheric CO<sub>2</sub> during plant photosynthesis. The C is stored within the above and below-ground vegetation, including *Sphagnum* mosses, shrubs, herbs, grasses, and trees, as well as within dead and decaying organic matter

below the surface. The majority of C stored in peatlands is located below the surface. Gorham (1991) estimated that peat accounts for ~98.5% of C sequestered. Loss of C occurs through the release of CO<sub>2</sub> and CH<sub>4</sub> (produced by plant (R<sub>a</sub>) and animal/microbial (R<sub>b</sub>) respiration) into the atmosphere and outflow of water containing DOC. A bog is a dynamic system with flows in and out occurring at the same time so whether or not C is being stored or lost depends upon the magnitude of the respective accumulation and release processes. Global warming is believed to occur as a result of increasing concentrations of greenhouse gases in the atmosphere such as CH<sub>4</sub> and CO<sub>2</sub> (Taylor 1991). These greenhouse gases absorb and emit infrared radiation, a phenomenon known as the greenhouse effect whereby the earth's surface is kept warmer than if energy was not being trapped within the system.

Peatlands are widespread north of 45° latitude (Gorham 1991). It has been noted that these regions are experiencing greater rates of warming than elsewhere (Kaplan and New 2006). Boreal, sub-arctic, and arctic peatlands comprising 60% of Canadian peatlands, are expected to be severely affected by global warming (Tarnocai *et al.* 2000). The role of peatlands as C stores and their potential feedback effects on global warming through emissions of CH<sub>4</sub> and CO<sub>2</sub> make the understanding of how these ecosystems function critical to future climate predictions. However, there is uncertainty about how the very complex nature of peatland functioning will react to forcings associated with global warming such as changes in precipitation or temperature. An example of this complexity is a study which contradicted the established idea that warmer temperatures would result in lowering of water table (WT) levels and decreased methane emissions

(Strack *et al.* 2006). This paper reported that with lowering of the WT, the vegetation community changes to sedges under certain conditions. As a result, methane emission would increase due to the aerenchymous tissues within sedges that allow CH<sub>4</sub> to pass from the saturated zone to the atmosphere and avoid oxidation within the expanded aerobic zone.

In an attempt to assess potential outcomes of a changing climate on peatlands, a model was developed. The Peatland Carbon Simulator (PCARS) simulates a complete peatland C balance on seasonal to interannual time scales. It was developed using C flux data from the MBPC and was designed to couple with a general circulation model to aid in predicting potential outcomes of global warming (Frolking *et al.* 2002). PCARS was designed particularly for an open bog and modelled data that differed from measured values. Modelled data was biased towards ecosystem respiration (ER) and C loss. The authors conclude that the discrepancy between measured and modelled data is due to differences in R<sub>a</sub> and/or R<sub>h</sub>.

The importance of different structural types on C budgeting has been recognised. Treed peatland C budgeting and anaerobic biogeochemistry simulation work has been carried out from a forestry management perspective. One study found that results of different management practices (e.g. duration of harvesting cycles) resulted in substantial differences in C sequestration (Cui *et al.* 2005). Ultimately, improving the current understanding of individual peatland type mechanisms and reactions to climate forcings is necessary to ensure accurate outcome assessments of future change.

### 1.2.3 Net Ecosystem Exchange

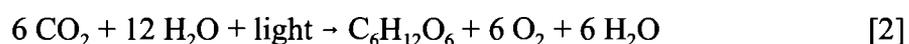
NEE is the difference between uptake of CO<sub>2</sub> by photosynthesis and loss due to aerobic respiration and decomposition. NEE has much greater magnitude and interannual variability than annual fluxes of DOC and CH<sub>4</sub> (Roulet *et al.* 2007). As such, NEE is the principal C flux examined in this study. NEE is the difference between ER, which is comprised of both R<sub>a</sub> and R<sub>h</sub>, and gross ecosystem productivity (GEP).

$$NEE = (R_a + R_h) - GEP \quad [1]$$

When the ecosystem is acting as a C source (more C leaving the system than entering) NEE has a positive value. NEE is determined by the factors that influence photosynthesis, respiration, and decomposition. Accumulation and loss processes occur simultaneously; therefore, they may affect each other and/or be influenced by the same environmental forcings.

### 1.2.4 Photosynthesis

Photosynthesis is a multi-step anabolic process undertaken by plants during which light energy from the sun is harnessed as biochemical energy in the bonds of a sugar molecule (Eq. 2). These sugars are converted to structural materials such as wood and fibres as well as carbohydrate storage molecules such as starch. It has been stated that 94% of a plant's dry weight is produced by photosynthesis (Stern 2006). C from atmospheric CO<sub>2</sub> is utilized in the sugar molecule glucose which results in C being sequestered within the plant. A simplified equation for photosynthesis is:



where CO<sub>2</sub>, H<sub>2</sub>O, and light are utilized by plant chlorophyll and enzymes to produce glucose (C<sub>6</sub>H<sub>12</sub>O<sub>6</sub>), oxygen (O<sub>2</sub>), and H<sub>2</sub>O. The main controls on photosynthesis are availability of CO<sub>2</sub>, H<sub>2</sub>O, and light but temperature also has an influence. A decrease in photosynthetic rates results from low concentration of CO<sub>2</sub>, low H<sub>2</sub>O content, limited availability of light, or extreme temperatures.

In peatlands, the main contributors to C uptake through photosynthesis are mosses, shrubs, and trees. Vascular plants contain transport systems which move materials such as water and nutrients through the plant. There are four main vascular functional groups in bogs: trees (e.g. *Picea mariana*), deciduous shrubs (e.g. *Vaccinium myrtilloides*), evergreen shrubs (e.g. *Ledum groenlandicum*), and graminoids (e.g. *E. vaginatum*). Non-vascular species, namely *Sphagnum* mosses, lack transport systems as well as the leaf, root, and stem growth forms associated with them. As a group, vascular plants are at a photosynthetic advantage over non-vascular plants but there is variation between vascular functional groups (van Breeman 1995). For example, a study on vascular plant species from the Arctic tundra reported that photosynthetic capacity of an evergreen shrub < graminoid species < a deciduous shrub (Limbach *et al.* 1982). It was suggested that differences in photosynthesis among functional groups was the result of different physiological controls. Evergreen shrubs balance a lower photosynthetic capacity by carrying out photosynthesis for a longer period of time during the growing season and retaining nutrients with minimal dieback. On the other hand, deciduous shrubs maximize photosynthetic C uptake in the limited time they have available. *Sphagnum* is at a photosynthetic disadvantage compared to vascular plants because it has

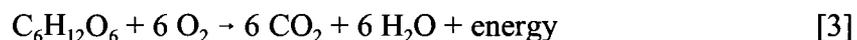
low light-use efficiency (van Breeman 1995). Light saturation at  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ , accompanied by a gross  $\text{CO}_2$  exchange (C loss during dark respiration not accounted for) of  $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ , was reported for *Sphagnum spp.* in a boreal forest (Goulden and Crill 1997). In comparison, *P. mariana* NPP rates were  $5.8 \pm 0.6$  ( $\pm 1$  standard error (SE))  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in an Alberta bog (Syed *et al.* 2006).

Similarly, physiological controls are different for vascular and non-vascular species. Photosynthesis in vascular plants is carried out within chlorophyll found in the leaves (Stern 2006). The water needed in photosynthesis is transported up from the roots while  $\text{CO}_2$  enters through adjustable openings on the surface of leaves called stomata. Air exchanges freely between the leaf and the atmosphere when the stomata are open which means that the plants can lose water vapour through a process called transpiration. Photosynthesis is inhibited by factors, such as a lack of available moisture, that cause the stomata to close. A lack of soil water, and/or increased water vapour loss due to a strong moisture gradient between the leaf and the atmosphere, are two factors that can result in a moisture deficit. *Sphagnum* mosses thrive under wet conditions but are able to alleviate moisture stress by using capillary suction to pull water up from depth through spaces between the branches and stems (van Breeman 1995). Photosynthesis is inhibited when limited light is available and under both saturated and desiccated moisture conditions (Williams and Flanagan 1996, Goulden and Crill 1997). Vascular canopy layers have the potential to impact the microclimate and productivity of underlying mosses. Shading reduces available light and decreases temperature while transpiration transfers water from the surface to the atmosphere. Overall, since peat is predominantly composed of

*Sphagnum* material, it is the non-vascular plant production that is important to long-term C sequestration. The vascular plants are more productive on the short-term and likely dominate NEE on this time scale.

### 1.2.5 Respiration

The multi-step catabolic process that breaks down glucose for use by autotrophic and heterotrophic organisms is respiration. During this process, energy from the bonds of the glucose molecule is released as heat or transferred to adenosine triphosphate (ATP). The energy in ATP, accounting for ~39% of energy stored in the initial glucose molecule, is then available for life processes (Stern 2006). There are various types of respiration: photorespiration (aerobic), dark respiration (aerobic), anaerobic respiration, and fermentation (anaerobic) (Jones 1994). They vary in light requirement, presence of oxygen, processes, molecules produced, and efficiency with the more efficient aerobic respiration (requires oxygen) accounting for 94% of total respiration and inefficient anaerobic respiration (requires absence of oxygen) the remaining 6% (Stern 2006). The simplified equation for aerobic respiration is:



where glucose is broken by enzymes in the presence of oxygen with CO<sub>2</sub>, H<sub>2</sub>O, and energy being produced. Anaerobic respiration that occurs at depth in the peat profile produces CH<sub>4</sub>. The CH<sub>4</sub> is released directly to the atmosphere or is transformed into CO<sub>2</sub> via oxidative processes during passage through the aerated surface zone of the peat profile. The main controls on respiration are temperature, H<sub>2</sub>O, and O<sub>2</sub>. Temperatures outside of the optimal 20-30 °C range, low water content, or low O<sub>2</sub> concentration result

in decreased respiration rates. This is a method of C loss because C stored in plants within the glucose molecule join with O<sub>2</sub> and are released into the atmosphere as CO<sub>2</sub>. Plants (e.g. mosses, shrubs, trees) and microorganisms (e.g. *Burkholderia* genus bacteria (Belova *et al.* 2005)) are the main contributors to C loss via respiration in peatlands. The contribution of *Sphagnum* moss to respiration is relatively small (0.5-1.5 μmol m<sup>-2</sup> s<sup>-1</sup>) and comes mainly from a shallow region below the surface (Goulden and Crill 1997). The different vascular plant functional groups differ in respiration rates with Limbach *et al.* (1982) reporting root respiration of a deciduous shrub < graminoid species < evergreen shrub.

#### 1.2.6 Decomposition

Decomposition is the breakdown and subsequent loss of organic material as a gas, in solution, or by removal by small invertebrates. In bogs, the majority of decomposition occurs in the acrotelm (aerobic surface zone) but it still occurs at depth in the catotelm (anaerobic zone below the acrotelm). The transition between the two zones can be roughly estimated as the mean minimum water table depth (WTD) during the summer (Clymo 1984). Decomposition rates are controlled by O<sub>2</sub>, temperature, nutrients, and phenolic compounds. Phenolic compounds aid in the breakdown of cyclic carbon compounds under aerobic conditions. High temperature, available nutrients, presence of oxygen, and abundance of phenolic compounds all encourage decomposition (Moore 2002). In general, decomposition rates are low in bogs but the rates vary between species with *Sphagnum* having lower decomposition rates than other plants (van Breeman 1995). It is for this reason that *Sphagnum* is often the main component of peat.

### 1.2.7 Peatland Bog Dynamics

As noted earlier (section 1.2.1), peatlands cover a broad spectrum of vegetation, hydrological, and chemical gradients. As a result, these ecosystems have considerable variation in structure (arrangement of components such as vegetation and H<sub>2</sub>O) and function (role of structural components). Bogs, whether treed or open, are characterised by acidic, nutrient-poor conditions but may be wetter or drier or with a dynamic WT (Zoltai and Vitt 1995). This is due mainly to nutrient and water input solely by precipitation and the properties of the *Sphagnum* mosses that dominate these ecosystems. *Sphagnum* acidifies as it decomposes which can create extremely acidic conditions, has the ability to hold large amounts of water which limits lateral flow, and over time can dome which increases the movement of nutrients obtained from precipitation to the outer edges of the bog. Overall plant productivity, vascular and non-vascular, is low in bogs due to acidity and lack of nutrients. Similarly, acidity, cold, and lack of oxygen create difficult conditions for below-ground fauna which limits decomposition. In effect, the moss initiates a positive feedback whereby it creates the conditions that it thrives in and sustains them by regulating ecosystem conditions. While the genesis of bogs, through either the process of terrestrialization (in-filling of lakes) or paludification (invasion of uplands), is well-understood, a definitive explanation has not been presented for why some bogs are treed and some are not. However, it is possible to explore key water and vegetation dynamics that have an influence on C cycling in bogs, as well as the environmental parameters that influence them, and speculate upon how trees relate to bog functioning.

As water dominated ecosystems, it is not surprising that water chemistry and availability play a key role in bog ecosystem function. WTD affects many processes by controlling oxygen and water availability within the peat profile. As  $\text{CH}_4$  produced by respiration and decomposition in the anoxic zone of the peat migrates upwards towards the surface, it can be oxidized by methanotrophic bacteria into  $\text{CO}_2$  while traversing the unsaturated zone of the peat (Clymo 1984, Roulet *et al.* 1993). The depth of the unsaturated zone determines how much C is emitted as  $\text{CH}_4$  versus  $\text{CO}_2$  with high  $\text{CH}_4$  emissions associated with a high WT. This is a universal mechanism which holds true across very different temperature, vegetation, and hydrological gradients from the Arctic to the Tropics (e.g. Roulet *et al.* 1993, Jauhiainen *et al.* 2005). The undulating hollow-hummock terrain which characterises many peatlands results in localised variations in WTD and subsequent adjacent micro-environments. Rouse *et al.* (1995) indicate that hollows lose more C as  $\text{CH}_4$  than adjacent hummocks. However, C loss as  $\text{CH}_4$  (hollows and hummocks) is estimated to be relatively small because of the acidic nature of peatland water (Roulet *et al.* 1994, Rouse *et al.* 1995). Tree presence has also been linked with micro-environments. Peat depth measurements at the study site revealed that tree presence in the open bog was associated with areas where the underlying undulating substrate was higher and produced thinner peat depth (Julie Talbot, personal communication). It is possible that a thinner peat profile provides more stability for tree rooting or is associated with the relatively older perimeter where trees have had time to infiltrate. WTD plays a role in C loss through decomposition by determining the zone available for aerobic respiration. A lowered WT and resulting increase in both oxygen

concentration and depth of zone for aerobic composition has been noted to increase decomposition in general and specifically allow fungi decomposers to thrive (Moore 2002).

Due to its importance to the photosynthetic process (see section 1.2.4) and biological functions, water availability has an impact on C uptake as well. Vascular plants take up water through absorption by roots while the growing tops, the capitula, of *Sphagnum* acquire water through capillary rise of ground water, absorption of dew, and interception of precipitation. The saturated nature of peatlands results in shallow rooting depths of trees and shrubs relative to rooting depths by similar species in mineral soil. Moss pulls up water from within the peat profile and helps keep the near-surface plant roots supplied with moisture (Hayward and Clymo 1982). However, the hydraulic conductivity of *Sphagnum* mosses decreases as they dry. It has been reported that peatlands become less productive during the latter part of the growing season when the WT drops below the rooting zone and *Sphagnum* moss desiccates (Lafleur *et al.* 2005). Water availability can also be a problem during the cold season. As water in the root zone freezes, vascular plants respond to the lack of water by closing their stomata and photosynthesis is effectively inhibited by lack of CO<sub>2</sub> (Öquist 1983). The effects of WTD on plants likely relates to tree cover in bogs. In general, the bog tree species *P. mariana* and *L. laricina* do not prefer flooded conditions. This relationship is present in a study which reported a raised treed bog island within a minerotrophic fen (Zoltai and Johnson 1985). It is not known if the same relationship is present within the peatland bog class. It is possible that trees have an optimal WTD zone below that of fens but on

the upper end of bogs. This balance would relate to having an oxygenated zone which provides adequate tree stability while still providing enough moisture for plant functioning.

Vegetation, including mosses, is an important factor in determining spatial and temporal patterns of peatland NEE. Lafleur *et al.* (1997) reported variations in NEE associated with uptake before leafout at a boreal fen while Thormann and Bayley (1997) reported that moss productivity accounted for ~50% of total productivity in a raised ombrotrophic bog over a 2 year period. Of note, the latter study also reported upon the contribution of other vegetation groups to short-term C sequestration within the bog with moss productivity > shrubs > trees. Despite being reported as the least productive vegetation type in a peatland, trees have been associated with inter-peatland NEE differences. Humphreys *et al.* (2006b) reported that from a selection of seven Canadian peatlands, the treed fens took up more CO<sub>2</sub> on a diurnal and growing season basis than the other fens and the bog without trees. Similarly, varying shrub and graminoid species have been associated with spatial and temporal variation in NEE. A study within a single peatland complex stated that while a deciduous dominated rich fen had the highest rates of daytime NEE and ER over a growing season, an ericaceous shrub bog and graminoid dominated poor and intermediate fens surpassed the rich fens in CO<sub>2</sub> uptake during the spring and fall (Bubier *et al.* 1998). The results in this study most likely relate to differences in ericaceous vs. deciduous shrub physiology discussed earlier (section 1.2.4). Lafleur *et al.* (1997) reported that deciduous vegetation phenology (leafout, peak foliage, senescence) influenced CO<sub>2</sub> flux at a minerotrophic fen. Seasonal variations in NEE

have been reported for coniferous *P. mariana* forests as well. All of this indicates that *P. mariana*, the dominant tree type in ombrotrophic bogs, as well as other evergreen plants, are able to contribute to C uptake early in the spring and late in the fall. The exact duration of this extended growing season is dependent upon weather and soil microclimate. Reduced plant activity during the spring and fall has been associated with physiological (e.g. recovery from winter dormancy) and environmental variables (air and/or soil temperature) (Frolking *et al.* 1998). It is possible to extrapolate that NEE for a treed bog could differ from that of an open bog on growing season and annual time scales due to the different physiological and phenological characteristics of the tree canopy.

Seasonal and interannual variations in WT and phenology are linked with weather variables such as sunlight, temperature, and precipitation. Roulet *et al.* (2007) reported that the NEE of a bog ecosystem was very responsive to weather variability with a range of  $100 \text{ g C m}^{-2} \text{ y}^{-1}$  over a 6 year period. Szumigalski and Bayley (1997) reported that productivity varied more between years as a result of weather influences than between different peatland types. The vegetation of a treed bog has the potential to influence NEE in a different way than that of an open bog due to potential differences in the way these vegetation communities respond to environmental conditions and specific microclimates. For example, evergreen and deciduous species might recover differently from a late frost. Dang *et al.* (1992) reported that *L. laricina* recovered photosynthetic capacity more quickly (after one day) after a summer frost than *P. mariana* (at least four days).

