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Spatial relationships of grassland net ecosystem carbon dioxide exchange in a first-order agricultural basin in southern Ontario

Patrick S. Chahil
Wilfrid Laurier University

SPATIAL RELATIONSHIPS OF GRASSLAND NET ECOSYSTEM CO_2 EXCHANGE IN A FIRST-ORDER AGRICULTURAL BASIN IN SOUTHERN ONTARIO

by

Patrick S. Chahil

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THESIS

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ABSTRACT

This study quantified the midday (10:00 – 16:00) summer source/sink CO_2 relationships of various land-use types, particularly grass-dominated riparian areas, using dynamic chamber techniques, while evaluating the relative contribution of root and microbial components towards the overall soil respiration.

The influence of nearby agriculture and was related to elevated N and P, which were 40 and 1000% larger, respectively. A site adjacent to cropped fields showed similar (within 8%) study averaged soil respiration as an open grassland site, but 22% lower soil respiration than a riparian site 250 - 300 m downstream, which is adjacent to an open grassland fallow. A maple woodlot site exhibited the lowest soil respiration. Patterns were different for vegetative dynamics, such that a grass-dominated riparian site adjacent to agriculture showed 18 and 40% larger ecosystem (soil and vegetation) respiration, 36 and 60% greater net ecosystem CO_2 exchange (NEE) and 23 and 45% higher net ecosystem productivity (NEP) than a grass-dominated riparian area adjacent to an open grassland and an open grassland site, respectively.

Ambient air (T_a) and soil temperatures (T_g) at 5 cm were the best predictors of the temporal variability in soil and ecosystem respiration for all grass-dominated sites, whereas T_g was the best predictor of the temporal variability of soil respiration at the maple woodlot site. Volumetric soil moisture content (VSM) also exerted substantial temporal control on soil respiration through a quadratic relationship. Weak temporal relationships between T_a, T_g and VSM, with NEE and NEP, were shown. Spatially, study averaged site ecosystem respiration, NEE and NEP for vegetated plots showed strong positive relationships, close to unity, with the site averaged total nitrogen, C/N ratio and above-ground biomass.

Results showed that grass-dominated riparian and non-riparian areas, with similar vegetation that appear to be homogenous, located approximately 250 - 300 m from one another, exhibited spatially differing CO_2 exchange dynamics based primarily on location within the watershed. In addition, soil and ecosystem dynamics exhibited differing spatial and temporal responses to soil N inputs. This highlights the need to better assess CO_2 fluxes from heterogeneous agricultural landscapes. Furthermore, it emphasises that estimates based solely on soil or vegetated surfaces can be rather conservative and may not capture the inherent spatial variability and small scale processes that drive CO_2 exchange.

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ACRONYMS/ABBREVIATIONS	DESCRIPTION	UNITS
SITES		
LR	Riparian site adjacent to an open grassland fallow	---
MR	Riparian site adjacent to cropped (soybean on left and corn on right)	---
OG	Open grassland fallow	---
WOOD	Maple woodlot site	---
Veg	Ecosystem plots (mainly grasses)	---
Bare	Soil plots in which vegetation was removed	---
CARBON FLUXES		
R_{TOT}	Gross respiration (for Bare plots this is soil, microbes and roots, and for Veg plots above-ground vegetation is included)	mg CO_2 m^{-2} hr^{-1}
NEE	Net ecosystem CO_2 exchange	mg CO_2 m^{-2} hr^{-1}
NEP	Net ecosystem productivity/photosynthesis	mg CO_2 m^{-2} hr^{-1}
GEP	Gross ecosystem productivity/photosynthesis	mg CO_2 m^{-2} hr^{-1}
PR	Plant respiration	mg CO_2 m^{-2} hr^{-1}
%PR	Percent contribution of plant respiration	---
R_{R+S}	Standardized root and soil carbon fluxes for laboratory experiment	mg CO_2 m^{-2} hr^{-1} / g dry wt of soil
R_S	Standardized soil carbon flux for laboratory experiment	mg CO_2 m^{-2} hr^{-1} / g dry wt of soil
R_R	Root carbon flux for laboratory experiment	mg CO_2 m^{-2} hr^{-1} / g dry wt of soil
SRR	Specific root respiration	mg CO_2 m^{-2} hr^{-1} / mg dry wt of root
%RC	Percent contribution of root respiration	---
RUE	Respiration use efficiency (R_{TOT}/NEP)	---
CUE	Carbon use efficiency (NEE/NEP)	---

METEOROLOGICAL VARIABLES		
T_a	Ambient temperature	°C
T_g	20 cm depth integrated ground temperature	°C
VSM	12 cm depth integrated volumetric soil moisture content	%
PAR	Photosynthetically active radiation	W m^{-2}
Ppt	Precipitation	mm
SOIL PROPERTIES		
TC	Total carbon content	g C $(g\ soil)^{-1}$
%TC	Percent total carbon	%
TN	Total nitrogen	G N $g\ soil^{-1}$
%TN	Percent total nitrogen	%
C/N	Carbon to nitrogen ratio	---
EXT-P	Water extractable phosphorus	mg kg^{-1}
ρ_b	Bulk density	g cm^{-3}
NO_3^-	Nitrate	---
C	Carbon	---
PLANT VARIABLES		
AGB	Above-ground green biomass	G m^{-2}
RBM	Below-ground root biomass	G m^{-2}
H_M	Peak seasonal vegetation height	m
MISCELLANEOUS		
EG	Early Green Period (May 7 – June 20)	---
G	Green Period (June 21 – August 3)	---
LG	Late Green Period (August 4 – October 21)	---
GWP	Global warming potential	---
BREB	Bowen Ratio Energy Balance	---
EC	Eddy Correlation	---

