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Spatial Relationships of Carbon Dioxide Exchange in an Upland Forested Wetland Complex in the Western Boreal Plain, Alberta, Canada

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By

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ABSTRACT

This study examined the midday (10:00 - 16:00) growing season (April - October) surface cover CO_2 relationships with different canopy closures and microtopography (lawn and depression) in a forested upland - peatland - pond complex in the Western Boreal Plain, north – central Alberta, Canada. A dynamic - closed chamber technique was used to: evaluate the relative contributions of heterotrophic and autotrophic respiration and photosynthesis and assess the relative roles of substrate, plant communities, hydrology, and microclimates on CO_2 exchange.

Large differences were observed among the forest floors of landscape units with different canopy covers with respect to midday total respiration (R_{tot}= vegetation respiration (R_{veg}) + soil respiration (R_{soil})) and gross ecosystem production (GEP), and the seasonal pattern of GEP and R_{tot}. Highest rates of R_{tot} followed the general progression of riparian > upland > open peatland > covered peatland, with high R_{soil} contributions. Strong correlations were observed between C:N, soil temperature, moisture and R_{tot}. Photosynthetic Active Radiation (PAR) controlled GEP, which was highest in the open and covered peatland. GEP and R_{tot} were highest in the middle of the growing season when soil and air temperatures were warmest, in addition R_{veg} contributed more to R_{tot} during this time, however R_{soil} dominated the flux.

Small differences were observed between lawn and depression sites in terms of net ecosystem CO_2 exchange (NEE). The general trend was for warmer, drier lawn sites to have higher GEP and R_{tot} than the topographically lower, cooler and wetter depressions. The moisture and temperature differences between microtopography drove differences in the productivity of species but did not drive differences in vegetation distribution.

This study demonstrated that degrees of spatial and seasonal temporal variability as well as controlling environmental factors on CO_2 exchange cannot necessarily be extrapolated to a sub – humid region, such as Canada's Western Boreal Plain. In addition, forest floors of different land cover units, and microtopography should be taken into account when discussing understory contributions to CO_2 exchange.

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Chapter 1

Introduction

1.0 Atmospheric CO_2 and Global Change

The primary cause of global warming over the past century is believed to be due to the increased combustion of fossil fuels (for industrial or domestic usage), biomass burning and land use change that has lead to increased greenhouse gases (GHGs) in the atmosphere (IPCC, 2001; Schlesinger, 1997). As a result, the mean global temperature has risen 0.6 ± 0.2°C over the 20th century, and 0.2 – 0.3°C over the past 40 years (IPCC, 2001). Global circulation models (GCMs) predict that if these trends continue ambient temperatures are expected to rise anywhere from 1.4 - 5.8 °C by 2100 (IPCC, 2001) and may be augmented by land use change (Vitousek et al., 1997). There are many implications that may result from warmer ambient temperatures such as sea - level rise, changing precipitation, and transpiration patterns, and altered dynamics of the soil - atmosphere carbon exchange (IPCC, 2001). However, climate change and its effects on our future environment requires a better understanding and quantification of the processes contributing to global change (Fang and Moncrieff, 2001). Global change predictions are difficult to generalize since the magnitudes, feedback directions and interactions are unknown (Goulden et al., 2007; Schlesinger and Andrews, 2000).

The most abundant and prominent GHG is water vapour, but human activity is not believed to have directly affected its average global concentration (IPCC, 2001). However, other prominent anthropogenic GHGs such as carbon dioxide (CO_2),

methane (CH_4) and nitrous oxide (N_2O) (greenhouse warming potentials of approximately 1, 23 and 296 respectively) (IPCC, 2001) may directly affect the hydrological cycle due to positive feedbacks from radiative forcing (William and Ruddiman, 2002). Although the greenhouse warming potentials of CH_4 and N_2O are much larger than CO_2, actual increases due to CO_2 are dominant and estimates indicate it has contributed 60% of the total increase in radiative forcing, followed by CH_4 (16%), and a combination of other gases (24%) (William and Ruddiman, 2002).

Natural systems and biogeochemical cycles have historically maintained carbon pools in dynamic equilibrium. However, due to anthropogenic activities large shifts among carbon pools have occurred (IPCC, 2001), and the fate of the CO_2 loaded into the atmosphere has been uncertain (Quay et al., 1992). Measurements of terrestrial carbon dynamics have been measured for nearly 80 years (Gainey, 1919), and the biosphere is now recognized as a reservoir that can exchange significant amounts of CO_2 on the time scale of the observed anthropogenic perturbations (Quay et al., 1992). The total global emission of CO_2 from soil is recognized as one of the largest fluxes in the global carbon cycle, and small changes in the magnitude of soil respiration could have a large effect on the concentration of CO_2 in the atmosphere (Schlesinger and Andrews, 2000; Rustard et al., 2000).

Vegetation is considered the regulator of carbon exchange in terrestrial ecosystems (Schlesinger 1997). Some authors believe that warming may stimulate plant production (e.g. Silvola, 1996). Higher CO_2 concentrations in the atmosphere may result in larger biomass uptake (increased photosynthesis) (Barton and Jarvis, 1999), which would act as a negative feedback to climate change. However, it is

expected that this effect would be modest as the soil currently stores more carbon than a mature temperate or boreal forest, and any indirect stimulation of production would have to be large to offset the expected loss of carbon (Goulden et al., 1998). Thus, understanding the feedbacks between terrestrial ecosystems and the atmosphere is a key instrument to predict the evolution of atmospheric CO_2 concentrations and global cycling of CO_2.

Currently, there is much uncertainty about the role of terrestrial ecosystems in the global carbon budget (Swanson and Flanagan, 2001; Fan et al., 1998). Direct measurements of the increase in atmospheric CO_2 levels when compared to the rates of fossil fuel combustion, indicated that about 57% of the CO_2 produced has been accumulated in the atmosphere (Quay et al., 1992), and the other 43% of the industrially derived CO_2 is either in the biosphere or ocean. However, recently a number of techniques (atmosphere - based methods (eddy covariance, tracer - transport inversion), and land - based approaches (chamber measurements, ecosystem models)) have all indicated that the terrestrial biosphere is a significant sink for the industrially derived CO_2. In fact, 70 - 100% of the missing sink may be in northern sub - arctic and arctic wetlands and forest ecosystems (Swanson and Flanagan, 2001; Fan et al., 1998). The mechanisms responsible for the carbon sequestration and the relative combination from different land covers of exact spatial location of the ecosystems contributing most to the terrestrial sink remain controversial (Swanson and Flanagan, 2001; Lloyd, 1999). Therefore, a major research challenge is to identify more accurately the mechanisms and location of the terrestrial sinks and sources for atmospheric CO_2, and how they will respond to changes in climate, land

use and management practices (Swanson and Flanagan, 2001; Pacala et al., 2001; Rustard et al., 2000).

1.1 Terrestrial Carbon Exchange

The general carbon balance for any terrestrial ecosystem can be expressed by:

$$\Delta C(NEE) = CO_2(GEP) - CO_2(R_{tot}) - CH_4 - DOC \qquad (1.1)$$

where ΔC (NEE) is the net change in carbon storage within the ecosystem (mg C m^{-2} sec^{-1} or g C m^{-2} day^{-1}), GEP is the net primary productivity, which represents total plant uptake or release of carbon from the system, R_{tot} represents CO_2 loss from roots, microbial activity (decomposition) and vegetation respiration, CH_4 is methane and DOC represents dissolved organic carbon. However, within this study only part of the carbon balance is examined, that is photosynthesis and total respiration are observed in detail to allow for the examination of spatial and temporal variability and the controlling variables on the fluxes. Thus, the terrestrial CO_2 exchange can be simplified as:

$$NEE = GEP + R_{tot} \qquad (1.2)$$

1.1.1 Photosynthesis

In terrestrial ecosystems atmospheric vegetation is able to convert light energy to chemical energy through photosynthesis. Photosynthesis (directly or indirectly) provides energy for many forms of life in the biosphere (Schlesinger, 1997). Atmospheric CO_2 is fixed by the vegetation and then converted to a carbohydrate ($C_3H_6O_3$) and oxygen:

$$6CO_2 + 12H_2O \rightarrow C_3H_6O_3 + 6O_2 + 6H_2O \qquad (1.3)$$

Some of the carbohydrates are used by the vegetation during metabolism and carbohydrate production, which is referred to as heterotrophic respiration (Raven et al., 1999). The remaining carbon is partitioned between above - ground (shoots and leaves) and below - ground biomass (roots) (Raven et al., 1999).

1.1.2 Respiration

The release of CO_2 from soils due to the production of CO_2 by roots and soil micro - organisms, and to a lesser extent chemical oxidation of carbon compounds, is commonly referred to as soil respiration (Lloyd and Taylor, 1994). Soil respiration exceeds all other terrestrial - atmosphere carbon exchanges with the exception of gross photosynthesis (Raich and Schlesinger, 1992). The overall carbon flux from soils will herein be referred to as R_{soil} for soil plots and R_{tot} and R_{veg} for vegetated plots. R_{tot} and R_{soil} is comprised of biotic (rhizosphere (root and root exudates)), heterotrophic (microbial and faunal respiration), chemical (chemical oxidation and soil carbonates) and physical factors (soil degassing) (Suyker et al., 2003; Raich and Schlesinger, 1992). However, R_{tot} will also include the above - ground biomass respiration (plant metabolism). R_{veg} will only be comprised of the above - ground vegetation respiration which can be described as:

$$R_{veg} = R_{tot} - R_{soil} \qquad (1.4)$$

When the vegetation enters senescence, large amounts of organic carbon is contained within the dead bodies of the plants and contribute to the soil organic matter (SOM) and detritus, which is then consumed by decomposers (small invertebrates, bacteria and fungi) (Raven et al., 1999). The carbon cycle is then

completed through the return of CO_2 to the atmosphere from the mineralization of SOM (Rustad et al., 2000):

$$C_6H_{12}O_6 + 6O_2 + 6H_2O \rightarrow 6CO_2 + 12H_2O + heat \qquad (1.5)$$

Soil carbon represents a major proportion of the total carbon budget (1500 Pg C), comprising twice the amount of carbon present in the atmosphere (750 Pg C) (Eswaran et al., 1993). It has been shown that 10% of the atmosphere's CO_2 passes through soils each year (Raich and Tufekcioglu, 2000), which represents more then 10 times the CO_2 released from anthropogenic sources (Raich and Tufekcioglu, 2000). Consequently, understanding the magnitudes and processes that regulate the transfer of carbon in the soils of forest floors in terrestrial ecosystems is essential from a global change perspective.

1.2 Significance and Uniqueness of Boreal Forests

Boreal forest ecosystems constitute the second largest biome on Earth (Heijmans et al., 2004), and is a region where the climate has warmed significantly in this century and is predicted to warm further in the next century (IPCC, 2001). The Western Boreal Plain (WBP) spans 6.5x 10^5 km^2 of land in the prairies, from southeastern Manitoba to northwestern Alberta (Env. Canada, 2007a), which is part of the boreal forest. Within the boreal forest seasonally and perennially frozen soils contain one of the largest pools of carbon in the terrestrial biosphere (200 to 500 gigatons of carbon, 1 GT= 10^9 metric tons) (Schlesinger, 1997). The accumulation of carbon here is believed to be the result of slow rates of decomposition of plant matter rather than large rates of net primary production (Vitt, 1990). Thus, the large amount of soil carbon stored could increase the concentration of CO_2 in the atmosphere by as

much as 50% if it were released by climatic warming (Oechel et al., 1993; Goulden et al., 2007). In addition, regions such as the WBP may respond to changes in the climate and land use more dramatically as this area is operating in a potential moisture deficit, such that in most years potential evapotranspiration is higher then precipitation (Env. Canada, 2007a). Thus, under heavy industrial pressures (for example, forestry and oil extraction) landscape alteration may cause significant changes to its biogeochemical cycling. For example, road establishment may compact the soil restricting the flow of gases such as CO_2, and in a region where water may be limiting, changes to the hydrology may release large amounts of CO_2 to the atmosphere. Thus, it is important to understand the fate of this carbon in response to global climate change and land use change since its release to the atmosphere could act as a positive climatic feedback (Strack et al., 2006).

The role of boreal forests, including the WBP in the global carbon cycle is determined by the net exchange of CO_2 between the terrestrial ecosystem and the atmosphere (commonly referred to as net ecosystem exchange (NEE)) (Gower et al., 1997), which is driven by the balance between the uptake of CO_2 by photosynthesis and its emission via plant and soil respiration (Bubier et al., 2003). As a result of differences in photosynthetic uptake and respiratory loss, there can be considerable spatial and interannual variability in NEE. A better understanding of the influence of the environmental and ecological factors on the major components of NEE is required to determine the causes of spatial and temporal variability in NEE (Gower et al., 1997; Suyker et al., 1997).

Despite the importance of these regions in the global carbon budget there are few studies that examine these areas as a diverse set of land cover units that are structured by a variety of factors (Bridgham et al., 1998). Most studies have viewed them as homogeneous land cover units in budget estimates (Gorham, 1991), focused only on peatlands breaking them down into only two or three vegetation communities (Botting and Fredeen, 2006; Swanson and Flanagan, 2001), microtopographical units (e.g. depressions and lawns) (Kim and Verma, 1992; Potter et al., 2001) or examined upland canopy CO_2 dynamics without partitioning between forest floor and canopy fluxes (Gower et al., 1997). In addition, estimates of above ground productivity is generally easier as they can be determined from satellites, however, below canopy forest floors are very important as they are a major component of CO_2 exchange but are poorly studies. Thus, the forest floor is poorly represented in models, and predictions for climate and land use change for the boreal forest, and therefore the WBP will likely be variable due to the heterogeneity of the area. Thus, the key to understanding the biogeochemical cycling in the boreal forest is to understand how heterogeneity in soil characteristics, vegetation and canopy conditions interact with the atmosphere and ecosystem in terms of hydrology and microclimate. That is, by studying a process – based local site (Utikuma Research Study Area (URSA)) within the boreal forest, the aforementioned interactions can be examined and ways to extrapolate and generalize can be applied to larger scales.

1.3 Study Rational

Climate change will continue as long as humans continue transforming the land surface, much of which has already been altered by humans (30 - 50%)

(Vitousek et al., 1997). It was with the initiation of the Kyoto Protocol that quantifying global carbon emissions has become of great significance (IPCC, 2001). Anthropogenic increases of carbon dioxide (CO_2) already represent a 30% increase relative to the pre - industrial era (Vitousek, 1997).

There have been studies on CO_2 effluxes from northern peatlands for nearly a decade that can be attributed to their importance in climate change scenarios (c.f. Gorham, 1991; Waddington et al., 1998; Moren and Lindroth, 2000). However, due to GMC predictions of increased temperatures in northern boreal forest and subarctic areas, research has recently increased. Controls on trace gas fluxes are fairly well known qualitatively, thus many studies try and quantify CO_2 emissions and establish links to physical process (Amiro, 2001; Black et al., 1996; Petrone et al., 2003). This has lead to research examining atmospheric conditions, (Megonigal and Schlesinger, 1997), surface conditions (snowmelt, growing season, understory species) (Griffis et al., 2000b; Heijmans and Chapman, 2003; Bisbee et al., 2000; Petrone et al., 2004), and subsurface properties (water table, peat temperature, soil temperature) (Bubier et al., 2003; Petrone et al., 2004) in relation to CO_2 exchange. However, the controls on the dynamics of these fluxes, and in particular the relationships between them are currently not well understood, particularly for differing vegetation types and potentials for carbon storage (Joabsson et al., 1999; Hobbie, 2000).

Ecosystem - scale measurements such as eddy covariance systems while allowing for continuous measurements only provide CO_2 exchange from the entire ecosystem, and do not differentiate among the combined effects of the species, functional groups, or microtopography within the ecosystem; and chamber

measurements required for such a study are labor intensive (Lund et al., 1999). This allows for understory species to be poorly represented in climate change models. Thus, the primary focus of this study was to explore forested boreal wetland complexes to obtain region - specific flux variability and examine the environmental controls on CO_2 exchange to improve the understanding and modeling of forest wetland exchange, which is lacking in the literature (Heijmans et al., 2003; Bubier et al., 1998)

1.4 Research Objectives

This research has two main objectives involving the examination of forest floors within the Western Boreal Plain (WBP) in a forested upland peatland – pond complex: (1) characterize the seasonal rates of forest floor gross ecosystem production (GEP) and total respiration (R_{tot}) from closed to open canopy of three land forms (upland, riparian and peatland) and to assess the relative roles of substrate, plant communities, hydrology, and microclimates on CO_2 exchange; and (2) measure the rates of understory NEE, GEP and R_{tot} from peatland lawn and depression mictotopographical units through the growing season to determine if there are differences in CO_2 exchange between microtopographical units and if vegetation types can be used as a proxy for photosynthesis and respiration.

Chapter 2

Forest Floor Carbon Dioxide Fluxes within an Upland Forested Peatland - Pond Complex in the Western Boreal Plain

2.0 Introduction

The Canadian boreal forest zone has been a centre for research for many years through collaborative projects such as BOREAS and BERMS (AEP, 1998). However, the boreal forest consists of two distinct geologic and climatic zones: glacial deposits and sub - humid climate in the Western Boreal Plain (WBP), and bedrock dominated and humid climate in the Canadian Shield zone. Differences in the hydrologic cycle between these zones (Devito et al., 2005) will have a large influence on biogeochemical cycling and carbon dynamics, and therefore trace gas exchange. Currently there is limited work on these linkages between the hydrology and biogeochemical cycling in the WBP, and it is not yet known if carbon dynamics within the runoff - dominated Shield can be extrapolated to the complex hydrology of the sub - humid WBP.

The WBP is within the Boreal Forest, which is a diverse biome, including a wide climatic range, from dry aspen forests of interior Alaska, to cold, wet peatlands of Hudson Bay (Gulledge and Schimel, 2000). Even a single watershed can encompass great variation. For example, closed dry aspen stands that occur adjacent to wet open canopy black spruce peatlands (Gulledge and Schimel, 2000). Forested wetland systems within the WBP also have a unique suite of external natural

(drought, climate variability and fire) and anthropogenic (forestry, petroleum development, agriculture and recreation) stressors (Schindler et al., 1990) which control the mosaic of vegetation. The importance of the WBP to global carbon cycling is known (IPCC, 2001; Heijmans et al., 2004), but the sensitivity of the component landcover units (i.e. forested upland, wetland and pond) to environmental changes are not well understood (Margolis and Ryan, 1997). Therefore, more information is needed on the processes that control the storage and fluxes of energy, water and carbon in this region; particularly the linkages between carbon and water cycling within the different land cover units that comprise the WBP landscape. Consequently, understanding the ecohydrological and biogeochemical connections in the sub - humid WBP is essential to predict the impact of climatic changes and resource development in the region on water resources and greenhouse gas emissions.

The carbon cycling in this region is controlled by the amount of water the land cover receives and stores, which is a function of precipitation (PPT), evapotranspiration (ET), underlying glacial deposits and land cover physiography. Peat formations within the riparian zones of many ponds in the WBP have formed forested wetland complexes (N.W.W.G.,1988), and influence the shallow hydrological connections between the ponds and surrounding mineral uplands (Devito et el., 2005; Ferone and Devito, 2003) whose hydrologic cycling is dominated by ET (Devito et al., 2005; Petrone et al., 2006). Wetlands here exist at a hydroclimatic threshold where their carbon exchange (storage) changes dynamically in response to climatic variability. However, they may persist in a homeostatic state where negative feedbacks with larger scale hydroclimatology maintain their current

water and carbon storage status, by limiting decomposition despite lower productivity rates. Further, in a sub - humid forested environment, ET also dominates the water balance of the adjacent uplands that generally produce little runoff (Ferone and Devito, 2003). Therefore, understanding all aspects of the hydrologic cycle in the context of these interactions between land cover units is essential to quantify the carbon cycle functioning of these systems, as patterns in water cycling will produce temporal and spatial variability in moisture conditions and vegetation communities that is important to carbon cycling. Preliminary results show that substantial amounts of carbon are stored in these systems (Petrone et al., 2005). Therefore, understanding the linkages between the hydroclimatology and carbon exchange within these landscapes is essential in understanding carbon storage in wetland systems (Branfireun and Roulet, 1998; Waddinton and Roulet, 1997).

One of the key questions to be addressed is the fate of the large amounts of carbon that is currently stored in soil organic matter (Fang and Moncrieff, 2001), and the possible positive feedback effects that warming could have on the release of CO_2 from these terrestrial carbon pools. For example, soil carbon is highly sensitive to changes in near surface temperature (Fang and Moncrieff, 2001) and relatively small changes in surface temperature may have a major role in the magnitude of the soil carbon flux. In addition, models generally predict that temperatures will increase in the WBP, but the predictions for precipitation and soil moisture vary (IPCC, 2001). Therefore, predictions for changes in boreal carbon exchange also vary (Gulledge and Schimel, 2000). Thus, the boreal wetlands and ponds that are sustained by a balance between pond and peatland evaporation and hydrologic connectivity with surrounding

forested uplands are likely to show large spatial variability and could be interrupted as the result of external stressors. For instance, higher soil temperatures that will accompany increased atmospheric temperatures could increase soil decomposition (Oechel et al., 1993; Raich and Schlesinger, 1992). However, the response of the terrestrial vegetation in the upland forested areas and wetlands that comprise this region could increase their uptake as a result of higher temperatures and atmospheric CO_2 concentrations (Goulden et al., 1998; Heijmans et al., 2004). Thus, it is critical to understand the spatial variability in soil respiration, as changes in climate and land use may not cause uniform changes in the cycling of carbon.

Most previous research in this area has focused on ecosystem scale measurements of CO_2 exchange, but very little is known about the role of the understory vegetation (Heijmans et al., 2004). An understanding of the factors controlling the exchange dynamics in understory vegetation could be especially important in areas where forests and wetlands meet or merge, which will be especially important in highly heterogeneous regions like the WBP. Further, changes in species composition or vegetation structure in response to climatic or land use change could alter water and energy feedbacks to the regional climate system (Heijmens et al., 2004; Chapin et al., 2000).

Optimal productivity in any ecosystem requires inter - plant interactions to be understood – both between, and within, land cover units (i.e. including over - and understory vegetation) (Powell and Bork, 2005). Understory production in boreal forests and wetlands can be as high as the above tree production (Oechel and Van Cleve, 1986; Bisbee et al., 2001). For example, mosses in the wetland and riparian

areas, as well as litter and understory vegetation, can insulate the soil, intercept water and nutrients, and decompose slowly, which reduces soil temperatures and rates of nutrient supply (Heijmans et al., 2004; Oechel and Van Cleve, 1986; Hobbie et al., 2000). However, vegetation growth under an aspen stand is also a strong function of the microclimate controlled by that aspen, which can produce a mixture of competitive and facilitative effects for understory productivity (Callaway and Walker, 1997; Powell and Bork, 2005). An aspen canopy can serve to reduce frost and insect damage, and alter competition among other understory species (Man and Lieffers, 1999). Thus, by altering the microclimate, and vegetation interactions, the biogeochemical characteristics of an aspen forest floor may also facilitate the cycling of CO_2 exchange within, and from, the canopy (Kishchuk, 2002; Hannam et al., 2004). However, thus far the differing effects, and interactions, between over - and understory vegetation productivity, and the resultant effects on CO_2 exchange in an aspen dominated stand are not well understood (Powell and Bork, 2005).