The complex microclimate, WT, and vegetation characteristics present in peatland bogs result in the CO<sub>2</sub> balance that determines NEE. As a result, trees have the potential to affect annual and growing season CO<sub>2</sub> flux. The importance of cold season NEE to the annual C balance of peatlands has been noted with annual variations in NEE characterised by a wintertime source of C and a summertime sink (e.g. Lafleur *et al.* 2003, Bonneville *et al.* 2008). One study stated that loss in the winter accounts for 30-70% of the uptake during the summer (Lafleur *et al.* 2003) while another reported that the magnitude of winter C loss at a site was greater than the annual net C balance (Aurela *et al.* 2002). To my knowledge, there are no specific studies that investigated the association of trees to wintertime CO<sub>2</sub> flux but there are several possibilities. One is that during periods favourable for photosynthesis, trees are able to take up C while other bog vegetation is not. Indications that trees have the potential to carry out photosynthesis during early spring and late fall when other bog vegetation is dormant supports this conjecture. Rouse *et al.* (2002) noted that photosynthesis begins earlier at a forested site because of evergreen spruce trees than at a fen with deciduous vegetation that must leaf out. Another effect of trees is the potential for warmer surface conditions as a result of a deeper insulating snowpack. Tree presence decreases windspeed at the surface and branches trap snow which results in a deeper snowpack than on a windswept open bog. This could then result in greater respiration during the winter. Lafleur *et al.* (2005) suggested that interannual variability in NEE at the low-shrub portion of the study site was dependent upon WT and snowdepth.

During the growing season, vegetation leafout, peak foliage, and senescence are associated with changes in NEE with peatlands acting as a C source during leafout/senescence and sink during peak foliage (e.g. Lafleur *et al.* 1997, Syed *et al.* 2006). Often, maximum C uptake occurs during the period of peak leaf area in peatlands (e.g. Lafleur *et al.* 2005). Growing season variations are also noted by Bergeron *et al.* (2007) and Arneeth *et al.* (2002). The first study noted that the relationship between temperature and NEP is strongest during the early part of the growing season. This is due to high temperatures promoting leaf out and plant photosynthesis, which initiates growing season CO<sub>2</sub> uptake by the vegetation. The second study noted interannual variability associated with varying moisture conditions during the growing season at a boreal bog site in European Russia.

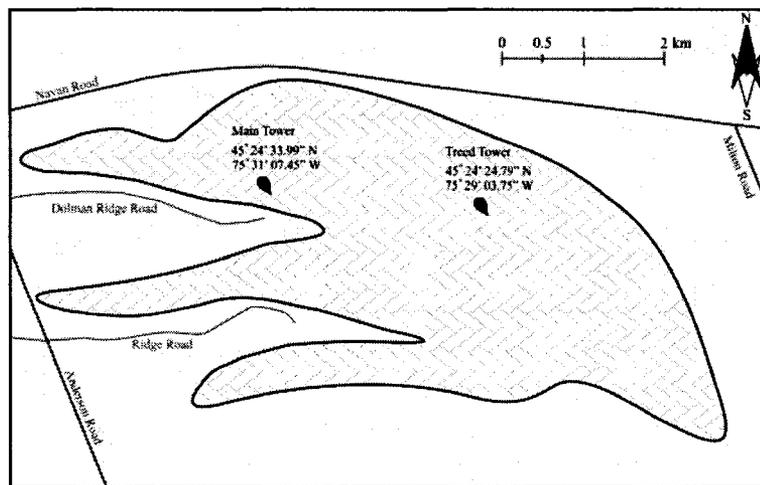
In summary, a treed canopy has the potential to impact bog microclimate, vegetation, soil conditions, and NEE. Trees increase shading which reduces light availability while decreasing temperature in the lower-canopy and at the ground surface. Reduced light means that photosynthesis by shrubs and mosses may be reduced. The cooler temperatures and lack of sunlight at the surface result in less water being evaporated from the surface while physiological limitations in the vascular trees limits transpiration. Less water transfer from the surface to the atmosphere is the result. During the winter trees trap snow which can result in warmer soil temperatures and increased below-ground respiration activity. A WT increase would also result from an increased snowpack since bogs only receive moisture input from precipitation. As an extra vegetation layer, trees may increase or decrease C uptake. Trees photosynthesis

directly contributes to ecosystem productivity and may increase overall C uptake. It is also possible that increased competition for nutrients and light reduces the productivity of the other vegetation and results in similar or less C uptake. Ultimately, whether or not these impacts enhance or reduce annual CO<sub>2</sub> uptake depends upon weather conditions and existing bog ecosystem functioning. For example, a decrease in C uptake may occur in an extremely wet year due to inhibition of both moss and tree photosynthesis.

Amplifying already saturated conditions by trapping winter precipitation and reducing both tree and non-tree vegetation growing season C uptake due to moisture related inhibition are two roles that trees would play. Trees have the potential to influence peatland functioning and, as a result, the C balance. The complexities of peatland dynamics reveal several possible functions of trees within bog ecosystems but supply no definitive answers. This present study is a unique opportunity to try to assess the role that trees play in an ombrotrophic bog ecosystem. Differences in NEE due to varying climate and time scales are minimised. The result should be a clearer understanding of the influence that trees have on C uptake and bog functioning.

## 2. Methodology

### 2.1 Site Description



**Figure 2.1:** Schematic diagram of MBPC with the location of study sites identified.

The study area is located within the 2800 ha MBPC located 10 km east of Ottawa, ON (Fig. 2.1) (Roulet *et al.* 2007). MBPC provides a research location with diverse surface cover and is comparable to the extensive Canadian northern peatlands in terms of climate as well as peat and vegetation composition. The peatland (45.41°N latitude, 75.48°W longitude, and 69 m a.m.s.l) was formed approximately 8400 years ago and lies in a river channel complex eroded by the Ottawa River into Champlain Sea sediments (Roulet *et al.* 2007). The study area changed from a fen to bog ca. 6000 years ago (Lafleur *et al.* 2003). The complex currently hosts open bog, treed bog, poor fen, and cattail marsh terrain. The open bog research site (OB) is located in the northern arm with the tower at 45° 24' 33.99" N, 75° 31' 07.35" W. The treed bog research site (TB) tower is located at 45° 24' 24.79" N, 75° 29' 03.75" W. Peat depth at OB varies between 3-6 m

due to the undulating underlying substrate. At TB, peat depth is greater than 3 m and tapers to ~1 m near a north-south oriented drainage ditch to the east of the treed tower.

### 2.1.1 Climate

The region has a cool continental climate with a mean annual air temperature ( $\text{MAT}_a$ ) of  $6.0 \pm 0.8$  °C, minimum average monthly temperature in January of  $-10.8 \pm 2.9$  °C, and maximum monthly temperature in July of  $20.9 \pm 1.1$  °C. It has 943.5 mm of precipitation annually with July being the wettest month (90.6 mm of rain) and February the driest (58.9 mm of rain and snow mixture ) (Environment Canada 2002a).

### 2.1.2 Vegetation

The bog presents challenging growing conditions that include its waterlogged nature, acidity, and low nutrient levels. The vegetation species found within this bog are capable of tolerating these conditions and are typical of other northern bogs. Both OB and TB have *P. mariana* (black spruce) and *L. laricina* (tamarack) trees with a mixed-moss ground layer composed mainly of *Sphagnum* mosses with *S. capillifolium* and *S. fuscum* the dominant species. The tree stand originated in the mid-1800s with the largest *L. laricina* trees dating to the 1860s and the largest *P. mariana* trees dating to the 1920s. Tree distribution was determined to be non-random using Parker's randomness test (Parker 1979) and visually assessed to be clumped. This is consistent with reproduction of trees in organic soils via rooting of attached branches (layering) rather than through seed germination (Farrar 1995). The understory (trees < 0.5 m tall and shrubs) is composed mainly of tree seedlings, *Ledum groenlandicum* (Labrador tea), *Chamaedaphne calyculata* (leatherleaf), *Kalmia angustifolia* (sheep laurel), *Kalmia*

**Table 2.1:** Site characteristics. <sup>†</sup>± 1 SE. <sup>‡</sup>Numbers in brackets represent 95% confidence intervals.

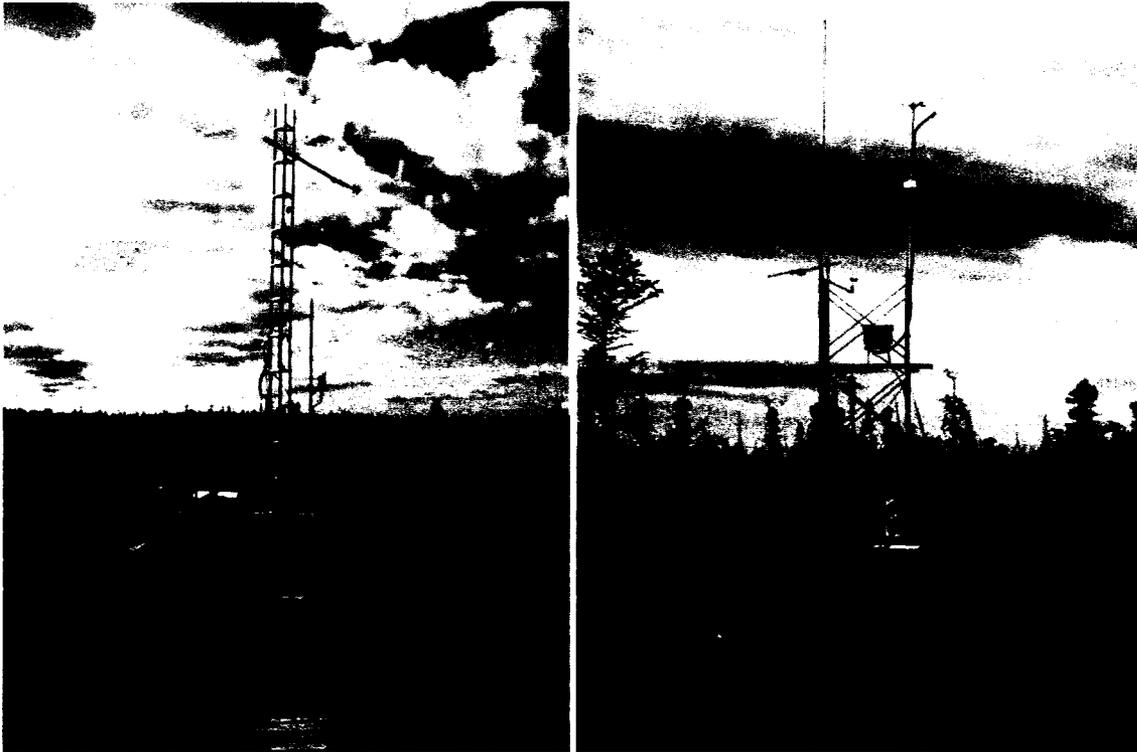
	Units	TB	OB
Total Shrub Biomass <sup>†</sup>	g m <sup>-2</sup>	470.6 ± 40.8	467.3 ± 43.7
Understory Tree Biomass <sup>†</sup>	g m <sup>-2</sup>	163.6 ± 31.5	0.8 ± 0.6
Tree Density <sup>‡</sup>	stems ha <sup>-1</sup>	5812 (5275, 6397)	negligible
Peat Depth	m	> 3	3 to 6 m
u <sub>s</sub> <sup>†</sup>	m s <sup>-1</sup>	0.27 ± < 0.01	0.20 ± < 0.01

*polifolia* (pale laurel), *Andromeda glaucophylla* (bog rosemary), *Vaccinium myrtilloides* (velvetleaf blueberry), *Vaccinium oxycoccos* (small cranberry), and *E. vaginatum* (cotton grass). The sites have similar above-ground understory vascular vegetation biomass of 467.3 g m<sup>-2</sup> (OB) and 470.6 g m<sup>-2</sup> (TB) but vary greatly in tree cover with a negligible total overstory tree density (trees > 0.5 m tall) at OB while at TB, there were 5812 stems ha<sup>-1</sup> (Table 2.1). Understory tree biomass was 0.8 g m<sup>-2</sup> at OB and 163.6 g m<sup>-2</sup> at TB. As a result of vegetation composition, surface roughness at TB is higher than OB. Average horizontal frictional wind velocity for the sites are 0.27 and 0.20 m s<sup>-1</sup>, respectively.

## 2.2 Data Collection

### 2.2.1 Tower NEE

CO<sub>2</sub> flux was measured using the EC technique. When combined with appropriate environmental sensors, EC is an ideal tool for studying ecosystem physiology and related forcings (Baldocchi 2003). It has become a popular technique with a worldwide network contributing to databases on CO<sub>2</sub> fluxes (e.g. Rocha *et al.* 2006 for Fluxnet-Canada, Grünwald and Bernhofer 2007 for EuroFlux, Yamamoto *et al.* 1999 for AsiaFlux). Baldocchi (2003) has identified four key reasons for EC popularity: 1) it is



**Figure 2.2:** Towers and vegetation at OB (left) and TB (right). For scale, tower heights are 6.0 m at OB and 9.2 m (including pole the sonic anemometer is affixed to) at TB, respectively.

ecosystem scale appropriate, 2) it directly measures exchange of  $\text{CO}_2$  over the canopy-atmosphere surface, 3) measurements can cover multiple time scales, and 4) it covers a large footprint. Site selection and instrument setup need to fall within certain parameters to ensure measurement accuracy. Comprehensive reviews of these needs have been presented (e.g. Baldocchi 2003, Oke 1987) but, in general, instrumentation should be located on flat terrain with homogenous surface cover in the upwind direction to ensure a uniform atmospheric boundary layer.

To obtain an adequate footprint in the direction of the prevailing wind, instrumentation at OB and TB was placed at 3.0 m and 9.2 m above the overstory canopy layer, respectively. Instrumentation at both sites was mounted on a wooden platform-

**Table 2.2:** Eddy covariance equipment and measurement characteristics.

	<b>TB</b>	<b>OB</b>
CO <sub>2</sub> and H <sub>2</sub> O	LI-COR 6262 IRGA	LI-COR 7000 IRGA
Windspeed	GILL R3-50 sonic anemometer	GILL R3-50 sonic anemometer
Logging Device	CR 1000	computer
Measurement Height	9.2 m	3.0 m
Sampling tube length and sample flow rate	5.3 m, 9 L min <sup>-1</sup>	4.0 m, 15 L min <sup>-1</sup>
Sampling Frequency	10 Hz	20 Hz
Power	solar	AC

based tower (antenna tower at OB and scaffolding tower at TB) upon which lightning rods and grounding wires were affixed (Fig. 2.2). At OB, fetch varies from 200-300 m in the least dominant wind direction (S) to 1500 m while at TB it varies from 150 m in the least dominant wind direction (S) to 500 m. The fetch for both sites is greatest in the NW dominant wind direction. Instrumentation at OB consists of a Gill R3-50 sonic anemometer (Gill Instruments Ltd., Lymington, England) used to measure high frequency fluctuations in windspeed in three coordinates, LI-7000 infrared gas analyser (IRGA) (LI-COR Inc., Lincoln, USA) used to measure fluctuations in the concentrations of CO<sub>2</sub> and H<sub>2</sub>O in a sample of air drawn through a tube, and a computer logger (Table 2.2). The IRGA is located in a temperature controlled box at the base of the tower while the computer is located in a small hut ~20 m tower. At TB, EC equipment consists of a Gill R3-50 sonic anemometer (Gill Instruments Ltd., Lymington, England), a LI-6262 IRGA (LI-COR Inc., Lincoln, USA) (also in a box, insulated during the winter), and a data logger (model CR1000, Campbell Scientific Ltd. (CSI), Edmonton, Canada). The

closed path tube lengths and flow rates are 4.0 m and 15 L min<sup>-1</sup> at OB while at TB they are 4.5 m and 4-9 L min<sup>-1</sup>. Corresponding delay times for CO<sub>2</sub> and H<sub>2</sub>O were changed in accordance with the flow rate. Data sampling frequency is 20 Hz at OB and 10 Hz at TB. EC equipment was run at OB using AC power from the city grid while at TB solar power from five solar panels was used. Manual IRGA calibration was carried out every two weeks at OB while logistical limitations at TB resulted in calibrations every 4-5 months. However, IRGA H<sub>2</sub>O was checked against humidity moisture probe (HMP) H<sub>2</sub>O every 2-3 weeks when data was collected from the site.

### 2.2.2 Chamber NPP

A closed, non-steady state chamber system was constructed to take species and branch level CO<sub>2</sub> flux measurements. Chamber systems of various configurations (e.g. steady-state or non-steady-state, manual or automated) have been used, alone or to complement EC measurements, for vegetation, soil, and mesocosm measurements (e.g. Rayment and Jarvis 1999, Reth *et al.* 2005, Moore *et al.* 2002, respectively). The system devised here is similar to an earlier one utilized at OB (Bubier *et al.* 1998, Moore *et al.* 2002) but has a few notable differences: 1) the chamber does not fit into a grooved collar inserted into the ground and 2) temperature is controlled using a cooler rather than a water heat exchanger. The system was comprised of two acrylic testing chambers (0.0042 m<sup>3</sup> and 0.0246 m<sup>3</sup>), quantum sensor (model LI-190, LI-COR Inc., Lincoln, USA) affixed to a tripod, and sampling equipment housed in a case. The chambers were of similar design and consisted of a hinged circular base plate upon which a cylindrical chamber was placed. A fine wire thermocouple located inside the chamber measured air

temperature ( $T_a$ ) while a Peltier cooler and mixing fan affixed to the top of the chamber kept  $T_a$  within  $\pm 2$  °C of ambient conditions and circulated the air, respectively. To minimise leaks, clamps were used to hold the unhinged side of the base plate and attach the two pieces together while closed cell weather stripping was applied to connection points. A LI-840 IRGA (LI-COR Inc., Lincoln, USA), CR23X data logger (CSI), pump, desiccant cylinder, and 12 V battery were located inside the case. Flow rate through the system was  $2 \text{ L min}^{-1}$  with 600-800 cc diverted into the IRGA. Bev-a-line tubing was used to transport air within the system and indicating drierite was used to dry the air slightly. Date, time,  $\text{CO}_2$  concentration,  $\text{H}_2\text{O}$  concentration,  $T_a$ , and  $\text{PPFD}_d$  were recorded every second. Data was downloaded via storage module or computer after one to two days of measurements. Varying light conditions were created by leaving the chamber uncovered, using single or double layers of standard 50% shading cloth, and a double layer of heavy duty black plastic garbage bags.

12 weeks of measurements were completed between June 20<sup>th</sup> and September 13<sup>th</sup>. A sampling set at OB was composed of one each of four species: *C. calyculata*, *K. angustifolia*, *L. groenlandicum*, and *V. myrtilloides*. A set at TB included four additional samples (*L. laricina* branch, *L. laricina* tree, *P. mariana* branch, *P. mariana* tree) for a total of eight samples from six species. This range covered the dominant shrub species (in terms of biomass) located at both sites as well as overstory and understory trees. Typically, two and three sampling sets were run at TB and OB, respectively. Four runs at varying light levels (clear, 1 shade cloth, 2 shade cloths, opaque), lasting for 2 min or a minimum of 10 ppm drop in  $\text{CO}_2$ , were carried out for each sample. The pump was run

briefly at the start of measurements and between each run to allow time for the system to equilibrate with ambient conditions. Samples were measured for two consecutive weeks and then clipped and taken to the lab for determination of leaf area. Clipped samples were individually placed into bags and stored in a shaded location before being transferred to the lab and stored in a refrigerator. Leaves and needles were pulled from stems and arranged in a single layer between two sheets of clear plastic. Care was taken to ensure individual specimens were not in contact with each other. The leaves were then scanned using a CanoScan 4400F flatbed scanner (Canon Inc., Tokyo, Japan). The number of foliage scans required for a single sample varied due to sample size and leaf phenology and ranged from one to seventy-one. Samples were then dried to obtain foliar and woody biomass.