DOY	Day of Year (i.e. July 9)	---
JD	Julian Day (i.e. July 9 = JD 190)	---
Q_{10}	Metabolic-temperature dependence of respiration for a 10°C temperature rise	---
SD	Standard deviation of study sample	same as variable
SE	Standard error of the mean of the study sample	same as variable
CV	Coefficient of variation (SD/mean)	%
RE	Root exclusion method	---
CI	Component integration	---
P	Phosphorus	---
IRGA	Infrared Gas Analyzer	---

--- Dimensionless

Chapter 1
INTRODUCTION

1.1 Atmospheric CO_2 and Global Change

The primary cause of global warming is believed to be the increasing emissions of greenhouse gases (GHGs) stemming from accelerated fossil fuel combustion and land-use change (Pacala et al., 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, which is the period with the most reliable data (IPCC, 2001). If the trends continue it is expected that temperatures will rise anywhere from 1.4 - 5.8°C by 2100 (IPCC, 2001). There are many implications that may result from these warmer ambient temperatures, such as sea-level rise, changing precipitation and evaporation patterns, and altered dynamics of the soil-atmosphere carbon exchange. However, confounding these global change predictions are positive and negative climatic feedbacks with direction, rates and magnitudes of these interactions that are difficult to forecast (IPCC, 2001; Schlesinger and Andrews, 2000).

The most abundant and prominent GHG is water vapour, but human activity is believed not to have directly affected its average global concentration (IPCC, 2001). However, radiative forcing from other anthropogenic GHGs (the most prominent of which are carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), each with global warming potentials (GWP) of approximately 1, 23 and 296, respectively (IPCC, 2001)) may indirectly alter the hydrological cycle. Although the GWP of CH_4 and N_2O are larger than that of CO_2, it is estimated that 56% of the total greenhouse effect is caused by CO_2 (IPCC, 2001).

Atmospheric CO_2 concentrations have increased from 280 – 355 ppm since the industrial revolution and most originate from fossil fuels (coal, oil, and natural gas) (IPCC, 2001). However, a substantial component (20 - 25%) of the CO_2 increase over the last 100 years has been attributed to land-use change altering ecosystem carbon (C) responses (IPCC, 2001). Therefore, a quantitative evaluation of the global C budget (and CO_2 in particular) and the identification of potential sources and sinks of C are crucial to our understanding the impacts of climatic variability (changes in temperature and moisture regimes) and land-use contributions towards the global biosphere (Schlesinger and Andrews, 2000).

Vegetation is considered to be the regulator of C exchange and vegetation growth in terrestrial ecosystems may be affected by increased temperatures (Schlesinger, 1997; Sims and Bradford, 2001). Some authors believe that enhanced atmospheric CO_2 will result in larger biomass uptake (increased net primary productivity (NPP)) or reduced soil and root respiration, both of which may mitigate some of the rising levels of atmospheric CO_2 (Barton and Jarvis, 1999). Others suggest that more biomass will augment vegetation litter and enhance decomposition, given favourable temperature and moisture conditions (Schlesinger and Andrews, 2000). Furthermore, concurrent with the emission of CO_2 to the atmosphere, large amounts of other nutrients (i.e. nitrogen fertilization) may enhance the storage of C in terrestrial ecosystems (Schlesinger, 1997). The biospheric regulators of CO_2 exchange are plants and understanding their roles is crucial.

Large terrestrial sinks have been estimated and discovered in the northern hemisphere (70 - 100% of the missing sink may be in northern subarctic and arctic wetlands and forest ecosystems) (Fan et al., 1998). However, a 'missing carbon sink' of

about 1.8 ± 1.2 Pg C, still exists globally (Fan et al., 1998; Pacala et al., 2001), which may be comprised of unexamined northern and mid-latitude ecosystems (Keeling et al., 1996) or an array of smaller ecosystems, such as temperate agricultural watersheds (possibly cropped and riparian areas) (Schimel et al., 2001). Thus, not only should the C balance of previously unexamined apparently homogenous ecosystems be measured, but their inherent spatial heterogeneity, and factors which influence C exchange, should also be explored.

Currently, global C models have been unable to balance the increased amount of CO_2 released from fossil fuels and land-use change, with the total amount of CO_2 released, because of the spatial and, inter- and intra-annual variability of photosynthesis and respiration (Rustad et al., 2000). Since most models and climate change predictions generally assume homogeneous conditions (area-averaged land-use types and parameters for given pixel sizes) it will not be possible to comprehend how varying ecosystems will scale globally without an understanding of the effects of local spatial heterogeneity (Vourlitis et al., 2000). This heterogeneity may introduce more variability at the scales of most models. Furthermore, to implement policies that will mitigate or lessen the possible impacts of increased atmospheric CO_2 more knowledge of ecosystem function at the plot scale and responses to varying factors and stresses must be evaluated. This will require studying the response of individual ecosystem elements (terrain and vegetation units) under a range of conditions. Thus, more emphasis has to be given towards quantifying the magnitude and exploring the physical processes that influence CO_2 exchange.

1.2 STUDY RATIONALE

Numerous studies exploring CO_2 exchange have been conducted on vegetation types such as northern forests and wetland ecosystems (Amiro, 2001; Black et al., 1996; Griffis et al., 2000a; Lafleur et al., 2001; Petrone et al., 2003) as these northern areas are were believed to be C sinks. These regions are predicted to experience the greatest rise in temperature resulting from global change and possess a potential to shift to C sources owing to their large above-ground biomass and cool soil conditions (Waddington et al., 1998). However, fewer studies have focused on characterizing the net ecosystem CO_2 exchange (NEE) and respiration (R_{TOT}) for temperate and mid-latitude areas, especially grasslands (Falge et al., 2002; Law et al., 2002) and riparian areas (Tufekcioglu et al., 2001).