The objective of this study is to characterize the average rates of forest floor gross ecosystem production (GEP) and total respiration (R_{tot}) along a gradient from closed to open canopy and to assess the relative roles of substrate, plant communities, hydrology, and microclimates on CO_2 exchange to improve our carbon flux understanding and modeling of forest floors. Key research questions are: What is the spatial variability among forest floors in CO_2 exchange? Are there differences in average seasonal patterns of CO_2 exchange? To which environmental or biotic factors are the differences related? To answer these questions in situ CO_2 exchange was

measured on the forest floor of different land cover units using a dynamic - closed chamber system.

2.1 Study Site

The forested peatland - pond – upland complex in this study is situated on common disintegrated moraine (Redding et al., 2005), located in the Utikuma Region Study Area (URSA) near Utikuma Lake, northern Alberta (56°20' N, 115°30' W) within the Western Boreal Plains (WBP) ecozone (Figure 2.1) (Devito et al., 2005). The climate is characterized by warm summers and long, cold winters. The 30 – year average annual temperature and precipitation for the region are 1.7 °C and 485 mm, respectively and potential evapotranspiration (PET) is 515 mm (Environment Canada, 2007). The sampling year's (January – December) average temperature and precipitation for 2005 and 2006 (in parentheses) were 2.8 °C (2.9 °C) and 374 mm (396.5 mm), respectively. Therefore these years were slightly warmer and drier than the 30 - year climate normals.

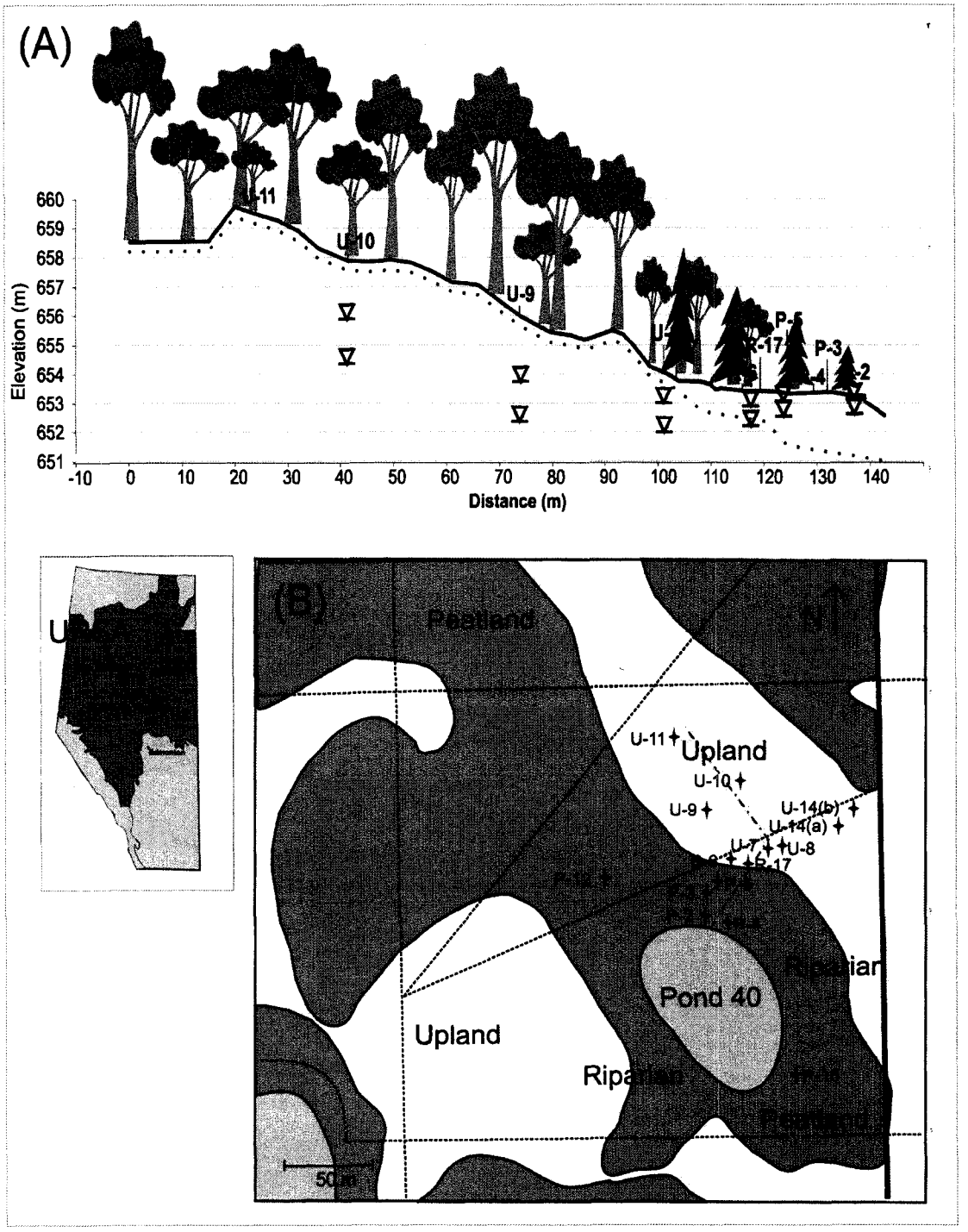

Figure 2.1: Study site Pond 40, located within the western boreal plain ecozone, Utikuma Region Study Area, Alberta, Canada. (A) Topographic relief showing distributions of sites along main collar transect (shown in (B) by red dashed line), canopy coverage, maximum and minimum depth to water table and dotted line represents average depth of organic layer. (B) Site locations within the study area, stars represent site locations, solid lines represent roads, dashed lines represent seismic lines.

Table 2.1: Midday point measure averages of total respiration (R_{tot}), and gross ecosystem production (GEP) (± standard error) for upland, riparian, and peatland (covered and open) showing the number of collars, and distribution of the fluxes within the uplands.

Land Cover Unit	Distribution	Number of Collars	Average R_{tot}	Average GEP
Upland				
	Top	1	-0.19± 0.011	0.019± 0.001
	Midslope	1	-0.17± 0.001	0.017± 0.002
	Toe	2	-0.19± 0.009	0.015± 0.003
	Depression	3	-0.17± 0.013	0.013± 0.004
Riparian		2	-0.21± 0.011	0.017± 0.001
Peatland	*Covered*	5	-0.05± 0.002	0.024± 0.12
	Open	6	-0.09± 0.004	0.078± 0.005

**Upland (top)- n=62; Upland (midslope)- n=62; Upland (toe)- n= 126; Upland (depression)- n=144; Riparian- n=96; Peatland (covered)- n=311; Peatland (open)- n=263*

Three land cover units were chosen within the catchment to span the continuum in canopy cover: upland aspen dominated (closed canopy), riparian (transition canopy), and peatland (covered and open canopies). In addition, the land cover units were defined by the depth of organic layer, water table location, and the degree of soil humification (Figure 2.1a). The depth of the organic layer in the upland was shallow and much less humified in comparison to the riparian and peatland. The water table in the riparian and peatland fluctuated close to the surface, whereas the depth of the water table in the upland sites were far from the surface, however it did fluctuate over the growing season. The upland sites were distributed at the top, midslope and slope toe (Figure 2.1). However, it was observed (Table 2.1) that there was little variation within the uplands (top, mid - slope, and slope toe); thus, they were grouped together to represent the uplands.

The three land covers (upland, riparian, and peatland (open and covered)) had variable canopy covers which will affect the moisture, thermal, and plant communities on the forest floors. Therefore, collars were placed along these gradients to capture a range of environmental conditions in addition to the variations observed in depth of organic layer, water table locations, and soil humification (Upland n= 7; Riparian n= 2; Peatland open n= 6; and Peatland covered n= 5). Forest floor plant community descriptions for each site are found in Table 2.2.

Table 2.2: Vegetation as percent coverage in vegetated collars for each site and land cover unit, and dominate canopy cover. Over 100% coverage is observed at some collars as moss mats were present with vascular vegetation growing through. Refer to Figure (2.1) for site locations.

Site	Canopy Cover	Dominant Canopy Coverage	Peatland				Riparian		Upland	
			Lawn		Depression					
40-16	Open	*Picea mariana*	*Cladina mitis*	15%	*Cladina mitis*	95%				
			Empetrum nigrum	30%	*Vaccinium vitis-idaea*	50%				
			Ledum groenlandicum	25%	*Oxycoccus microcarpus*	5%				
			Oxycoccus microcarpus	10%						
			Sphagnum fuscum	100%						
			Vaccinium vitis-idaea	3%						
40-12	Open	*Picea mariana*	*Empetrum nigrum*	10%	*Helodium blandowii*	4%				
			Ludum groenlandicum	25%	*Ledum groenlandicum*	5%				
			Oxycoccus microcarpus	30%	*Oxycoccus microcarpus*	3%				
			Sphagnum fuscum	90%	*Sphagnum fuscum*	85%				
			Vaccinium vitis-idaea	10%	*Vaccinium vitis-idaea*	15%				
40-2	Open	*Picea mariana*	*Cladina mitis*	95%	*Cladina mitis*	20%				
			Ledum geoenlandicum	15%	*Ludum groenlandicum*	10%				
			Pleurozium schreberi	25%	*Pleurozium schreberi*	95%				
			Vaccinium vitis-idaea	15%	*Vaccinium vitis-idaea*	30%				
40-3	Covered	*Picea mariana*	*Helodium blandowii*	10%	*Helodium blandowii*	95%				
			Viola renifolia	10%	*Vaccinium vitus-idaea*	30%				
40-4	Covered	*Picea mariana*	*Ludum groenlandicum*	30%	*Hylocomium splendens*	20%				
			Smilaciha trifolia	1%	*Helodium blandowii*	55%				
			Vaccinium vitis-idaea	25%						
40-5	Covered	*Picea mariana*			*Helodium blandowii*	65%				
					Hylocomium splendens	15%				
40-6		*Alnus spp.*					*Equisetum sylvaticum*	5%		
		Picea mariana					*Ribes Triste*	15%		
40-17		*Alnus spp.*					*detritus*			
		Picea mariana								
40-7		*Populus tremuloides*							*Cornus canadensis*	5%
									Mitella nuda	10%
40-8		*Populus tremuloides*							*detritus*	
40-9		*Populus tremuloides*							*Maianthemum canadense*	20%
									Mitella nuda	20%
40-10		*Populus tremuloides*							*Cornus candensis*	10%
									Epilobium angustifolium	25%
									Frageria virginiana	7%
40-11		*Populus tremuloides*							*detritus*	
40-14 (a)		*Populus tremuloides*							*detritus*	
40-14 (b)		*Populus tremuloides*							*Eurhynchium pulchellum*	10%
									Hylocomium splendens	50%

2.2 Materials and Methods

2.2.1 CO_2 Measurements

CO_2 exchange between the forest floor and atmosphere was measured using a dynamic - closed chamber system with an EGM - 4 Infrared Gas Analyzer (IRGA) (P.P. Systems, Maryland). Net ecosystem CO_2 exchange (NEE) and gross ecosystem productivity (GEP) were measured using clear lexan chambers, while total (R_{tot}) and soil respiration (R_{soil}) were measured using an opaque neoprene shroud over the lexan. Each site consisted of a vegetated and a bare plot (vegetation removed) to assess soil respiration by separating below - ground from above - ground plant respiration. This permitted the examination of whether the variability of CO_2 exchange was influenced more by soil or vegetation dynamics. Measurements were conducted from May to September, 2005 and April to October, 2006 (Table 2.3). Polyvinylchloride (PVC) collars (radius= 9cm) with a groove for collar placement were inserted one week prior to initial measurements. Due to the placement of the collars early in the season there was no vascular plant growth on the forest floor within the uplands and riparian land cover units. Therefore some sites contained only detritus, which is typical of the forest floors in this region. The groove in the top of the plastic collar was filled with water and remained throughout the measure to ensure an airtight seal when the chamber was inserted during the flux. A climate controlled system in each chamber consisted of a cooler with cold water pumped through a coolant tube to maintain chamber conditions within 2 °C of ambient conditions and a fan mounted on the inside of the chamber to minimize concentration build - up influencing the gradient, without ventilating the surface (Welles et al.,

2001). Five 1 minute CO_2 concentrations were sampled at each collar location midday (9 - 1600 hrs), twice a week. The rate of CO_2 concentration increase within the 5 minute interval was used to determine the average flux (Lund et al., 1999). The concentration of CO_2 was measured in ppm and then converted into mg CO_2 m^{-2} sec^{-1} using,

$$F = \frac{\Delta \times MM}{N} \times \frac{V}{A} \times CF \qquad (2.1)$$

where F is the gas flux (mg CO_2 m^2 sec^{-1}), Δ is the linear change in CO_2 concentration with time (ppm × sec^{-1}), MM is the molar mass of CO_2 (44010 mg mol^{-1}), N is the molar volume of a gas (22.4 L mol^{-1}) at standard temperature and pressure (STP), V is the temperature corrected volume within the chamber (m^3), A is the chamber area (m^2) and CF is the conversion factor from ppm to mol (1 ppm = 10^{-6}mol). Sampling times at each site were random and rotated to allow for different light, temperature and moisture regimes that may occur throughout the day to be measured.

Photosynthesis (GEP) was estimated by subtracting the gross respiration (R_{tot}= autotrophic and heterotrophic) from NEE which is the combined above - and below ground respiration and photosynthesis:

$$GEP = NEE - Rtot \qquad (2.2)$$

The sign convention of CO_2 uptake by the ecosystem as positive and CO_2 emissions from respiration as negative was adopted here. For comparative purposes the season was divided into different time periods (Table 2.3) (early green (EG), green (G), late green (LG) and senescence (S)).

Table 2.3: Time periods for 2005 and 2006. The periods fluctuated slightly between years; early green (EG), vascular species emerge but are immature; green (G), vascular species are maturing; late green (LG), vascular species reach maturity and leaf area index (LAI) reaches a maximum; senescence (S), onset of dormancy.

	Dates	
Time Period	**2005**	**2006**
Early Green	April 30- June 10	April 26- June 6
Green	June 10-August 6	June 6- July 31
Late Green	August 6- September 7	July 31- September 1
Senescence	N/A	September 1- October 3

The periods fluctuated slightly between the years as they were based on precipitation, temperature and understory vegetation growth. Early green in 2005 and 2006 (in parentheses) extended from DOY 120 (116) to 161 (157). At this time vascular species emerge but are immature. Green extended from DOY 161 (157) to 218 (212). During this time vascular species are maturing. Late green extended from DOY 218 (212) to 250 (244). During this time the vascular species reach maturity and leaf area index (LAI) reaches a maximum. The senescence period was only monitored in 2006 and extended from DOY 244 to 276. Onset of dormancy occurred at this time.

The relationship between GEP and PAR was fitted empirically using an equation for a rectangular hyperbola (Whiting, 1994; Waddington and Roulet, 1996):

$$GEP = \frac{(\alpha \times PAR \times GP_{max})}{(\alpha \times PAR + (GP_{max}))} \qquad (2.3)$$

where PAR is the measured PAR (in μmol m^{-2} sec^{-1}), GP_{max} is the empirically derived gross photosynthetic exchange of CO_2, and α is the initial slope of GEP versus PAR. To determine the temperature coefficients (Q_{10}) which represents the difference in

respiration rates over a 10°C interval, Fang and Moncrieff's (2001) first - order exponential equation was used:

$$Q_{10} = (R_2 / R_1)^{10/(T_2 - T_1)} \qquad (2.4)$$

where R_1 and R_2 were measured respiration rates at temperatures T_1 and T_2 respectively.

2.2.2 Environmental Variables

Relative humidity (RH), air temperature (T_a) and photosynthetically active radiation (PAR) were measured at each site during each 5 minute chamber sample, both inside and outside of the chamber (at approx. 0.5 m above the forest floor). Peat and soil temperatures were recorded at the same temporal and spatial scale as the CO_2 fluxes using a digital thermocouple at 2, 5, and 10 cm depths. Soil moisture was measured using time domain reflectometry (TDR) (tectronics) such that the probe was inserted horizontally at each collar site to give a bulk soil moisture value over 10 cm. TDR's were calibrated in the lab by extracting representative samples from the field and then allowing them to dry to different moistures. Hydro - sense (Campbell Scientific), theta soil moisture probe (Delta-T Devices), and recording 615 TDR were used to monitor the soil moistures and were recorded twice daily for 3 weeks. Soil properties for the representative samples were then determined in the lab, and calibration curves were determined and fitted to the data. Water table positions relative to the ground surface at each site were recorded weekly using wells constructed of PVC tubing. Wells were located within a 5 meter radius of each upland site. However, within the peatland and riparian area one well represented numerous sites due to the close proximity of the sites to each other.

2.2.3 Vegetation Sampling

Plant species composition was recorded in each collar by percent cover of vascular plant and bryophyte species. Nomemclature follows Anderson et al. (1990) for all species. Canopy closure was determined using digital photographs. The camera (Kodak DC-120) with a fixed 39 - 114mm *f*/2.5 - 3.8 lens and 1280 x 960 pixel image resolution was leveled above each collar and manual photos were taken. Photos from all sites were taken mid day on clear days to avoid large variations in brightness among the images. Photos were analyzed using Adobe Photoshop CS (Adobe Systems incorporated). The threshold to classify pixels into 'sky' and 'canopy' was determined on the first image and then applied to the rest of the images in that set. Classified images were then analyzed to calculate canopy area. The ratio of the canopy area to frame area of the image was expressed as a percentage and used to estimate canopy closure (Guevara - Escobar & Gonzalez - Sosa, 2005).

2.2.4 Soil Analysis

Soil cores were taken in duplicate for each collar site in August 2005 and were analyzed for bulk density (ρ_b), porosity (θ), soil organic matter (SOM), specific yield (Sy), VonPost and C:N ratios. Bulk density measured the mass of soil per unit volume, including pore space and was determined by:

$$BulkDensity = \frac{WeightOfOvenDriedSample(g)}{VolumeOfSample(cm^3)} \qquad (2.5)$$

Porosity measured the portion of soil occupied by air and water and was determined using:

$$\%Porosity = \frac{SaturatedMass(g) - DryMass(g)}{Volume(cm^3)} \times 100 \qquad (2.6)$$

Specific yield was determined by saturating the soils and then allowing them to drain for 48 hours:

$$SpecificYield = \frac{SaturatedMass(g) - DrainedMass(g)}{SaturatedMass(g)} \quad (2.7)$$

Total carbon (liable carbon and carbonate) for all sites were determined through loss on ignition (LOI) in a muffle furnace (Fang et al., 1998) using:

$$\%LossOnIgnition = \frac{\left[\left(W_{cso} - W_c\right) - \left(W_{csi} - W_c\right)\right]}{\left(W_{cso} - W_c\right)} \times 100 \quad (2.8)$$

Where W_c is the weight of the crucible (g), W_{cso} is the weight of the oven dried soil in crucible (g), and W_{csi} is the weight of the remaining (inorganic) soil and crucible (g). For the C:N there was no separation between organic and inorganic forms was made for the carbon component of the soil. The total percent carbon (%TC) and nitrogen (N) contents of the soil were determined through combustion using an Isochrom - elemental analysis, Carlo - Erba Isotope Ratio Mass Spectrometry, autocombustion carbon - nitrogen analyzer (Micromass UK, Ltd., Environmental Isotope Laboratory, Dept. of Earth Sciences, University of Waterloo, Waterloo, Ontario, Canada). Soil characteristics for each land cover unit are provided in Table 2.4.

Table 2.4: Soil Characteristics for each land cover unit as a function of depth.

Landscape Unit	Depth (cm)	LOI	BD (g/cm^3)	Porosity (%)	Sy	VonPost	TC (%)	TN (%)	C:N
Upland	LFH	87.79	0.013				43.44	1.53	28.48
	5-10	76.03	0.069	65.46	0.128	H7	44.26	1.92	23.03
	10-20	26.75	0.405	38.31	0.044	H9	16.51	0.55	30.08
	20-30	5.66	0.743	20.42	0.023	>10	0.99	0.08	11.96
	30-40	6.97	0.818	19.14	0.021	>10	0.83	0.08	10.74
Riparian	LFH	91.74	0.021				46.56	1.42	32.90
	5-10	88.66	0.030	87.53	0.133	H6	47.21	1.92	24.60
	10-20	87.71	0.055	85.22	0.054	H7	46.97	1.92	24.45
	20-30	86.99	0.054	89.44	0.039	H7	42.03	1.86	22.54
	30-40	88.90	0.053	91.40	0.036	H7	48.05	1.97	24.37
Covered	0-10	91.28	0.03	90.22	0.14	H3	46.49	0.95	49.10
	10-20	91.46	0.06	87.18	0.08	H4	47.80	1.57	30.45
	20-30	92.65	0.09	85.75	0.06	H5	46.98	1.53	30.80
	30-40	93.05	0.05	89.25	0.08	H6	45.50	1.35	33.71
Open	0-10	93.41	0.026	90.89	0.127	H1	45.474	0.771	58.956
	10-20	94.55	0.030	92.06	0.109	H2	45.816	0.704	65.043
	20-30	95.64	0.038	91.88	0.069	H3	47.248	0.723	65.384
	30-40	94.24	0.037	92.11	0.078	H3	43.032	0.863	49.877

** Uplands (at each depth)- LOI, BD, Vonpost n=14; Sy, Porosity, C:N, %TN, %TC n=7*

** Riparian (at each depth)- LOI, BD, Vonpost n=4; Sy, Porosity, C:N, %TN, %TC n=2*

** Open (at each depth)- LOI, BD, Vonpost n=12; Sy, Porosity, C:N, %TN, %TC n=6*

** Covered (at each depth)- LOI, BD, Vonpost n=10; Sy, Porosity, C:N, %TN, %TC n=5*

2.2.5 Statistical Analysis

Literature that examines chamber flux measurements uses standard deviation (Strack et al., 2006; Botting and Fredeen, 2006; McNeil and Waddington, 2003) or standard error (Tufekcioglu et al., 2001; Heijmans et al., 2004) to assess the daily uncertainty between and within sites. For this study standard error was used as it better describes the confidence of the reported mean, rather than the natural variability (Ambus, 2001).

When modeling temperature dependence with total respiration (R_{tot}), in some circumstances linear (Heijmans et al., 2004; Fang et al., 1998) or quadratic (Maestre and Cortina, 2003) relationships fit well, however most studies represent temperature and R_{tot} using exponential relationships (Fang and Moncrieff, 2001). This exponential relationship suggests that microbial activity increases at an accelerated, non – linear rate as temperature rises, thus exponential relationships were used to model temperature and R_{tot}.

A linear model can suitably explain variability in R_{tot} with volumetric moisture content (VMC) if small seasonal ranges of VMC occur. That is, if the majority of the measurements occur in conditions that are either 'wet' or 'dry' ends of the spectrum (Simek et al., 2004). However, when the range of 'wet' and 'dry' conditions occurs, a quadratic relationship is more representative (Davidson et al., 1998). Therefore, within this study a quadratic model was used to represent the relationships between R_{tot} and soil moisture as a range of VMC were observed over the study period.

2.3 Results

2.3.1 Canopy Closure

Canopy closure among the land cover units were not that variable except for the open peatland (Table 2.5). The upland was composed of a high aspen canopy where canopy closure increased throughout the growing season as leaf out occurred (31 - 64%). The riparian area had a variable canopy composed of aspen, black spruce, and alder that also increase in canopy closure as leaf out occurred ranging from 48 - 70%. The peatland was composed of two types of canopy, open and covered black spruce canopy. The canopy closure in the covered peatland (~50%) was 5 times larger than that of the open peatland (~11%). The peatland (open and covered) experienced little variation in percent coverage as the growing season increased as the majority of the canopy was composed of evergreen species. These different canopy covers allowed for different light regimes to reach the forest floor affecting the hydrological conditions and microclimates of the different land cover units.