### *2.2.3 Tower Site Characteristics*

Environmental data was collected in support of flux measurements. Recorded variables include  $PPFD_a$  and upwelling PPFD ( $PPFD_u$ ), net radiation ( $R_n$ ), relative humidity (RH), windspeed, air ( $T_a$ ) and soil ( $T_s$ ) temperatures, soil moisture, and WTD. A list of environmental variables and measurement equipment for each site is located in Table 2.3. Measurements were similar at both sites except for  $PPFD_a$  which was only measured at OB. Data was recorded as mV onto CR7X (OB) and CR23X (TB) loggers (CSI) at every 2 s at OB and every 5 s at TB.

### *2.2.4 Additional Site Characteristics*

The point quadrant method, initially outlined by Levy and Madden (1933) and variations of which are widely used (e.g. Hazlett 1992, Hoosbeek *et al.* 2001, Thomas

**Table 2.3:** Environmental equipment and measurement characteristics.

	TB	OB
Temperature and Relative Humidity	model HMP35C (CSI) probe housed in 12-plate gill radiation shield (RM Young Co., Traverse City, MI), 2.2 m	HMP35C (CSI) probe, housed in 12-plate gill radiation shield (RM Young, Traverse City, MI), 2.0 m
Windspeed	cup anemometer (model 12102, RM Young Co., Traverse City, MI)	cup anemometer (model 12102, RM Young Co., Traverse City, MI)
Net Radiation	net radiometer (REBS model Q7.1, CSI), 5.3 m	net radiometer (model CNR1, Kipp and Zonen B.V., Delft, Netherlands), 6 m
PPFD <sub>d</sub>	N/A	quantum sensor (model LI-190, LI-COR Inc., Lincoln, USA), 2.0 m
Upwelling Solar Radiation	pyranometer (model PSP, Eppley Laboratory Inc., Newport, USA), 5.3 m	pyranometer (model CM3, part of the CNR1, Kipp and Zonen B.V., Delft, Netherlands), 4.0 m
PPFD <sub>o</sub>	quantum sensor (model LI-190, LI-COR Inc., Lincoln, USA), 5.3 m	quantum sensor (model LI-190, LI-COR Inc., Lincoln, USA), 4.0 m
Ground Temperature	2 soil profiles, 7 chromel-constantan thermocouples each (0.025 to 1.5 m depth)	2 soil profiles, 9 chromel-constantan thermocouples each (0.01 to 2.5 m depth)
Water Level	1 well (float and counterweight system attached to a potentiometer)	2 wells (float and counterweight system attached to a potentiometer)
LAI	manual point frame method	manual point frame method
Ground Heat Flux	2 heat flux plates (REBS model HFT3, CSI), 10 cm depth	3 heat flux plates (REBS model HFT3, CSI, 7, 10, 30 cm depth)
Soil Moisture	2 soil water reflectometers (CS-616, CSI); 10 and 20 cm depth	7 soil water reflectometers (CS-615, CSI); 10, 20, 28, 30, 40, 40, 50 cm depth
Logger	CR23X (CSI)	CR7X (CSI)
Sampling Frequency	5 s	2 s

and Winner 2000), was used for determination of understory LAI. Ten permanent plots representing different elevation and terrain types, marked by bamboo poles, were located along the path to the tower at each site. The  $50 \times 50$  cm sampling frame consisted of a plastic water tubing square and 25 intersection-point fishing line grid. The frame was placed just above the height of the vegetation, resting upon bamboo poles, and aligned parallel to the ground. A fine gauge metal rod was dropped perpendicular to the ground at each intersection point and the number of green vegetation points touching the rod, species, and desiccation status of the moss was recorded. LAI was calculated for each plot as the total number of hits divided by the total number of intersection points while total site LAI was calculated as the mean LAI for the 10 plots. Sampling was carried out weekly during the height of the growing season, and every two to three weeks during the fall, for a total of 18 measurements between May 14<sup>th</sup> and October 26<sup>th</sup>.

Overstory tree density and distribution were determined using the variable area transect method and randomness test developed by Parker (1979). This method has been utilized for density estimations of a variety of populations from deer damaged cabbage (Engemann *et al.* 2002) to shrubs (Kirchhoff and Thomson 1998), and was determined by Engemann *et al.* (1994) to be one of the best performing plotless density estimators. A transect was marked in 20 m segments from a random starting point in the vicinity of the tower. Every 5 m (i.e. 0, 5, 10, etc.) a search started for the 3<sup>rd</sup> organism fitting the arbitrary criteria of a tree ( $> 0.5$  m) within 0.91 m of either side of the transect centre line. If more than 5 m were passed to find the third organism, the bypassed starting point was skipped. For example, if it took 6.79 m to find the third organism from the starting

point of 0 m, the search would begin again at 10 m. Winter fieldwork was carried out on February 17<sup>th</sup> of 2007 and 2008, respectively, to minimise damage to the surface of the bog. Four transects were completed in 2007 (4 × 100 m in N, S, E, and W directions) and two in 2008 (2 × 200 in NE and NW directions). Density (Eq. 5) and 95% confidence intervals as well as tree distribution were calculated.

$$\hat{D}_v = \frac{3n - 1}{w \sum (l_i)} \quad [5]$$

Where  $n$  is the sample number,  $w$  the width of the transect, and  $l_i$  is the total length of transect searched until the 3<sup>rd</sup> organism is found.

Overstory tree age was determined by the coring and dating of 10 *P. mariana* and 18 *L. laricina* segments, representing 5 and 9 trees, respectively. Fieldwork was carried out in October of 2007 and visual cross-dating and electronic measuring were carried out at the Carleton University Paleoecology Laboratory. Cross-dating involved visual inspection and dating of the cores to identify marker rings and subsequent comparison between cores to ensure correlation of identifying characteristics.

Understory vascular biomass was determined by clipping and drying of vegetation. 50 × 50 cm plots were randomly selected and the vascular vegetation was clipped and sorted by species. Samples were oven dried at 80 °C for a minimum of 24 hours, and subsequently weighed. 30 plots per site were sampled between June 5<sup>th</sup> and August 14<sup>th</sup>. Data for 19 OB plots was provided by researchers from Mount Holyoke College. They used a 60 × 60 plot size. Different plot sizes were taken into account when converting biomass values to g m<sup>-2</sup> and diversity of species composition between

plots was deemed acceptable via visual assessment of their data. Twelve species and species groups were selected for comparative analysis using the Student's T-test: *L. groenlandicum*, *C. calyculata*, *K. polifolia*, *K. angustifolia*, *A. glaucophylla*, *V. myrtilloides*, *V. oxycoccus*, *E. vaginatum*, understory trees (*P. mariana* and *L. laricina*), chamber NPP shrubs (*L. groenlandicum*, *C. calyculata*, *K. angustifolia*, and *V. myrtilloides*), total shrubs (everything except for understory trees), and total (all species). The hypotheses were tested at the 95% confidence level i.e. differences are significant when  $p < 0.05$ .

## 2.3 Data Processing

### 2.3.1 Tower NEE and Site Characteristics

Data from TB and OB were treated similarly. All analyses were carried out using Matlab software (MathWorks Inc., 2006). Existing OB data processing procedures, which are based on the Canadian Carbon Program (CCP, previously Fluxnet-Canada) protocols, were adjusted and used for flux calculation (Fluxnet-Canada Network Management Office 2003). 30 min fluxes were calculated from the covariance of CO<sub>2</sub> mixing ratio and vertical wind velocity, having undergone the 3-axis co-ordinate rotation described by Tanner and Thurtell (1969) to align it parallel with the surface (Eq. 4).

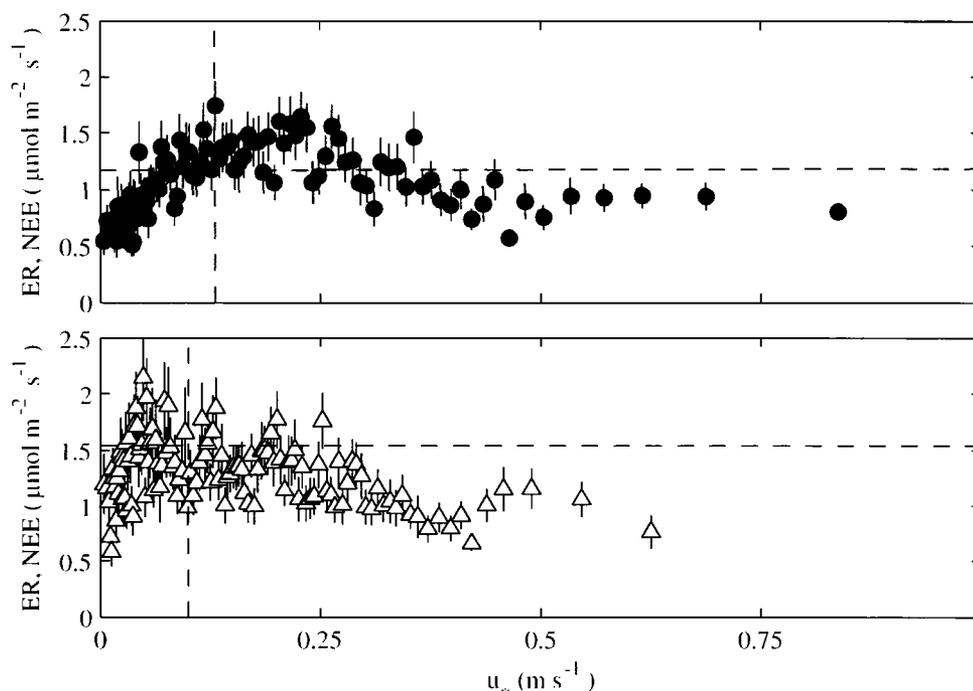
$$F_c = \overline{\rho_a} \overline{w' s'} \quad [4]$$

Where  $F_c$  is the CO<sub>2</sub> flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $\rho_a$  is the density of air ( $\text{mol m}^{-3}$ ),  $w$  is vertical wind velocity ( $\text{m s}^{-1}$ ), and  $s$  is CO<sub>2</sub> mixing ratio ( $\mu\text{mol mol}^{-1}$  dry air). The overbar indicates time averaging (e.g. 30 min periods) and primes indicate fluctuations from the mean. A complete review of flux treatment for OB eddy covariance data is outlined by

Roulet *et al.* (2007). Attempts were made to ensure the accuracy of EC data by dealing with systematic and random error. Lafleur *et al.* (2003) provide an analysis of the error associated with EC measurements at OB. These measures include manual calibration of IRGAs on a regular basis, post measurement investigation of calibration, and removal of data that was considered to be erroneous (i.e. nighttime periods of low turbulence and positive NEE during the cold season or at night).

Post-measurement assessment of IRGA calibration involved carrying out a linear regression between CO<sub>2</sub> and H<sub>2</sub>O mV readings from both sites for periods when the atmosphere was well-mixed. This work also revealed a high correlation between HMP and the IRGA humidity readings at OB and TB, which supports the assumption that these H<sub>2</sub>O and CO<sub>2</sub> concentrations are similar during these periods. In addition to adjusting the offset for both the H<sub>2</sub>O and CO<sub>2</sub> signals, this analysis revealed a 4% increase to the raw H<sub>2</sub>O and CO<sub>2</sub> signals at TB was necessary for the period May 20<sup>th</sup> to October 7<sup>th</sup> in 2007.

A correction was applied to deal with the problem, outlined by Moncrieff *et al.* (1996), of ER underestimation and C sequestration that is associated with periods of low atmospheric turbulence and mixing at night. Fluxes from periods of time below a designated frictional velocity ( $u_*$ ) were deemed to be erroneous and tossed. A procedure for determining  $u_*$  threshold (Humphreys *et al.* 2006a) was adapted to reproduce the  $u_*$  threshold of 0.1 m s<sup>-1</sup> identified by project researchers at OB (Lafleur *et al.* 2003). ER fluxes (non-gap-filled NEE nighttime fluxes) were binned and sorted into ascending order. The mean of the fluxes unaffected by  $u_*$  (designated as the highest 25%) was calculated and then multiplied by 80% to ensure a conservative estimate. Least squares



**Figure 2.3:** ER (NEE,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) plotted against friction velocity ( $u_*$ ,  $\text{m s}^{-1}$ ) for TB (top) and OB (bottom). Bin size of 50 with  $\pm 1$  SE. The vertical lines represent the  $u_*$  thresholds of  $0.13 \text{ m s}^{-1}$  and  $0.10 \text{ m s}^{-1}$  for TB and OB, respectively. The horizontal lines represent 80% of the flux unaffected by low  $u_*$ .

linear regression was used to find the  $u_*$  value corresponding to this calculated ER value. This procedure determined a  $u_*$  threshold of  $0.13 \text{ m s}^{-1}$  for TB (Fig. 2.3). As expected, the  $u_*$  threshold for TB is higher than OB due to increased surface roughness from the taller tree canopy layer at TB.

Gaps in TB winter data necessitated using both TB and OB data to determine when cold season specific gap-filling was necessary; therefore, both sites were processed the same way despite phenological differences. The cold season period (DOY 17-57) was determined by visual inspection of NEE data. This period is marked by consistent lack of diurnal patterns at OB and scarce diurnal patterns in the spotty TB data. It was assumed that the cold temperatures, snow cover, and limited light availability during the

cold season prevented C uptake; therefore, large negative NEE values were removed. Similarly, large negative NEE were removed during nighttime due to the assumption that plants are unable to carry out photosynthesis in the absence of sunlight. To alleviate the bias to positive fluxes, values within the error associated with wintertime measurements from closed path IRGA systems, as determined by Lafleur and Humphreys (2007),  $0 \pm 0.25 \mu\text{mol m}^{-2} \text{s}^{-1}$ , were kept. This value was determined to be the range within which 83% of cold season fluxes lie. The potential for cold season uptake by *P. mariana* at TB was considered but deemed negligible. Öquist (1983) notes three main causes of photosynthesis inhibition at low temperatures: 1) freezing of needles that generally occurs at approximately  $-5 \text{ }^\circ\text{C}$  which results in physical damage to the photosynthetic mechanism, 2) freezing of roots which occurs at approximately  $0 \text{ }^\circ\text{C}$  which results in water stress and closure of the stomata, and 3) increasing duration of cold temperatures. At TB, roots extending below the maximum freezing depth of  $\sim 20 \text{ cm}$  likely alleviate water stress but this is still presumed to be a factor. It is assumed this combination of factors negates potential C uptake by *P. mariana*. Extensive gaps mean that very few TB measurements were affected by the cold season data removal criteria described above. There were only 336 half-hours of data (out of possible 1968) available for TB during the cold season while OB had 1143. 17% and 13% of these measurements were removed at TB and OB, respectively.

Questionable data due to power outages, equipment failure, equipment maintenance, nighttime periods with low  $u_x$  or with C uptake, or unreasonable values were removed by automated cleaning programs according to thresholds (e.g.  $> \pm 3$

standard deviations from the monthly mean daytime/nighttime flux, relative humidity or soil volumetric water content > 100%). In addition, questionable data occurring immediately before or after data removed for the reasons listed above were removed manually. In total, 41% and 51% of the data at OB and TB, respectively, was not measured or removed. Gaps in selected traces (e.g.  $T_a$ ,  $T_s$ ,  $PPFD_d$ ,  $R_n$ ) were filled by regression adjusted data from the other site, if available. Following Roulet *et al.* (2007), 1 to 2 half-hour gaps in all data were linearly interpolated. Remaining small gaps were filled using mean diurnal variation with varying regressions, usually over a two week period. ER was filled with NEE at night and during the non-growing season and then gap-filled using the empirical model  $ER = f(T_s, t)$ . During the growing season GEP was estimated as  $-NEE + ER$  and then gap-filled with the empirical model  $GEP = f(PPFD_d, t)$  while nighttime and non-growing season GEP was assumed to be zero. In all cases  $t =$  time. Larger NEE gaps were filled with modelled  $-GEP + ER$  using an exponential relationship derived for negative of nighttime half-hour NEE (ER) and  $T_s$  for periods when  $T_s > 0$  °C. The relationship was adjusted for seasonality by moving through the year in 40 half-hour increments and doing a regression of modelled values against measured NEE values for 200 consecutive half-hour measurements. Data missing from daytime and nighttime cold season periods  $T_s < 0$  °C were filled with the mean from 200 consecutive half-hour measurements. The lack of TB data at the end of 2006 and beginning of 2007 resulted in the cleaning program treating the missing data as the end or beginning of the trace for each year, respectively, rather than a gap. As a result, the only difference between cleaning procedures for TB and OB is an additional condition for TB

that prevents modelled midday data from being removed during an 18 day period (DOY 356-8). Despite the use of standardised procedures to minimize error, it is acknowledged that TB has more potential for error due to a higher percentage of gaps (Falge *et al.* 2001). There are two main differences between the data processing procedures outlined here and those utilized by other OB researchers: 1) cold season delineated by arbitrary dates instead of periods of time when  $T_s < 0^\circ\text{C}$  and 2) cold season  $\text{NEE} < -0.25 \mu\text{mol m}^{-2} \text{s}^{-1}$  were removed rather than using a threshold of  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ . As a result, values reported here may be different than presented elsewhere.

### 2.3.2 Chamber NPP

An automated flux calculation program separated logger data into runs based on a minimum 30 s gap between measurements, converted  $\text{CO}_2$  concentration (ppm) into mixing ratio ( $\mu\text{mol mol}^{-1}$  dry air), and then calculated fluxes in units of  $\mu\text{mol m}^{-2}$  ground area  $\text{s}^{-1}$  using the linear regression method. Runs were visually assessed and manually corrected to ensure that step changes, indicating splicing together of separate runs, were not used for flux calculation. Barometric pressure (BP) as well as corrected tower  $T_a$  and  $\text{PPFD}_a$  data, as determined by regression analysis between chamber and tower data, were used when not measured directly due to instrument malfunction.  $\text{PPFD}_a$  values were adjusted to 92% of measured values to account for attenuation of  $\text{PPFD}_a$  during transmission through the acrylic chamber material. Kim *et al.* (2004) noted that ~92% of energy in the photosynthetically active radiation (PAR) wavebands is transmitted through a sheet of acrylic. This was confirmed by independent tests on the chamber system during which 90-92% of total incident  $\text{PPFD}_a$  was measured inside the chamber. To

allow comparison of species-level fluxes between the two sites, leaf area ( $\text{m}^2$ ) was determined using image analysis of scanned foliage and then used to convert fluxes to units of  $\mu\text{mol m}^{-2}$  leaf area  $\text{s}^{-1}$ . An automated program uploaded grayscale images, converted them to black and white, and then calculated leaf area as the total area of the image minus the area of white. In total, 4 outlying flux measurements were removed from the dataset that were indicative of a problem with the chamber system (3) or to enable reasonable light-temperature-response curve fitting (1).