The NEE for temperate grasslands have been examined (Frank and Dugas, 2001; Ham and Knapp, 1998; Meyers, 2001; Saigusa et al., 1998; Sims and Bradford, 2001; Suyker and Verma, 2001; Suyker et al., 2003) using eddy correlation (EC) or Bowen ratio energy balance (BREB) methods. While these studies will enhance our knowledge of C cycling at the ecosystem scale, the techniques employed area-average CO_2 exchange. This limits the examination of smaller, more diverse landscapes, such as those present in a typical first-order, temperate agricultural basin (Law et al., 2002). To assess the spatial heterogeneity of CO_2 at the plot scale (less than a metre), the use of dynamic chambers is preferred (Lund et al., 1999; Welles et al., 2000). However, only a few studies have directly explored soil CO_2 fluxes from grasslands using chambers (Bremer et al., 1998; Dugas et al., 1997; Frank et al., 2002; Mielnick and Dugas, 2000; Norman et al., 1992). Even fewer have explored the spatial variability of NEE in grasslands, and

those that do focus primarily on grazing (Knapp et al., 1998; LeCain et al., 2002) and fire influences (Bremer et al., 1998).

Many studies have demonstrated the importance of quantifying CO_2 exchange rates for all ecosystem components in order to better assess C dynamics from heterogeneous landscapes, such as desert (Maestre and Cortina, 2003), agricultural (Raich and Tufekcioglu, 2000; Tufekcioglu et al., 2001) and wetland (Waddington and Roulet, 1996) ecosystems. For example, studies in Alaska have shown riparian and snow-bed areas comprise approximately 25% of the landscape, but contribute over 72% of the total CO_2 respired over the winter (Fahnestock et al., 1998). This work suggests that CO_2 fluxes for relatively smaller land areas, such as riparian zones, may be a larger contributor to the overall ecosystem CO_2 fluxes, owing to their landscape position, vegetation composition and organic matter content (Tufekcioglu et al., 2001).

Landscape level monitoring is critical in verifying that all important community (spatially distinct vegetation types and unique locations) level processes have been identified and described as accurately as possible (Griffis et al., 2000a). As a result, the primary focus of this study is to explore riparian ecosystems to obtain a region-specific flux, which are lacking in the literature (Tufekcioglu et al., 2001).

1.2.1 Significance and Uniqueness of Riparian Areas

Temperate agricultural riparian systems are composed mainly of grass species with an extensive fibrous root system, soils that are often high in soil organic matter content (SOM), and large microbial populations and surface residues, all of which contribute to the overall CO_2 flux (Conant et al., 2001; Frank et al., 2002). These riparian zones are sinks for sediments and nutrients that are transported within subsurface and

surface waters (Tufekcioglu et al., 2001). Within agricultural ecosystems these areas may receive large anthropogenic influences through fertilizer applications (Robertson et al., 1996). Riparian zones have been shown to reduce nitrate (NO_3^-) levels that reach the stream through microbial denitrification, converting NO_3^- to nitrogen gas, and vegetation uptake (Hill, 1996). However, the addition of large quantities of nitrogen (N) and phosphorus (P) to cropped ecosystems may meet or exceed vegetation requirements. If N and P are applied in excess of plant requirements (it is estimated that 50% of the N is utilized by the vegetation) (IFA and FAO, 2001; Hill, 1996) these nutrients may be temporarily stored within the soil matrix. The stored nutrients can be accessed through root growth and by precipitation, which enhance available nutrients by chemical dissolution and transport aided by hydrologic connectivity. Since N is the limiting nutrient within terrestrial environments (Schlesinger, 1997) vegetation and soils in riparian areas, or in close proximity, may be more biologically active (CO_2 uptake by plants and/or released from soils) in response N inputs than areas not exposed to these nutrient inputs (Tufekcioglu et al., 2003).

Studies that examine the CO_2 exchange for riparian areas are lacking due to the difficulty of accessing such sites in agricultural basins as relatively small areas are not conducive to EC or BREB techniques, and the measurements required when using CO_2 chambers are labour intensive (Lund et al., 1999; Tufekcioglu et al., 2001). However, the limited literature that does exist exclusively evaluates soil respiration, neglecting vegetation dynamics (vegetation CO_2 uptake and vegetation respiration), for established riparian vegetation for larger stream channels (such as 3rd and 4th order streams) (Griffiths et al., 1997; Tufekcioglu et al., 2001) or in urban areas (Groffman et al., 2002). These

larger streams may 'mask', or minimize, the direct influences from land-use that smaller, first-order channels may exhibit. Furthermore, these ecosystems may have been influenced by nearby agricultural practices for decades, and as such, may differ in CO_2 exchange, arising from long-term N influences than exhibited by less disturbed environments.

1.3 Research Objectives

This research has three main objectives: 1) quantify and identify the processes regulating the midday (10:00 – 16:00) summer CO_2 source/sink components of ecosystem (vegetated) and soil terrains for grass-dominated riparian vegetation and non-riparian vegetation, and a maple woodlot site, using dynamic chamber techniques; 2) partition the soil and root contributions towards the overall soil CO_2 flux; and 3) evaluate the climatic (temperature and soil moisture), soil and vegetative determinants of the spatial and temporal variability of CO_2 exchange.