Table 2.5: Canopy coverage as a percent for upland, riparian, and peatland (covered and open) land cover units, Utikuma Region Study Area, Alberta, Canada.

Date	Canopy Percent Coverage			
			Peatland	
	Upland	Riparian	Covered	Open
29-Apr-06	30.5	48.2	44.1	10.2
19-May-06	54.5	63.0	46.3	11.7
15-Jun-06	58.0	66.1	49.0	11.6
22-Jul-06	62.9	70.3	51.1	12.5
15-Aug-06	63.5	69.9	51.4	11.5
22-Sep-06	60.9	69.0	47.5	10.1
5-Oct-06	41.5	57.5	46.5	10.5

2.3.2 Variability of Environmental Controls on CO_2 Exchange

The growing season was divided into four components to compare the hydro – climatic conditions and CO_2 exchange between land cover unit forest floors (Table 2.3). The hydrology (precipitation, soil moisture, water table, and depth to frost) between land cover units and years is shown in Figure 2.2. The water table gradient was from the peatlands (no separation between open and closed sites were made), toward pond and upland. The covered peatland had the highest average Volumetric Moisture Content (VMC) (51%) and was the most variable, whereas the riparian was least variable. The lowest average VMC (34%) was observed in the forest floor of the upland. Frost lasted longer in 2005 for all land cover types. Depth to frost at the measured sites was deepest in the uplands in both years and was the first land cover to lose its frost (ice lens). The frost in the open peatland sites was slightly deeper then those observed in the covered sites, and disappeared slightly earlier. However, within land cover units, spatial variability in frost depth was measured. Thus, depth to frost is an average for the land cover unit.

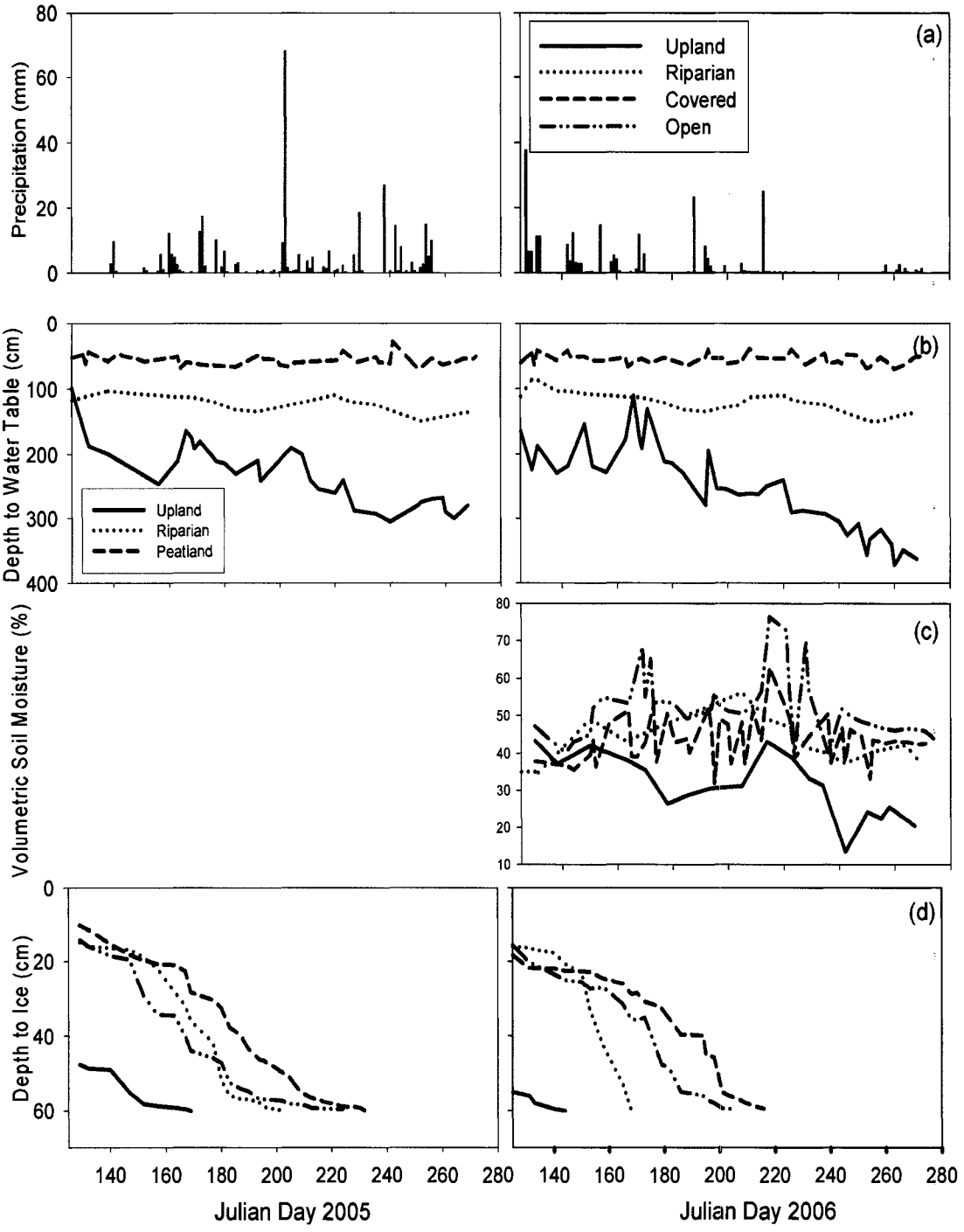

Figure 2.2: Average seasonal (a) precipitation, (b) water table depth, (c) soil moisture (θ) at 10 cm below surface, and (d) depth to frost, for the study site, Utikuma Region Study Area, Alberta, Canada 2005 and 2006. Upland water table depth shown is taken from the toe of the slope.

The microclimates at each site were examined at the same time as the CO_2 fluxes within each land cover unit to assess the relative roles of air temperature (T_a), soil temperature at 5cm (T_5), photosynthetically active radiation (PAR) and relative humidity (RH) on the exchange of CO_2 within each forest floor (Figure 2.3). T_a and T_5 show slight spatial variation between the land cover units but the variability between T_a of forest floors is insignificant. However, a significant difference in T_5 ($p< 0.001$) was observed which was driven by differences between the covered peatland and the other land cover forest floors. Distinct seasonal variations of T_a and T_5 were observed, peaking at the middle of the growing period (Figure 2.3b, 2.3c). T_a and T_5 were slightly higher in 2005 for all forest floors, particularly in the early growing season. However, maximum T_a and T_5 was reached approximately 2 weeks earlier in 2006, T_5 on Julian day 206 and T_a on Julian day 175 (T_5 and T_a on Julian day 219 and 190 in 2006, respectively). Maximum air temperatures and soil temperatures did not vary between years, however, the minima were lower in 2006.

Relative humidity (Figure 2.3d) is lowest in the early green for all forest floors, and increases with the growing season in 2005, however, trends were not statistically significant ($p= 0.86$). PAR (Figure 2.3a) was significantly different ($p< 0.001$) between the different forest floors which were driven by the difference between the open peatland and the other forest floors. Seasonality in PAR was also observed. PAR decreased in the upland and riparian forest floors as the season progresses and was significantly lower then the PAR in the open peatland. However, PAR values in the covered peatland were similar to the upland and riparian but did not show seasonal variability.

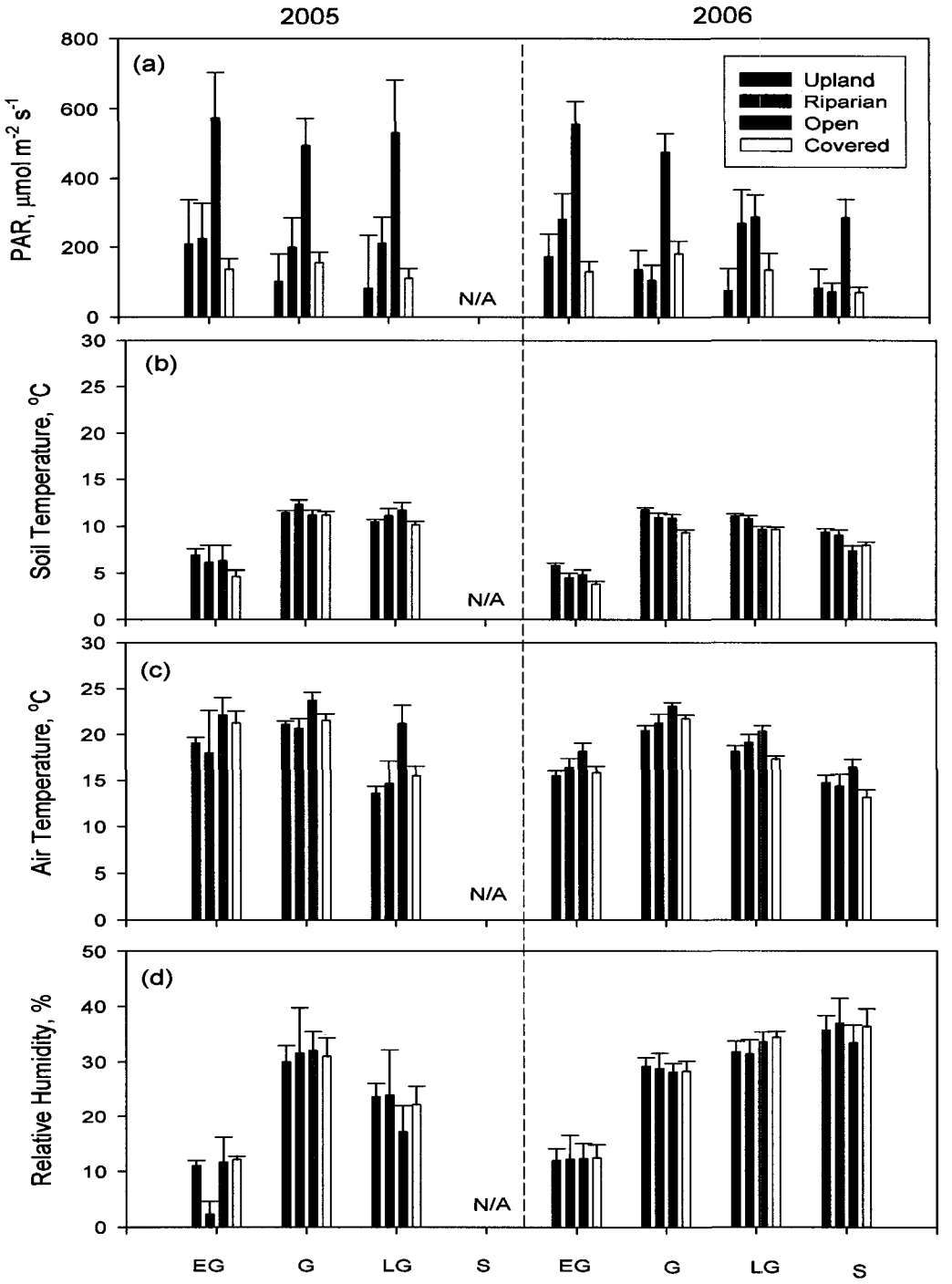

Figure 2.3: Average seasonal (a) PAR, (b) soil temperature at 5 cm (T_5), (c) air temperature at 20 cm above surface (T_a) , and (d) relative humidity (RH) during time of measurement at each upland, riparian and peatland (covered and open) land cover units, Utikuma Region Study Area, Alberta, Canada, 2005 and 2006. Error bars are standard errors, upland n= 394, riparian n= 96, covered n= 311 and open n= 263.

Small variations in seasonal average were observed in PAR between years (2005 and 2006 (in parentheses), upland 126 (122); riparian 180 (175), open 516 (428), and covered 141 (135) μmol m^{-2} s^{-1}).

2.3.3 Seasonal variation in measured CO_2 exchange

Measurements of day time forest floor CO_2 exchange from April through October in both years showed a similar pattern of CO_2 uptake and release, but a difference in magnitude between forest floors (Figure 2.4). Note that the fluxes in this study represent instantaneous midday fluxes, which cannot be extrapolated to daily or seasonal carbon gain or loss (Heijmans et al., 2004). Maximum, minimum and average R_{tot} values for each forest floor are shown in Table 2.6. Point measure maximum R_{tot} in all forest floors were observed in the EG or G. The average R_{tot} in both 2005 and 2006 was the highest in upland and riparian forest floors (-0.19 and -0.21 mg CO_2 m^{-2} sec^{-1} respectively) and was not significantly different between these forest floors ($p= 0.47$). R_{tot} was lowest for all forest floors in the early green, but increased throughout the growing season. The average R_{tot} for both years was higher in the open peatland sites than covered sites (-0.09 and -0.05 mg CO_2 m^{-2} sec^{-1} respectively), but was not significantly different. Soil respiration (R_{soil}) for all forest floors followed the same trend as R_{tot} and represented >75 % of the total respiration.

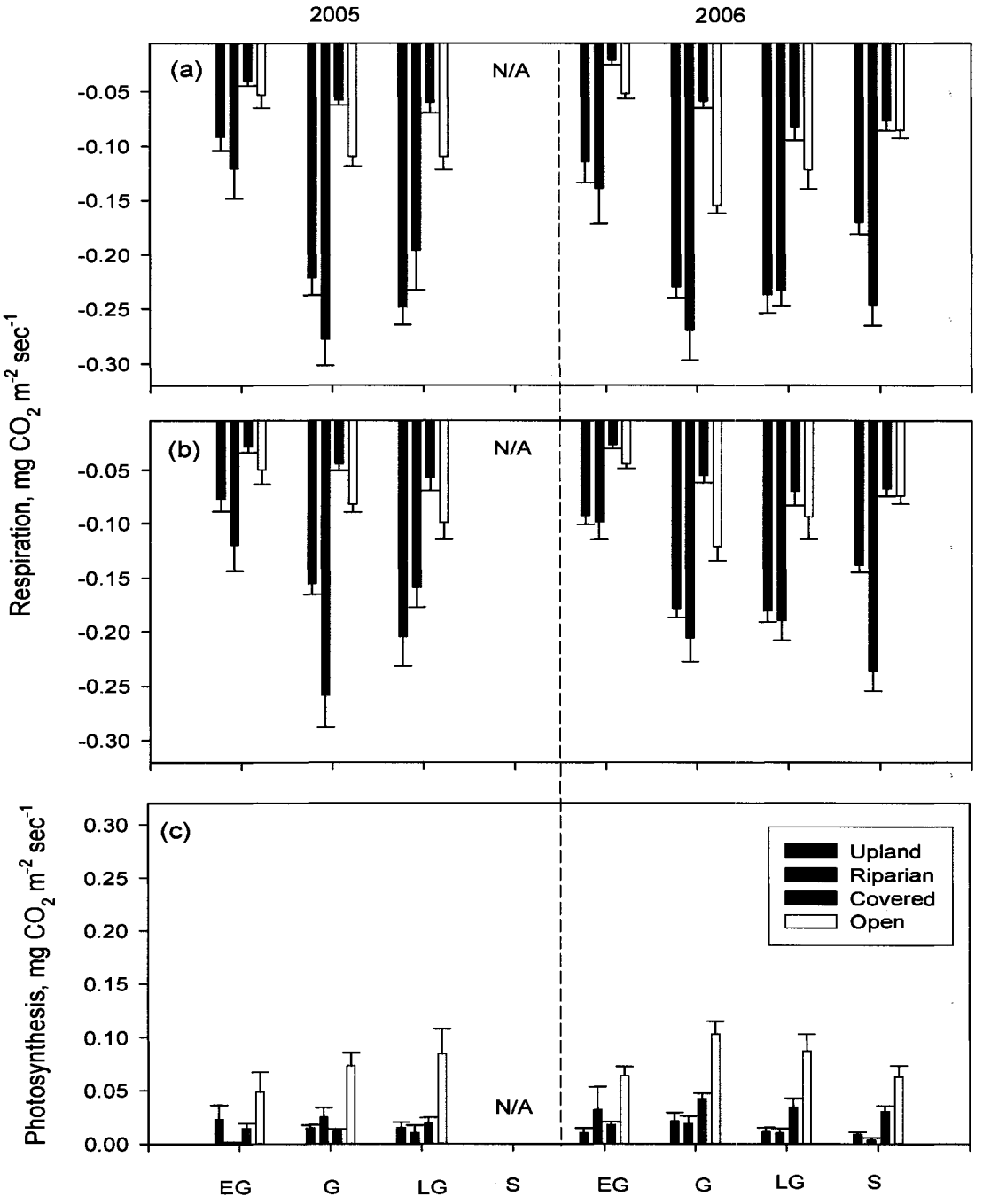

Figure 2.4: Average seasonal chamber measurements of (a) total respiration (R_{tot}), (b) soil respiration (R_{soil}), and (c) gross ecosystem production (GEP) from forest floors of uplands, riparian, and peatland (covered and open) land cover units (n= 86 – 176), 2005 and 2006 during the early green (EG), greening (G), late green (LG) and senescence (S) periods, for Utikuma Region Study Area, Alberta, Canada. Negative values indicate CO_2 release from respiration; positive values represent uptake by the ecosystem, error bars are standard error.

Gross ecosystem production was faintly variable between land covers, however the open peatland was had considerably higher GEP (Figure 2.4c, Table 2.6). The peatlands (open and covered) generally had the highest GEP for forest floors of different land covers, however the open sites were much higher then the covered sites. The GEP averages for 2005 and 2006 (in parentheses) were open peatland 0.071, (0.081); and covered peatland 0.014, (0.032) mg CO_2 m^{-2} sec^{-1}. All land cover units except the uplands showed higher GEP and R_{tot} values in 2006 than 2005. There was no significant difference in GEP observed between the upland and riparian sites ($p= 0.99$). However, significant differences were observed between the open and covered peatland sites ($p< 0.001$) as well as with the other forest floors ($p< 0.001$).

The largest range in GEP and R_{tot} were in the riparian land cover unit while the closed peatlands had the smallest range (Table 2.6). The timing of the maximum CO_2 uptake and maximum R_{tot} are closely coupled to one another. All land cover units exhibited the lowest CO_2 exchange (photosynthesis and respiration) early in the growing season when the soils were still partially frozen and air temperatures low. Greatest fluxes were measured during the mid growing season when vegetation was fully developed and air and soil temperatures were at a maximum.

Table 2.6: Maximum, minimum, and average point measures of total respiration (R_{tot}), soil respiration (R_{soil}), and gross ecosystem production (GEP) (mg CO_2 m^{-2} sec^{-1}) at upland, riparian, and peatland (covered and open) land cover units for 2005 and 2006, Utikuma Region Study Area, Alberta, Canada. ± Standard error.

Land Cover Unit	Year	Total Respiration (Rtot)			Soil Respiration (Rsoil)			Gross Ecosystem Production (GEP)		
		Maximum	*Minimum*	*Average*	*Maximum*	*Minimum*	*Average*	*Maximum*	*Minimum*	*Average*
Upland	2005	0.620	0.009	0.196± 0.001	0.476	0.009	0.164± 0.001	0.186	0.001	0.016± 0.001
	2006	0.682	0.011	0.191± 0.004	0.542	0.001	0.137±0.002	0.256	0.001	0.016± 0.002
Riparian	2005	0.612	0.011	0.162± 0.002	0.485	0.006	0.116± 0.005	0.075	0.001	0.015± 0.001
	2006	0.656	0.017	0.207±0.005	0.462	0.012	0.178± 0.003	0.167	0.001	0.017± 0.003
Covered	2005	0.199	0.003	0.051± 0.004	0.178	0.003	0.043± 0.006	0.153	0.002	0.014± 0.001
	2006	0.286	0.006	0.054± 0.002	0.264	0.005	0.041± 0.004	0.295	0.001	0.032± 0.006
Open	2005	0.309	0.005	0.073± 0.001	0.286	0.004	0.054± 0.001	0.267	0.001	0.071± 0.003
	2006	0.411	0.011	0.091± 0.001	0.375	0.011	0.071± 0.001	0.328	0.002	0.081± 0.001

Upland n=394; Riparian n=96; Peatland (covered) n=311; Peatland (open) n=263 for average R_{tot}, R_{soil} and GEP

The seasonal partitioning of total respiration (R_{tot}) into soil respiration (R_{soil}) and vegetation respiration (R_{veg}) is shown in Figure 2.5. During the early greening (EG) in all forest floors R_{veg} was low. As the growing season progresses R_{veg} contributed more to R_{tot} but always <20%. The contribution of R_{veg} observed within the uplands and riparian was larger than expected in the G and LG (~25 % in uplands ~20% in riparian) owing to the low percent coverage of vegetation within these plots. This may be due to the decomposition of the detritus within the collars, which cannot be partitioned and is being observed as R_{veg}. R_{veg} contributes ~30% of the R_{tot} in the middle of the growing season to the open peatland. However, within the covered peatland, R_{veg} was only ~20% of the R_{tot}.

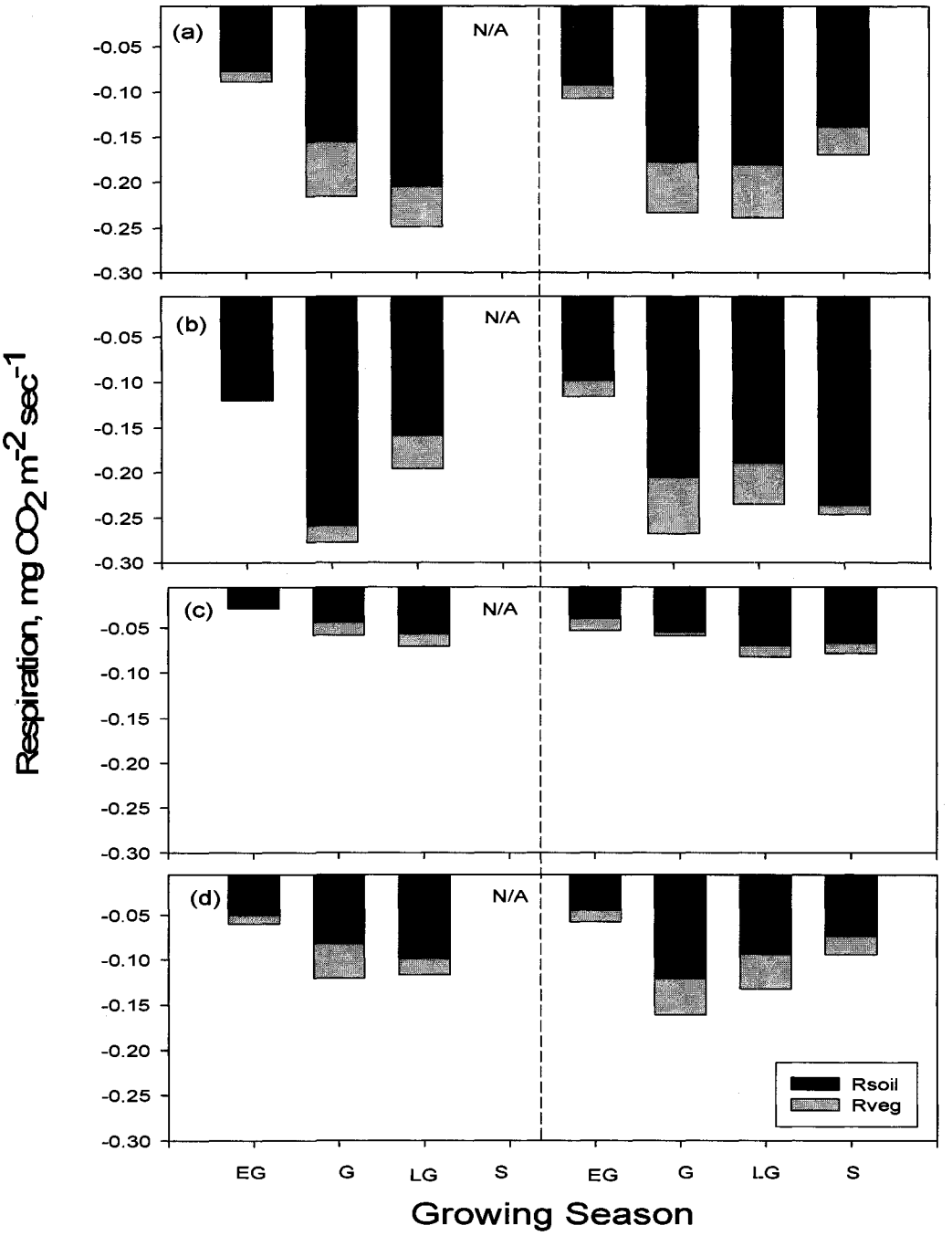

Figure 2.5: Average partitioning of total respiration (R_{tot}) into soil respiration (R_{soil}), and vegetation respiration (R_{veg}) in (a) upland, (b) riparian, (c) covered peatland and (d) open peatland during the growing season (April- October). Utikuma Region Study Area, Alberta, Canada, 2005 and 2006.