#### 2.4 Light-Temperature-Response

$P_{\text{max}}$  (absolute maximum gross primary productivity at saturating light,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $\alpha$  (sensitivity of NEE to change in light,  $\text{mol CO}_2 \text{ mol}^{-1}$  photons), and  $R_{10}$  (ER at  $10^\circ\text{C}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), given a  $Q_{10}$  of 2 (rate of increase in ER for a  $10^\circ\text{C}$  increase in temperature), were calculated using a combination of rectangular hyperbolic and exponential relationships (Eq. 6). Froelking *et al.* (1998) determined a rectangular hyperbolic fit to be a better relationship for peatland NEE-PPFD data than a linear one.

$$NEE = - \frac{\alpha \text{PPFD } P_{\text{max}}}{\alpha \text{PPFD} + P_{\text{max}}} + R_{10} 2^{\left(\frac{T-10}{10}\right)} \quad [6]$$

In Eq. 6, NEE is a function of  $\text{PPFD}_d$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and temperature ( $^\circ\text{C}$ ). When applied to chamber measurements, NEE is replaced by NPP and  $R_{10}$  represents plant respiration at  $10^\circ\text{C}$ . For tower data, non-gap-filled  $\text{CO}_2$  fluxes, daytime  $\text{PPFD}_d$  ( $\text{PPFD}_d > 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and  $T_s$  were used for calculation. NPP in units of  $\mu\text{mol m}^{-2}$  leaf area  $\text{s}^{-1}$ ,  $\text{PPFD}_d > 0 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and  $T_a$  were used for chamber calculations.

## 2.5 Environmental Correlations

Relationships between NEE normalised for light and temperature (i.e.  $P_{\max}$ ,  $\alpha$ ,  $R_{10}$ ) and environmental variables were tested for significance using Spearman correlation analysis. Environmental variables used for correlation analysis were  $T_a$ ,  $T_s$ ,  $PPFD_d$ ,  $PPFD_u$ , vapour pressure deficit (VPD), vapour pressure (VP), RH, BP, soil moisture at 10 cm depth (SM1), soil moisture at 20 cm depth (SM2), WTD, and total precipitation (TP). TP was measured at MacDonald-Cartier International Airport (Environment Canada 2002b) while all other variables were recorded at TB or OB. Annual light-temperature-response parameters and averages of environmental variables were determined using a 5-day window that moved through the year in a 5-day increment. Correlations were limited to segments with  $R^2 > 0.50$  for the light-temperature-response fits and  $P_{\max} < 15 \mu\text{mol m}^{-2} \text{s}^{-1}$  to ensure that quality data were used. A 3-day window and increment as well as  $P_{\max} < 20 \mu\text{mol m}^{-2} \text{s}^{-1}$  were used for spring (May-Jun), summer (Jul-Aug), and fall periods (Sep-Oct).

### 3. Results

#### 3.1 Site Characteristics

##### 3.1.1 Biomass

**Table 3.1:** Average biomass  $\pm$  1 SE for species and groupings. Selections identified with an asterisk (\*) are significantly different at the 95% confidence level.

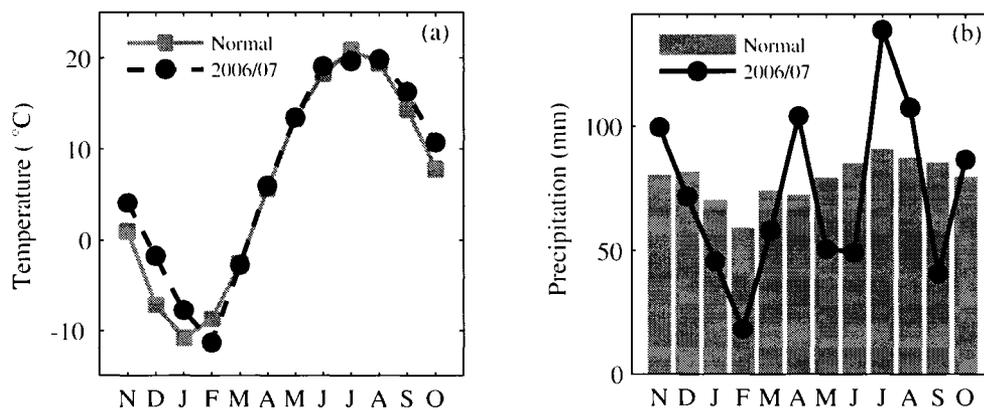
Species	TB (g m <sup>-2</sup> )	OB (g m <sup>-2</sup> )	Species	TB (g m <sup>-2</sup> )	OB (g m <sup>-2</sup> )
<i>L. groenlandicum</i>	100.8 $\pm$ 13.9	75.6 $\pm$ 12.4	<i>V. oxycoccus</i> *	28.7 $\pm$ 5.9	12.6 $\pm$ 2.4
<i>C. calyculata</i>	81.3 $\pm$ 23.9	153.4 $\pm$ 34.3	<i>E. vaginatum</i>	14.3 $\pm$ 3.1	9.6 $\pm$ 3.4
<i>K. polifolia</i> *	36.4 $\pm$ 6.1	0.7 $\pm$ 0.4	Total Non-Tree Understory*	307.0 $\pm$ 25.7	441.7 $\pm$ 39.3
<i>K. angustifolia</i> *	2.4 $\pm$ 1.1	70.0 $\pm$ 12.3	Total Tree Understory*	163.6 $\pm$ 31.5	0.8 $\pm$ 0.6
<i>A. glaucophylla</i> *	22.1 $\pm$ 6.5	0.5 $\pm$ 0.5	Total Understory Vegetation	470.6 $\pm$ 40.8	467.3 $\pm$ 43.7
<i>V. myrtilloides</i> *	20.9 $\pm$ 6.4	118.0 $\pm$ 31.5			

OB has significantly higher *V. myrtilloides* and *K. angustifolia* biomass while TB has significantly higher *K. polifolia* and *A. glaucophylla* biomass (Table 3.1).

Differences in  $T_s$  and WTD between the two sites help explain the variation in vegetation. Research conducted to investigate effects of manipulated  $T_s$  and WTD on bog vegetation revealed complex species-specific responses to these parameters (Weltzin *et al.* 2003). The study found that when  $T_s$  increases and WTD decreases, shrub cover increases by 50% and species composition changes. Higher *K. polifolia* biomass found at wetter TB corresponds to these results, but higher *A. glaucophylla* biomass as well contradicts them. However, it has been noted that *A. glaucophylla* tends to grow in fens

and occasionally bogs which indicates a preference for wetter, or possibly richer nutrient, terrain (Johnson *et al.* 1995). In contrast, although *V. myrtilloides* is able to grow in peat soils, it prefers to grow on gravelly or sandy soils, indicating a preference for the drier conditions present at OB. The difference between total understory biomass at the two sites is not significant. This indicates that at TB greater understory tree (trees < 0.5 m tall) biomass is balanced by less biomass for other shrubs. Of the two tree species, *P. mariana* was visually observed to be more abundant than *L. laricina* at TB. During the survey of overstory tree density, only 7.6% of the overstory trees were *L. laricina*. Biomass of the overstory trees was not quantified but it is assumed that TB has higher total above-ground vegetation biomass given the similarities in understory biomass.

### 3.1.2 Weather and Microclimate

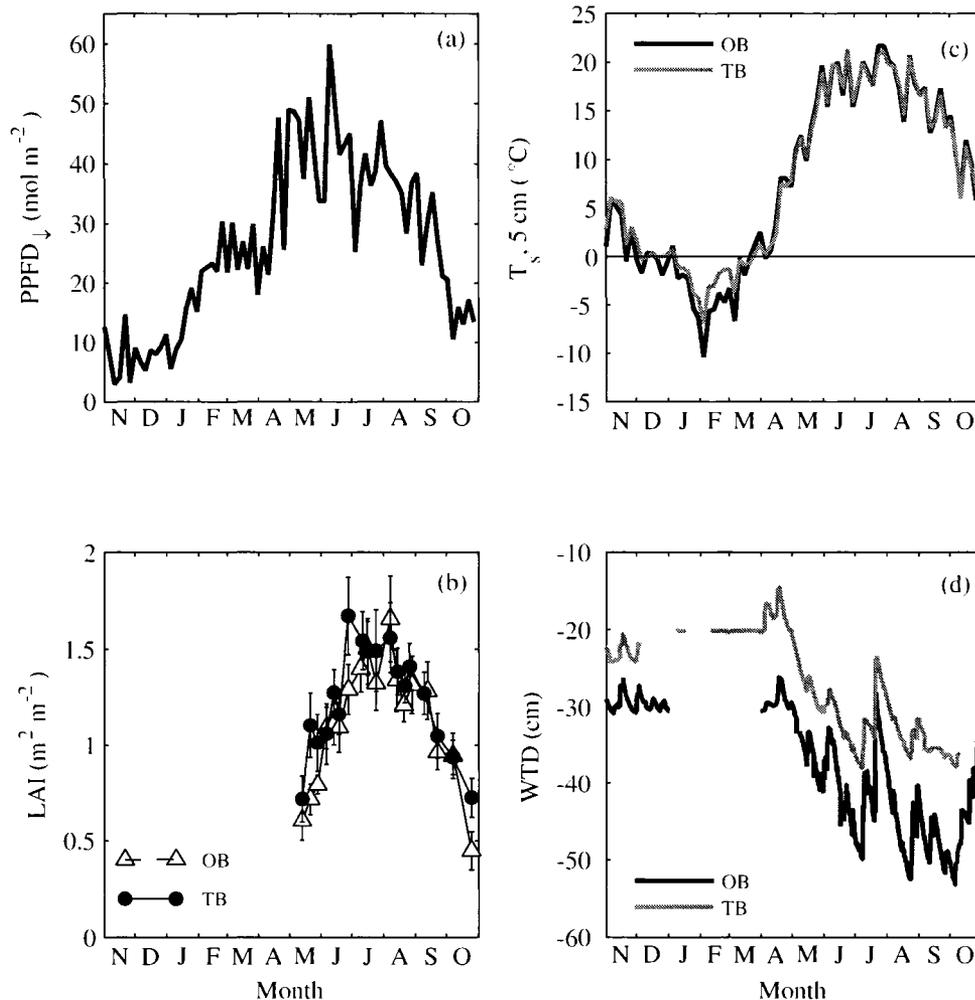


**Figure 3.1:** Climate normal and 2006/07 average monthly temperature (a) and precipitation (b). All data from Environment Canada for Ottawa MacDonal-Cartier International Airport (Environment Canada 2002a, Environment Canada 2002b).

The study year was warmer than normal (study year  $MAT_a = 7.2$  °C, normal = 6.0 °C) with below average precipitation (study year total precipitation = 871.0 mm, normal total precipitation = 943.5 mm). The fall periods and early winter were warmer

than normal while below normal precipitation occurred during the winter (Dec-Mar), spring (May-Jun), and early fall (Sep) (Fig. 3.1). The summer (Jul-Aug) and late fall periods (Nov 2006 and Oct 2007) were wetter than normal. The dry winter resulted in a shorter duration of snow on the ground and below normal snow depth. November and March did not have any snow on the ground at the end of the month, as indicated by  $PPFD_u$  (Fig. 3.3c), and December (12 cm), January (12 cm), and February (16 cm) had ~50% of normal month end snow depth (Dec = 24 cm, Jan = 30 cm, Feb = 30 cm). Both the climate normals and the monthly values were taken at the MacDonald-Cartier International Airport located ~16 km SW of the study sites.

Given that TB and OB are only 2.7 km from each other, these sites experience very similar weather. The average  $MAT_a$  values recorded at each site at approximately 3 m above the peatland surface are 6.5 °C for TB and 6.7 °C for OB. Jan-Mar  $T_a$  are -7.5 °C (TB) and -7.4 °C (OB) while Jun-Aug  $T_a$  are 17.5 °C (TB) and 17.7 °C (OB) (Fig. 3.3b). As a result, site specific microclimate variables such as 5 cm  $T_s$  and WTD also exhibited similar seasonal variations with some differences (Fig. 3.2). Mean annual soil temperature (5 cm depth) is 8.0 °C at TB and 7.6 °C at OB. The difference is due to wintertime rather than growing season differences. Jun-Aug  $T_s$  at both sites is 18.7 °C while  $T_s$  at TB is more moderate during the winter than at OB. Average  $T_s$  for Jan-Mar is -1.8 °C at TB and -3.2 °C at OB. This is most likely due to higher moisture content in the surface moss at TB due to a higher WT (Fig. 3.3a, Fig. 3.2b). Average WTD at TB is 27.2 cm below the average hummock surface while at OB it is 38.0 cm. There is the possibility that TB has a deeper insulating snowpack than OB. Manual snow depth

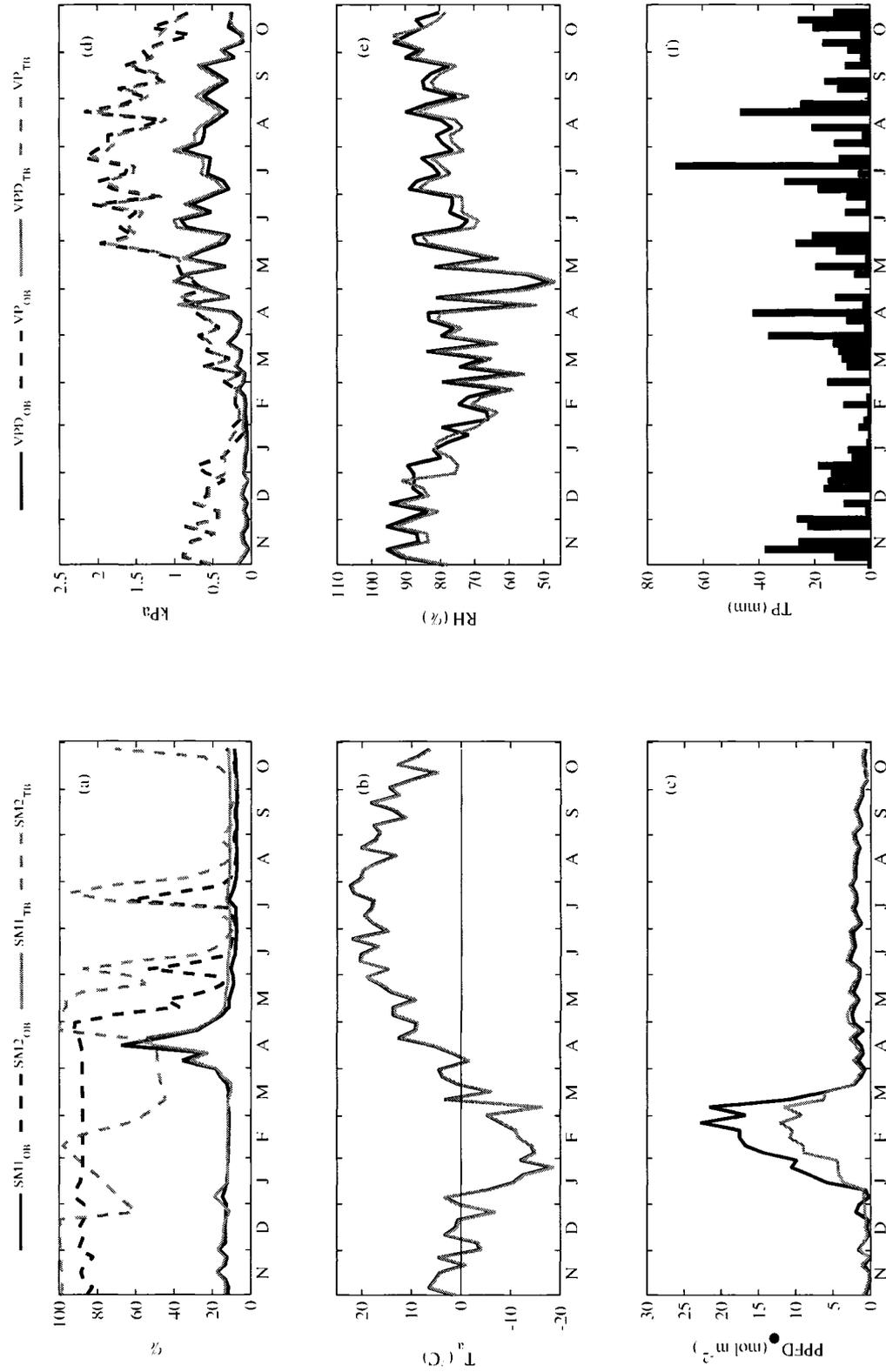


**Figure 3.2:** Study year site characteristics: (a) 5-day average PPFD<sub>d</sub> measured at OB. (b) Growing season (DOY 135-299) LAI  $\pm$  1 SE for understory vascular plants. (c) 5-day average soil temperature at 5 cm depth. (d) Depth of WT below peat surface.

measurements were available for three dates at OB (February 20, 26, and March 11) and one day at TB (March 18). There was no consistent difference in snow depth between OB and the MacDonald-Cartier weather station (-4.6 to +9.4 cm), but estimates of OB snow depth for March 18 by using the difference from the closest date (-9.4 cm) or adding the average of the differences (2.8 cm) results in TB having an estimated ~3-15 cm more snow. The difference between estimated OB and recorded TB snow

depth is likely due to trapping of snow by trees and reduced windspeed at the surface but these variables were not recorded.