Although CH_4 and N_2O are also potent GHGs, with GWP of 23 and 296 times greater than CO_2, respectively (IPCC, 2001) only CO_2 will be examined in this study. This is because CH_4 and N_2O are predominately emitted under anaerobic conditions (Hill et al., 2000) and within this study location the soils have good drainage, due to the presence of drainage tiles (Macrae, 2003). Thus, stagnant water during the growing season (May - September) is rarely observed (Mike English, Pers. Comm., 2003). Since, the primary focus of this research is to explore the spatial variability and underlying controls of riparian CO_2 fluxes, the issue of temporal variability will be coarsely discussed.

Chapter 2
LITERATURE REVIEW

2.1 INTRODUCTION

Globally, agricultural lands cover 62 x 10^5 km^2 with croplands, rangelands and wetlands comprising 45.5 x 10^5 km^2, 15.5 x 10^5 km^2 and 7 x 10^4 km^2, respectively (Follet, 2001). Within Canada 13% of the agricultural land is located in Ontario and Quebec (Paustian et al., 1998). Many temperate agricultural ecosystems within southern Ontario are characterized by diverse land-use types (croplands, grasslands and riparian areas of first-order streams) usually located within a small area (3 - 6 km^2) (Romero et al., 2002). Primarily, the studies of CO_2 exchange within agricultural areas have focused on crop management techniques (no-till versus tillage) (Follet, 2001; Paustian et al., 2000) and crop types (Duiker et al., 2000; Lohila et al., 2003; Soegaard et al., 2003). However, few studies have examined the grass-dominated riparian areas adjacent to agriculture (Bremer et al., 1998; Knapp et al., 1998; LeCain et al., 2002). Grass-dominated areas, including riparian grasses, can comprise up to 60% of the total land area within these agricultural basins (Mike English, Pers. Comm., 2003). Moreover, many temperate agricultural basins contain first-order streams neighboured by narrow grass-dominated riparian areas. These areas have the potential to show high biological activity owing to their landscape position. However, few studies have explored the carbon (C) exchange dynamics of agricultural riparian areas and those that do focus exclusively on soil respiration (Griffiths et al., 1997; Groffman et al., 2002; Tufekcioglu et al., 2001). To my knowledge none have explored the NEE of these ecosystems, which may show that

enhanced soil respiration is accompanied by increased plant CO_2 uptake. Consequently, there is a need to gain a better understanding of ecosystem specific magnitude, variability and processes controlling the R_{TOT}, NEE and net ecosystem productivity (NEP) within natural and riparian grasslands, and to explore anthropogenic influences such as nitrogen fertilization.

2.2 Characteristics of Grassland Ecosystems

Grasslands are defined as terrestrial ecosystems dominated by herbaceous and shrub vegetation, which are maintained by anthropogenic (fire and grazing) and climatic (drought and/or freezing temperatures) means (White et al., 2000). According to this definition, grasslands encompass not only non-woody temperate and humid grasslands, but also savannas, shrublands and tundra. Globally, grasslands cover about 41%, or 52.5 million km^2 of the earth's natural terrestrial land surface and contain about 284 Gt C in both above- and below-ground biomass (Adams et al., 1990). They are most commonly found in temperate (38% of the world's grasslands), humid (23%), cold (20%), and arid zones (19%) (White et al., 2000). Temperate grasslands, savannas and shrublands have experienced heavier conversion to agriculture (White et al., 2000). For example, in North American, prairie grasslands have declined on average 79% over the past century (White et al., 2000). This substantial change in land-use suggests that within the context of global change and management it is important that the CO_2 dynamics of grassland ecosystems are examined to evaluate possible consequences and shifts of C dynamics created by land-use change.

Grasslands in North America can be classified into three predominant groups (Tall grass prairie, Mixed grass prairie and Short grass prairie) with tall grass prairie

being the predominant type of grassland present in temperate agricultural basins (Meyers, 2001; Soegaard et al., 2003). Characteristics of each of these grassland types are presented in Table 2.1.

Table 2.1: Characteristics of the three main types of grasslands found in North America (White et al., 2000).

Grassland Type	Characteristics
Tall grass prairie	Tall grass prairie lies mainly in the eastern portion of the US Midwest and Canada. Grasses often grow to be five feet tall and annual precipitation approaches 760 mm
Mixed grass prairie	Mixed grass prairie is mainly found in the middle portion of the US Midwest and Canada. Grasses often grow to be two and three feet tall and annual precipitation is about 380 to 640 mm
Short grass prairie	Short grass prairie is contained primarily in the western portion of the US Midwest, beside the coast of deserts and the Rocky Mountains into Canada. Grasses grow to be no more than two feet tall and the yearly precipitation is below 260 mm

Grasslands have been shown to be more productive than peatland ecosystems and similar in production to forests (growing season NEE ranges from -446 g C m^{-2} yr^{-1} to +155 g C m^{-2} yr^{-1}, -90 g C m^{-2} yr^{-1} to +20 g C m^{-2} yr^{-1} and -700 g C m^{-2} yr^{-1} to + 105 g C m^{-2} yr^{-1} for grasslands, peatlands and forests, respectively (Griffis et al., 2000b; Joiner et al., 1999; Lafleur et al., 2001; Law et al., 2002) (negative and positive values represent biospheric CO_2 uptake and loss, respectively). However, much less attention has been given to grassland ecosystems although measurements have shown their importance in the global C budget (Dugas et al., 1999; Frank et al., 2002; Mielnick and Dugas, 2000; Norman et al., 1992; Novick et al., 2004). Furthermore, the large species diversity that is present in grassland ecosystems and subsequent wide range in grassland NEE (mentioned above) suggests that the spatial variability between and within ecosystem needs to be addressed (Suyker et al., 2003).