2.3.4 Environmental Controls on Photosynthesis and Respiration

The relationship between GEP and PAR for each land cover unit was compared and modeled (Figure 2.6), and varied according to land cover units and canopy coverage. However, there was no relationship observed between the upland forest floor and PAR due to the lack of vegetation located within the collars as potential photosynthetic rates and light use efficiency are found to be related to leaf area index (Ueyama, et al., 2006). The forest floors displays considerable scatter, which can be attributed to the moisture variations between microtopography as well as the timing of frost out. The open peatland responded to higher light levels with higher photosynthesis, and the highest PAR values were observed here. GEP ranged from 0.0001 and 0.328 mg CO_2 m^{-2} sec^{-1}, with maximum PAR values of 2200 μmol m^{-2} s^{-1} in the open peatland. GEP from the covered peatland ranged from 0.002 and 0.145 mg CO_2 m^{-2} sec^{-1}, and had a max PAR value of 1500 μmol m^{-2} s^{-1}. The riparian exhibited only slight increases in photosynthesis with increases of PAR (range 0.0001 and 0.189 mg CO_2 m^{-2} sec^{-1}) and had the lowest maximum PAR values (975 μmol m^{-2} s^{-1}) aside from the upland sites.

Ecosystem respiration is closely tied to changes in the near surface soil temperatures at 5 cm depth and volumetric moisture content (VMC) in all forest floors (Figure 2.7). All sites showed bell shape curves, lowest total respiration at low and high moisture, and peaks at 30 – 50%. Correlations between VMC and R_{tot} were high in all forest floors at all land cover units (R^2= 0.34 – 0.70). R_{tot} was highest in both upland and riparian land cover units, however the peak in R_{tot} was reached at different VMC. This may correspond to percent saturation that occurs for different VMC from differences in soils. The riparian area had a higher maximum R_{tot} than the

upland but peaked at higher VMC. Fluxes varied according to canopy coverage in the peatland. The open peatlands had slightly higher R_{tot} and peaked at a lower VMC then that of the covered peatlands.

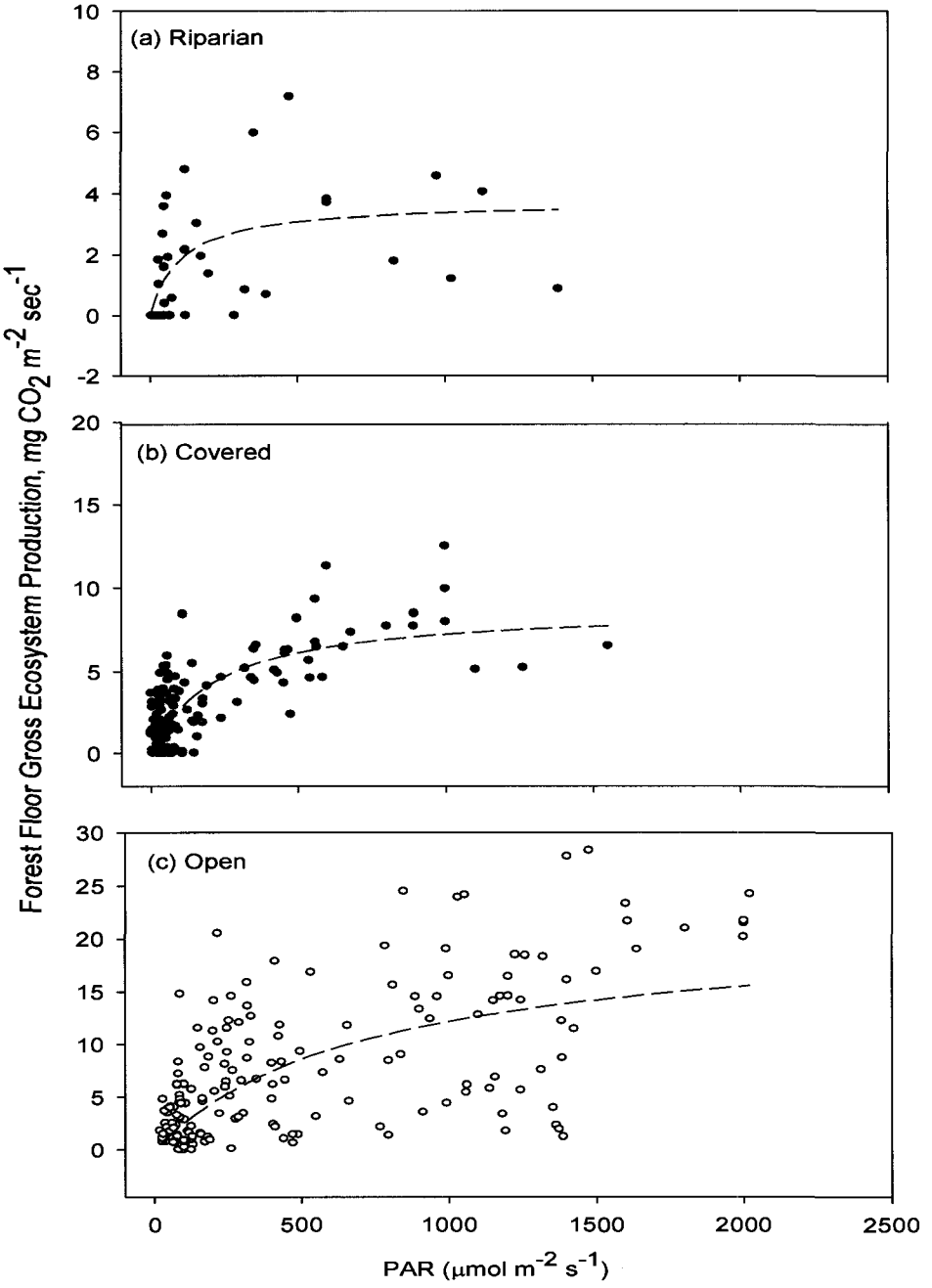

Figure 2.6: Relationship between photosynthetically active radiation (PAR) and gross ecosystem production of CO_2 (GEP) for combined data of 2005 and 2006, showing variation in the rates of GEP between land cover units ((a) riparian; (b) peatland covered; and (c) peatland open)), Utikuma Region Study Area, Alberta, Canada. Curve fits for PAR versus GEP are calculated with rectangular hyperbola model from Eq. (2.3). Note change in scale between land cover units. Upland forest floor site not shown as no relationship was observed for PAR versus GEP.

Soil temperatures at 5 cm for all land cover units (Figure 2.7b) were also strongly associated with R_{tot} but the slopes of the regressions vary significantly between sites. The uplands responded with higher R_{tot} for lower soil temperatures than those observed within the peatlands. Total carbon (organic and inorganic) to total nitrogen (no separation between nitrogen species, e.g. nitrate and ammonia) ratios in the top 10 cm of soil during this study show that lower C:N ratios are associated with the uplands and riparian forest floors where CO_2 exchange to the atmosphere is highest. C:N ratios are variable between open and covered peatland sites. However, the range of variability between them are similar.

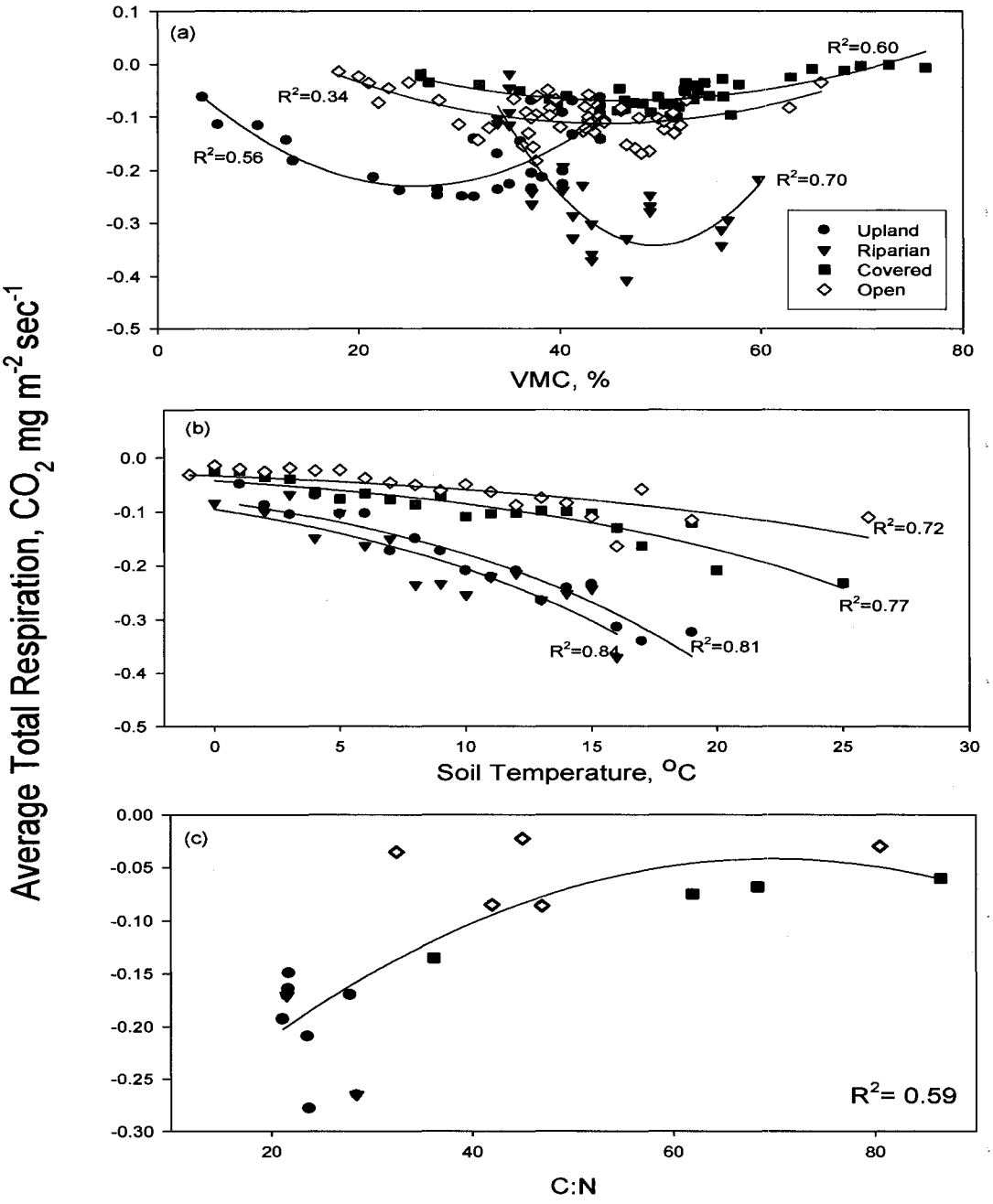

Figure 2.7: Relationships between total respiration (R_{tot}) and (a) soil moisture content (θ) at 10 cm depth, (b) temperature at depth of 5 cm, (c) C:N ratio in the top 10 cm of the uplands, riparian, and peatlands (open and covered) land cover units. 2005 and 2006 data are combined. Utikuma Region Study Area, Alberta, Canada. Negative values indicate CO_2 release from respiration.

The relationship between photosynthesis and respiration shows a positive correlation at all sites during all seasons in 2005 and 2006 (Figure 2.8), (R^2 ranging from 0.21 - 0.42). The slope of the regression varies between land cover units: upland -0.11; riparian -0.13; covered -0.32; and open -0.74. The slope of the regression line is -0.28 for the combined data set in 2005 and 2006, indicating that the ratio of combined autotrophic and heterotrophic respiration to maximum CO_2 uptake is approximately 1/3 in both years. However, it is important to note that the peatland (open and covered) forest floors have the highest photosynthesis, and most respiration is occurring within the upland and riparian.

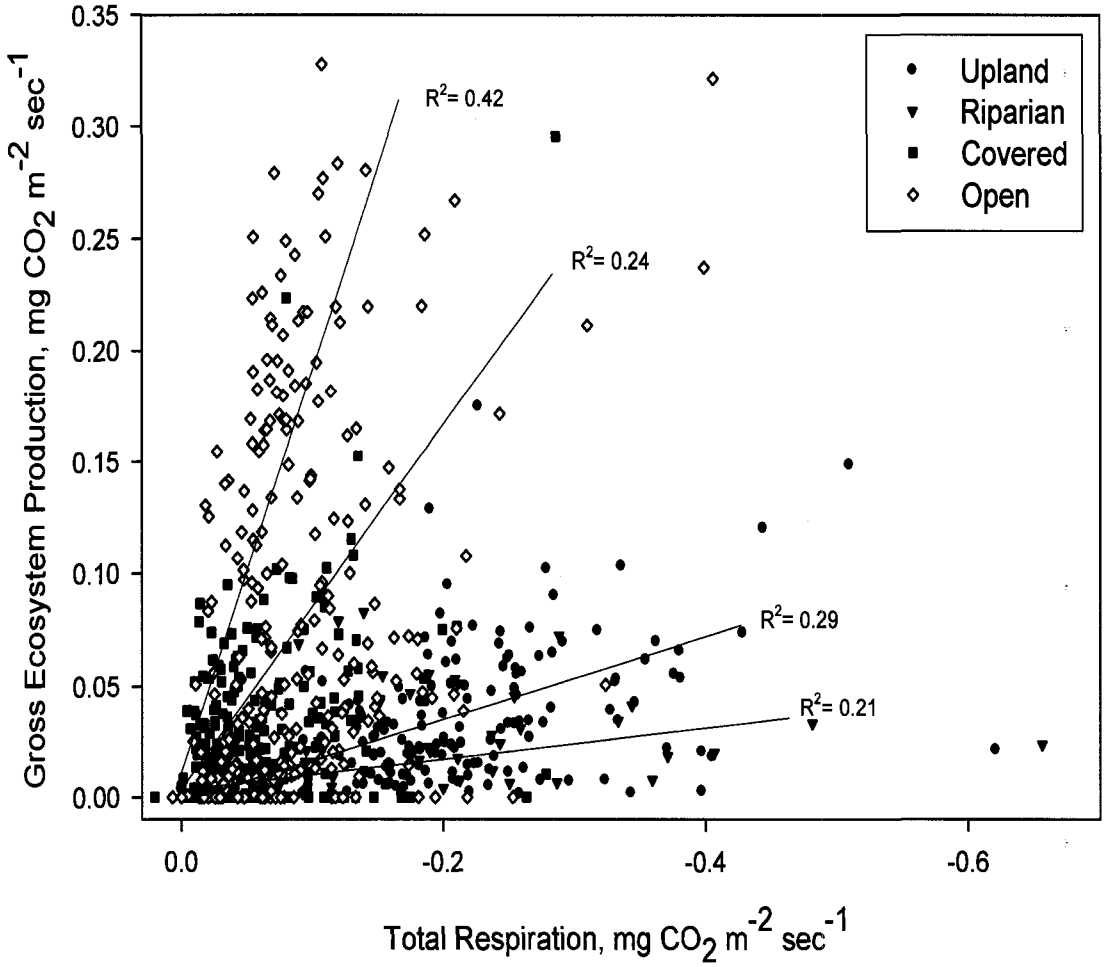

Figure 2.8: Relationship between total respiration (R_{tot}) and gross ecosystem production (GEP) for each upland (n=175), riparian (n= 43), peatland (covered (n= 311) and open (n= 263) land cover units, from April through October, 2005 and 2006. Utikuma Region Study Area, Alberta, Canada. Positive values represent uptake by the ecosystem

2.4 Discussion

2.4.1 Spatial and Temporal Variability of CO_2 Exchange

The rate of total respiration (R_{tot}), soil respiration (R_{soil}) and gross ecosystem production (GEP) varied within, and between, land cover forest floors both spatially and temporally within the season. Spatial variability in R_{tot} and GEP across a peatland in terms of microtopography (e.g. Moore, 1989; Strack and Waddington, 2007), variation in vegetation (e.g. Heijmans et al., 2004; Botting and Fredeen 2006), and canopy coverage (e.g. Connell et al., 2003; Swanson and Flanagan, 2000) has been reported previously. The variability in R_{tot} and GEP within upland and riparian areas have also been explained to be a function of the above ground biomass (Gulledge and Schimel, 2000), variability in soil organic matter (Longdoz et al., 2000) and soil temperatures (Swanson and Flanagan, 2001), which can be attributed to the light regime under the canopy, and the presence of a few key species (Tremblay and Larocque, 2001). Thus, the variability of CO_2 exchange observed within the land cover units is not uncommon for northern forested wetland complexes.

The timing of maximum CO_2 uptake and the timing of highest R_{tot} are closely coupled to one another (Figure 2.4). In the early growing season when the vegetation first emerges (mid May) the light levels are high, which allows the system to quickly initiate and reach maximum R_{tot} and GEP values in a shorter time (Bubier et al., 1998) than it takes for the ecosystem to senesce in the fall. In 2006, during the late greening period there is a decrease in GEP but R_{tot} is still high, this can be attributed to high temperatures and very low precipitation during that time which would cause vegetation productivity to decrease due to water limitations. However, microbial

activity likely continued as the temperature and moisture deficits that occurred were not strong enough to cause a break down of the microbes.

Ranges of maximum R_{tot} and R_{soil} followed the general progression of riparian > upland > open peatland > covered peatland (Figure 2.4). This corresponds to the water table being close to the surface within the peatland allowing anoxic conditions to limit microbial and root respiration slowing the rates of decomposition. Vegetation cover has been shown to alter soil temperature and moisture conditions (Raich and Tufekcioglu, 2000), and soil temperatures significantly influence soil respiration rates (Goulden et al., 1998). As a result, observed differences in soil respiration among plant communities can frequently be attributed directly to plant - mediated effects on soil microclimate. Within the peatland, R_{soil} was higher in the open peatland, even though C:N ratios were lower in the covered peatland which would favour decomposition (Tufekcioglu et al., 2001). However, high VMC within the covered peatland likely limited decomposition due to anoxic conditions and lower soil temperatures. Higher R_{tot} and R_{soil} values within the riparian land unit can be attributed to higher litter quality (high organics, minerals and nutrients) of the forest floor compared to those within the upland (Table 2.3) which allow for efficient decomposition (Rejmankova and Houdkova, 2006; Longdoz et al., 2000). These areas also had higher VMC than the uplands. Thus, water was not limiting in the soil processes.

In this study the average daily R_{tot} fluxes (Table 2.6) in the peatland (open and covered) are similar in magnitude to other studies (Strack et al., 2006; Swanson and Flanagan, 2001) even though fluxes were exclusively measured during midday, with

no dormant season measurements. The R_{tot} in the upland and riparian land cover units were as much as four times higher than those within the peatland (open and covered). R_{tot} values of the riparian forest floors were similar to those found by Tufekcioglu et al. (2001) in a mid - latitude multi - species riparian buffer, and the uplands were similar to these findings in a cropped field. This may be due to the high C:N ratios found in the upland, which is an important determinant on soil respiration and soil moisture (Tufekcioglu et al., 2001).

Gross ecosystem production in the open peatland forest floor was about 4 times higher then that in the forest floor of the upland, riparian and covered peatland forest floors (Table 2.6). This large uptake of CO_2 from the forest floor can be attributed to the large above ground biomass and the light response of the vegetation. The relationship between GEP and PAR (Figure 2.6) varied among the four land cover forest floors with maximum photosynthetic capacity following the gradient from open peatland > covered peatland > riparian with no relationship for the uplands due to the lower amounts of vegetation located within the collars. The open peatland forest floor had the largest maximum GEP fluxes, which were similar to that found by Swanson and Flanagan (2001). This can be associated to the shading of the above canopy and the light levels that reached the understory. Also, it was observed that the open and covered peatland forest floors in this study had highly variable VMC, which suggest that they may not have been photosynthesizing optimally during drier parts of the growing season due to low water content, lowering metabolic activity.

Many studies have shown that peatlands store large amounts of carbon (e.g. Bubier et al., 2003; Griffis et al., 2000; Waddington and Roulet, 1996). However, it

was observed that average midday chamber measurements in this study were dominated by R_{tot}, indicating net CO_2 flux to the atmosphere. Although, studies that examine inter - annual CO_2 exchange variability have shown that there can be large differences in carbon exchange from year to year (e.g. Lafleur et al., 1997; Shurpali et al., 1995). Trends throughout the growing season in the peatland were similar to those determined by Swanson and Flanagan (2001) within a mature black spruce forest in central Saskatchewan and by Botting and Freedeen (2006) in a sub - boreal spruce forest. Both studies report a net loss of CO_2 to the atmosphere during the growing season (April – October). Within the uplands and riparian land units, there were large CO_2 fluxes to the atmosphere during all growing periods. This can be attributed to the high quality soils and lower water tables (Table 2.4 and Figure 2.2b). However, the above canopy in these land cover units generally has high photosynthetic light - use efficiency, making them highly productive, thus compensating for loss of CO_2 from the forest floor. Aspen productivity can be highly variable between years depending on temperature and precipitation (Arian et al., 2002). During senescence, high R_{tot} could be associated with the decomposition of the understory vegetation and the above canopy leaves. Deep soil warming also may be playing a role in the consistent R_{tot} into senescence.

2.4.2 Interactions of Environmental Variables

Fluxes were collected midday within a 0.4 km^2 area and there was spatial variability in air and soil temperature, VMC, soil quality and PAR between sites and land cover units. Canopy coverage controlled the light that penetrated to the forest floor which influenced photosynthesis. However, R_{tot} dominated the CO_2 flux. Soil

temperature and moisture showed the largest influence on R_{tot} but differed spatially between land cover units (Figure 2.7). As a result, the spatial variability in R_{tot} can be attributed to both hydro - climatological and biological (C:N, vegetation) variables, and to explain seasonal patterns of CO_2 exchange.

T_a (air temperature 50 cm above forest floor) and T_5 (soil temperature at 5cm below surface) showed slight spatial variation between the land cover units, and show distinct seasonal variation peaking at the middle of the growing period (Figure 2.3). It is during the middle of the growing season when maximum R_{tot} and GEP values were also observed (Figure 2.4). This may be associated with the deepening of the active layer increasing decomposition and CO_2 exchange. The correlation between respiration and 5 cm soil temperature is strong for all land cover units when water is not limiting the soil processes but the slopes of the regressions vary between sites (Figure 2.7b). This may be due to the quality of the soil at the different land cover units (Figure 2.7c). Higher quality soils (lower C:N) have more nutrient availability for soil organisms, roots, and mycorrhizae (Raich and Schlesinger, 1992). Thus, small increases in soil temperature provide an optimal situation for decomposition (Fang and Moncrieff, 2001), whereas a soil with less nutrient availability will not profit the same with a similar temperature input. In this study the uplands and riparian areas react with higher total respiration to similar temperatures, than that observed in the peatland.