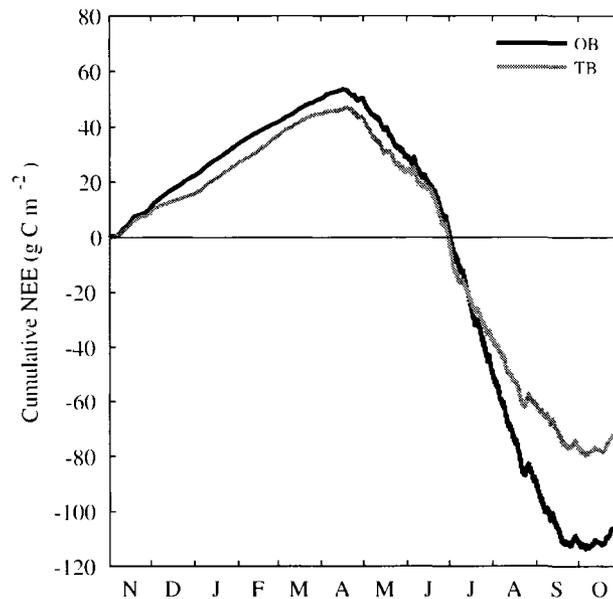
The seasonal pattern of understory LAI varied only slightly between sites with peak LAI occurring in mid-summer (Fig. 3.2b). At OB, a substantial amount of the increase in LAI is attributable to leafing out of *V. myrtilloides*. It accounts for  $0.25 \pm 0.01$  ( $\pm 1$  SE)  $\text{m}^2 \text{m}^{-2}$  during DOY 179-256. Deciduous *M. trifolium* and the evergreen shrubs *L. groenlandicum*, *C. calyculata*, *K. angustifolia*, and *V. oxycoccos* are the other main species that contribute during this time period. At TB, the LAI is not as influenced by deciduous *V. myrtilloides* ( $0.07 \pm < 0.01 \text{ m}^2 \text{m}^{-2}$ ) or *L. laricina* (not present in the LAI plots) during this period. The main species contributing to the increase in mid-summer LAI at this site are *L. groenlandicum*, *C. calyculata*, *K. polifolia*, *V. oxycoccos*, and *E. vaginatum*. As peak LAI follows the period of peak radiation by ~2 weeks at TB and ~5 weeks at OB (Fig. 3.2b, a), this indicates a spring lag period where plants are reestablishing themselves for the growing season. Understory LAI is similar between sites throughout the growing season but deviates slightly during the spring and fall. This is probably due to the different proportions of deciduous and evergreen vegetation. For example, the principle deciduous shrub, *V. myrtilloides* made up 25.2 % of the total biomass at OB while it made up only 4.4% at TB. In contrast, coniferous *P. mariana* made up 34.8% of the biomass at TB but was not present at OB within the 30 randomly located biomass sample plots. LAI for the overstory trees (trees > 0.5 m tall) at TB was not quantified but it is assumed that TB has higher total LAI than OB given the differences in overstory tree density and similarities in understory LAI.



**Figure 3.3:** Study year 5-day averages for SMI and SM2 (a), T<sub>a</sub> (b), PPF<sub>OB</sub> (c), VPD and VP (d), RH (e), and 5-day total for TP (f). Legends for (a) and (d) are located above their respective graphs. Black lines represent OB and grey lines represent TB for (b), (c), and (e). TP totals were calculated from Environment Canada data (Environment Canada 2002b).

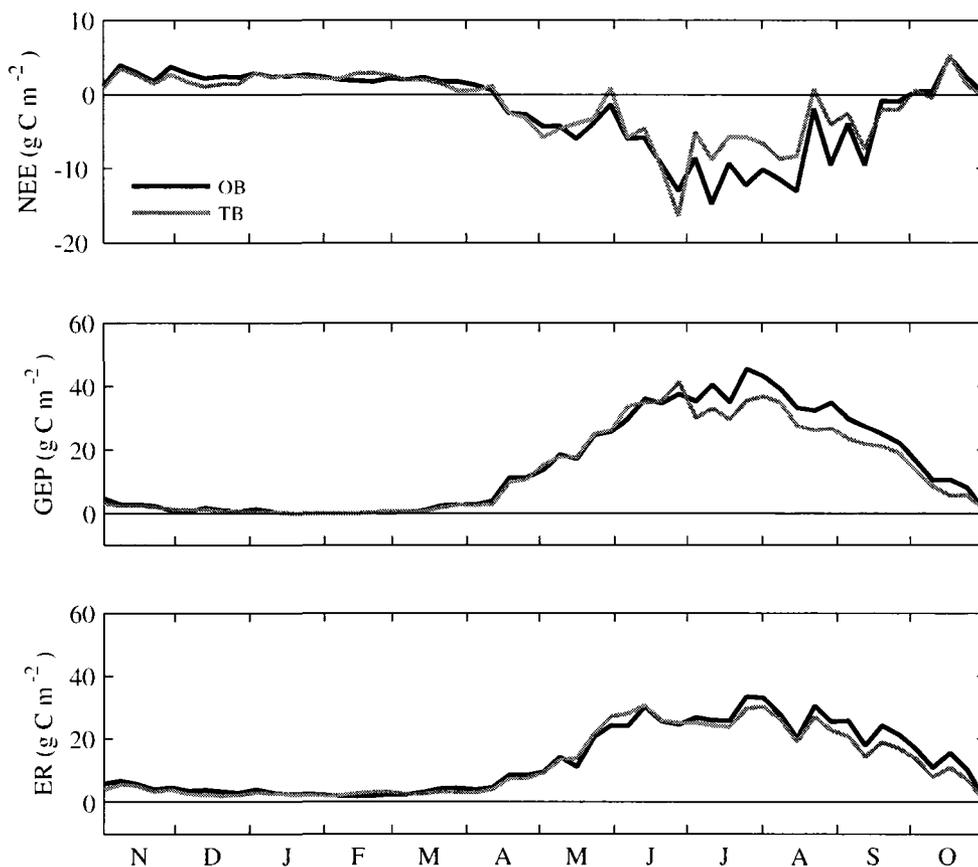
## 3.2 Ecosystem NEE

### 3.2.1 Annual



**Figure 3.4:** Cumulative NEE. Total NEE is  $-71.8 \text{ g C m}^{-2} \text{ y}^{-1}$  for TB and  $-104.1 \text{ g C m}^{-2} \text{ y}^{-1}$  for OB.

On an annual scale, OB is a greater sink for CO<sub>2</sub> than TB with NEE totals of  $-104.1 \text{ g C m}^{-2} \text{ y}^{-1}$  and  $-71.8 \text{ g C m}^{-2} \text{ y}^{-1}$ , respectively. The cumulative curve for ecosystem NEE shows that while TB and OB have a similar pattern for NEE, TB releases less CO<sub>2</sub> during the winter and takes up less during the growing season (Fig. 3.4). Growing season differences are due to small but consistently greater GEP and ER at OB (Fig. 3.5). Average growing season (Jun-Sep) GEP and ER are  $4.87 \text{ g C m}^{-2} \text{ d}^{-1}$  (GEP) and  $3.72 \text{ g C m}^{-2} \text{ d}^{-1}$  (ER) at OB while they are  $4.30 \text{ g C m}^{-2} \text{ d}^{-1}$  (GEP) and  $3.48 \text{ g C m}^{-2} \text{ d}^{-1}$  (ER) at TB. These differences in component C exchange processes could be due to differences in vegetation composition and/or differences in microclimatic conditions such as soil moisture, temperature, and understory radiation. The greater growing season CO<sub>2</sub>



**Figure 3.5:** 7-day means for NEE (top), GEP (middle), and ER (bottom). Annual values are: TB NEE =  $-71.8 \text{ g C m}^{-2} \text{ y}^{-1}$ , OB NEE =  $-104.1 \text{ g C m}^{-2} \text{ y}^{-1}$ , TB GEP =  $695.6 \text{ g C m}^{-2} \text{ y}^{-1}$ , OB GEP =  $783.7 \text{ g C m}^{-2} \text{ y}^{-1}$ , TB ER =  $623.8 \text{ g C m}^{-2} \text{ y}^{-1}$ , and OB ER =  $679.7 \text{ g C m}^{-2} \text{ y}^{-1}$ .

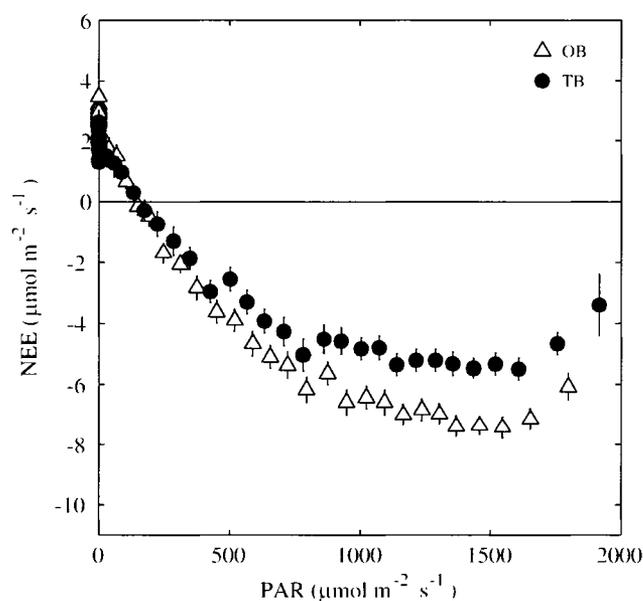
uptake at OB vs. TB appears to be a result of greater photosynthesis rather than less respiration. Growing season (Jun-Sep)  $P_{\max}$  at OB,  $14.86 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (14.31, 15.42), is significantly greater than at TB,  $12.63 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (12.05, 13.20) (Fig. 3.6, Table 3.2). Numbers in brackets are upper and lower 95% confidence intervals.  $R_{10}$  values are not significantly different where  $R_{10}$  is  $1.08 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (0.99, 1.16) at OB and  $1.09 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (1.01, 1.18) at TB. Since  $5 \text{ cm } T_s$  is similar at both sites, this suggests that ER associated with decomposition/respiration processes within the acrotelm should be similar. However, the slightly greater ER at OB may be related to WTD. With the WT

further from the surface, a larger aerobic zone at OB could result in more CO<sub>2</sub> production through aerobic respiration, more oxidation of CH<sub>4</sub> into CO<sub>2</sub>, or both.

Similar environmental conditions as well as comparable measurement and data processing techniques most likely mean that relative certainty between the two sites is strong enough to conclude that the differences in annual CO<sub>2</sub> fluxes noted here are significant. However, it is important to note there is a higher certainty associated with

**Table 3.2:** Growing season (Jun-Sep) light-temperature response parameters and their 95% confidence intervals (in parentheses) for TB and OB. Selections identified with an asterisk (\*) are significantly different at the 95% confidence level.

	TB	OB
$P_{\max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	12.63 (12.05, 13.20)*	14.86 (14.31, 15.42)*
$\alpha$ ( $\text{mol CO}_2 \text{ mol}^{-1} \text{ photons}$ )	0.018 (0.016, 0.019)	0.020 (0.019, 0.022)
$R_{10}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	1.09 (1.01, 1.18)	1.08 (0.99, 1.16)
$R^2$	0.62	0.73
N	2648	2633



**Figure 3.6:** Growing season (Jun-Sep) light-temperature-response curves. Bin size of 100 with 95% confidence intervals. Curve parameters are located in Table 3.2.

the annual estimate of NEE at OB than at TB due to the larger percentage of gaps in TB data (Roulet *et al.* 2007, Falge *et al.* 2001). The uncertainty associated with measurements at OB over a 6 year period was discussed by Roulet *et al.* (2007). The authors conclude that uncertainty associated with random error is small ( $< 1.6 \text{ g C m}^{-2} \text{ y}^{-1}$ ) while the uncertainty associated with systematic error, due mainly to gap-filling procedures, is large (e.g. changing the method used to estimate ER from an annual exponential relationship to a running mean increased NEE on average by 13-39  $\text{g C m}^{-2} \text{ y}^{-1}$ ).

It is possible that the magnitude of difference in total C sequestration between OB and TB would be lessened by accounting for C loss via  $\text{CH}_4$  and DOC at the respective sites although  $\text{CO}_2$  flux (NEE) is the greatest contributor to the total C budget at OB (Roulet *et al.* 2007). Roulet *et al.* (2007) reported that  $\text{CH}_4$  and DOC related C loss at OB was only responsible for  $3.7 \pm 0.5 \text{ g m}^{-2} \text{ y}^{-1}$  and  $14.9 \pm 3.1 \text{ g m}^{-2} \text{ y}^{-1}$ , respectively. Values presented with  $\pm 1$  SD.  $\text{CH}_4$  emission is most likely higher at TB due to a higher WTD. At the treed site, peat depth decreases towards a man-made drainage ditch located  $\sim 600$  m from the tower. It is possible that more DOC is lost via drainage of water than at OB. However, it is very likely that the difference in annual NEE of  $32.3 \text{ g m}^{-2} \text{ y}^{-1}$  between the sites would not be completely offset by differences in  $\text{CH}_4$  and DOC losses.

### 3.2.2 Annual and Seasonal Environmental Relationships

Spatial and temporal variations in weather and microclimate can result in spatial and temporal variations in NEE. Temporal variations in 5-day derived  $P_{\text{max}}$  and  $R_{10}$  are

shown in Fig 3.9. Not surprisingly,  $P_{\max}$  and  $R_{10}$  have significant negative correlations with soil moisture (SM1, SM2, WTD) and significant positive correlations with temperature ( $T_a$ ,  $T_s$ ) and VP through the entire year at both sites (Table 3.3). It is during the growing season that temperature and VP are highest (Fig. 3.3b, d), WTD and surface moisture content are lowest (Fig. 3.3a, Fig. 3.2d), and C uptake is greatest (Fig. 3.5). The most notable differences between the sites are the correlations for  $R_{10}$  and soil moisture variables.  $R_{10}$  at TB is significantly negatively correlated with WTD and soil moisture while at OB it is not. The differing influence of WTD on ER at both sites is interesting. This difference likely has to do with the consistently lower, and greater fluctuation in, WT at OB. The majority of decomposition (aerobic and anaerobic) takes place in the

**Table 3.3:** Annual Spearman correlation coefficients ( $r$ ) and significance ( $p$ , in parentheses) for 5-day averaged light-temperature-response parameters and environmental variables. Significant correlations are in bold.

Environmental Variable	TB $P_{\max}$	OB $P_{\max}$	Environmental Variable	TB $R_{10}$	OB $R_{10}$
$T_a$	<b>0.44 (0.02)</b>	<b>0.72 (&lt;0.01)</b>	$T_a$	<b>0.37 (0.05)</b>	0.24 (0.34)
$T_s$	<b>0.58 (&lt;0.01)</b>	<b>0.81 (&lt;0.01)</b>	$T_s$	<b>0.49 (0.01)</b>	0.30 (0.22)
PPFD <sub>d</sub>	-0.24 (0.20)	0.3 (0.23)	PPFD <sub>d</sub>	-0.33 (0.08)	-0.19 (0.46)
PPFD <sub>n</sub>	-0.24 (0.21)	0.4 (0.10)	PPFD <sub>n</sub>	-0.36 (0.06)	-0.12 (0.63)
VPD	-0.19 (0.33)	0.33 (0.18)	VPD	<b>-0.36 (0.05)</b>	-0.15 (0.56)
VP	<b>0.55 (&lt;0.01)</b>	<b>0.75 (0.01)</b>	VP	<b>0.52 (&lt;0.01)</b>	<b>0.54 (0.02)</b>
RH	0.35 (0.06)	-0.11 (0.66)	RH	<b>0.48 (0.01)</b>	0.42 (0.08)
BP	<b>-0.45 (0.01)</b>	-0.14 (0.59)	BP	-0.33 (0.08)	<b>-0.5 (0.03)</b>
SM1	<b>-0.47 (0.01)</b>	<b>-0.53 (0.03)</b>	SM1	<b>-0.46 (0.01)</b>	-0.38 (0.12)
SM2	<b>-0.38 (0.04)</b>	<b>-0.51 (0.03)</b>	SM2	<b>-0.44 (0.02)</b>	-0.33 (0.19)
WTD	<b>-0.37 (0.05)</b>	<b>-0.64 (0.01)</b>	WTD	<b>-0.43 (0.02)</b>	-0.29 (0.24)
TP	0.26 (0.18)	-0.29 (0.25)	TP	0.30 (0.12)	0.33 (0.18)

upper peat depths. As such, the consistently lower WT at OB probably means that more easily decomposable material is exposed to aerobic decomposition than at TB.

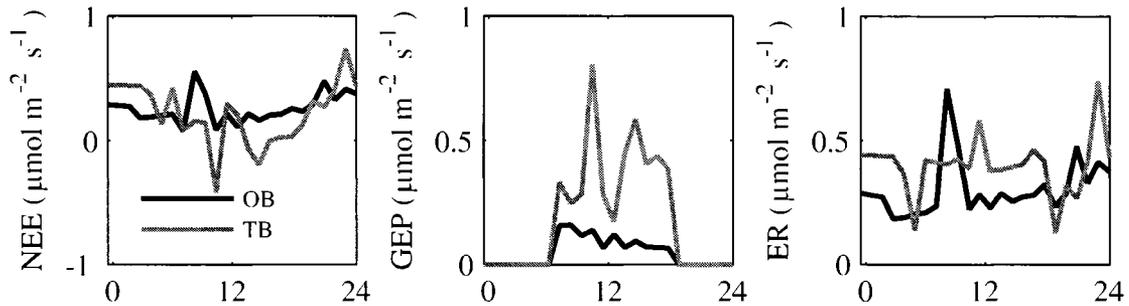
Therefore, lowering of the WT by the same amount exposes more material for decomposition at TB than at OB. In addition, the correlation for  $P_{\max}$  and RH at TB is positive and, although not significant at the 95% confidence level, it is associated with a p value of 0.06. This is likely due to the tree canopy at TB. As air moisture content increases, plants lose less  $H_2O$  through transpiration and are able to keep stomata open for photosynthesis. This has the potential to affect trees more than shrubs because of the proximity of the shrub canopy to the surface. Maximum tree height is ~4 m while the average height of the shrub layer is 0.2-0.3 m (Roulet *et al.* 2007). The surface is the transition between the ground and the atmosphere. Close to this plane where water evaporates and heat is released, temperature and moisture conditions are conducive to plant productivity. As a result, trees benefit more from not being exposed to dry air, especially conifers which are known to be very conservative with water loss. A drop in transpiration and leaf conductance in response to high  $T_a$  and humidity deficits has been reported for *P. mariana* in Saskatchewan (Rayment and Jarvis 1999).

During the spring, summer, and fall there are seasonal and study site differences in  $CO_2$  exchange and associated light-temperature response curve parameters (Fig. 3.8, Table 3.4). These differences are explored in section 3.2.3; however, there are several general findings that deserve mention here because of the insight they provide into annual and seasonal environmental influence. A lack of significant environmental correlations with either  $P_{\max}$  or  $R_{10}$  at the study sites during the summer (Table 3.5)

indicates that growing season climatic variation does not affect GEP or ER as much as at other times of the year because plants have adequate growing conditions (e.g. sunlight, moisture, warmth). There is the possibility that years with normal or below normal precipitation would result in stronger WT correlations because the plants would be more sensitive to a generally lower WT. In addition, the lack of significant correlations between  $P_{\max}$  and environmental variables at TB during the spring and fall, while OB has several significant correlations, indicates that OB is more sensitive to environmental change. As such, interannual NEE at OB may vary more than at TB and it might respond more quickly and dramatically to a changing climate. Although the correlations are not significant, TB  $P_{\max}$  is negatively correlated to soil moisture variables during the summer season while at OB they are positively correlated. This suggests that TB vegetation may have an optimal WT zone and that when the upper or lower threshold is surpassed there is a negative effect on plant productivity.