The NEE for grasslands in Japan (Saigusa et al., 1998), temperate grasslands in the Midwest (Frank and Dugas, 2001; Meyers, 2001; Sims and Bradford, 2001; Suyker and Verma, 2001; Suyker et al., 2003), northern temperate grasslands (Flanagan et al., 2002; Kim et al., 1992; Redmann, 1978; Ripley and Saugier, 1978) and grasslands in semiarid environments (Angell et al., 2001; Dugas et al., 1999; Emmerich, 2003; Hunt et al., 2002; Valentini et al., 1995) have been explored using eddy correlation (EC) or Bowen ratio energy balance (BREB) micrometeorological techniques. These micrometeorological approaches generally determine fluxes using atmospheric elements above a surface without modifying surface characteristics, and provide a spatially and temporally integrated flux measurement (Law et al., 2002). While these studies will enhance our knowledge of C cycling at the ecosystem scale (1000's of metres) these methods limit the examination of smaller, more diverse landscapes. Conversely, chamber methods do allow for process based examination and are useful for making replicated plot measurements, although they are more labour intensive and provide only discrete analysis periods (Lund et al., 1999; Welles et al., 2001). However, few studies have directly explored soil CO_2 and NEE fluxes from grasslands using chambers (Bremer et al., 1998; Frank et al., 2002; LeCain et al., 2002; Norman et al., 1992; Mielnick and Dugas, 2000; Tufekcioglu et al., 2001).

2.3 Temperate Agricultural Riparian Zones

Riparian zones represent an interface between terrestrial and aquatic ecosystems and are defined as the area that encompasses the stream channel between the low and high water mark toward the uplands where vegetation may be influenced by a high water table and changing hydrologic conditions (Naiman and Decamps, 1997). Although they

occupy a small area of a watershed, their location between streams and cropped fields places them in a unique position to serve as sinks for sediments and nutrients (Naiman and Decamps, 1997; Tufekcioglu et al., 2001). That is, riparian zones may reduce non-point source pollutions derived from upland agricultural lands (Hill, 1996; Hill et al., 2000). The possibility of elevated C and N availability in riparian areas suggests that vegetation and soils may exhibit larger release and uptake of CO_2 than surrounding upland areas (Griffiths et al., 1997; Tufekcioglu et al., 1999).

The rooting system of any vegetation is the key component for nutrient uptake and soil respiration (Bouma and Bryla, 2000). Root densities have been shown to be greater under grass (600 g m^{-2}) than cultivated crops (230 g m^{-2}) (Tufekcioglu et al., 1999). Moreover, the roots in riparian areas can extend to depths greater than 1.0 m and exhibit respiration rates two times greater than in adjacent cropped fields (Tufekcioglu et al., 1999). In fact, Tufekcioglu et al. (2003) showed that root biomass in a riparian switch grass accounted for 57% of the total biomass and C/N ratios were lower compared to the adjacent crops. The authors suggest that riparian vegetation adds more organic C (and more N) to the soil, therefore providing a better opportunity for the sequestration of nutrients (e.g. energy source for soil microbes to utilize N) (Tufekcioglu et al., 1999), thus enhancing the biological activity and total respiration.

2.4 Terrestrial Carbon Exchange

The general C balance for any terrestrial ecosystem can be represented by,

$$\Delta C\,(NEE) = CO_2(NEP) - CO_2\,(R_{TOT}) - CH_4 - DOC \qquad (2.1)$$

where ΔC (NEE) is the net change in C storage within the ecosystem (g C m^{-2} d^{-1} or μmol C m^{-2} d^{-1}), NEP is the net primary productivity, which represents total plant uptake or

release of C from the system, R_{TOT} represents CO_2 loss from roots, microbial activity and vegetative respiration, CH_4 is methane and DOC represents dissolved organic carbon. DOC and CH_4 contributions towards the C balance are more important under saturated conditions (after storm events and spring melt) but contribute less during the summer, even more so within terrestrial dominated environments (Novick et al., 2004; Schlesinger, 1997). Thus, the terrestrial CO_2 exchange can be simplified as,

$$NEE = NEP + R_{TOT} \tag{2.2}$$

Figure 2.1 presents a more complete conceptual model for sources and transfer mechanisms of C between the biosphere and atmosphere.

2.4.1 Photosynthesis

In terrestrial systems atmospheric CO_2 is fixed by vegetation through photosynthesis, in which CO_2 is converted to a carbohydrate ($C_6H_{12}O_6$),

$$6CO_2 + 12H_2O + Sunlight = C_6H_{12}0_6 + 6O_2 + 6H_2O \tag{2.3}$$

Approximately 50% of the C fixed is utilized by vegetation during metabolism and carbohydrate production (loss of C) via internal plant metabolism, which is referred to autotrophic respiration (Schlesinger, 1997). The remaining C is partitioned between above-ground (shoot and leaves) and below-ground biomass (roots), such that 50 - 75% can be allocated to below-ground root C (Bremer and Ham, 2002; Frank and Dugas, 2001).