Temperature coefficients (Q_{10}) for the temperature interval 10°C to 20°C between the land cover units ranged from 1.24 - 1.68. These low values are similar to those generally associated with upland mineral soils (Bubier et al., 1998). However,

this may be attributed to maximal rates of decomposition occurring at higher moisture values then those observed during this study (Ise & Moorecroft, 2006). The Q_{10} value is an estimate because it only considers the direct affect of temperature and ignores other factors that may influence microbial and root respiration, but is often used to explain the temperature dependence of R_{tot} (Fang et al., 1998). The larger the Q_{10} value the more sensitive the reaction (SOM decomposition) is to temperature increases. Ise and Moorecroft (2006) suggest that the temperature sensitivity of decomposition at global scales is Q_{10}= 1.37. This is significantly less than those values suggested in respiration studies (mean Q_{10}= 2.5) (Reich & Schlesinger, 1992), which directly apply temperature sensitivity from small - scale studies, and that maximal rates of decomposition occurs at higher moisture values then is assumed by these studies (Ise and Moorecroft, 2006). However, comparing the Q_{10} values obtained from different studies is difficult because some are calculated from observed data and others from fitted relationships, in which different models were used to obtain Q_{10} (Fang et al., 1998). In addition, Q_{10} can vary spatially and seasonally (Davidson et al., 2000) and is related to VMC distribution. For example higher Q_{10} values have been reported for wetter soils at the same temperatures and decreases with VMC, suggesting that soil CO_2 flux is more sensitive to low temperature soils under high moisture conditions (Lloyd and Taylor, 1994), and has also been observed to be more sensitive under acidic and organic soils (Chapman and Thurlow, 1996). With all the abovementioned uncertainties, values in this study were still comparable to the literature.

Water table location was also an important control on R_{tot} on a seasonal basis as well as a daily basis between the land cover units. The spatial variation in water table position can be as significant as interannual differences in affecting carbon accumulation rates (Bubier et al., 1999). Within the peatland (open and covered) microtopographic features respond differently to changes in temperature and water table. For example, Waddington and Roulet (1996) found that drier hummocks generally accumulate more carbon than wetter hollows. The four land cover forest floors respond to changes in VMC differently (Figure 2.6a). The riparian, open and covered peatland forest floors optimally respire at the same VMC. However, the riparian forest floor responds with much higher R_{tot} than the covered and open sites. This is likely attributed to the quality of the soils. The riparian land cover unit had a much lower C:N ratio, thus microbial decomposition could occur at a higher rate than that observed in the peatland sites. If the VMC were to increase in the upland and riparian land cover units, it is likely that higher R_{tot} rates would be observed as optimal conditions for decomposition would be expected.

Heterotrophic respiration can be limited by substrate quality and quantity, in addition to temperature and moisture. This can have a large effect on total ecosystem respiration (Law et al., 2002). Figure 2.7c shows that the quality of the soil plays an important role in total respiration. The C:N ratio (Table 2.3) of the open canopy peatland was nearly double that of the closed canopy peatland sites. Thus the substrate within the covered peatland is of better quality. The low substrate quality in the open peatland is likely due to high nutrient resorption resulting in poor litter quality, and consequently, lower decomposition. The covered peatland C:N ratios

were slightly higher than those observed within the riparian and upland sites, which is likely due to the boundary of oxic and anoxic conditions occurring very close to the surface. Thus, nitrification and denitrification are coupled, which allows for the rapid formation of N gas rather than assimilation into biomass (Baldwin & Mitchell, 2000). In addition, larger amounts of recalcitrant litter produced annually by the above aspen canopy can decrease the C:N ratios (Chastain et al., 2006).

Seasonal variability in PAR, soil and air temperatures and soil moisture can control the CO_2 exchange in the land cover units. The relative controls of temperature and light on photosynthesis vary seasonally with changes in leaf area and biochemistry (Law et al., 2002). Generally PAR values were high in the riparian and upland in the early growing season as the above canopy leaf out had not yet occurred (Figure 2.3a). This allowed for more radiation to reach the forest floor, increasing the soil and air temperatures, which favoured R_{tot}. Similar PAR was observed throughout the growing season within the covered peatland as the above canopy was dominated by evergreen species. Therefore canopy cover did not fluctuate a great deal during the growing season. The compact structure of the foliage and the narrow canopy of black spruce trees resulted in gaps between individual trees that allowed the passage of sunlight to the ground throughout the growing season in the open peatland. However, throughout the growing season the mosses insulated the soil, thereby reducing the soil temperatures (Van Cleve et al., 1983). An increase in PAR was also observed in the upland during senescence as the canopy began to lose its leaves. Variation in vegetation distribution on the forest floor is generally due to the PAR that reaches it (Heijmans et al., 2004). Seasonal variability in PAR allows for species to use the light

most efficiently during different times during the growing season and soil temperatures to vary seasonally with PAR.

The correlation between photosynthesis and respiration (Figure 2.8) in the combined data set suggests that the two processes are coupled in the open and covered peatland even though different factors are controlling the uptake and release of CO_2, however no correlation was observed for the riparian and upland land cover units. However, under closer observation it can be seen that within the uplands and riparian areas the slope of the regression was much lower. This suggests that the two processes are controlled by different factors, or that there is an offset in the timing of carbon uptake and release during the season, implying that deep soil warming may be playing an important role (Bubier et al., 1998). The ratio of combined (auto - and heterotrophic) respiration to maximum CO_2 uptake is 1/3. This may be attributed to the relationship of respiration and photosynthesis to biological factors such as %TC (Maeste et al., 2003), N content (Tufekcioglu et al., 2001), and C:N ratios (Tufekcioglu et al., 2001). The strong correlation in the peatland suggests that there may be a strong physical link between photosynthesis, plant metabolism, and respiration (Bubier et al., 1998). The close relationship between surface temperatures and respiration (Figure 2.7b) suggests that root associated processes may be responsible for a substantial portion of the total respiration. Further, PAR is the primary control on photosynthesis, but increased light levels are correlated with increased soil temperatures, which is a dominant control on respiration (Bubier et al., 1998).

2.4.3 Implications for Climate or Land use Change

Within a wetland - forest ecosystem, both photosynthesis and respiration occur in a range of species and functional groups as well as along variable topographic gradients. Subsequently the environmental controls on carbon exchange processes are quite different in these ecosystems. Northern peatlands represent a globally significant stock of soil carbon (Gorham, 1991). Although they have been a net sink of carbon for thousands of years, the balance between CO_2 uptake and release may be so close that a small change in water table, temperature, or timing of thaw and senescence could favour decomposition over plant production (Bubier et al., 1998). Anticipated climate change scenarios in these regions may be further complicated by altered land use practices. Impacts on these areas such as timber removal, road establishment, and corridor creation enables industry to access prime regions for extraction of timber and oil. However, this may cause significant changes to the WBP hydrological and biogeochemical cycling. For example, increased soil moisture resulting from forest harvesting could decrease decomposition in the peatlands, or provide more optimal conditions for decomposition in the dry uplands.

Since different land cover units respond to environmental variables differently it is essential that they be examined separately when predicting R_{tot} and GEP under such scenarios. Warming at high latitudes would expose larger amounts of organic carbon to microbial activity by lowering the depth to frozen soil, lowering the water table (assuming sufficient drainage) and extending the duration of thawed conditions (Goulden et al., 1998). Silvola et al. (1996) estimated that an increase in 2 °C - 4 °C in the boreal region would cause a 30 - 60% increase in CO_2 emissions from peatlands. This calculation was based on average Q_{10} values that were higher than those in this

study, suggesting that a comparable increase in temperature would result in lower CO_2 fluxes. However, because temperature only correlates well on daily and weekly time scales (Law et al., 2002) temperature based predictions on CO_2 exchange is complicated.

It is suggested that warming may also stimulate plant production in the boreal forest although it is expected that this effect would be modest (Goulden et al., 1998). Furthermore, the soil currently contains more carbon than is stored in the vegetation of a mature temperate deciduous or boreal forest (Gorham, 1991). Thus, indirect stimulation in production would have to be large to offset the expected loss of soil carbon (Goulden et al., 1998). That is, over long periods of time (years to decades), heterotrophic decomposition might be more influenced by substrate quality and quantity (Giardina and Ryan, 2000). Further, boreal forests in northern latitudes typically have soil that is wetter for longer periods (Grace and Rayment, 2000). Thus, respiration rates can be higher than those of terrestrial ecosystems at lower latitudes that experience periods of soil water deficits (Law et al., 2002).

Changes in land use due to industrial pressures within this area may also cause enhanced aerobic soil respiration under lower water tables and higher peat temperatures (Devito et al., 2005; Petrone et al., 2006) causing a release in stored carbon to the atmosphere, which could act as a positive feedback to climate change. When soils are disturbed, their content of organic matter declines. The decline is observed because the conditions for decomposition (soil aeration and moisture content) are often improved when the soils are disturbed, leading to greater rates of soil respiration (Schlesinger and Andrews, 2000). Clearing of trees creates conditions

that affect the soil biota, including restructing, vegetation, modification in quality and quantity of litter, alteration of root exudates, leaching of plant nutrients, changes in the microclimate (Marshall, 2000; Raich & Schlesinger, 1992), and compaction of soils all of which may restrict water, nutrient and gas movement (Childs et al., 1989). Thus, harvesting in the uplands and riparian will increase soil temperatures, which if the soil moisture remains adequate, increased microbial activity will occur leading to enhanced organic decomposition and increases in inorganic nitrogen production (Hazett et al., 2007). However, production of the understory vegetation may be stimulated by the availability of resources (e.g. PAR, water, nutrients) and the peatland may become more productive if nutrients are leached from the upland, offsetting increased R_{tot}. Understanding of the spatial and temporal variability in CO_2 exchange between land cover units is essential when hypothesizing anticipated changes with climate and land use change.

2.5 Conclusion

CO_2 exchange between the forest floors of differing canopy closures is variable both spatially and temporally. Within an aspen upland and a transitional riparian the forest floor is dominated by detritus and small vascular vegetation, and is responsible for only part of the ecosystem CO_2 exchange. Such that, the aspen in the upland and the variable canopy closure in the riparian as well as the shrub layer are largely contributing to the CO_2 exchange. In the covered and open peatland the forest floor is playing a more dominant role and community scale fluxes encompass nearly the entire ecosystem. Thus, the highest R_{tot} was found within the riparian and uplands, which was dominated by R_{soil}. The highest GEP was found within the peatland, with

lower R_{tot}, and higher R_{veg} contribution to it. Although canopy cover controlled PAR at the forest floor, small spatial variability was observed in the microclimates between forest floors (T_a p= 0.034; T_5 P<0.001; RH p= 0.859). However, seasonal variability and spatial variability was observed in the hydrology (water table location, soil moisture, depth to frost) of the forest floors. Each of the forest floors responded to VMC and T_5 with differing magnitudes of R_{tot} and had differing responses to light. Examining the forest floors of land covers with different canopy coverage is important when predicting changes in the cycling of CO_2 within these ecosystems after changes to land covers from industry or climate change. With the deforestation in the uplands the understory may start to act like the peatland due to enhanced resources (increased LAI, temperature, etc), or will it may become a greater source of CO_2 to the atmosphere as the water table lowers further increasing the oxic zone, and soil temperatures warm. Changes in the upland hill slope may also directly affect the peatland CO_2 exchange by altering the hydrologic connections, for example increased runoff.

Due to the variability between the forest floors of different land cover with different canopy coverage they should be assessed separately in biogeochemical models as they will likely not respond to external changes on the same spatiotemporal scales.

Chapter 3

Microtopographical Controls on Carbon Dioxide Exchange in a Western Boreal Plain Pond - Peatland Complex

3.0 Introduction

There have been many studies on CO_2 exchange from northern peatlands over the past decade because of their importance in greenhouse scenarios (c.f. Gorham, 1991; Waddington et al., 1998; Moren and Lindroth, 2000). Many studies try to quantify CO_2 emissions and establish links to physical processes (Amiro, 2001; Black et al., 1996; Petrone et al., 2003). However, the quantification of, and interactions between the environmental controls on the dynamics of net ecosystem CO_2 exchange are currently not well understood (Joabsson et al., 1999; Hobbie et al., 2000).

It has been observed that measurements of net ecosystem exchange show large spatial variability (e.g. Heijmans et al., 2004; Bubier et al., 1998; Waddington, 1996) within, and among, northern peatlands. These ecosystem carbon budgets are controlled by the balance between carbon uptake during photosynthesis and carbon loss during respiration (Bubier et al., 2003; Potter et al., 2001). However, within a peatland, both respiration and photosynthesis are occurring among a range of species and functional groups, so the environmental controls on the carbon exchange processes are quite different in the distinct ecosystem components (Swanson and Flanagan, 2001; Bubier et al., 2003). Much of this variance in CO_2 exchange is related to differences in the factors controlling the fluxes, such as plant community, hydrological conditions, nutrient availability, temperature and peat substrate

(Waddington, 1996). Much of the previous research has taken a vegetation community or microform (microtopograhical) approach to explain, and predict, the spatial variables in CO_2 exchange and these controlling factors within a peatland (Waddington and Roulet, 1996; Carrill and Clark, 1998; Biasi et al., 2005; Yavitt et al., 2000; Potter et al., 2001; Bubier et al., 2003).

Much of this research, however, has focused the discussion of these interrelationships largely on hydrologic and microtopographical controls. That is, the live biomass of a system greatly influences the net function of the ecosystem by affecting the hydrology, thermal regimes and nutrient availability (Oechel and Van Cleve, 1986; Bisbee et al., 2001; Heijmans et al., 2004). Further, dominant peatland communities such as *Sphagnum* mosses will insulate the soil, intercept atmospheric nutrients, and decompose very slowly, thereby reducing the soil temperatures and rates of nutrient supply (Oechel and Van Cleve, 1986). However, this approach to vegetation controls on ecosystem CO_2 exchange requires the assumption that vegetation is the primary control on local - scale hydrologic conditions compared to other factors such as surficial geology, or microtopography, and climate.

Another approach is to assume that the microtopography drives hydrological gradients, which in turn controls vegetation patterns and therefore CO_2 exchange (Bubier et al., 1998; Waddington and Roulet, 1996). Therefore, in any system, hydrological gradients will exist along with variations in micotopography. For example, microtopographic highs (e.g. hummocks, lawns, moss cushions) will generally be drier than adjacent microtopographic lows (e.g. hollows, depressions) (Waddington and Roulet, 1996; Petrone et al., 2005). These hydrological differences

will drive vegetation distributions, which will control patterns of CO_2 exchange. Thus, in sub – humid regions, such as Canada's Western Boreal Plain (WBP), where peatlands and surface water systems persist in much drier conditions (Devito et al., 2005), the correlation between CO_2 exchange and patterns in vegetation and microtopography may differ from studies conducted elsewhere.

Peatland – pond complexes dominated by Black Spruce (*Picea mariana*) overstories with *Sphagnum* (*Sphagnum* spp.) and feather moss (e.g. *Pleurozium schreberi and Hylocomium splendens*) ground covers are widespread not only within North America (Bisbee et al., 2001), but are also common place within the WBP. Here they represent important water resources, wildlife habitat and sites of potentially significant greenhouse gas exchange (Swanson and Flanagan, 2001). The narrow nature and low density of trees allows for a substantial portion of solar energy to reach the moss - covered floor (Heijmans et al., 2004), contributing significantly to ecosystem CO_2 exchange due to the large above ground biomass (Waddington et al., 1998; Goulden et al., 1997). However, since these complexes exist in a sub - humid climate soil moisture storage and groundwater - surface water connections are controlled largely by surficial geology (Devito et al., 2005). Thus, these mosses can have potentially strong effects on ecosystem CO_2 exchange (Petrone et al., 2004; Waddington and Roulet, 1996) but their interactions with hydrologic conditions may differ than those described above. That is, the complex hydrology and sub - humid climate of the WBP (Devito et al., 2005) may produce a relationship between microtopography and vegetation patterns that is highly variable and dissimilar to other systems. Further, the required moisture thresholds (differences) between

microtopographical highs and lows may not be the same as that which is needed to drive vegetation differences relative to CO_2 differences. For example, a difference in CO_2 exchange may be observed between lawns and depression, but not a difference in relative ground cover vegetation distributions, which in the WBP is largely comprised of bryophytes.

Currently, the inclusion of the role of the ground layer comprised of such bryophytes is limited in estimates of boreal forest net ecosystem exchange (NEE) (Gower et al., 2001), and as such these communities are poorly represented in models used to predict the effects of climate and land - use change on ecosystems (Frokling et al., 1996). A better understanding of the factors influencing bryophyte distribution, such as interactions with canopy cover, microtopography, and NEE is needed to quantify the boreal forest carbon cycle because of the large contribution of bryophytes to this flux and their influence on the microenvironment of systems dominated by black spruce (Bisbee et al., 2001).

The objectives of this study are to measure the rates of understory net ecosystem exchange (NEE), gross ecosystem production (GEP) and total respiration (R_{tot}) through the growing season to determine (1) if there are differences in CO_2 exchange between different microtopographical units and if these units can be used as a proxy for photosynthesis and respiration, and (2) whether vegetation patterns are controlled more by microclimate, hydrology or canopy cover.

3.1 Site Description

The forested peatland - pond – upland complex in this study is situated on common disintegrated moraine (Redding et al., 2005), located in the Utikuma Region Study Area (URSA) near Utikuma Lake, northern Alberta (56°20' N, 115°30' W) within the Western Boreal Plains (WBP) ecozone (Figure 2.1) (Devito et al., 2005). The climate is characterized by warm summers and long, cold winters. The average 30 year climate normals in annual temperature, precipitation, and potential evapotranspiration for the region are 1.7°C, 485 mm, and 515 mm respectively (Environment Canada, 2007). The average temperature and precipitation for 2005 and 2006 (in parentheses) were 2.8°C (2.9°C) and 374 mm (396.5 mm), respectively, making them slightly warmer and drier than the 30 year normal.

In most years, PET exceeds precipitation in this region, making it a sub - humid climate. Up to 84 % of the area in this ecozone is covered in conifer and deciduous forests (Environment Canada, 2007). Typical vegetation of drained uplands includes trembling aspen (*Populus tremuloides.*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana)* in sandy areas, while balsam poplar (*Populus balsamifera*) and black spruce (*P. mariana*) dominate in the lowland areas (Environment Canada, 2007).

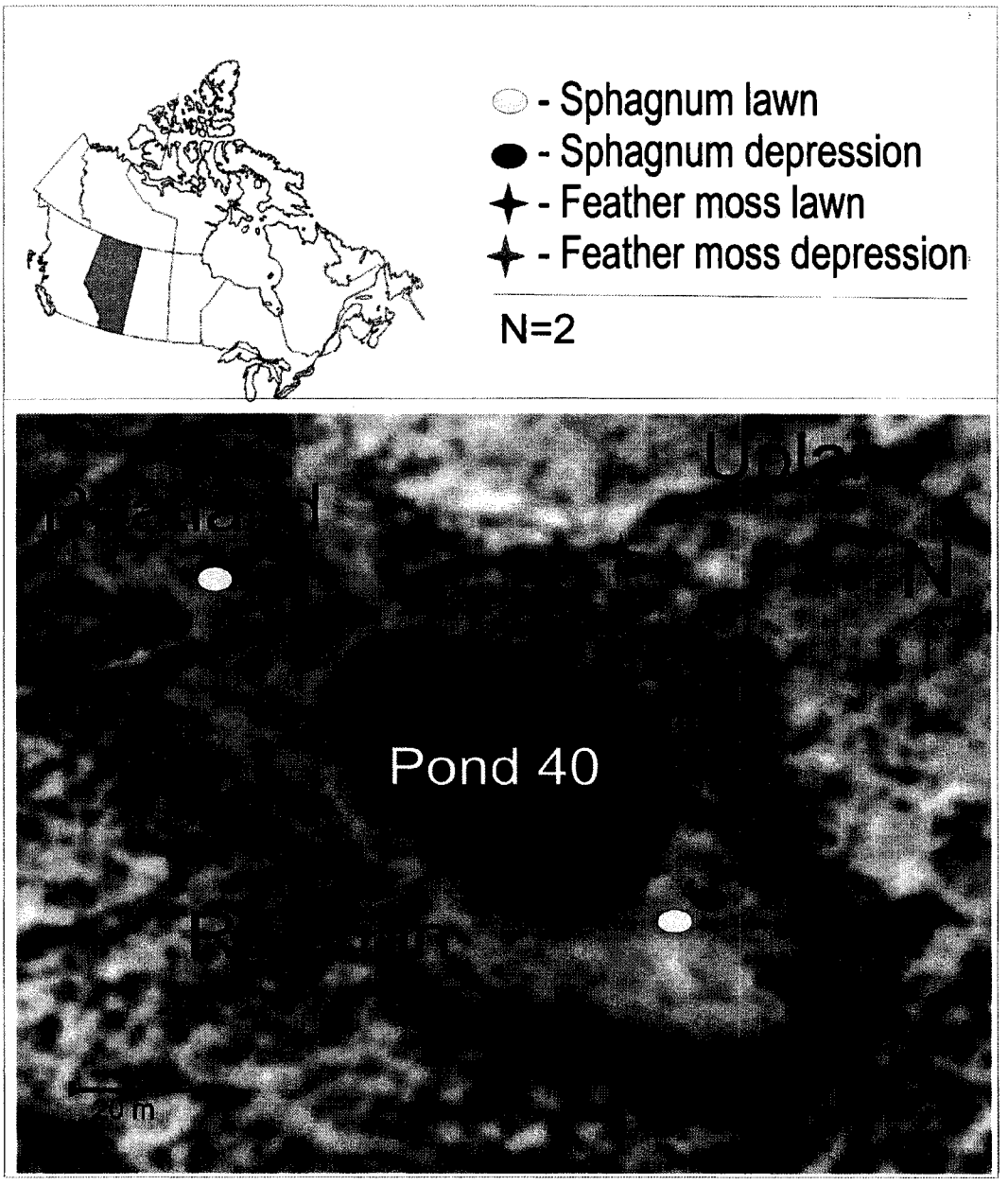

Figure 3.1: Study site Pond 40, located within the western boreal plain ecozone, Utikuma Region Study Area, Alberta, Canada. Stars and circles represent site locations.

The study site is comprised of a shallow pond (< 1 m depth) surrounded by riparian treed bog/fen and thicket swamp grading to aspen dominated uplands similar to that described by Ferone and Devito (2004). The peatland - pond complex is located on a topographical high glacial till moraine adjacent to an upland forested hill slope reaching a height of 7 m above the pond surface. There is some disturbance associated with access roads for oil drilling and seismic lines where strips of vegetation are removed located outside the study pond - peatland complex.

The ground cover of the peatland – pond complex is comprised mainly of continuous mats of vegetation with some microtopographical differences. Peat depths ranged from 1.5 – 4 meters. Although vegetation communities varied throughout the peatland – pond complex, similar vegetation was located both on lawns and in depressions. Lawns are classified as topographically high moss mounds, whereas depressions are low lying. Therefore, collars were placed throughout the complex to capture the range of microtopography and the different vegetation communities (lawn n= 5 (*Sphagnum* lawn n= 2; Feather moss lawn n= 3) depression n= 6 (*Sphagnum* depression n= 2; Feather moss depression n= 4).