### 3.2.3 Seasonal Case Studies

Diurnal NEE follows a similar pattern at OB and TB during each season but deviates in the magnitude of the fluxes (Fig. 3.8). Variation between seasons and between sites can be attributed to differing influences of vegetation and microclimatic variables on NEE. During the winter, TB and OB have similar ER and therefore, similar rates of  $\text{CO}_2$  loss. Jan-Mar ER is  $0.40 \text{ g C m}^{-2} \text{ d}^{-1}$  at both sites while NEE is  $0.32 \text{ g C m}^{-2} \text{ d}^{-1}$  and  $0.31 \text{ g C m}^{-2} \text{ d}^{-1}$  at TB and OB, respectively. Snow cover during this period of time insulated the ground and covered surface vegetation at both sites. Lafleur *et al.* (2005) suggested that interannual variability in NEE at the open bog portion of the



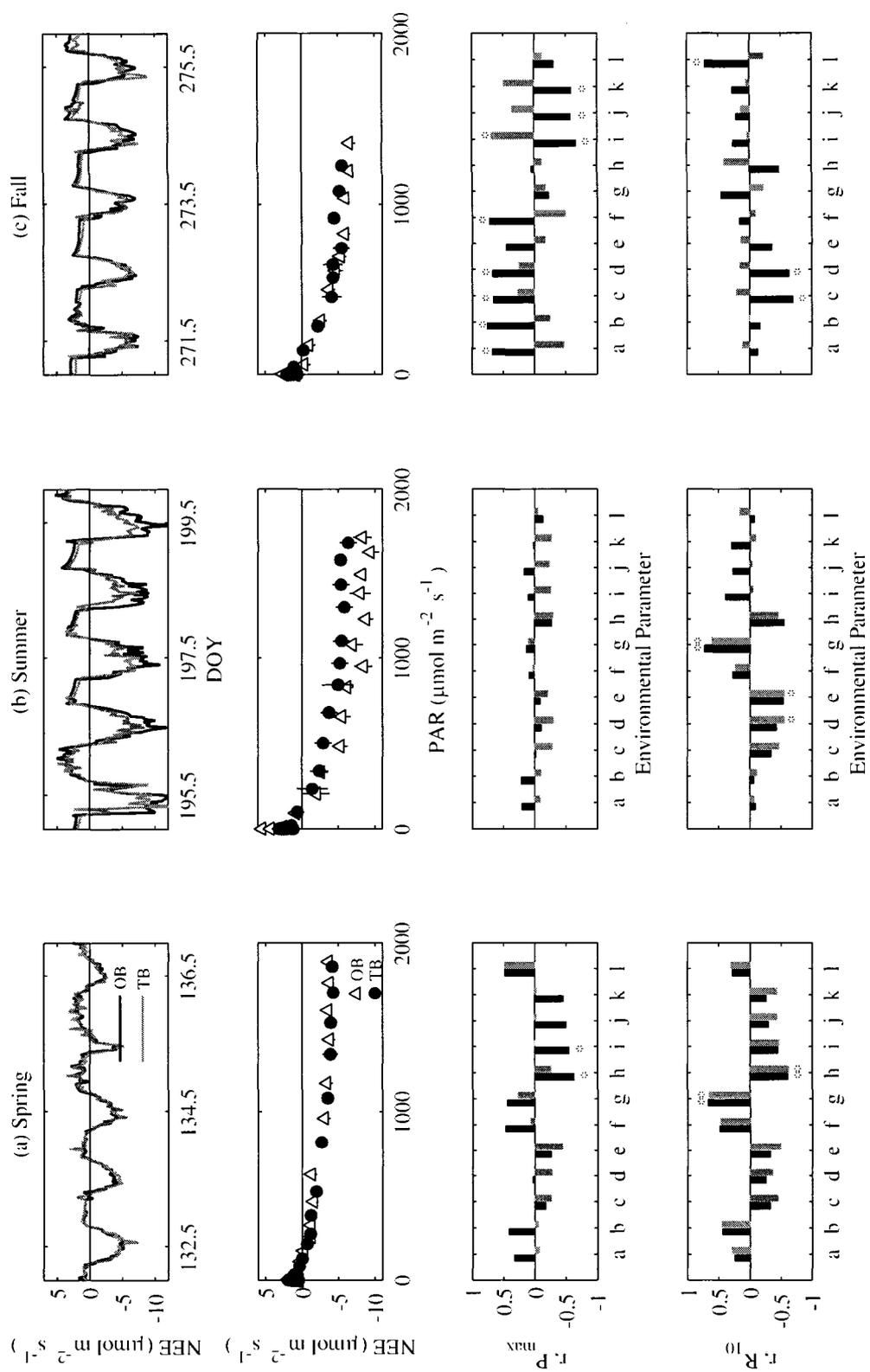
**Figure 3.7:** Diurnal NEE, GEP, ER for DOY 59-60. 95% confidence intervals overlap.

study site was dependent upon water table and snow depth. There is potential for snow depth to be responsible for spatial variability as well. Warmer  $T_s$  at TB during the winter, most likely due to higher WTD and speculated deeper snowpack, indicates that TB has an advantage over OB. Higher  $T_s$  results in a shallower freezing depth and, as a result, more water is available in the rooting zone. At TB the root zone extends below the maximum freezing depth of  $\sim 20$  cm (data not shown). It appears that during favourable conditions (e.g. warm and sunny periods), the taller trees at TB photosynthesized while the majority of low shrubs at OB remained dormant under the snow (Fig. 3.7). DOY 59-60 showed C uptake during the day at TB despite relatively cold  $T_a$  (TB =  $-8.5$  °C, OB =  $-8.2$  °C) and  $T_s < 0$  °C (TB =  $-1.1$  °C, OB =  $-5.6$  °C). Snow depth at OB was between 25.6 cm (DOY 57 manual measurement) and 9.6 cm (DOY 70 manual measurement). OB does not display the same diurnal NEE, GEP, or ER patterns during this period. Higher ER at TB resulted in a loss of  $0.82$  g C  $m^{-2}$  while at OB ER loss was only  $0.63$  g C  $m^{-2}$ . GEP uptake for the two days is  $0.38$  g C  $m^{-2}$  and  $0.10$  g C  $m^{-2}$  for TB and OB, respectively. As a result, NEE is similar (TB =  $0.45$  g C  $m^{-2}$ , OB =  $0.53$  g C  $m^{-2}$ ) despite different processes.

To continue the comparison of C exchange processes at OB and TB throughout the seasons, NEE fluxes are examined for the following periods: 1) DOY 132-136 during spring, 2) DOY 195-199 during summer, and 3) DOY 271-275 during autumn (Fig. 3.8, Table 3.4, Table 3.5). C uptake starts earlier at TB (DOY 87,  $-0.09 \text{ g C m}^{-2} \text{ d}^{-1}$ ) than at OB (DOY 104,  $< -0.01 \text{ g C m}^{-2} \text{ d}^{-1}$ ). The same favourable environmental conditions that potentially enhance tree photosynthesis at TB during the winter are most likely responsible for the earlier start to the growing season. Due to their dominance, *P. mariana* and moss are likely responsible for much of the GEP at TB in early spring. While all of the plants require an adjustment period to recover from winter dormancy, deciduous *V. myrtilloides* requires more time for leafout. As a result, there is less vegetation contributing to photosynthesis at OB. Higher productivity of the less abundant evergreen shrubs at OB balancing out the lower productivity of more abundant evergreen shrubs and coniferous trees at TB could be the cause of similar NEE at the

**Table 3.4:** Light-temperature-response parameters and their 95% confidence intervals (in parentheses) for three different periods for spring, summer, and fall. Selections identified with an asterisk (\*) are significantly different at the 95% confidence level.

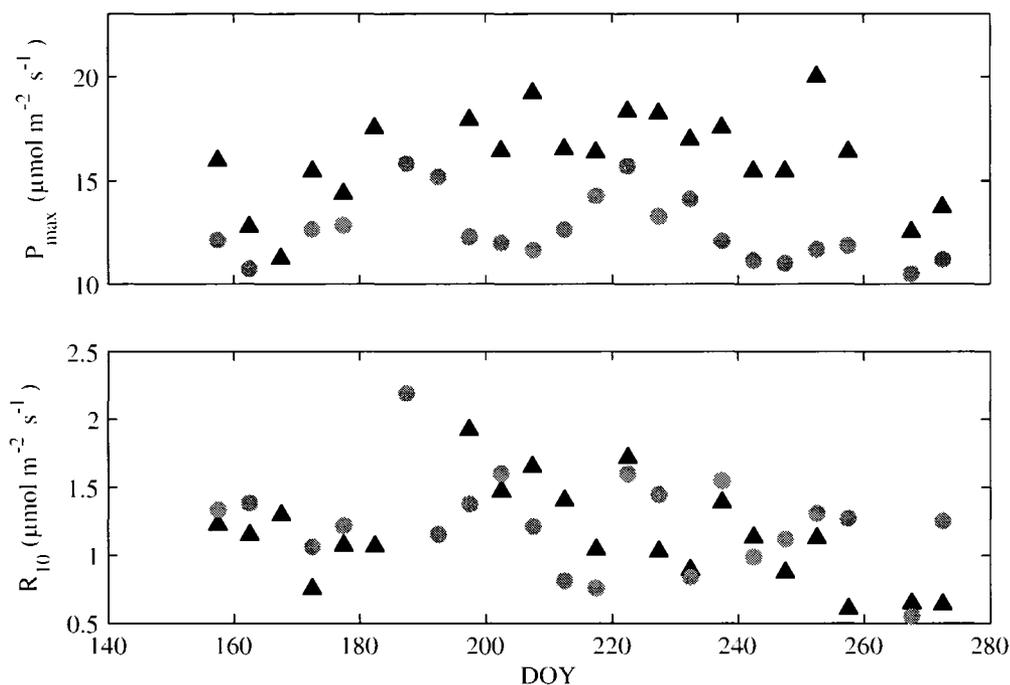
	Spring (DOY 132-136)		Summer (DOY 195-199)		Fall (DOY 271-275)	
	TB	OB	TB	OB	TB	OB
$P_{\max}$ ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	9.35 (6.51, 12.20)	8.15 (5.85, 10.44)	13.15 (10.60, 15.69)	17.02 (15.30, 18.73)	11.15 (9.10, 13.19)	13.19 (9.06, 17.32)
$\alpha$ ( $\text{mol CO}_2$ $\text{mol}^{-1}$ photons)	0.006 (0.004, 0.008)	0.006 (0.004, 0.008)	0.019 (0.012, 0.026)	0.031 (0.022, 0.040)	0.021 (0.014, 0.029)	0.012 (0.007, 0.017)
$R_{10}$ ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	0.44 (0.14, 0.74)	0.44 (0.16, 0.71)	1.08 (0.64, 1.52)	1.57 (1.12, 2.02)	1.13 (0.69, 1.57)	0.2 (-0.28, 0.67)
$R^2$	0.77	0.77	0.62	0.8	0.76	0.78
N	131	134	122	127	100	93



**Figure 3.8:** Half-hour NEE (top row), light-temperature-response curves (second row), and environmental correlations for ecosystem  $P_{\max}$  (third row) and  $R_{10}$  (bottom row) for spring (a), summer (b), and fall (c). Spring, summer, and fall periods are DOY 132-136, 195-199, and 271-275, respectively, for NEE and light-temperature-response curves. Grey lines and black circles represent TB while black lines and white triangles represent OB. Environmental correlations are for 3-day averages for May-Jun (spring), Jul-Aug (summer), and Sep-Oct (fall). Light-temperature-response parameters and correlation values are located in Table 3.4 and Table 3.5, respectively. Grey bars represent TB, black bars represent OB, and asterisks indicate significant correlations. Environmental variables: a =  $T_{ab}$ , b =  $T_s$ , c =  $PPFD_{tp}$ , d =  $PPFD_{tp}$ , e =  $VPD$ , f =  $VP$ , g =  $RH$ , h =  $BP$ , i =  $SM1$ , j =  $SM2$ , k =  $WTD$ , l =  $TP$ .

**Table 3.5:** Spearman correlations ( $r$ ) and significance ( $p$ , in parentheses) for relationships between NEE light-temperature-response parameters and environmental variables. Significant correlations are in bold.

	Spring (May-Jun)		Summer (Jul-Aug)		Fall (Sep-Oct)	
	TB - $P_{max}$	OB - $P_{max}$	TB - $P_{max}$	OB - $P_{max}$	TB - $P_{max}$	OB - $P_{max}$
$T_a$ (a)	-0.06 (0.82)	0.33 (0.24)	-0.09 (0.75)	0.20 (0.53)	-0.46 (0.15)	<b>0.68 (0.01)</b>
$T_s$ (b)	-0.05 (0.87)	0.41 (0.13)	-0.10 (0.72)	0.22 (0.50)	-0.25 (0.47)	<b>0.75 (&lt;0.01)</b>
PPFD <sub>d</sub> (c)	-0.26 (0.35)	-0.17 (0.55)	-0.28 (0.29)	-0.02 (0.96)	0.26 (0.43)	<b>0.65 (0.02)</b>
PPFD <sub>u</sub> (d)	-0.27 (0.33)	0.03 (0.93)	-0.30 (0.26)	-0.10 (0.75)	0.25 (0.47)	<b>0.66 (0.02)</b>
VPD (e)	-0.44 (0.10)	-0.25 (0.37)	-0.21 (0.44)	-0.08 (0.80)	-0.16 (0.63)	0.45 (0.13)
VP (f)	-0.18 (0.52)	0.46 (0.09)	0.02 (0.94)	0.08 (0.80)	-0.50 (0.12)	<b>0.71 (0.01)</b>
RH (g)	0.27 (0.33)	0.43 (0.11)	0.10 (0.70)	0.13 (0.69)	-0.17 (0.61)	-0.23 (0.46)
BP (h)	-0.26 (0.35)	<b>-0.62 (0.01)</b>	-0.29 (0.27)	-0.27 (0.39)	-0.12 (0.73)	0.04 (0.91)
SM1 (i)	0.00 (0.99)	<b>-0.54 (0.04)</b>	-0.26 (0.34)	0.10 (0.77)	<b>0.68 (0.03)</b>	<b>-0.66 (0.02)</b>
SM2 (j)	-0.02 (0.95)	-0.5 (0.06)	-0.23 (0.39)	0.17 (0.60)	0.35 (0.30)	<b>-0.58 (0.04)</b>
WTD (k)	-0.02 (0.95)	-0.46 (0.09)	-0.26 (0.32)	0.02 (0.96)	0.48 (0.14)	<b>-0.59 (0.04)</b>
TP (l)	0.48 (0.07)	0.48 (0.07)	-0.05 (0.85)	-0.12 (0.70)	-0.11 (0.74)	-0.31 (0.30)
	TB - $R_{10}$	OB - $R_{10}$	TB - $R_{10}$	OB - $R_{10}$	TB - $R_{10}$	OB - $R_{10}$
$T_a$ (a)	0.29 (0.30)	0.24 (0.38)	-0.07 (0.80)	-0.09 (0.78)	0.10 (0.78)	-0.13 (0.68)
$T_s$ (b)	0.44 (0.11)	0.44 (0.10)	-0.11 (0.68)	-0.06 (0.85)	0.00 (1.00)	-0.17 (0.58)
PPFD <sub>d</sub> (c)	-0.45 (0.09)	-0.32 (0.24)	-0.47 (0.07)	-0.34 (0.29)	0.20 (0.56)	<b>-0.69 (0.01)</b>
PPFD <sub>u</sub> (d)	-0.36 (0.19)	-0.26 (0.35)	<b>-0.55 (0.03)</b>	-0.42 (0.18)	0.15 (0.67)	<b>-0.63 (0.03)</b>
VPD (e)	-0.48 (0.08)	-0.32 (0.24)	<b>-0.55 (0.03)</b>	-0.54 (0.07)	0.14 (0.69)	-0.36 (0.23)
VP (f)	0.47 (0.08)	0.48 (0.07)	0.22 (0.40)	0.27 (0.40)	-0.10 (0.78)	0.15 (0.62)
RH (g)	<b>0.66 (0.01)</b>	<b>0.67 (0.01)</b>	<b>0.61 (0.01)</b>	<b>0.72 (0.01)</b>	-0.22 (0.52)	0.46 (0.12)
BP (h)	<b>-0.62 (0.02)</b>	<b>-0.61 (0.02)</b>	-0.46 (0.07)	-0.55 (0.07)	0.39 (0.24)	-0.48 (0.10)
SM1 (i)	-0.46 (0.09)	-0.44 (0.10)	-0.05 (0.86)	0.38 (0.22)	0.03 (0.95)	0.25 (0.40)
SM2 (j)	-0.43 (0.12)	-0.29 (0.29)	-0.04 (0.89)	0.26 (0.42)	0.13 (0.71)	0.21 (0.49)
WTD (k)	-0.43 (0.12)	-0.26 (0.34)	-0.09 (0.73)	0.29 (0.37)	0.05 (0.90)	0.27 (0.37)
TP (l)	0.30 (0.27)	0.27 (0.33)	0.15 (0.58)	-0.07 (0.82)	-0.23 (0.50)	<b>0.71 (0.01)</b>



**Figure 3.9:**  $P_{max}$  (top) and  $R_{10}$  (bottom) light-temperature-response parameters for 5-day segments throughout the growing season. Black triangles represent OB while grey circles represent TB.

sites during the majority of the spring period (see section 3.4). As a result,  $P_{max}$  is not significantly different between the two sites despite differences in vegetation (Table 3.4). The greatest similarity in both light-temperature-response parameters and  $R_{10}$  correlation with environmental variables occurs during springtime. DOY 132-139  $P_{max}$  is  $9.35 \mu\text{mol m}^{-2} \text{s}^{-1}$  at TB and  $8.15 \mu\text{mol m}^{-2} \text{s}^{-1}$  at OB while  $R_{10}$  is  $0.44 \mu\text{mol m}^{-2} \text{s}^{-1}$  at both sites (Fig. 3.8a, Table 3.4). NEE, GEP, and ER are also similar during this time period with NEE of  $-0.59 \text{ g C m}^{-2} \text{ d}^{-1}$  at TB and  $-0.51 \text{ g C m}^{-2} \text{ d}^{-1}$  at OB. GEP is  $2.14 \text{ g C m}^{-2} \text{ d}^{-1}$  (TB) and  $1.96 \text{ g C m}^{-2} \text{ d}^{-1}$  (OB) while ER is  $1.55 \text{ g C m}^{-2} \text{ d}^{-1}$  (TB) and  $1.45 \text{ g C m}^{-2} \text{ d}^{-1}$  (OB). While the difference is not significant, NEE has the general trend of slightly greater daytime uptake and nighttime loss at TB. This may be representative of

belowground respiration at TB benefiting from higher  $T_s$  (TB = 10.2 °C, OB = 9.4 °C) and lack of productive vegetation at OB. For both sites, RH (+) and BP (-) are significantly correlated with  $R_{10}$  while  $T_a$ ,  $T_s$ , and WTD have insignificant positive correlations (Fig 3.8a, Table 3.5). In addition, there is a positive correlation between  $P_{max}$  and TP ( $r = 0.48$ ,  $p = 0.07$ ) at both sites. A study on two swamps in China reported that ER was significantly positively correlated with water temperature as well as surface  $T_s$  (0-10 cm depth) (Changchun *et al.* 2003). Precipitation is generally associated with increased RH and decreased BP at this time of year. This may result from direct warming of water at depth due to mixing with relatively warm precipitation. Increased soil water temperature may allow respiration processes to commence at a greater depth within the peat profile than would be possible if relying solely upon warmth from  $T_a$  to penetrate the surface.  $P_{max}$  at TB does not correlate significantly with any environmental variables while at OB  $P_{max}$  correlates significantly with BP (-) and SM1 (-). Dry conditions due to a combination of lower WT, little snowmelt, and below normal precipitation in May-Jun affected vegetation at OB. However, since TP was positively correlated with  $P_{max}$  for both sites ( $r = 0.48$ ,  $p = 0.7$ ), it appears that GEP was enhanced at both sites by increased moisture and humidity.