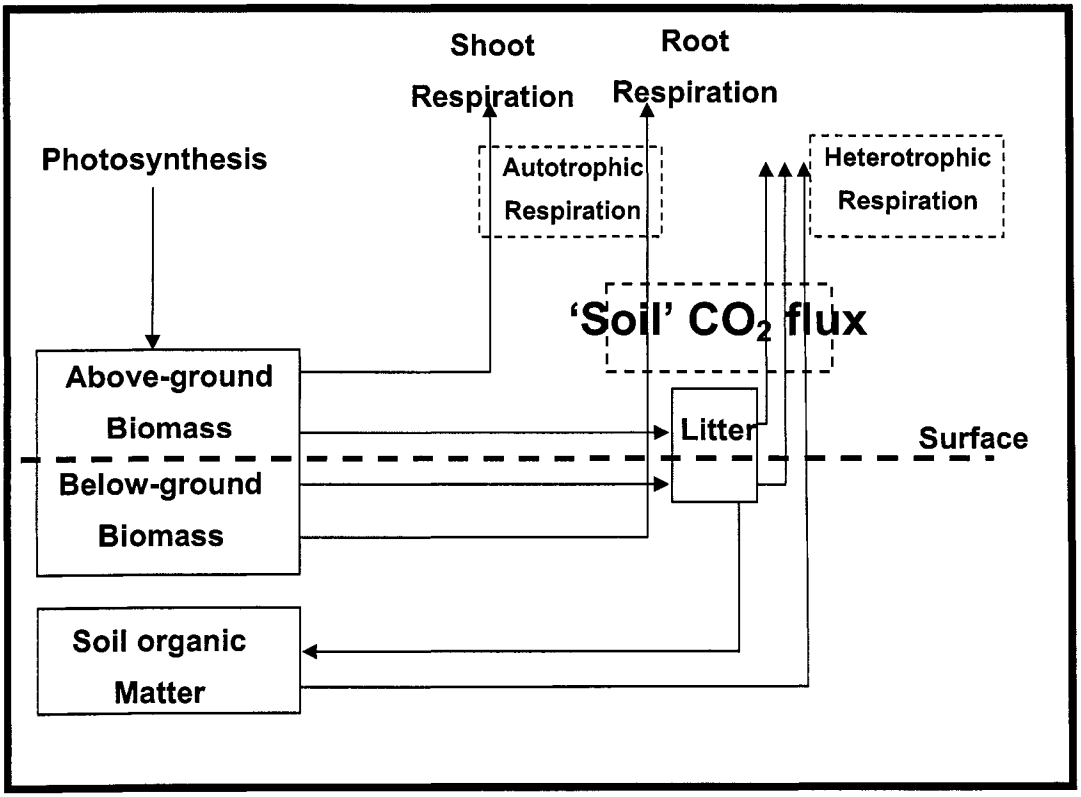

Figure 2.1: Representation of the main components contributing to the carbon (C) flux within terrestrial ecosystems (Modified from Kirschbaum et al., 2001; Schlesinger and Andrews, 2000).

2.4.2 Soil Respiration

Respiration is the process of gas exchange between organisms and the environment (Schlesinger, 1997). The overall C flux from soils, or vegetated plots including soils, will be referred to herein as R_{TOT} with the terrain distinction of Bare and Veg representing soil and vegetated areas, respectively. In other words, ecosystem and soil fluxes are represented by Veg R_{TOT} and Bare R_{TOT}, respectively. Soil R_{TOT} is comprised of biotic (rhizosphere (root and root exudates), heterotrophic (microbial and faunal respiration) and chemical (chemical oxidation of soil carbonates, which is relatively small compared to other sources (Emmerich, 2003)), and physical factors (soil

degassing) (Meyers, 2001; Suyker et al., 2003). When vegetation enters senescence, a portion of the above- and below-ground biomass contributes to detrial litter and soil organic matter (SOM). The C cycle is completed through the return of CO_2 to the atmosphere from the mineralization of SOM (Rustad et al., 2000) as described by,

$$C_6H_{12}0_6 + 6O_2 + 6H_2O = 6CO_2 + 12H_2O + Heat \qquad (2.4)$$

Globally, 1500 Pg C is contained within the surface metre and this represents a major proportion of the total C budget, comprising twice the C present in the atmosphere (760 Pg C) (Eswaran et al., 1993) and about three times that in terrestrial biomass (560 Pg C) (Rustad et al., 2000; Schlesinger, 1997). Hence, soils with large primary production and C storage, such as that of grasslands, can be expected to have high CO_2 fluxes (Bremer et al., 1998; Flanagan et al., 2002).

Assessing R_{TOT} is important for several reasons. First, R_{TOT} itself provides a useful index of ecosystem productivity or biological activity through decomposition (Bouma and Bryla, 2000; Raich and Schlesinger, 1992). Secondly, it has been noted that annually 10% of the atmospheric CO_2 cycles between the biosphere and atmospheric (Bouwmann and Germon, 1998), which represents 10 times the amount of CO_2 released from fossil fuel combustion (Raich and Tufekcioglu, 2000). Soils transfer about 75 Pg C yr^{-1}, or 25% of the annual emitted CO_2, to the atmosphere (Schlesinger, 1997), and following gross photosynthesis (120 Pg C yr^{-1}) represents the second largest flux of C within terrestrial ecosystems (Rustad et al., 2000; Schlesinger and Andrews, 2000). It has been estimated that an increase of 0.03°C yr^{-1} may enhance R_{TOT} by 60 Pg C between 1990 and 2050 (Xu and Qi, 2001), which is equivalent to a 19% increase in fossil fuel

emissions over that same time period. As a result, understanding the magnitudes and process that regulate the transfer of C is crucial from a global change perspective.

2.4.3 Root Respiration

Wiant (1967) defines root respiration as all respiration derived from organic compounds originating in plants. This includes root respiration of live tissues, the respiration of symbiotic myccorrhizal fungi and associated microorganisms, decomposing root exudates (water, sugars, amino acids, etc. released into the soil matrix by healthy roots) and recently dead root tissues in the rhizosphere. Since the respiration of root-derived C by symbionts (mycorrhizae) and other microorganisms closely associated with the roots are difficult to separate, their contributions are typically combined and referred to as rhizosphere or root-respiration (Hanson et al., 2000; Meharg, 1994; Rochette et al., 1999). While live roots contribute to the R_{TOT} flux directly, dead root material can provide the organic matter energy source for microorganisms (Rustad et al., 2000).