3.2 Materials and Methods

3.2.1 CO_2 Measurements

CO_2 exchange between the surface and atmosphere was measured using a dynamic - closed chamber system with an EGM - 4 Infrared Gas Analyzer (IRGA) (P.P. Systems, Maryland). Net ecosystem CO_2 exchange (NEE) and gross ecosystem productivity (GEP) were measured using clear lexan chambers, while total respiration

(R_{tot}) was measured using an opaque neoprene shroud over the lexan similar to that used by Wadding and Roulet (1998, 2000). Measurements were conducted from April 30th (DOY120) to September 7th (DOY 250) 2005 and April 26th (DOY 116) to October 3rd (DOY 276), 2006. Polyvinylchloride (PVC) collars (radius = 9cm) with a groove for collar placement were inserted one week prior to initial measurements. The groove was filled with water and remained throughout the measurements to insure an airtight seal when the chamber was inserted during the flux. A climate controlled system in each chamber consisted of a cooler with cold water pumped through a coolant tube to maintain chamber conditions within 2 °C of ambient conditions and a fan mounted on the inside of the chamber to minimize concentration build - up influencing the gradient without ventilating the surface (Welles et al., 2001). Five 1 - minute CO_2 concentrations were sampled at each collar location midday (9 - 1600 hrs), twice a week. The rate of CO_2 concentration increase within the 5 minute interval was then used to determine the average flux (Lund et al., 1999). The concentration of CO_2 was measured in ppm and then converted into mg CO_2 m^{-2} sec^{-1} using,

$$F = \frac{\Delta \times MM}{N} \times \frac{V}{A} \times CF \qquad (3.1)$$

where F is the gas flux (mg CO_2 m^2 sec^{-1}), Δ is the linear change in CO_2 concentration with time (ppm sec^{-1}), MM is the molar mass of CO_2 (44010 mg mol^{-1}), N is the molar volume of a gas (22.4 L mol^{-1}) at standard temperature and pressure (STP), V is the temperature corrected volume within the chamber (m^3), A is the chamber area (m^2)

and *CF* is the conversion factor from ppm to mol (1 ppm = 10^{-6}mol). Sampling times at each site were random and rotated to allow for different light, temperature and moisture regimes that may occur throughout the day to be measured.

Gross ecosystem production (GEP) was estimated by subtracting the gross respiration (R_{tot} = autotrophic and heterotrophic) from net ecosystem exchange (NEE) which is the combined above - and below ground respiration and photosynthesis:

$$GEP = NEE - Rtot \tag{3.2}$$

The sign convention of CO_2 uptake by the ecosystem as positive and CO_2 emissions from respiration as negative was adopted here. The measurement period includes the majority of the growing season at this boreal location. For comparative purposes the season was divided into different time periods (early green (EG), green (G), late green (LG) and senescence (S)). The periods fluctuated slightly between the years as they were based on precipitation, temperature and vegetation growth. Early green in 2005 and (2006) extended from DOY 120 (116) to 161 (157). At this time vascular species emerge but are immature. Green extended from DOY 161 (157) to 218 (212). During this time vascular species are maturing. Late green extended from DOY 218 (212) to 250 (244). During this time the vascular species reach maturity and leaf area index (LAI) reaches a maximum. The senescence period was only monitored in 2006 and extended from DOY 244 to 276. Onset of dormancy occurred at this time.

The relationship between GEP and PAR was fitted empirically using an equation for a rectangular hyperbola (Whiting, 1994; Waddington and Roulet, 1996):

$$GEP = \frac{(\alpha \times PAR \times GP_{max})}{(\alpha \times PAR + (GP_{max}))} \quad (3.3)$$

where PAR is the measured PAR (in μmol m^{-2} sec^{-1}), GP_{max} is the empirically derived gross photosynthetic exchange of CO_2, and α is the initial slope of GEP versus PAR.

To determine the temperature coefficients (Q_{10}) which represent the difference in respiration rates over a 10 °C interval, Fang and Moncrieff's (2001) first - order exponential equation was used:

$$Q_{10} = (R_2 / R_1)^{10/(T_2 - T_1)} \quad (3.4)$$

where R_1 and R_2 were measured respiration rates at temperatures T_1 and T_2 respectively.

3.2.2 Environmental Variables

Relative humidity (RH), air temperature (T_a) and photosynthetically active radiation (PAR) were also measured at each site during each 5 minute chamber sample period, both inside and outside of the chamber (at approx. 1.5 m above the forest floor) using an EGM - 4 atmospheric probe (P.P. Systems, Maryland). Peat and soil temperatures were recorded at the same temporal and spatial scale as the CO_2 fluxes using a digital thermocouple at 2, 5 and 10 cm. Soil moisture was measured using a Theta soil moisture probe (Delta-T Devices) inserted into the top 7cm of the soil substrate. Theta soil moisture probe were calibrated in the lab by extracting

representative samples from the field and then allowing them to dry to different moistures. Theta soil moisture measures and weights of the soil were recorded twice daily for 3 weeks. Soil properties for the representative samples were then determined in the lab, and calibration curves were determined using theta soil moisture measures and VMC relationships and then fitted to the data.

3.2.3 Vegetation Sampling

Plant species composition was recorded in each collar by percent cover of vascular plant and bryophyte species. Nomemclature follows Anderson et al. (1990) for all species. Canopy closure was determined using digital photographs. The camera (Kodak DC - 120) with a fixed 39 - 114mm *f*/2.5 - 3.8 lens and 1280 x 960 pixel image resolution was levelled above each collar and manual photos were taken (Guevara - Escobar & Gonzalez - Sosa, 2005). Photos from all sites were taken mid-day on clear days to avoid large variations in brightness across the pictures. Images were analyzed using Adobe Photoshop CS (Adobe Systems incorporated). The threshold to classify pixels into 'sky' and 'canopy' was determined on the first image and then applied to the rest of the images in that set. Classified images were then analyzed to calculate canopy area. The ratio of the canopy area to frame area of the image was expressed as a percentage and used to estimate canopy cover (Guevara - Escobar & Gonzalez - Sosa, 2005).

Table 3.1: Biomass partitioning and soil organic matter in plots where CO_2 flux measurements were made. Utikuma Region Study Area, Alberta, Canada. Data are means ± S.E. (n= 2 - 8 plots). All data are in g dry mass m^{-2}. Plots were harvested to a depth of 12 - 17 cm (bottom of collar). Samples were taken and analyzed in 2005.

		Vegetation dominated by			
		Feathermoss		***Sphagnum***	
		Lawn	Depression	Lawn	Depression
Total Biomass		1075	1362	1576	1228
Vascular plants (aboveground)					
	Evergreen shrubs	46±10	32±4	56±28	31±9
	Herbs	5±5	3±3	2±2	1±1
	Graminoids	0±0	3±3	0±0	1±1
Mosses					
	Feathermoss	1024±101	1302±78	0±0	0±0
	Sphagnum	0±0	0±0	1402±184	1205±97
Lichens		708±650	22±6	10±10	784±745
Vascular plants (belowground)		301±42	281±31	108±45	184±55
Soil Organic Matter		3901±402	5298±640	4205±325	5105±348

Species (occuring in more then one plot) were- evergreen shrubs: *V. vitis- idaea, L. Groenlandicum, O. microcarpus, E. nigrum*; feathermoss: *P. schreberi, H. splendens, and H. blandowii.*

To determine above - ground biomass (Table 3.1) two representative plots per collar were harvested to a depth of 12 - 17 cm (bottom of collar). The cores were separated into aboveground vascular - plants (clipped from above the moss surface), moss, below - ground vascular plant parts (fine roots, rhizomes, below - ground stem parts), and soil organic matter (the remainder) (Heijmans et al., 2004). The above - ground vascular plant parts were sorted into three categories: (1) herbaceous plant material (2) graminoids, and (3) woody leaf and stem (evergreen) (Bubier et al., 1998; Thormann and Bayley, 1997). The moss fraction was 4 - 6 cm thick and only green moss was included, clearly decomposed and compacted moss was included in the soil organic matter fraction (Heijmans et al., 2004). The mosses were separated into *Sphagnum*, and feather mosses (*P. schreberi, H. blandowii, H. splendens*), and lichens were separated from the mosses. All plants were oven dried at 60 °C for 2 days, whereas the large soil organic matter fraction was dried for a week, and then all

samples were weighed. The below - ground biomass was determined by taking two 20 cm representative cores for each site. Roots were removed and separated into living and dead, live roots were oven dried at 60 °C for 2 days.

Table 3.2: Vegetation as percent coverage in vegetated collar for each lawn and depression site (n = 1), and above canopy closure. Bare collars are not shown as no live material was present. Over 100% coverage is observed at some collars as moss mats were present with vascular vegetation growing through. Canopy closure at all sites was composed of Black spruce (*P. mariana*). Utikuma Region Study Area, Alberta, Canada.

Lawn (L)			Depression (D)		
Canopy Closure	**Vegetation**		**Canopy Closure**	**Vegetation**	
8%	*Cladina mitis*	15%	**5%**	*Cladina mitis*	90%
	Empetrum nigrum	30%		*Vaccinium vitis-idaea*	30%
	Ledum groenlandicum	25%		*Oxycoccus microcarpus*	5%
	Oxycoccus microcarpus	10%		*Sphagnum fuscum*	100%
	Sphagnum fuscum	100%			
	Vaccinium vitis-idaea	3%			
4.50%	*Empetrum nigrum*	10%	**2%**	*Helodium blandowii*	4%
	Ludum groenlandicum	25%		*Ledum groenlandicum*	5%
	Oxycoccus microcarpus	30%		*Oxycoccus microcarpus*	3%
	Sphagnum fuscum	90%		*Sphagnum fuscum*	85%
	Vaccinium vitis-idaea	10%		*Vaccinium vitis-idaea*	15%
29%	*Cladina mitis*	95%	**84%**	*Cladina mitis*	20%
	Ledum geoenlandicum	15%		*Ludum groenlandicum*	10%
	Pleurozium schreberi	90%		*Pleurozium schreberi*	95%
	Vaccinium vitis-idaea	15%		*Vaccinium vitis-idaea*	30%
64%	*Helodium blandowii*	40%	**62%**	*Helodium blandowii*	95%
	Viola renifolia	10%		*Vaccinium vitus-idaea*	30%
40%	*Helodium blandowii*	40%	**40%**	*Hylocomium splendens*	20%
	Ludum groenlandicum	30%		*Helodium blandowii*	55%
	Smilaciha trifolia	1%			
	Vaccinium vitis-idaea	25%			
			69%	*Helodium blandowii*	65%
				Hylocomium splendens	15%

** Canopy closure n=12 for each site, percent coverage of vegetation is average of 2005 and 2006.*

3.2.4 Soil Analysis

Soil cores were taken in duplicate for each collar site in August 2005 and were analyzed for bulk density (ρ_b), porosity (θ), soil organic matter (SOM), specific yield (Sy), VonPost and C:N ratios. Bulk density measured the mass of soil per unit volume, including pore space and was determined by:

$$BulkDensity = \frac{WeightOfOvenDriedSample(g)}{VolumeOfSample(cm^3)} \quad (3.5)$$

Porosity measured the portion of soil occupied by air and water and was determined using:

$$\%Porosity = \frac{SaturatedMass(g) - DryMass(g)}{Volume(cm^3)} \times 100 \quad (3.6)$$

Specific yield was determined by saturating the soils and then allowing them to drain for 48 hours:

$$SpecificYield = \frac{SaturatedMass(g) - DrainedMass(g)}{SaturatedMass(g)} \quad (3.7)$$

Total carbon (liable carbon and carbonate) for all sites were determined through loss on ignition (LOI) in a muffle furnace (Fang et al., 1998) using:

$$\%LossOnIgnition = \frac{\left[\left(W_{cso} - W_c\right) - \left(W_{csi} - W_c\right)\right]}{\left(W_{cso} - W_c\right)} \times 100 \quad (3.8)$$

Where W_c is the weight of the crucible (g), W_{cso} is the weight of the oven dried soil in crucible (g), and W_{csi} is the weight of the remaining (inorganic) soil and crucible (g). For the C:N there was no separation between organic and inorganic forms was made for the carbon component of the soil. The total percent carbon (%TC) and nitrogen (N) contents of the soil were determined through combustion using an Isochrom -

elemental analysis, Carlo - Erba Isotope Ratio Mass Spectrometry, autocombustion carbon - nitrogen analyzer (Micromass UK, Ltd., Environmental Isotope Laboratory, Dept. of Earth Sciences, University of Waterloo, Waterloo, Ontario, Canada). Soil characteristics for each land cover unit are provided in Table 3.3.

3.2.5 Statistical Analysis

Literature that examines chamber flux measurements uses standard deviation (Strack et al., 2006; Botting and Fredeen, 2006; McNeil and Waddington, 2003) or standard error (Tufekcioglu et al., 2001; Heijmans et al., 2004) to assess the daily uncertainty between and within sites. For this study standard error was used as it better describes the confidence of the reported mean, rather than the natural variability (Ambus, 2001).

When modeling temperature dependence with total respiration (R_{tot}), in some circumstances linear (Heijmans et al., 2004; Fang et al., 1998) or quadratic (Maestre and Cortina, 2003) relationships fit well, however most studies represent temperature and R_{tot} using exponential relationships (Fang and Moncrieff, 2001). This exponential relationship suggests that microbial activity increases at an accelerated, non – linear rate as temperature rises, thus exponential relationships were used to model temperature and R_{tot}.

A linear model can suitably explain variability in R_{tot} with volumetric moisture content (VMC) if small seasonal ranges of VMC occur. That is, if the majority of the measurements occur in conditions that are either 'wet' or 'dry' ends of the spectrum (Simek et al., 2004). However, when the range of 'wet' and 'dry' conditions occurs, a quadratic relationship is more representative (Davidson et al.,

1998). Therefore, within this study a quadratic model was used to represent the relationships between Rtot and soil moisture as a range of VMC were observed over the study period.

Table 3.3: Soil characteristics for microtopographical units (lawn and depression) as a function of depth, Pond 40, Utikuma Region Study Area, Alberta, Canada. 2005 and 2006.

Microtopography	Depth (cm)	LOI	BD (g/cm3)	Porosity (%)	Sy	VonPost	TC (%)	TN (%)	C:N
Lawn	5-10	92.86	0.02	0.92	0.14	H1	45.06	0.86	52.67
	10-20	94.29	0.03	0.91	0.10	H2	43.82	0.62	70.38
	20-30	95.51	0.05	0.93	0.08	H3	47.09	0.91	51.95
	30-40	93.42	0.06	0.93	0.10	H3	45.27	1.04	43.68
Depression	5-10	93.12	0.04	0.91	0.14	H2	45.10	0.91	49.66
	10-20	93.50	0.04	0.91	0.10	H2	47.35	1.33	35.65
	20-30	94.92	0.06	0.88	0.05	H3	47.31	1.16	40.87
	30-40	85.70	0.04	0.92	0.06	H4	44.39	1.07	41.43

** Lawn (at each depth, and microtopography)- LOI, BD, Vonpost n=10; Sy, Porosity, C:N, %TN, %TC n=5*

** Depression (at each depth, and microtopography)- LOI, BD, Vonpost n=12; Sy, Porosity, C:N, %TN, %TC n=6*

3.3 Results

The plots in the lawns and depression were dominated by *Sphagnum* and feather moss (*Pleurozium schreberi* and *Hylocomium splendens*), and all contained similar total biomass (above - and below ground) (Table 3.1). The soil organic matter was similar across all plots, ranging from 3901 to 5298 g dry mass m^{-2} in feather moss lawn and depression, respectively. Below - ground vascular plant biomass was highest within the feather moss plots, which may be associated with the quantity of evergreen shrubs with deep roots on these plots. The depression sites had higher bulk densities (BD), lower C:N and further decomposed peat (Table 3.3). Specific yield (Sy), loss on ignition (LOI), and porosity was similar between the lawn and depression microtopographical units.

3.3.1 Variability in Environmental Controls on CO_2 Exchange

The growing season (2005 and 2006) was divided into four intervals to compare the hydrology, microclimate and CO_2 exchange between the different microtopographical units. There were large fluctuations in soil moisture for the lawns and depressions throughout the growing season (Figure 3.2b). However, the depression sites were considerably wetter than the lawn sites throughout the entire season in both years with average VMC of 68 and 63% in 2005 and 2006, respectively (lawn VMC's for 2005 and 2006 were 31 and 28% respectively). In both years the depth to frost at the beginning of the season was similar (~10cm below surface) (Figure 3.2c). Frost out occurred later in 2005 for both microtopographical

units. However, in 2005, frost out occurred first in the depressions and in 2006, lawns lost the ice lenses first.

The microclimate (air temperature (T_a), soil temperature at 5cm (T_{soil}), photosynthetically active radiation (PAR) and relative humidity (RH)) was examined at the same temporal scale as the CO_2 fluxes to determine if there was variation between the microtopographical units (Figure 3.3). No significant difference was observed in T_a between units. However, average temperatures for 2005 and 2006 at the depression sites (7.9°C) were generally cooler then the lawns (9.6°C) throughout the study seasons. Seasonality in T_a and T_{soil} was observed at both microtographical units, with maximum T_{soil} being reached during the green (G) period when maximum T_a values were also observed. The lawn and depression units had similar PAR values for the early green (EG) and G periods; however, during the late green (LG) and senescence (S) periods the depressions had lower average PAR. This could be attributed to the on average higher percent canopy closure in the depressions, and the differential shading by the canopy when the sun was lower in the sky. Maximum PAR values were observed in the EG period for the lawn (1862 μmol m^{-2} s^{-1}) and during the G period for the depression (1616 μmol m^{-2} s^{-1}). Relative humidity increases slightly through the study season, but did not vary between microtopographical units.

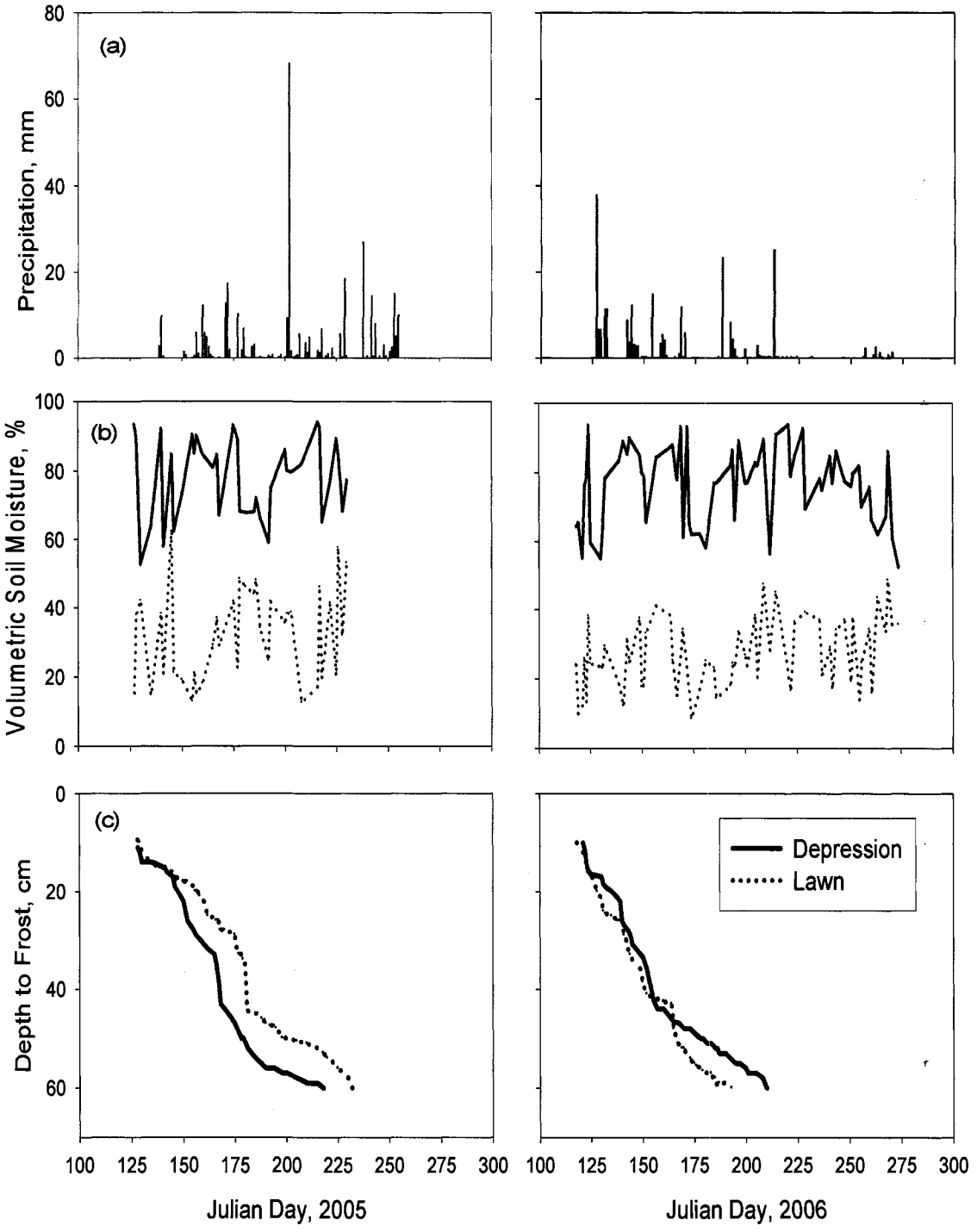

Figure 3.2: Average seasonal (a) precipitation, (b) soil moisture (θ) at 7 cm below surface, and (c) depth to frost, for the study peatland – pond complex, 2005 and 2006. Utikuma Region Study Area, Alberta, Canada.

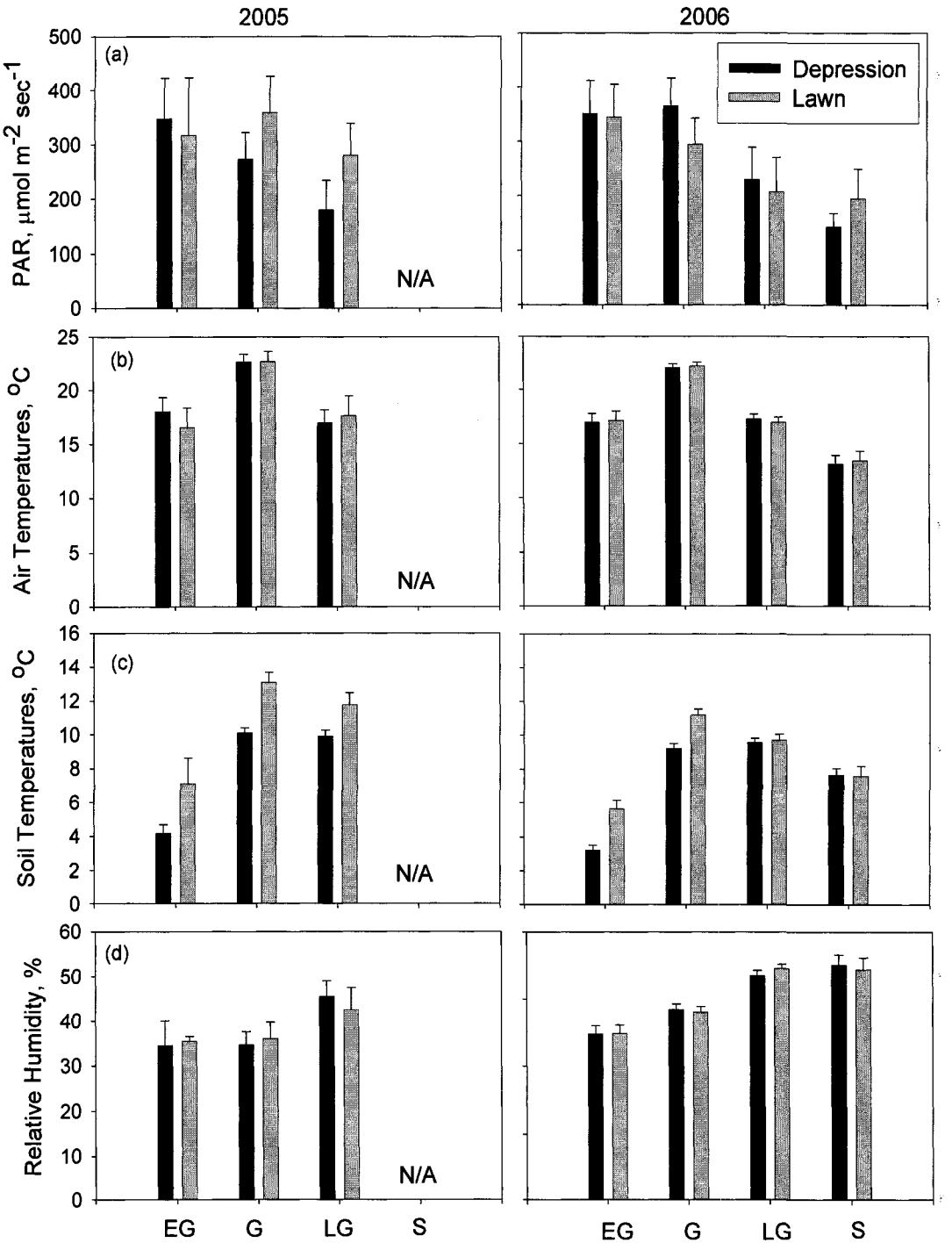

Figure 3.3: Average seasonal (a) PAR, (b) soil temperature (T_{soil}), (c) air temperature (T_a), and (d) relative humidity (RH) at each microtopographical (lawn and depression) unit, for 2005 and 2006 (error bars are standard error, n= 30 - 70). Utikuma Region Study Area, Alberta, Canada.