The greatest difference in NEE between the two sites occurred during the summer. During this period of time TB takes up less  $CO_2$  during the day and loses less at night than OB (Fig. 3.8b). DOY 195-199 GEP and ER are greater at OB (6.06 g C m<sup>-2</sup> d<sup>-1</sup> and 3.77 g C m<sup>-2</sup> d<sup>-1</sup>, respectively) than TB (4.88 g C m<sup>-2</sup> d<sup>-1</sup> and 3.50 g C m<sup>-2</sup> d<sup>-1</sup>, respectively). Subsequently, NEE is -2.29 g C m<sup>-2</sup> d<sup>-1</sup> at OB and -1.38 g C m<sup>-2</sup> d<sup>-1</sup> at TB.

The minimal difference in ER between the sites means that vegetation governed GEP is largely responsible for the difference in NEE. This is reflected by a difference in the light-temperature-response curves for OB and TB for DOY 195-199 (Fig. 3.8b, Table 3.4).  $P_{\max}$  is  $17.02 \mu\text{mol m}^{-2} \text{s}^{-1}$  at OB and  $13.15 \mu\text{mol m}^{-2} \text{s}^{-1}$  at TB. During the summer, GEP decreases to a greater extent than ER at TB (Fig. 3.5). Between the end of June to the beginning of September, GEP at TB decreased by  $1.41 \text{ g C m}^{-2} \text{ d}^{-1}$  while ER decreased by  $0.48 \text{ g C m}^{-2} \text{ d}^{-1}$ . The dominant *P. mariana* at TB are most likely the reason for this pattern of decline. Bergeron *et al.* (2007) reported a similar plateau and decline in NEP during the month of July for a boreal *P. mariana* forest. This trend is apparent in the light-temperature-response parameters for this period as well.  $P_{\max}$  at OB increased between June and September (not shown). In contrast,  $P_{\max}$  at TB decreased. Similar to  $P_{\max}$ ,  $R_{10}$  increased at OB and decreased at TB. At TB, the difference in  $P_{\max}$  ( $-2.76 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) is much greater than for  $R_{10}$  ( $-0.26 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). While not significant, high soil moisture had a negative impact on photosynthesis at TB (e.g. SM1  $r = -0.26$ ,  $p = 0.34$ ) at this time (Fig. 3.8b, Table 3.5). Above normal precipitation during the summer, coupled with a higher WT at TB, is likely the reason for the appearance of these correlations. SM1 is a measure of moisture content at a very shallow depth (10 cm). Excess moisture this close to the surface limits available oxygen in the majority of the root zone for the plants. Although not conclusive, this indicates that there is an optimal soil moisture range at TB and the heavy precipitation in the summer caused the upper threshold to be surpassed. As a result,  $P_{\max}$  at TB went from having no correlation with soil moisture in the spring (e.g. SM1  $r = < 0.01$ ,  $p = 0.99$ ) to a negative one in the

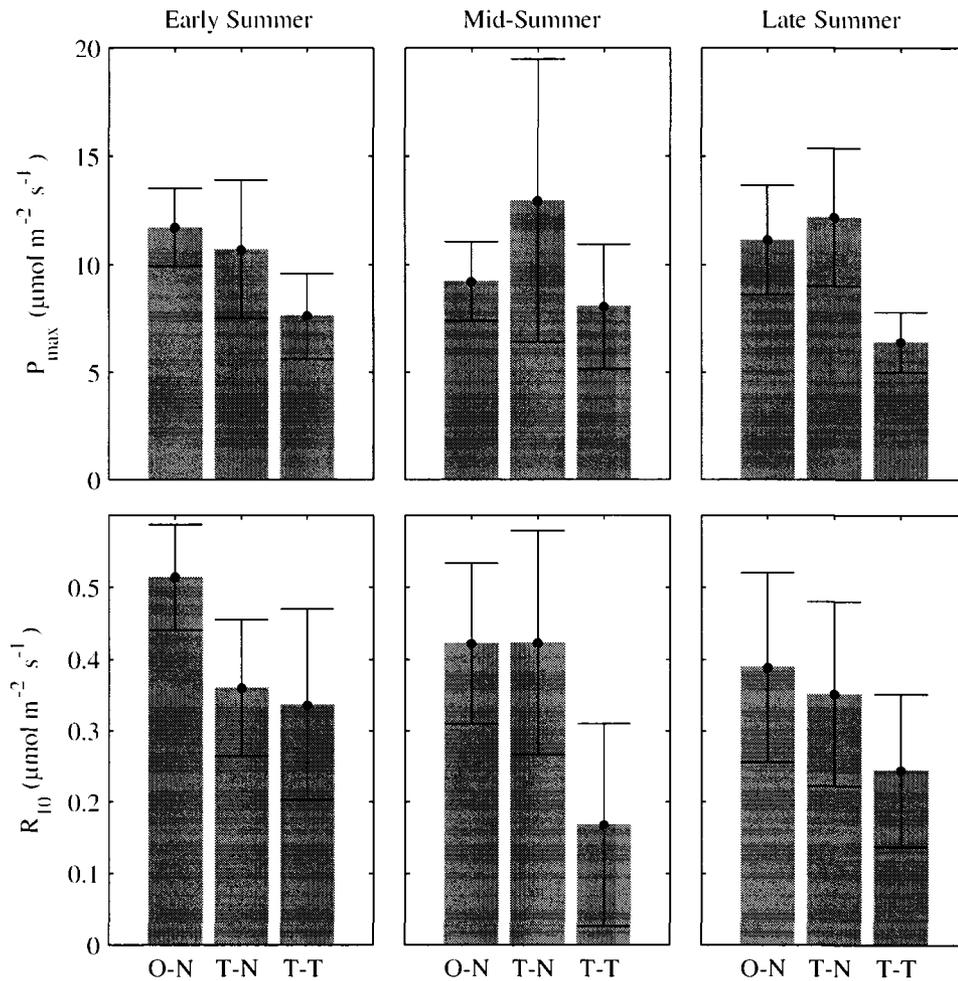
summer. The lack of significant environmental correlations with  $P_{\max}$  at either site during Jul-Aug further indicates that the growing season differences in NEE between the sites, as well as the differential decline in GEP and ER at TB, are related to shifts in plant physiology and functioning rather than short-term changes in weather.

By the fall, NEE and light-temperature-response are back to being similar at TB and OB (Fig. 3.8c, Table 3.4). DOY 271-275 TB values are  $-0.77 \text{ g C m}^{-2} \text{ d}^{-1}$  for NEE,  $11.15 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$  for  $P_{\max}$ , and  $1.13 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$  for  $R_{10}$  while OB values are  $-0.67 \text{ g C m}^{-2} \text{ d}^{-1}$ ,  $13.19 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and  $0.20 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ , respectively (Table 3.4). However, OB is still more productive than TB with a GEP of  $3.30 \text{ g C m}^{-2} \text{ d}^{-1}$  (TB =  $2.84 \text{ g C m}^{-2} \text{ d}^{-1}$ ) and ER of  $2.6 \text{ g C m}^{-2} \text{ d}^{-1}$  (TB =  $2.07 \text{ g C m}^{-2} \text{ d}^{-1}$ ). During the fall, TB and OB differ in their relationships with temperature and soil moisture (Fig. 3.8c, Table 3.5). OB  $P_{\max}$  has significant positive correlations with many variables (e.g. VP,  $\text{PPFD}_d$ ,  $T_a$ ) and significant negative correlations with soil moisture reappearing. Warm temperatures (e.g.  $T_s$ ,  $r = 0.75$ ,  $p < 0.01$ ) allow continued photosynthesis of moss and evergreen shrubs during the fall. The appearance of a significant correlation between OB  $P_{\max}$  and  $\text{PPFD}_d$  ( $r = 0.65$ ,  $p = 0.02$ ) is likely related to *V. myrtilloides* productivity. Plant senescence is dependent mainly upon sunlight; therefore, the *V. myrtilloides* growing season will be extended if there is sufficient sunlight that allows it to continue up C. Interestingly, the only significant correlation with TB  $P_{\max}$  during the growing season occurs in the fall (SM1  $r = 0.68$ ,  $p = 0.03$ ) and it is opposite to OB. The lowest WTD occurs during the fall (Fig. 3.2). It appears that TB has surpassed the bottom threshold of its preferred soil moisture range and at this time an increase in soil moisture correlates with an increase in

productivity. NEE patterns throughout the spring, summer, and fall reveal that functioning at TB and OB are different and that the annual difference in C uptake is attributable to greater productivity at OB during the summer. Overall, at both sites environmental variables do not correlate well with productivity during the height of the summer while relationships between environmental variables and ER are similar between sites. This suggests that annual NEE differences are the result of differing productivity due to summer vegetation composition differences.

### 3.3 Vegetation NPP

There is evidence that productivity varies between plant type, within plant type, and between *V. myrtilloides* species located at different sites.  $P_{\max}$  and  $R_{10}$  are typically greater for shrubs than trees, as a group (Fig. 3.10). However, the only significant difference occurs in late summer. During this period of time tree  $P_{\max}$  at TB is  $6.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (5.0, 7.8) while shrub  $P_{\max}$  is  $12.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  (9.0, 15.4) and  $11.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  (8.6, 13.7) at TB and OB, respectively. Numbers in the brackets are upper and lower 95% confidence limits. Consequently, growing season differences in  $P_{\max}$  at the ecosystem level (Fig 3.6, Table 3.2) could relate to the higher proportion of shrubs at OB. The biomass of shrubs selected for species-level NPP analysis, *L. groenlandicum*, *C. calyculata*, *K. angustifolia*, and *V. myrtilloides*, at OB is  $416.9 \pm 40.4 \text{ g m}^{-2}$  while at TB it is only  $205.5 \pm 24.9 \text{ g m}^{-2}$  ( $p < 0.01$ ). The seasonal trend of ecosystem-level GEP declining more at TB vs. OB during mid-summer could be related to decreasing productivity of trees during the growing season. While the differences were not significant, TB tree (*P. mariana* and *L. laricina*)  $P_{\max}$  declined from mid-summer



**Figure 3.10:** Seasonal variation in  $P_{max}$  and  $R_{10}$  for non-tree understory vegetation at OB (O-N), non-tree understory vegetation at TB (T-N), and trees (understory and overstory) at TB (T-T). Error bars represent 95% confidence limits. Early summer = DOY 171-193, mid-summer = DOY 197-233, late summer = DOY 235-256. N varied between 103 and 193 while  $R^2$  varied between 0.51 and 0.83.

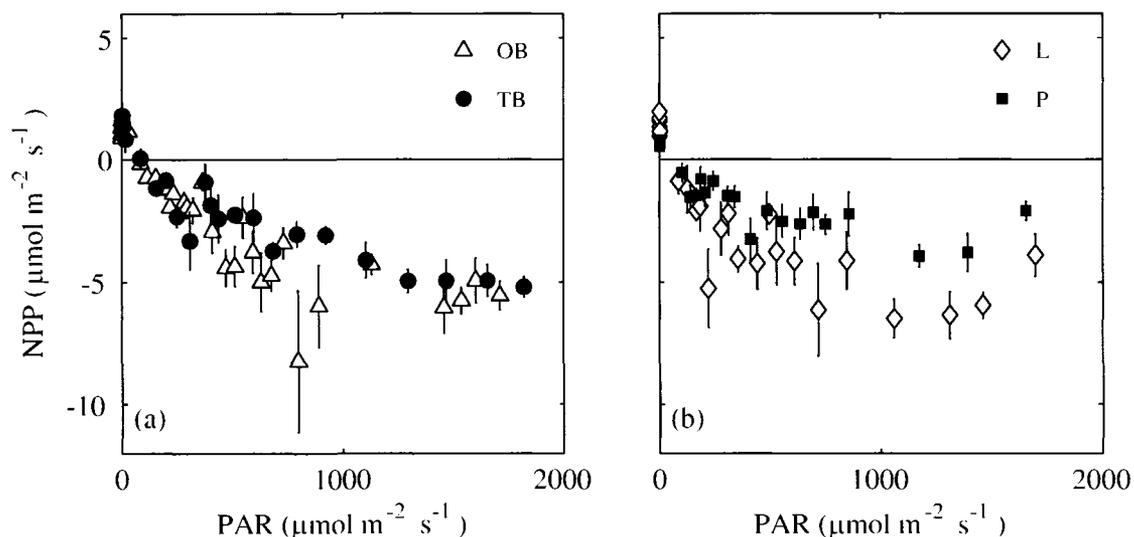
8.06  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (5.16, 10.96) to late summer 6.40  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (5.00, 7.80) and  $R_{10}$  increased from 0.17  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (0.03, 0.31) to 0.25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (0.14, 0.35). During the same period, shrub  $P_{max}$  at OB increased from 9.22  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (7.37, 11.07) to 11.15  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (8.63, 13.67) while  $R_{10}$  remained stable varying only from 0.42  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (0.31, 0.53) to 0.39  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (0.26, 0.52). Notably, *V. myrtilloides*, one of the dominant species at OB, had late summer  $P_{max}$  and  $R_{10}$  values of 14.82  $\mu\text{mol m}^{-2} \text{s}^{-1}$

(10.31, 19.32) and  $0.29 \mu\text{mol m}^{-2} \text{s}^{-1}$  (0.12, 0.45), respectively. The significant difference in ecosystem productivity noted at the end of the summer suggests that the dominant trees at TB are more susceptible to the moisture and heat stresses associated with the end of the growing season than the dominant *V. myrtilloides* are at OB. Diminishing growing season C uptake by *P. mariana*, due to high humidity deficits and low stomatal conductance, has been reported (Rayment and Jarvis 1999). At TB, conditions that could result in stomatal closure (i.e. water table below main rooting zone and high temperature) increase during the latter part of the growing season.

Significantly different light-temperature-response for *L. laricina* suggests that it is more productive than *P. mariana* with growing season  $P_{\text{max}}$  and  $R_{10}$  of  $7.70 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $0.20 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively (Fig. 3.11b, Table 3.6). *P. mariana* branch  $P_{\text{max}}$  and  $R_{10}$  are  $4.72 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $0.18 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively. However, *L. laricina* are less productive than shrubs at either site. TB growing season shrub  $P_{\text{max}}$  is

**Table 3.6:** Light-temperature-response parameters and their 95% confidence intervals (in parentheses) for *V. myrtilloides* (TB and OB), *L. laricina* (TB), and *P. mariana* (TB). Selections identified with an asterisk (\*) are significantly different at the 95% confidence level.

	(a) <i>V. myrtilloides</i>		(b) TB Tree Branches	
	TB	OB	<i>L. laricina</i>	<i>P. mariana</i>
$P_{\text{max}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	8.91 (7.25, 10.57)	10.11 (8.13, 12.09)	7.70 (5.86, 9.53)*	4.72 (3.78, 5.66)*
$\alpha$ ( $\text{mol CO}_2 \text{ mol}^{-1}$ photons)	0.013 (0.009, 0.017)	0.017 (0.012, 0.022)	0.027 (0.012, 0.043)	0.017 (0.009, 0.024)
$R_{10}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	0.28 (0.20, 0.36)	0.33 (0.21, 0.46)	0.20 (0.02, 0.34)	0.18 (0.10, 0.26)
$R^2$	0.82	0.71	0.63	0.68
N	96	140	95	95



**Figure 3.11:** Growing season light-temperature-response curves (DOY 197-256) for (a) *V. myrtilloides* at OB and TB and (b) *L. laricina* and *P. mariana* branches at TB. Light-temperature-response parameters are in Table 3.6.

10.49  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (8.69, 12.29) ( $R^2 = 0.63$ ) while OB  $P_{\text{max}}$  is 10.23  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (9.12, 11.4) ( $R^2 = 0.68$ ). Within the shrub group, the least productive species, *L. groenlandicum*, had similar  $P_{\text{max}}$  values of 8.87  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (6.33, 11.42) and 8.88  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (6.78, 11.00) at OB and TB, respectively (not shown). Associated  $R_{10}$  values are 0.43  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (2.9, 5.7) for OB and 0.55  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (0.38, 0.72) for TB. In general, the trees that balance out the biomass at TB are less productive than the shrubs at OB and result in a lower  $P_{\text{max}}$ . It appears that dominant functional group vegetation differences contribute to contrasting GEP rates between the study areas.

It appears that productivity is lower at TB than OB for some species. Growing season  $P_{\text{max}}$  and  $R_{10}$  are 10.11  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 0.33  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for *V. myrtilloides* at OB (Fig. 3.11a, Table 3.6). Equivalent values at TB are 8.91  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 0.28  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively. While the difference is not significant, it suggests variations in functioning of the same species at different sites. Therefore, a change in structure

(vegetation composition) at OB due to establishment of tree species may not result in NEE similar to that of TB. Spatial differences in species NPP within a site were not tested but the clumped distribution of trees at TB may result in a more variable microclimate than the relatively homogenous open bog terrain. Shading, temperature differences due to shading and competition for nutrients could all result in variations in NPP within species at TB.

Overall, ecosystem-level differences in NEE appear to be largely related to GEP differences at TB and OB and result from variability of both vegetation composition (e.g. TB = trees dominant, OB = *V. myrtilloides* dominant) and functioning (e.g. TB = lower productivity trees, OB = higher productivity *V. myrtilloides*).

## 4. Discussion

### 4.1 Ecosystem Comparison

The comparison carried out here indicates that structural and microclimate differences between a treed bog and an open bog result in differences in ecosystem functioning. Annual CO<sub>2</sub> sequestration varied between the two with the treed bog taking up 31% less CO<sub>2</sub> than the open bog. While this is a relatively large difference, when put into the context of interannual variability for a given peatland and with other ecosystems, this absolute difference of 32.3 g C m<sup>-2</sup> y<sup>-1</sup> may not be as important. In addition, interannual variation could minimize differences between these sites and result in long-time NEE in line with the 20-30 g C m<sup>-2</sup> y<sup>-1</sup> estimated by Gorham (1991) for long-term C sequestration.

Structural differences between TB and OB are minor compared to the variation in vegetation and water properties for peatlands as a whole (see section 1.2.1). However, these differences result in different functioning. This is because while ecosystem NEE at TB and OB has similar annual correlations with environmental variables, the two sites respond to seasonal environmental forcings in different ways. Temperature (T<sub>a</sub>, T<sub>s</sub>) and VP are positively correlated with NEE while soil moisture (WTD, SM1, SM2) is negatively correlated on an annual scale. These relationships stem from the benefits of warm temperature, high atmospheric H<sub>2</sub>O content, and soil moisture availability to photosynthesis and respiration. The same relationships are found in a variety of vegetated ecosystems including North American (e.g. Humphreys *et al.* 2006a, Griffis *et al.* 2003) and European forests (e.g. van Dijk and Dolma 2005) as well as peatlands (e.g.