The proportion of the total R_{TOT} flux that is attributed to roots, compared to microbial sources, varies among ecosystems, being high in cold, northern regions, representing approximately 50 - 93% and 62 - 89% in boreal forests (Billings et al., 1977; Ryan et al., 1997). These large values were attributed to cooler temperatures that limit microbial decomposition while the root respiration of larger trees and certain plants could still operate (Law et al., 2002). In temperate regions, it is estimated that root respiration contributes 30 - 50% in broad-leaved forests (Bowden et al., 1993) and 17 - 40% in grasslands (Kucera and Kirkham, 1971; Buyanovsky et al., 1987). Root contribution in cropped fields contributes 12 - 38% of R_{TOT} due to the short duration of live roots and

low root biomass (Hanson et al., 2000). During the dormant season the contribution of root respiration can be much lower in magnitude (<20%) than over the growing season (Rochette et al., 1999), however, percentage contributions have been shown to be largest during senescence when roots allocate C below-ground and microbial decomposition is still occurring (Yazaki et al., 2004). In addition, the highest root respiration has been shown to occur in late May and June, a period characterized by intensive nutrient uptake, rapid root growth and root turnover (Hanson et al., 1993; Lohila et al., 2003).

Roots have been shown to be responsive to temperature increases showing a Q_{10} (the change in microbial activity given a 10°C increase in temperature) (Winkler et al., 1996) of 4.6 compared to 3.5 for bulk respiration (Bekku et al., 2003). Under moderate temperature conditions, the acclimatization of R_{TOT} to warming, (temperature sensitivity of R_{TOT}) decreased (Luo et al., 2001). It has also been observed that Q_{10} ratios decreased with depth (Bekku et al., 2003), decreased at higher temperatures (Fang and Moncrieff, 2001; Winkler et al., 1996) and can be constrained by soil moisture, such that Q_{10} was larger for wetter soils at the same temperature (Conant et al., 2004; Davidson et al., 2000).

2.5 Spatiotemporal Controls on CO_2 Exchange

The temporal and spatial variability of NEE and R_{TOT} have been related to numerous climatic, vegetative and soil variables. Climatic factors such as soil temperature (Fang and Moncrieff, 2001; Frank et al., 2002; Winkler et al., 1996), soil moisture (Davidson et al., 2000; Frank et al., 2002) and photosynthetic active radiation (PAR) (Griffis et al., 2001b; Petrone et al., 2003) have been shown to influence the temporal variability of CO_2 exchange in many ecosystems. Furthermore, biological

factors, such as leaf area index (LAI) (Flanagan et al., 2002), above- and below-ground biomass (LeCain et al., 2000), vegetation type (Raich and Tufekcioglu, 2000), soil carbon content (Maeste and Cortina, 2003; Tufekcioglu et al., 2001) and N content (Bowden et al., 2004; Burton et al., 2004; Verburg et al., 2004) have been shown to be related to the spatial variability of C dynamics. However, these controls differ in their relative importance depending on the scale and time of interest. At the plot scale (magnitudes of cm's) these controls can be highly variable and regulated by microsites ("hotspots") (Parkin et al., 1987; Simek et al., 2004). For example, the coefficient of variation (CV) for R_{TOT} can range from 35% in grasslands (Pol-van Dasselaar et al., 1998), 50% for ponderosa pine soil (Fang et al., 1998) and 150% in corn and soybean fields (Cambardella et al., 1994). This larger variation in agricultural fields may be the result of historical fertilizer applications and tillage influences (Reicosky et al., 1997).

Temporally, NEP is primarily dependant on PAR and water supply, and varies throughout the growing season as ecophysiological parameters and leaf area change (Frolking et al., 1998; Griffis et al., 2001b). R_{TOT} is usually explained by soil temperature and soil water content. Spatially, vegetative properties (root biomass, above-ground biomass) and soil nutrient status dictate C fluxes. However, soil temperature and moisture, related to microtopography can indirectly influence nutrients status and hence C fluxes (Waddington and Roulet, 1996).

2.5.1 Soil Temperature and Moisture Influences on Soil Respiration

Generally, soil temperature has been shown to explain 50 - 90% of the temporal variability in seasonal Bare R_{TOT} (Buchmann, 2000; Xu and Qi, 2001) through linear (Dong et al., 2000) or exponential relationships (Franzluebbers et al., 2002; Mielnick and

Dugas, 2000; Xu and Qi, 2001). The general seasonal trend is lower R_{TOT} values in the winter and autumn months and peak values in mid-summer (July) (Mielnick and Dugas, 2000). Normally, soil temperature and moisture are negatively related, however during drought the relationship can become decoupled and as a result the temperature and/or moisture control on R_{TOT} is reduced as plant mediated influences tend to dominate (Meyers, 2001). Spatially, temperature can dictate the variability of R_{TOT}, but this is usually a weak control (Xi and Qi, 2001).

The effect of soil water content on CO_2 efflux has been described by linear, logarithmic, quadratic or parabolic functions of soil water content, matric potential, precipitation indices and depth of the water table (Davidson et al., 2000). The control of soil moisture content on soil CO_2 flux is complicated through its influence on root respiration, microbial activity and soil gas transport (Mielnick and Dugas, 2000). The inhibition of soil moisture on R_{TOT} is revealed at 'high' (wet soil > 0.5 m^3 H_2O m^{-3} soil) and 'dry' (low soil < 0.15 m^3 H_2O m^{-3} soil) contents. Linn and Doran (1984) explain this phenomena mechanistically for microbial respiration as reduced diffusivity and limited O_2 diffusion through pore spaces in very wet soils (anaerobic conditions) and the limited supply of soluble organic substrates (energy source for respiration) within water films in very dry soils. Similarly, Raich and Potter (1995) hypothesize three phases of moisture effects on soil respiration: 1) when soils are relatively dry, metabolic activity increases with increasing moisture content; 2) when soil pores are 50 - 80% saturated, soil biological activity proceeds at about the potential rate; and 3) when soils are saturated, anoxic conditions inhibit aerobic and favour anaerobic conditions. The moisture

influences can be confounded by temperature, such that higher temperatures influence soil moisture loss (Davidson et al., 2002).