3.3.2 Microtopographical effects on spatial and temporal variability of CO_2 exchange

There were differences observed in midday CO_2 exchange from April through October among the microtopographical units (Figure 3.3). Note that the fluxes in this study represent instantaneous midday fluxes, which cannot be extrapolated to daily or seasonal carbon gain or loss (Heijmans et al., 2004). There was little difference in NEE, GEP and R_{tot} between 2005 and 2006 (Table 3.4), and differences between the two years could be accounted for by the addition of new sites in 2006. Thus, the two years were grouped together for the analysis of the CO_2 exchange. The lawns showed an average net CO_2 uptake during the early green (EG) period, but an average loss of CO_2 to the atmosphere for the remainder of the study season. The depression sites also showed an average net loss of CO_2 to the atmosphere during the entire study season. Net ecosystem exchange (NEE) for both microtopographical units was closest to zero during the EG. The average NEE for the lawn (-0.018 mg CO_2 m^{-2} sec^{-1}) was less than that for the depression (-0.029 mg CO_2 sec^{-2} m day^{-1}). The timing of maximum GEP occurred earlier than maximum R_{tot}. However, the timing was different in the two microtopographical units. Daily point measure maximum GEP in the lawn (0.32 mg CO_2 m^{-2} sec^{-1}) occurred during the G period and maximum R_{tot} (-0.29 mg CO_2 m^{-2} sec^{-1}) was reached in the LG. Conversely, maximum GEP in the depression (0.32 mg CO_2 m^{-2} sec^{-1}) occurred during the LG period and maximum R_{tot} (-0.40 mg CO_2 m^{-2} sec^{-1}) was reached during senescence. The timing of the flux maxima correspond with the highest GEP and R_{tot} averages. The lowest R_{tot} and GEP averages and minimums were observed in the EG when the soils were still cold and

had a shallow frost depth, and the lawn sites had higher average R_{tot} and GEP (-0.087 and 0.074mg CO_2 m^{-2} sec^{-1} respectively) for the study season than the depressions (-0.54 and 0.031 mg CO_2 m^{-2} sec^{-1}, respectively). The spatial variability of instantaneous CO_2 fluxes between microtopographical units suggests that the moisture and temperature regimes are important in the exchange of CO_2 between the peatland – pond complex and the atmosphere.

Total respiration (R_{tot}) was partitioned into vegetation (R_{veg}) and soil (R_{soil}) respiration to examine the variability in the exchange throughout the growing season (Figure 3.5). The highest R_{tot} was observed in the lawns, and approximately 26% originated from the vegetation, whereas only 13% originated from the vegetation in the depressions. Throughout the growing season moss respiration contributed only a small proportion of the total respiration from the forest floor. However, a seasonal variation of R_{veg} was observed for both mircotopographical units.

Table 3.4: Average measured net ecosystem exchange (NEE), gross ecosystem production (GEP) and total respiration (R_{tot}) within the understory, for lawn and depression microtopographic units. Values are in mg CO_2 m^{-2} sec^{-1} per growing season, negative values indicate a release of carbon to the atmosphere. Utikuma Region Study Area, Alberta, Canada. 2005 and 2006.

Period	Year	NEE		GEP		Rtot	
		Lawn	Depression	Lawn	Depression	Lawn	Depression
Early Green	*2005*	0.003	-0.028	0.020	0.023	-0.047	-0.044
Green		-0.012	-0.045	0.068	0.018	-0.087	-0.061
Late Green		-0.018	-0.032	0.087	0.015	-0.104	-0.044
Senescence		N/A	N/A	N/A	N/A	N/A	N/A
Early Green	*2006*	0.007	-0.007	0.059	0.027	-0.047	-0.025
Green		-0.019	-0.021	0.105	0.048	-0.106	-0.062
Late Green		-0.057	-0.035	0.068	0.048	-0.112	-0.071
Senescence		-0.039	-0.035	0.064	0.034	-0.097	-0.062

* Values are averages, n= 30 - 70.

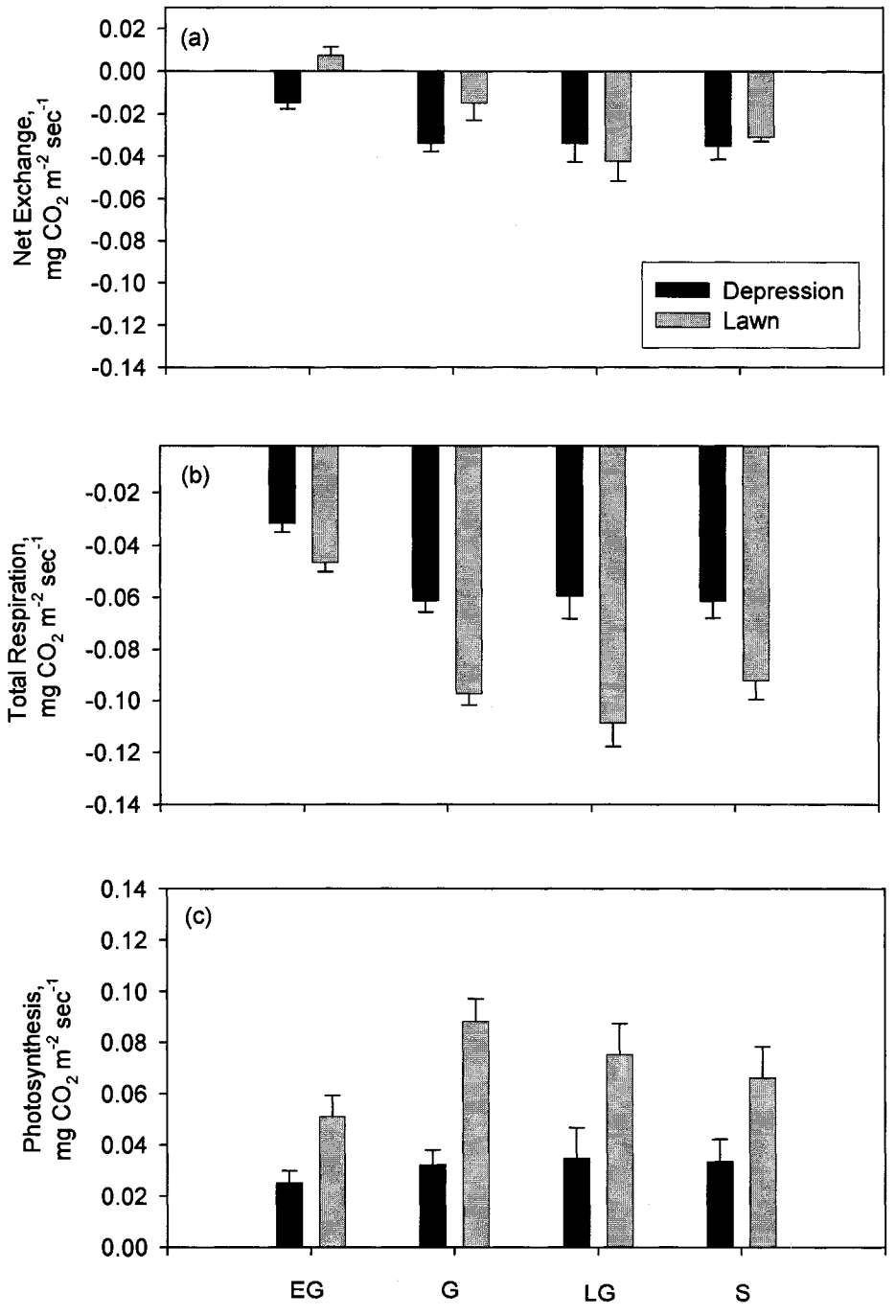

Figure 3.4: Average seasonal (a) net ecosystem exchange (NEE), (b) total respiration (Rtot), and (c) gross ecosystem production (GEP) from microtopographical lawn and depression units, Utikuma Region Study Area, Alberta, Canada for 2005 and 2006. Negative values indicate CO_2 release from respiration; positive values represent uptake by the ecosystem. (Error bars are standard error, for depression EG n=63, G n= 148, LG n=63, S n= 42; and for lawn EG n= 58, G n= 106, LG n= 45, S n= 34).

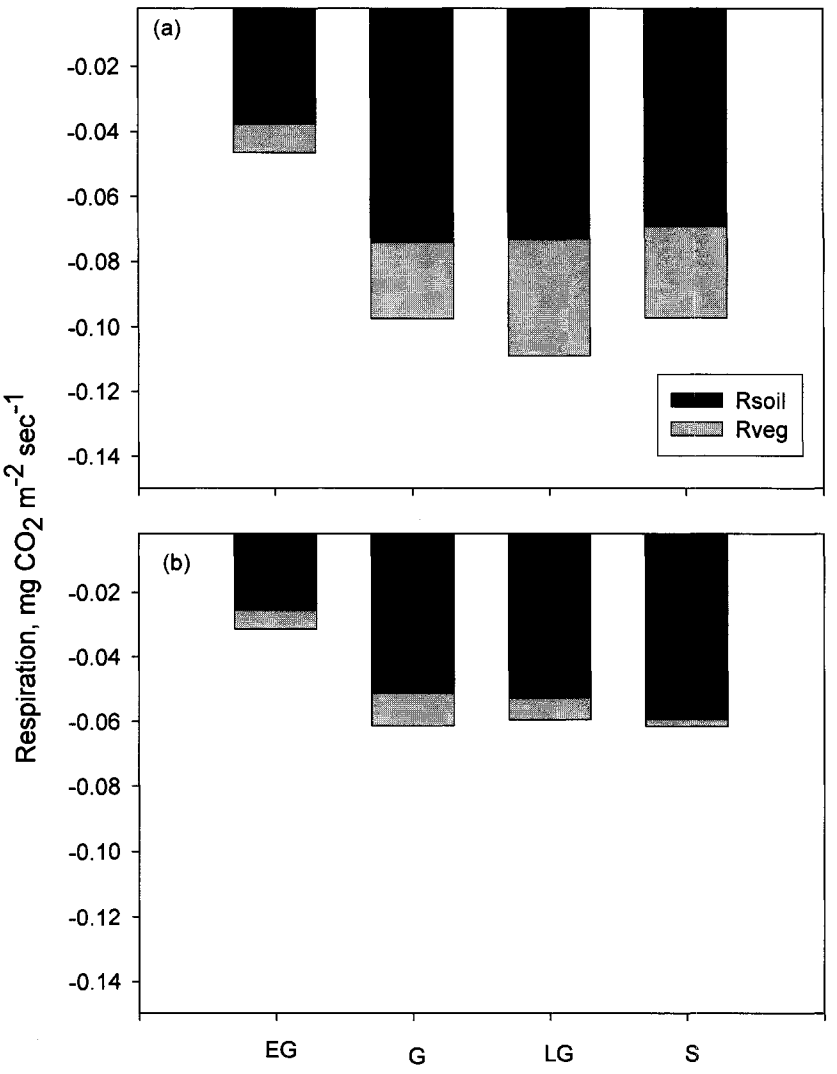

Figure 3.5: Partitioning of total respiration (R_{tot}) into soil respiration (R_{soi}l) and vegetation respiration (R_{veg}) for (a) lawn (b) depression microtopographical communities throughout the growing season. Utikuma Region Study Area, Alberta, Canada. Values are averages of 2005 and 2006 data; depression EG n=63, G n= 148, LG n=63, S n= 42; and for lawn EG n= 58, G n= 106, LG n= 45, S n= 34.

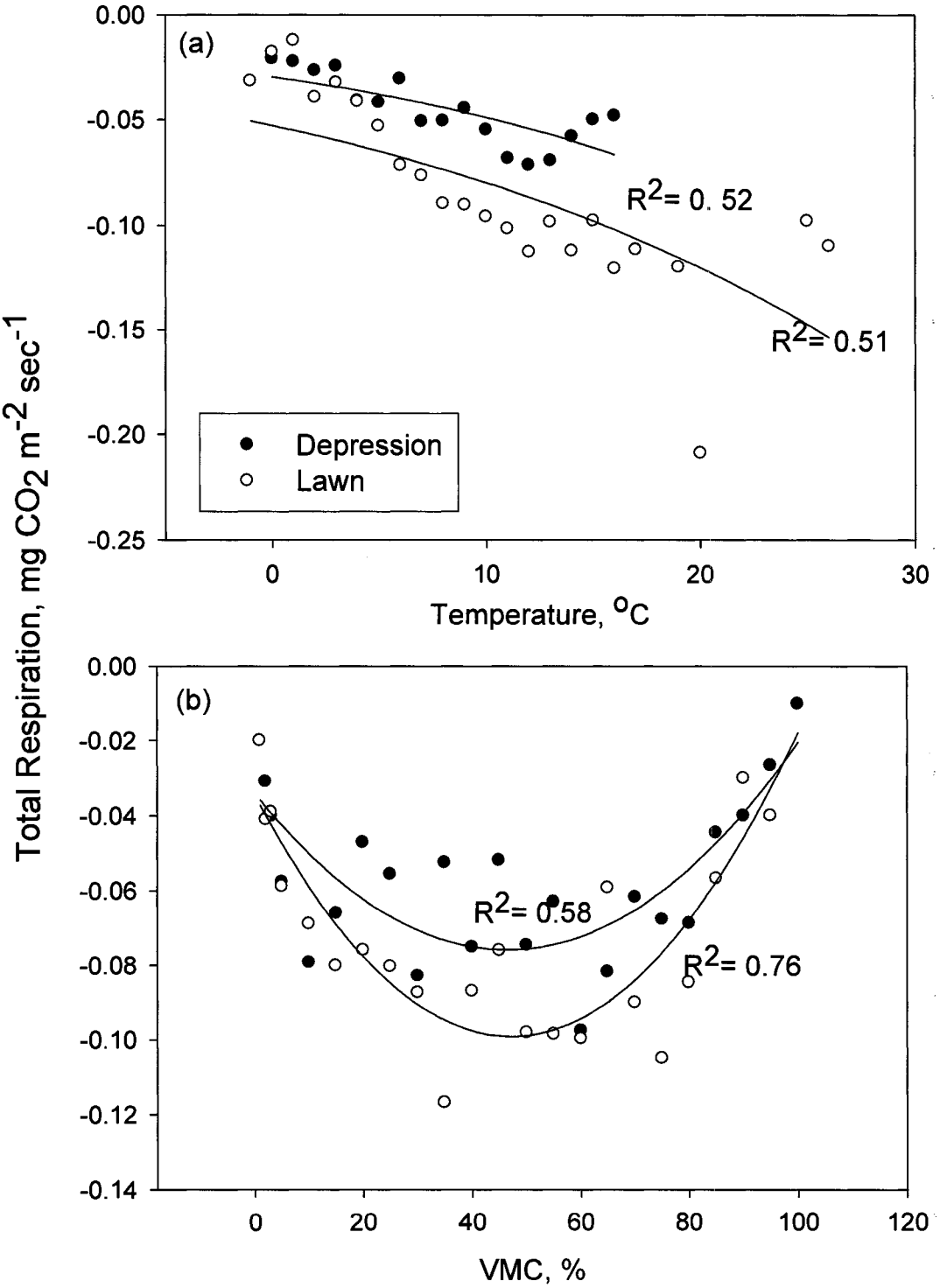

Figure 3.6: Variations in total respiration (R_{tot}) with soil temperatures at 5cm below the surface, (b) variations in total respiration (R_{tot}) with VMC (%). Utikuma Region Study Area, Alberta, Canada. 2005 and 2006.

Soil temperatures and volumetric moisture content (VMC) were tightly linked to total respiration (Figure 3.6). However, the lawn sites responded with higher R_{tot} to similar temperatures and VMC's observed in the depression sites. Soil moisture and R_{tot} curves were bell shaped and peaked at 40-60%. Average Q_{10} values calculated using a standard exponential equation, were higher in the depression (1.61) than lawn (1.58) microtographical unit for the range of soil temperatures observed (10 – 20 °C).

3.4 Discussion

The differences in midday net ecosystem CO_2 exchange among microtopographical units (lawns and depressions) in this study were small (Figure 3.4a). However, when partitioned into R_{tot} and GEP (Figure 3.4 b and c), spatial variability was observed between lawns and depressions, suggesting that the CO_2 exchange is sensitive to the microtopography of the understory. Spatial variability in R_{tot} and GEP across a peatland in terms of microtopography (e.g. Moore, 1989; Strack and Waddington, 2007; Waddington, 1996), variation in vegetation (e.g. Heijmans et al., 2004; Botting and Fredeen 2006), and canopy coverage (e.g. Connell et al., 2003; Swanson and Flanagan, 2000) has been reported previously. Thus, the variability of CO_2 exchange observed within this riparian peatland is not uncommon for northern forested wetland complexes. However, CO_2 exchange for sites with microtopographical differences but little variation in the composition of the vegetation has not been well documented.

3.4.1 Peatland - pond complex NEE, respiration and photosynthesis

Differences in midday CO_2 exchange among the lawns and depressions were observed (Figure 3.4), suggesting that the CO_2 exchange in the peatland - pond complex is sensitive to the microtopography of the area. However, with this set of measurements it cannot be said with certainty whether the observed differences are sustained when integrated over day and night, or year. Still, these data are useful for comparing sites with seasonal patterns with respect to midday CO_2 exchange.

Net ecosystem CO_2 rates were generally highest in the depressions, and both lawns and depressions were a source of CO_2 during the growing season (Figure 3.4a). However, NEE was only significantly different in the early green (EG) and green (G) periods, and no significant differences were observed for the remainder of the growing season between lawn and depression microtopographic units. Other studies (e.g. Waddington and Roulet, 1996; Strack et al., 2006; Kim and Verms, 1992) have shown significant differences between lawn (hummock) and depression (hollow) CO_2 exchange at sites located in Sweden, Quebec, and Minnesota. However, these studies had larger magnitudes of GEP and lower R_{tot} then this sub – humid site. The variability in net ecosystem CO_2 exchange between lawn and depression microtopographical units has been strongly linked to changes in the water table position and near surface temperatures (Waddington and Roulet, 1996; Kim and Verms, 1992). Therefore, the greater spatial variability of NEE between lawns and depression in previous studies relative to this WBF site could be due to more extreme moisture and temperature gradients. For example, the depressions described in Waddington and Roulet (1996) were generally saturated. However, in the current

study the depressions had an average VMC of 65% and were rarely saturated. The extreme variability in the moisture and temperature gradients that drive spatial variability in CO_2 exchange in other studies is likely why differences in NEE were observed in the EG and G periods when moisture and soil temperature varied the greatest between the microtopographical units. In addition, depression sites in this study had higher bulk densities, therefore the water holding capacity was higher. In the *Sphagnum* sites this may reflect the need for a tighter growth form (smaller pore space) to maintain hydrologic connectivity around non – *Sphagnum* shoots (c.f. Bauer et al., 2007). Additionally, studies have shown that bulk densities of *Sphagnum* increase with distance from water (Luken, 1985; Bauer et al., 2007). This suggests that the depression sites in this study are drier, and more closely resemble the soil characteristics of the lawns than those of studies completed in more humid Eastern peatlands. That is, higher bulk densities in depressions are a result of an increased need maintain hydrological connectivity that resembles the lawn sites due to distance from the water table, whereas larger topographical gradients (i.e. lawns are topographicaly higher then depressions) exist in more humid peatlands that cause the bulk densities of the lawns to be larger as the depressions are located closer to the water table. In addition, feather moss productivity has been shown to be tightly linked to availability of water (Bauer et al., 2007. Therefore, due to small moisture gradients between the lawns and depressions it is likely that productivity is similar, however the depression with a slightly higher VMC likely results in slower decomposition, thus higher bulk densities.

The larger topographical gradients in humid peatlands cause larger moisture gradients that tend to drive vegetation differences (Moore, 1990; Vitt, 1990) in other regions, which have been documented to alter CO_2 dynamics (Botting and Fredeen, 2006; Heijmans et al., 2004). This may further explain the lack of spatial variability of NEE observed between lawns and depressions in this study. That is, although moisture and temperature gradients were observed between lawn and depression microtopographical units, there was little to no variation in the vegetation patterns in the lawns and depressions in this study. Although NEE was not always significantly different between depressions and lawns, significantly different average gross ecosystem production (GEP) and total respiration (R_{tot}) (in parentheses) values were observed between depression and lawn sites (0.03 (-0.053) and 0.07 (-0.086) mg CO_2 m^{-2} sec^{-1} respectively) (Figure 3.4 b and c). Bubier et al. (2003) observed similar NEE for lawns and depressions at a site in Ottawa, Canada. However, GEP and R_{tot} were very similar, and vegetation patterns were different between microtographical units. Thus, moisture thresholds in this more humid climate are required to produce variation in vegetation distribution, and CO_2 exchange are similar to which, or more closely related.

Studies have shown that temporal variability in GEP is strongly related to PAR, and that respiration rates are coupled to soil and air temperatures (Botting and Fredeen, 2006; Law et al., 2002; Bubier et al., 1998; Waddington and Roulet, 1996). Thus, gross photosynthesis rates, calculated from the chamber measurements made in the light and dark were related to changes in PAR (Figure 3.7). A rectangular hyperbole was fitted to the GEP – PAR data at individual collars to calculate values

for the A_{max}. The scatter in the GEP - PAR model for this study is typical of that found in other studies (Lafleur, 1999, Bubier et al., 1998), which is often attributed to limiting environmental conditions (e.g. high temperature or vapour deficit) (Lafleur, 1999) and differential timing of snowmelt and thaw (Bubier et al., 1998). The fluxes here appeared to vary according to microtopography (Figure 3.7) with fluxes being slightly larger from the lawns. However, partitioning these data into the dominant ground cover vegetation communities shows that *Sphagnum* lawns (Figure 3.7b) had three times higher A_{max} than *Sphagnum* depressions and both feather moss depressions and lawns.