Bonneville *et al.* 2008, Roulet *et al.* 2007). A key difference is the relationship that TB and OB have with soil moisture at their respective sites. During the study year, GEP at OB was enhanced by drier conditions during the spring and fall with WTD and  $P_{\max}$  negatively correlated during these periods of time (spring  $r = -0.49$ ,  $p = 0.09$ ; fall  $r = -0.59$ ,  $p = 0.04$ ) while TB has no relationship during the spring ( $r = -0.02$ ,  $p = 0.95$ ) and a positive one during the fall ( $r = 0.48$ ,  $p = 0.14$ ). It appears that ER at TB is inhibited by its higher WT with the site having consistently slightly smaller ER values (e.g. summer NEE at TB =  $3.50 \text{ g C m}^{-2} \text{ d}^{-1}$ , OB =  $3.77 \text{ g C m}^{-2} \text{ d}^{-1}$ ). Overall, the correlations suggest that there are different ideal moisture zones at the respective sites and that one site can cross an upper or lower threshold which results in a correlation switch while the other one remains the same.

Slight differences in phenology at TB and OB due to differences in species composition and abundance appeared to play a role in varying NEE values. Before leafout of *V. myrtilloides*, TB has slightly higher LAI than OB which enables it to take up more  $\text{CO}_2$ . This is evident in earlier startup (TB = DOY 87, OB = DOY 104) and slightly greater (TB =  $0.59 \text{ g C m}^{-2} \text{ d}^{-1}$ , OB =  $0.51 \text{ g C m}^{-2} \text{ d}^{-1}$ ) NEE during the spring at the study sites. This coincides with work by Rouse *et al.* (2002) and Lafleur *et al.* (1997) that also show seasonal changes in  $\text{CO}_2$  flux linked to changes in surface cover in northern Manitoba. Rouse *et al.* (2002) compared a fen composed of a lichen and brown moss ground layer under sedges and sparse vascular shrub coverage with an adjacent forest composed of ~25 cm of *Sphagnum* moss ground layer under a sedge and vascular plant understory and mixed *P. mariana* and *L. laricina* overstory. The LAI of the trees was

estimated to be 1.5 while the peak growing season LAI for the fen was estimated at 0.4. The authors speculated that the evergreen trees were able to carry out photosynthesis earlier in the growing season. Further, they stated that the higher LAI at the forested site was a factor in its performance as a CO<sub>2</sub> sink through 3 years of study while the fen was only a sink for one of those years (forest = -73.1 g C m<sup>-2</sup> y<sup>-1</sup>, fen = -30.0 g C m<sup>-2</sup> y<sup>-1</sup>). Lafleur *et al.* (1997) also examined the fen in northern Manitoba using the EC technique. The vegetation reported was slightly different with a *L. laricina* overstory (~3 m height), *Betula glandulosa* (~0.8 m height) and sedge (~0.5 m height) understory, and a *Sphagnum* moss ground layer. They noted that the fen only acted as a CO<sub>2</sub> sink when the vascular vegetation was actively photosynthesising during the growing season and that the ascent and decline in CO<sub>2</sub> uptake coincided with changing LAI of deciduous vegetation. Consequently, environmental forcings and species assemblages that influence LAI (e.g. high T<sub>a</sub> resulting in early snowmelt or low light due to cloudy skies delaying leafout) has a different impact at sites with dominant evergreen or deciduous vegetation.

A notable omission to the vegetation analysis in the present study is quantification of the contribution of moss to productivity. According to research, moss ground cover composition and its contribution to CO<sub>2</sub> exchange changes with tree cover (e.g. Goulden and Crill 1997). This has the potential to further influence ecosystem level CO<sub>2</sub> exchange since moss is believed to contribute up to 50% of ecosystem productivity (Thormann and Bayley 1997; Goulden and Crill 1997). Goulden and Crill (1997) looked at *Sphagnum* moss ground layer sites with a sparse tree canopy and feather moss ground

layer sites with substantial canopy within the same black spruce forest. They used multiple automated chambers placed on the forest floor and related them to an associated EC tower. They reported midday gross photosynthesis values of 0.5-1.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for feather moss and 0.5-2.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for *Sphagnum* moss. Total soil and moss respiration in the chambers were 1-2.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  above feather moss and 0.5 to 1.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  above *Sphagnum* moss. As already stated, there are no comparative values for these numbers within the present study but quantifying moss contribution and its relationships with environmental forcings may help to better explain the differences in NEE between the study sites.

Peak growing season (Jul-Aug) NEE was 1.38  $\text{g C m}^{-2} \text{d}^{-1}$  at TB and 2.29  $\text{g C m}^{-2} \text{d}^{-1}$  at OB. It is the persistence of these generally small differences over much of the growing season that results in the 32.3  $\text{g C m}^{-2} \text{yr}^{-1}$  difference in C uptake. This coincides with recent work by Humphreys *et al.* (2006b) who reported that 24-hour NEE is similar across a variety of peatland types, including treed peatlands. The treed fen sites had slightly higher  $\text{CO}_2$  uptake of 2.8  $\text{g C m}^{-2} \text{d}^{-1}$  and 1.8  $\text{g C m}^{-2} \text{d}^{-1}$  compared to the  $1.5 \pm 0.2$   $\text{g C m}^{-2} \text{d}^{-1}$  reported for the peatlands as a group. The results showed that while C uptake by trees increased GEP, the gain was offset by increased C loss due to ER and NEE remaining similar. The magnitude of the difference in NEE between OB and TB on a daily basis was small for most of the year, similar to the results in Humphreys *et al.* (2006b). The growing season values for NEE at OB and TB are similar to those reported by Humphreys *et al.* (2006b) for other treed peatlands as well as the average for peatlands as a whole.

On the annual scale, TB and OB are average C sinks in relation to other peatlands. NEE values such as  $-144 \text{ g C m}^{-2} \text{ y}^{-1}$  (Syed *et al.* 2006),  $-4$  to  $-53 \text{ g C m}^{-2} \text{ y}^{-1}$  (Aurela *et al.* 2004),  $-112$  to  $+2 \text{ g C m}^{-2} \text{ y}^{-1}$  (Roulet *et al.* 2007), and  $-53.5$  to  $+41.4 \text{ g C m}^{-2} \text{ y}^{-1}$  (Rouse *et al.* 2002) are reported in the few papers available on peatland annual NEE.

The relatively large difference in NEE between the OB and TB ( $32.3 \text{ g C m}^{-2} \text{ y}^{-1}$ ) may not be as important in the long-term given the variability in annual NEE reported for OB (Lafleur *et al.* 2003, Roulet *et al.* 2007). Roulet *et al.* (2007) reported that over a 6 year period NEE varied between  $-112$  to  $+2 \text{ g C m}^{-2} \text{ y}^{-1}$  and pointed out that using only one year of data from OB, or 5 of 6 in combination, results in a very different assessment of C sequestration at the site. The greatest  $\text{CO}_2$  uptake recorded for OB was  $-112 \text{ g C m}^{-2} \text{ y}^{-1}$  in 2003/04. This would suggest that NEE measured at OB ( $-104.1$ ) and likely at TB ( $-71.8$ ) in 2006/07 was perhaps slightly greater than normal. This short-term variability is approximately 4 times greater than the difference between TB and OB measured during the study year. Due to the drier than normal winter and wetter growing season, the one year of data presented here quite possibly does not represent the average or normal conditions. It is likely that the magnitude of annual NEE at both sites will vary in response to changing weather and microclimate conditions. The large variability in NEE at OB, including switching from a source to a sink, and varying response to environmental forcings implies that over time long-term C sequestration rates between the sites may balance out. Small annual averages in long-term C stock gains for peatlands were discussed by Gorham (1991) and highlighted in results by Roulet *et al.*

(2007). They reported that a highly variable 6-year NEE record is not statistically different from a 3000-year record obtained via peat cores. Ultimately, the one year of comparative measurements for TB and OB does not effectively address the question of long-term C sequestration potential for these two peatland types.

Compared to other ecosystems, annual NEE values for peatlands in general are small. Mature forests or agricultural crops with different species assemblages have much larger differences in NEE and are broadly grouped. The difference in NEE between the treed and open bog in this study (Annual: TB =  $-0.20 \text{ g C m}^{-2} \text{ d}^{-1}$ , OB =  $-0.29 \text{ g C m}^{-2} \text{ d}^{-1}$ ; Growing Season: TB =  $-0.83 \text{ g C m}^{-2} \text{ d}^{-1}$ , OB =  $-1.15 \text{ g C m}^{-2} \text{ d}^{-1}$ ) is small compared to the range of  $-5.9$  to  $-17.4 \text{ g C m}^{-2} \text{ d}^{-1}$  for boreal forest stands (Griffis *et al.* 2003) or  $-34 \text{ g C m}^{-2} \text{ y}^{-1}$  and  $-193 \text{ g C m}^{-2} \text{ y}^{-1}$  reported for different crops at an agricultural site (Anthoni *et al.* 2004). The study sites, and comparison sites, have obvious structural differences relating to quantity and composition of above-ground vegetation as well as location differences relating to weather and microclimate. Yet, placing the results from the current study in the context of other findings suggests that the hypothesis that peatland ecosystems have relatively conservative C exchanges is tenable.

#### **4.2 Component Fluxes and Light-Response**

Trees have a greater impact on NEE, and subsequently ecosystem functioning, through their influence on other ecosystem components (e.g. plants) and forcings (e.g. warmer soil temperatures during the winter due to the insulating effect of trapped snow) than through direct CO<sub>2</sub> uptake. Tree NPP is similar in different peatland types and

despite obvious structural differences, many treed peatlands have CO<sub>2</sub> uptake similar to non-treed peatlands (Humphreys *et al.* 2006b).

Although growing season P<sub>max</sub> is significantly different between TB and OB, P<sub>max</sub> and ER are within the range for peatlands examined by Frohking *et al.* (1998). OB P<sub>max</sub> and ER values calculated with Eq. 7 (see below) are 11.4 μmol m<sup>-2</sup> s<sup>-1</sup> (11.1, 11.8) and -2.6 μmol m<sup>-2</sup> s<sup>-1</sup> (-3.0, -2.4), respectively. P<sub>max</sub> at TB is 8.8 μmol m<sup>-2</sup> s<sup>-1</sup> (8.5, 9.1) and ER is -2.1 μmol m<sup>-2</sup> s<sup>-1</sup> (-2.4, -1.9). Numbers in brackets are upper and lower 95% confidence intervals. P<sub>max</sub> values for OB and TB are significantly higher than Frohking *et al.* (1998) reported for bogs, 5.2 ± 0.11 μmol m<sup>-2</sup> s<sup>-1</sup>, but are within the range reported for the peatland ecosystem types where maximum P<sub>max</sub> was 12.1 ± 0.30 μmol m<sup>-2</sup> s<sup>-1</sup> (rich fens). Values are presented ± 1 SE. There was no significant difference in ER between OB and TB and these parameters were similar to the ER value of -2.44 ± 0.05 μmol m<sup>-2</sup> s<sup>-1</sup> reported for peatlands in general.

Frohking *et al.* (1998) looked at the relationship between NEE and PPFD for a number of different peatland types including treed peatlands but did not examine them as a specific peatland type. The four treed sites were allocated to the rich fen (2) and bog (2) groupings. Light-response parameters presented here were calculated using the following formula (Eq. 7) and growing season period outlined in Frohking *et al.* (1998).

$$NEE = \frac{\alpha PPFD P_{\max}}{\alpha PPFD + P_{\max}} + ER \quad [7]$$

In comparison to Eq. 6 (see section 2.4), this rectangular hyperbolic relationship does not include a temperature response and subsequently the three parameters obtained are P<sub>max</sub>,

$\alpha$ , and ER. The authors define mid-growing season data as the first and last days of the season when midday C uptake was greater or equal to  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Visual assessment of OB and TB data identified DOY 112-280 as the growing season.

The trees at TB contribute less to NEE during the growing season than shrubs with *L. laricina* sequestering more  $\text{CO}_2$  than *P. mariana*. This coincides with results from a treed rich fen in Alberta (Syed *et al.* 2006).  $\text{CO}_2$  fluxes of these two species, as well as the dominant deciduous shrub *Betula pumila*, were measured at full daylight using a portable LI-6200 (LI-COR Inc., Lincoln, USA) system equipped with a 250 mL leaf chamber. NPP of  $5.8 \pm 0.6$  ( $\pm 1$  SE)  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for *P. mariana*,  $8.7 \pm 0.5$   $\mu\text{mol m}^{-2} \text{s}^{-1}$  for *L. laricina*, and  $13.9 \pm 0.9$   $\mu\text{mol m}^{-2} \text{s}^{-1}$  for *B. pumila* were reported. In comparison,  $P_{\text{max}}$  values at TB for *L. laricina* (branch), *P. mariana* (branch), and the dominant shrub *V. myrtilloides* are  $7.70 \mu\text{mol m}^{-2} \text{s}^{-1}$  (5.86, 9.53),  $4.72 \mu\text{mol m}^{-2} \text{s}^{-1}$  (3.78, 5.66), and  $8.91 \mu\text{mol m}^{-2} \text{s}^{-1}$  (7.25, 10.57), respectively. Numbers in brackets are 95% confidence intervals. For comparison purposes, estimated NPP values ( $P_{\text{max}} - R_{10}$ ) for the three species at TB are  $7.50 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $5.54 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and  $8.63 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively. The overall patterns of *P. mariana* < *L. laricina* and trees < shrubs are the same at the rich fen and ombrotrophic bog. On average, the current tree stand at TB is older than the Alberta fen with *L. laricina* establishing first in ~1862 and *P. mariana* establishing later in ~1921. At the site studied by Syed *et al.* (2006), *P. mariana* is the older part of the tree stand with the establishment of the biggest trees occurring in ~1870 while the largest *L. laricina* were established in ~1958. While there is a lack of studies on undisturbed treed peatlands, studies of upland forests indicate that C sequestration of a

forest diminishes as it ages (e.g. Schulze *et al.* 1999). If the tree canopy reaches C equilibrium in peatlands (i.e. respire as much CO<sub>2</sub> as it sequesters), at some point the understory may become the most important contributor to NEE. Since the trees at these sites are similar in age and have similarly low NPP, this suggests that the other vegetation, namely the understory shrubs, trees, and moss, may be partly responsible for the differences in NEE between the two sites.

Despite the similarity in vegetation NPP measurements, a much greater annual CO<sub>2</sub> sequestration of  $-144 \text{ g C m}^{-2} \text{ y}^{-1}$  was reported for the treed fen examined by Syed *et al.* (2006), a value the authors note is greater than reported for other peatlands. In comparison, NEE for TB and OB is  $-71.8 \text{ g C m}^{-2} \text{ y}^{-1}$  and  $-104.1 \text{ g C m}^{-2} \text{ y}^{-1}$ , respectively. The difference results from considerably lower ER at the fen (fen =  $569 \text{ g C m}^{-2} \text{ y}^{-1}$ , TB =  $623.8 \text{ g C m}^{-2} \text{ y}^{-1}$ , OB =  $679.7 \text{ g C m}^{-2} \text{ y}^{-1}$ ) and slightly lower GEP at TB (fen GEP =  $713 \text{ g C m}^{-2} \text{ y}^{-1}$ , TB GEP =  $695.6 \text{ g C m}^{-2} \text{ y}^{-1}$ , OB GEP =  $783.7 \text{ g C m}^{-2} \text{ y}^{-1}$ ). GEP at the two treed sites is similar with a difference of only  $\sim 17 \text{ g C m}^{-2} \text{ y}^{-1}$ , potentially due to the presence of relatively conservative coniferous trees. However, the fen is cooler than OB and TB (both  $16.5 \text{ }^{\circ}\text{C}$ ) with a regional average growing season temperature of  $12 \text{ }^{\circ}\text{C}$  and had a  $\sim 15 \text{ cm}$  higher WT. It has the same overstory trees of *L. laricina* and *P. mariana* but differs in ground layer vegetation. The fen has a mixture of *Sphagnum*, brown, and feather mosses while TB and OB have *Sphagnum* mosses as the dominant ground cover. This suggests that microclimate factors such as WT and temperature, which are speculated to be responsible for ER differences between TB and OB, are in part responsible for differences in ER between the rich fen and TB. The lower

WT and higher temperatures at TB encourage CO<sub>2</sub> loss via below-ground respiration compared to the fen site. Subsequently, although the fen had less plant productivity than OB, albeit more than TB, NEE was greater. The same association was present between a wet and dry year at the fen (Syed *et al.* 2006). ER was greater during the year with a low WT period and warmer temperatures.

To my knowledge, the study on the moderately rich fen by Syed *et al.* (2006) is the only annual NEE study on a natural treed peatland available for comparison purposes. Further research in this area will allow for a better understanding of how structural differences influence C exchange processes in peatlands.

## 5. Conclusion

Patterns of NEE and environmental variables are similar throughout the year at the open and treed bogs on the seasonal and diurnal scales. The greatest differences in NEE occur during the summer when vegetation composition and related productivity are dissimilar. Both sites have moderate coverage of *L. groenlandicum* and *C. calyculata* while TB has more *P. mariana*, *L. laricina*, *A. glaucophylla*, and *K. polifolia*. OB has more *V. myrtilloides* and *K. angustifolia*. The dominant trees at TB are less productive than the dominant shrubs at OB. Differing influence of environmental variables during the summer do not have a significant impact on NEE. Varying environmental conditions are more significant during the spring and fall when peak growing conditions (e.g. high temperatures and PPFD<sub>d</sub>) are lacking. During these periods of time, C uptake and loss at OB are more susceptible to environmental influence than at TB. There is evidence that despite similar NEE, ecosystem functioning varies between the two sites. Notably, there is potential for winter differences due to tree photosynthesis at TB but more data is needed to support this premise.

The main findings of this study are:

- 1) Treed and open bog areas of a peatland complex have differing microclimates, structure, and function despite similar environmental forcings and vegetation species. Trees have an impact on NEE through their influence on GEP. The results suggest that *P. mariana* and *L. laricina* tree species have different physiological limitations than the ericaceous and deciduous shrubs present at TB and OB. It appears that the vegetation may be governing ecosystem response to environmental forcings and subsequent C

sequestration rates. Consequently, this implies that treed bog and open bog peatlands may respond differently to changes associated with changing climate.

2) The annual difference in CO<sub>2</sub> sequestration is due to the cumulative effect of small daily deviations in NEE. These daily and annual differences are minor when compared to established ranges of NEE for other ecosystem groups such as crops and forests, and when compared to interannual variability of NEE within a given peatland. As such, the idea of peatlands as conservative ecosystems, derived from Gorham's (1991) estimation that peatlands as a group have a long-term sequestration of 20-30 g C m<sup>-2</sup> y<sup>-1</sup>, is substantiated by the results of this study. While not conclusive, this implies that treatment of treed and non-treed peatlands as a single class in modelling efforts is valid. However, further research is required to assess the relationships between peatland types and environmental forcings to substantiate the applicability of these findings to peatlands under a regimen of climate warming.

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