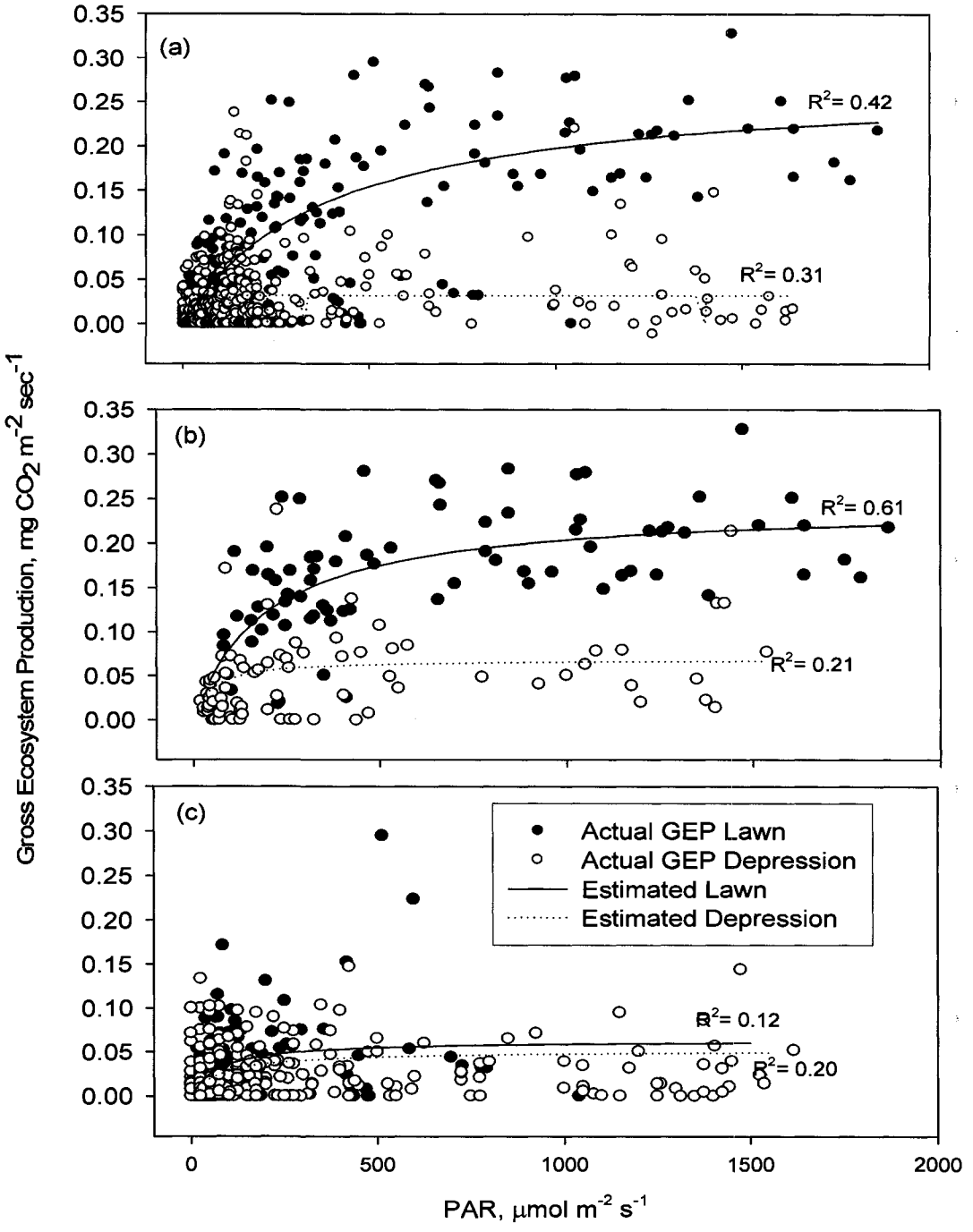

Figure 3.7: Relationships between gross ecosystem production (GEP) and photosynthetically active radiation (PAR) for combined data of 2005 and 2006 data for (a) all lawns and depressions (b) *Sphagnum* (lawns and depressions), and (c) feather moss (lawns and depressions). Curve fits for GEP versus PAR were calculated with a rectangular hyperbola model from Eq. (3.3). Utikuma Region Study Area, Alberta, Canada.

Previous studies have indicated that mosses (feather moss and *Sphagnum*) have different photosynthtically active periods over the growing season (e.g. Botting and Fredeen, 2006; Williams and Flanagan, 1998). Sites dominated with feather moss have been found to be consistently photosynthetic throughout the growing season and senescence, whereas *Sphagnum* plots generally exhibit stronger seasonal photosynthetic trends peaking in the middle of the growing season (Botting and Fredeen, 2006; Swanson and Flanagan, 2001). This difference is likely due to seasonal changes in photosynthetic capacity in *Sphagnum* as a result of physiological/ biochemical adjustments (Williams and Flanagan, 1998). *Sphagnum* usually grows in wetter, less dense portions of black spruce forests, while *Hylocolium* has higher abundance in the shaded, drier areas where tree density is higher (Gignac, 1992; Brisbee et al., 2001), therefore higher PAR (Table 3.2) in *Sphagnum* dominated areas favours GEP. Under field conditions, *Sphagnum* exhibits significant seasonal changes in biochemical capacity for photosynthesis, while photosynthesis in feather moss appears more strongly influenced by seasonal shifts in soil water content (Williams and Flanagan, 1998; Swanson and Flanagan, 2001). In addition, Bauer et al. (2007) found that feather moss (*P. schreberi and H. splendens*) did not show differences in actual productivity between wetter and drier plots. This suggests that the higher photosynthesis observed in the lawns in this study is more a function of increased productivity of the *Sphagnum* mosses. Net ecosystem exchange (NEE), total respiration (R_{tot}) and gross ecosystem production (GEP) for lawn and depression microtopographical units dominated by *Sphagnum* and feather moss are shown in Table 3.5. Both feather moss lawns and depression had higher bulk densities (BD)

than the *Sphagnum* sites (0.049 and 0.051 g cm^{-3}, respectively), which were associated with the highest volumetric moisture content (VMC) (34.4 and 80.8%, respectively). The lowest R_{tot} was observed in the feather moss depression, where the BD and VMC were the largest, suggesting that the water holding capacity of the feather moss at this site has a high water holding capacity which may be causing anoxic conditions to occur. However, the feather moss lawn had a similar BD but the highest R_{tot} for both feather moss and *Sphagnum* microtopographical units. This suggests that the feather moss depression sites were situated close to the water table which allowed for water to saturate the pore space. However, in the topographically high feather moss lawns, while they had the potential to hold water it was unable to draw water up. This likely allowed for the lawns to maintain an optimal VMC for decomposition, in addition to having warmer temperatures than the depressions which increased R_{tot}. However, as PAR values were similar there was little difference observed in GEP between feather moss lawns and depressions. Conversely, *Sphagnum* depressions had higher BD than the *Sphagnum* lawns, but similar VMC. In addition PAR values were similar between *Sphagnum* sites. This suggests that the difference in soil temperature between *Sphagnum* microtopographical units drove the differences GEP.

Table 3.5. Average measured bulk density, volumetric moisture content (VMC), photosynthetic active radiation (PAR), net ecosystem exchange (NEE), total respiration (R_{tot}) and gross ecosystem production (GEP) for lawn and depression microtopographical units dominated by *Sphagnum* and feather moss, 2005 and 2006. Negative values indicate a release of carbon to the atmosphere. Utikuma Region Study Area, Alberta, Canada.

Site	Bulk Density, $g\ cm^{-3}$	VMC, %	Soil Temperature, °C	PAR, $\mu mol\ m^{-2}\ s^{-1}$	NEE, $mg\ CO_2\ m^{-2}\ day^{-1}$	R_{tot}, $mg\ CO_2\ m^{-2}\ day^{-1}$	GEP, $mg\ CO_2\ m^{-2}\ day^{-1}$
Sphagnum Lawn	0.021	18.7± 0.81	10.3± 0.59	644.7± 55.2	-0.088± 0.006	0.075± 0.004	-0.163± 0.008
Sphagnum Depression	0.041	18.22± 0.98	8.05± 0.43	489.1± 50.2	0.057± 0.007	0.084± 0.008	-0.047± 0.006
Feather moss Lawn	0.049	34.4± 1.45	9.2±0.29	131.65± 13.5	0.07± 0.005	0.092± 0.004	-0.031± 0.003
Feather moss Depression	0.051	80.8± 1.22	7.83± 0.21	216.04± 21.1	0.02± 0.002	0.044± 0.002	-0.026± 0.002

The NEE from lawns and depressions exhibited marked seasonal variations (Figure 3.4). When the study began, there was no snow present but the peatland still had a shallow frost depth. Thus, sites were only slowly fixing CO_2 from the beginning of this study, while cool soil temperatures resulted in the lower GEP and R_{tot} measured during the EG. This is similar to Bubier et al. (1998), who found a peatland in northern Manitoba fixed CO_2 as soon as the top 5 cm of peat warmed above 0°C. During the middle of the growing season, maximum R_{tot} and GEP values were observed in both lawns and depressions. Deepening of the active soil layer from higher air temperatures was likely increasing decomposition, resulting in higher R_{tot}. In addition, during this period, light levels were high, soil conditions were warm and moist, and large leaf area index (LAI) favoured GEP. The CO_2 flux then declined with decreasing temperatures at the end of the growing season as soils cooled and plants began to senesce.

Moss respiration contributed only a small proportion of the total respiration from the peatland surface (Figure 3.5). Lawn vegetation contributed about 26% of the total respiration, whereas the depression vegetation contributed only 13%. In addition, in areas dominated by feather moss approximately 13% of the respired CO_2 came from the moss, while a slightly higher percentage (25%) originated from the moss in the *Sphagnum* dominated lawns and depressions. These were similar to observations by Swanson and Flanagan (2001) who found that 7% of R_{tot} originated from feather moss respiration, and 21% originated from *Sphagnum* respiration, and most of the R_{tot} occurs in the deeper soil layers. The lower contribution of feather moss respiration than *Sphagnum* moss was likely a combination of the low water

content in the feather moss, and therefore lowered metabolic activity (Swanson and Flanagan, 2001). Thus, the higher R_{tot} values in the lawns can be associated to the increased plant respiration from the higher productivity, more specifically the *Sphagnum*. Soil respiration rates correlate significantly with mean annual air temperatures and precipitation (Raich and Schlesinger, 1992). Thus, small changes to the climate or the landscape (e.g. removal of canopy cover) may dramatically increase the rates of deep soil respiration. For example, as this is a pre - harvest study, when this study site is logged, soil respiration rates may be very high following deforestation due to higher soil temperatures and decomposition of logging debris, and changes in the availability of water to vegetation may increase the metabolic activity of the understory vegetation increasing R_{tot}.

This study examined point CO_2 measurements. However, it has been observed that CO_2 fluxes vary diurnally (e.g. Suyker et al., 1997; Kim and Verma, 1992). Given that this study focused on midday CO_2 exchange the importance of GEP may be over estimated. For example, it has been observed that GEP exhibits a midmorning maximum (Shurpali et al., 1995; Suyker et al., 1997) and can be highly variable on diurnal timescales (Griffis et al., 2000). Whereas, total respiration generally peaks midday and the ecosystem continues to respire throughout the night (Jarvis et al., 1997). Therefore, it is likely that total respiration in this peatland – pond complex is higher when examining the exchange for the entire day, and GEP may be over estimated if extrapolated for the entire day.

3.4.2 Implications for Climate or Land use Change

Average daytime peatland NEE for all understory vegetation communities was a net loss of CO_2 to the atmosphere for the combined 2005 and 2006 growing seasons. The average range in summer NEE for the 2 years was -0.057 to 0.007 mg CO_2 m^{-2} sec^{-1} (Table 3.4). The upper end of this range is considerably lower then those observed in other studies (e.g. Lafleur, 1998; Waddington and Roulet, 1996; Bubier et al., 1998) who showed a large net uptake in CO_2 over the entire season, which may be due to these studies having been conducted in areas where soil moisture and temperatures were different than those in this study. For example, the study by Bubier et al. (1998) had depressions with standing water, and higher soil temperatures, which likely increased NEE. However, studies that have examined interannual NEE variability have observed that there can be large differences in carbon exchange from year to year (e.g. Lafleur et al., 1997; Shurpali et al., 1995). For example, Griffis et al. (2000) reported interannual variability ranging from a net sink of 2.71 mg CO_2 m^{-2} sec^{-1} in an early snowmelt year to a net source of -0.88 mg CO_2 m^{-2} sec^{-1} in the same peatland a few years earlier. Shurpali et al. (1995) observed seasonal net exchange from bogs ranged from -0.82 to 0.37 mg CO_2 m^{-2} in contrasting dry, warmer years, and cool, wetter years. Therefore, the fluxes observed in this study are within the ranges of previous studies. However, even though both field seasons were slightly warmer and drier then the 30 year normal of the area they did not come close to the lower end of this range. This is likely due to the season not being as warm and dry as that observed by Shurpali et al. (1995). Consequently, as it is anticipated that climate change is going to be most pronounced in these areas, a

further increase in temperature and decrease in precipitation may drive the study site to be a larger source of CO_2 to the atmosphere.

The strong relationships observed between T_5, VMC and R_{tot} (Figure 3.6) illustrates how enhanced soil temperatures and changes in the soil moisture may act as a positive feedback to climate change. For example, industrial pressures will play a significant role in altering the CO_2 biogeochemical cycles within these areas by altering land use practices. Corridor creation to access prime regions for the extraction of timber and oil may cause enhanced aerobic soil respiration due to the lowering of water tables and higher peat temperatures due to canopy removal (Devito et al., 2005; Petrone et al., 2006) causing a release in stored carbon to the atmosphere. As alterations to the upland and riparian areas occur (e.g. forest harvesting) it is likely that the peatlands will be affected as these different land cover units are hydrologically connected. Thus, if the peatlands dry out, or wet up it is likely that R_{tot} will decrease as both lawns and depressions optimally respires between 50 - 70% VMC (Figure 3.6). In addition increased warming could influence the depth to frozen soil, decrease the water table and extending of thawed conditions, therefore exposing larger amounts of organic carbon to microbial activity (Goulden et al., 1998). This could act as a positive feedback to climate change in a system that is already acting as a source.

The average Q_{10} coefficient observed in this study (1.7) is lower than those observed in other respiration studies (e.g. Lafleur, 2001; Bubier et al., 1998) and marginally lower then the global median (2.4) reported by Raich and Schlesinger (1992), but was within the overall values they reported (1.3 - 3.3). Higher Q_{10} values

generally correspond to a high sensitivity to temperature change in low temperature soils (Lloyd and Taylor, 1994), as well as wet, acidic, and organic soils (Chapman and Thurlow, 1996). The observed lower Q_{10} values observed suggests that this study area may not be as sensitive to changes in temperature. For example, Silvola et al. (1996) estimated that an increase in 2°C - 4°C in the boreal region would cause a 30 - 60% increase in CO_2 emissions from peatlands. However, this calculation was based on average Q_{10} values that were higher than those in this study, suggesting that a comparable increase in temperature would result in less of an increase in CO_2 fluxes. Currently, however, it is difficult to conclude with confidence how these climate changes will immediately affect the NEE of CO_2 exchange at high latitudes due to the uncertainty surrounding changes in evaporation rates, active layer deepening, water balance, water table elevation and soil moisture content (Griffis et al., 2000). Therefore studies such as this are important as they allow for the development of predictive relationships among photosynthesis, respiration and the environmental controls on these processes, which help to improve the understanding and modeling of peatland – pond complex CO_2 exchange.

3.5 Conclusion

Midday growing season ecosystem CO_2 exchange shows small differences between lawn and depression microtopographic units, including different controls on the seasonal pattern. This suggests that species composition of the peatland surface cover should be taken into account when evaluating understory contributions or when interpreting eddy covariance data for the entire forest or peatland ecosystem. The general trend was for lawn sites to have higher CO_2 uptake and respiration than the

topographically lower, denser depressions. Changes in volumetric soil moisture and soil temperature are important in many peatland environments as they cause gradients that also drive changes in vegetation. However, they did not control the distribution of vegetation in this study. That is, similar surface cover vegetation was located in areas with different hydrological and microclimatic conditions. *Sphagnum* lawns had higher maximum rates of GEP than feather moss lawns and depressions, and *Sphagnum* showed a pronounced seasonal change in photosynthetic capacity. While most studies treat peatlands as discrete units, this study has tied fluxes to different microtopographic units and shows that moisture and temperature gradients that can drive changes in fluxes may not be related to eco - hydrology of vegetation distribution. Thus, the variability observed in CO_2 exchange between microtopograhy and similar vegetation communities demonstrates that vegetation communities alone cannot be used as a proxy for CO_2 exchange. In addition, higher bulk densities in depression sites suggests that the water holding capacities in the WBP is different then those observed in more humid peatlands, thus it is likely that these different types peatlands be not react the same to climatic and environmental changes. Therefore, peatlands located in a moisture deficit ecozone (peatlands in a sun- humid climate), considerable micotopography and different vegetation communities should not be lumped together as one component of a boreal forest ecosystem.

Therefore, in a sub – humid environment like the WBP, moisture differences (gradients) between microtopographical highs and lows are reduced compared to other environments wetter conditions and larger gradients (i.e. saturated conditions or standing water in depressions). This results in moisture gradients with

microtopography that are not significant enough to result in differences in vegetation distribution, but are large enough to cause differences in the level of productivity within a species.

Chapter 4

Summary and Conclusions

4.1 Spatial and temporal variability in CO_2 exchange within a forested wetland complex

Examining CO_2 exchange from different land cover units in a forested wetland complex allows for the enhancement of: (1) our understanding of CO_2 dynamics in forested wetland systems between different canopy closures and vegetation communities, and to better quantify, and represent, the role of the these land covers within the context of northern greenhouse gas emissions; and (2) evaluate whether these land covers can be assessed as a homogeneous unit during the growing season, or that they exhibit large spatial and temporal variability.

This study demonstrated that there is large spatial and temporal variability in CO_2 exchange between forest floors of differing canopy closures. The forest floors in the upland and riparian land covers are dominated by R_{tot}, which is a function of R_{soil} rather than R_{veg}. However, high R_{tot} values for the forest floors in these areas are likely compensated for by the uptake of the large aspen canopy cover as well as the shrub layer. Within the covered and open peatland sites, the forest floors play a more dominant role in CO_2 exchange as these areas encompass a high proportion of the total ecosystem. However, the canopy cover in this study controlled the light available to the forest floors, allowing for small variations in the microclimate to occur. In addition, variations in the substrate quality (C:N) is observed between sites, which is likely the reason for the differences in the magnitude of the responses to

changes in soil temperature and moisture. All sites exhibit enhanced R_{tot} and GEP during the middle of the growing season when soil and air temperatures where highest, and when depth to frost was 20 cm below the surface.

It is observed that there is little spatial variability between the top, middle, and slope toe within the uplands (Table 2.1). Therefore, these sites are able to be grouped together to represent the uplands. However, within the peatland spatial variability is found between covered and open peatlands in CO_2 exchange as well as moisture regimes and vegetation communities. As a result, the peatlands are examined to better understand the CO_2 dynamics as well as to determine if peatlands can be grouped together when modeling CO_2 exchange or if they need to be addressed according to the microtopography, or vegetation composition. This study shows that temporal variability is similar for lawns and depressions, but different in magnitude. Moisture and temperature gradients are observed between the lawns and depressions. The drier and warmer microclimate of the lawn causes differences in the productivity of the species affecting GEP and R_{tot}, which are higher at the lawn sites. Although temperature and moisture gradients are observed between lawn and depression sites they are not enough to cause variation in the vegetation composition. However, *Sphagnum* plots (lawn and depression) show higher maximum rates of GEP than feather moss plots. In addition the *Sphagnum* plots have a lower canopy closure, which increases PAR availability at the peatland. This is likely why higher productivity is observed at the *Sphagnum* plots. This suggests that microtopography and species composition of the peatland should be taken into consideration when describing CO_2 exchange for the peatland ecosystem.

4.2 Global carbon cycle and management

The boreal forest constitutes a large biome on Earth, and as we attempt to monitor and model the dynamics of it there is an increasing need to recognize the directions and magnitudes of the CO_2 flux in different land covers. This is especially important when considering the northern boreal regions as a possible carbon sink for elevated atmospheric CO_2 concentrations (IPCC, 2001). Since this study uses instantaneous midday fluxes (which cannot be extrapolated to daily or seasonal carbon gain or loss) (Heijmans et al., 2004), whether this forested wetland complex increases, sustains, or decreases the atmospheric CO_2 concentration cannot be confirmed. However, it is known that soil CO_2 emissions are negatively linked to the water table (Bubier et al., 1998) and positively linked to changes in the near surface soil temperature (Raich and Tufekcioglu, 2000). However, they may react to changes with different CO_2 fluxes as shown in this study. For example, warming of the soils in a particular land cover in this study would result in an increase of CO_2 to the atmosphere (as long as water is not limiting), but not all land cover units would react with the same magnitude of change. Generally, peatland lawns have higher R_{tot} and GEP, thus changes in the water table and soil moisture could significantly change the peatland CO_2 flux. For instance, a decrease in water table and soil moisture could change the depression areas to operate more like a lawn site increasing the R_{tot} and GEP. Although the increase in photosynthesis would act as a positive feedback, respiration would likely also increase. In addition, the lawn sites may dry out with an increase in water table, increasing respiration, and minimizing GEP. Thus, it is

important to recognize that small changes to these ecosystems could result in large shifts in the CO_2 exchange.

As the WBP is altered by land use change, the dynamics and cycling of CO_2 will be altered as well. This study illustrates how the forest floors of the peatlands are responsible for most of the understory photosynthesizing in the watershed. However, as this area is altered we will likely observe a shift in the exchange. For example, if the aspen canopy in the upland and riparian is removed, the forest floor will likely receive more resources. An increase in PAR and precipitation received at the forest floor may stimulate the understory species and the forest floors of the upland and riparian will encompass the entire ecosystem and may start to operate like the peatlands with higher GEP. As a result, R_{tot} may increase as soil and air temperatures increase, and the aspen canopy will no longer be present to counteract the increase in R_{tot} with high productivity. However, runoff of nutrients from the upland and riparian due to the removal of the aspen canopy may stimulate growth in the peatlands (Hazlett et al., 2007), as well as increase soil moisture, which will act as a positive feedback for global climate change. Compaction of soils, alteration of out and in - flows, and other human interferences are also likely to alter the microclimates, vegetation interactions and biogeochemical characteristics of these forest floors. Therefore, as climate change occurs and the alteration of these landscapes continues, understanding the interactions of the physical and environmental variables and the processes involved will help with the parameterization and interpreting of climate change and biogeochemical models.

4.3 Conclusion

This study observed the region – specific CO_2 flux variability and some of the controlling variables on the exchange. The large spatial variability in net ecosystem CO_2 exchange that is observed demonstrates how the forest floors of different land cover units needs to be assessed independently as they will likely not respond to changes the same. In addition, microtopographical differences within the peatland caused gradients in the moisture and thermal regimes that resulted in higher productivity, therefore variation in the CO_2 exchange. Although the results are comparable to other studies, the sub – humid environment appeared to have unique qualities. For example, moisture gradients with microtopography did not drive vegetation differences, but did drive differences in CO_2 exchange. Thus, this study demonstrated that although degrees of spatial and temporal variability as well as controlling environmental factors on CO_2 exchange have previously been examined, they cannot necessarily be extrapolated to a sub – humid region, such as Canada's Western Boreal Plain.

Chapter 5

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