Field experiments have shown that the soil moisture of the litter layer (Gärdenäs, 2000; Rochette et al., 1992a) influences the temporal variability of R_{TOT}. The increased water holding capacities of organic matter can provide better conditions for root growth and microorganisms, which may lead to higher R_{TOT} rates. Lab experiments (incubations under various moisture regimes) have demonstrated a convex relationship (R_{TOT} lowest under wet and dry conditions and highest for intermediate moisture conditions), but these relationships are rarely observed in the field, except during short-term droughts (Sinkyu et al., 2003; Suyker and Verma, 2001). As a result, measurements of R_{TOT} can be inaccurate (especially for finer textured soils) following precipitation or flooding events. Furthermore, the spatial variability of soil moisture has been thought to regulate other factors, such as temperature and nutrient status, which can exert a greater control on R_{TOT} (Simek et al., 2004).

2.5.2 Organic Content and Nitrogen Influences on Soil Respiration

Decomposition of soil organic matter (SOM) is the source of energy that microbes require to obtain essential nutrients, and as a by-product release CO_2 to the atmosphere (Conant et al., 1998). R_{TOT} has been shown to be spatially (Franzluebbers et al., 2002; Lohila et al., 2003) and temporally (Tufekcioglu et al., 2001) correlated with SOM. This suggests that higher TC should lead to greater rates and magnitudes of decomposition. The importance of the organic layer was shown by Buchmann (2000) where they removed the litter and less than 70% of the fine organic matter layer of soil within a Norway Spruce stand. The R_{TOT} decreased 10 - 20% and by 30 - 40% when the entire

organic layer was removed. Thus, the underlying mineral soil contributed a substantial amount (60%) of the CO_2 flux.

N is one of the primary macronutrients in terrestrial ecosystems and is often the limiting nutrient (Schlesinger, 1997), which in addition to C has to be present to facilitate energy towards the decomposition of organic matter (Kane et al., 2003). It is important because elevated N inputs can increase the productivity of ecosystems (Brady and Weil, 1999; Schlesinger, 1997). N is used by microbes for growth purposes and by plants for the production of chlorophyll, amino acids, enzymes and hormones, as well as root development, which supports the uptake of other essential nutrients (Brady and Weil, 1999). Furthermore, plants obtain N from the soil solution principally as nitrate (NO_3^-) or ammonium (NH_4^+) through flow in the unsaturated zone or through soil leaching activated by precipitation.

C/N ratios are important for two main reasons: 1) competition among soil microbes when C/N ratios are wide (higher) and; 2) the C/N ratios dictate the rate of SOM decay and rate of nitrogen supplied to the soil (Brady and Weil, 1999). The C/N ratios in arable (cultivated land) surface horizons is usually between 8:1 to 15:1, however, narrower (lower) ranges can be present in subsoils (Brady and Weil, 1999) with little variation for similarly managed soils. Thus, the C/N ratio can be used as an indicator of nutrient status and to assess the relative decomposition rates. C/N ratios of 30/1 are adequate for soil microbes and as that ratio increases, decomposition rates decline (Brady and Weil, 1999). However, R_{TOT} has been shown to be both weakly (Flanagan et al., 2002) and strongly (Xu and Yi, 2001) related to N suggesting that

although in theory N should exert a strong control, other factors are required for decomposition, such as labile C.

The N control is exemplified in manipulated plot studies in which elevated N supplies are applied. Inorganic N applications at high rates ($\geq$ 10 g N m^{-2} yr^{-1}) (Bowden et al., 2000) and chronic low level rates (3 g N m^{-2} yr^{-1}) (Burton et al., 2004) within forest ecosystems, and moderate levels (~6 g N m^{-2} yr^{-1}) for grassland ecosystems (Verburg et al., 2004) have been shown to reduce R_{TOT} through suppressed microbial activity, while increasing NEP and NEE, through greater biomass.

2.5.3 Vegetation and Soil Texture Influences on Soil Respiration

R_{TOT} rates vary significantly among various plant ecosystems suggesting vegetation type may have some influence on the decomposition of SOM as well as root respiration. Vegetation may affect R_{TOT} by influencing the soil microclimate and structure, the quantity and quality of detritus supplied to the soil (Raich and Tufekcioglu, 2000). To explore this Raich and Tufekcioglu (2000) compiled a large data set from the literature comparing various crop types, under the same soil and climatic conditions, in which R_{TOT} was measured simultaneously. There were no significant differences in R_{TOT} between cropped and vegetation-free soils, forested and cropped soils, and grasslands and cropped soils (Raich and Tufekcioglu, 2000). There was however, a difference between grassland and forest soils, where grassland soils had on average 20% higher R_{TOT} rates forests. The larger value in grasslands was attributed to the extensive rooting system (Dugas et al., 1999). Tufekcioglu et al. (2001) also showed that root biomass was temporally related to the production CO_2 for riparian grasslands, but related to monthly measurements. Had measurements been confined to one season the strong relationship

may not exist because rapid fluxes changes would me driven by climatic variables, rather than slight changes in root biomass content (Franzluebbers et al., 2002).

Soil texture affects the movement of water and gasses into and out of the soil, and as such may have a profound influence on CO_2 efflux rates. Theory suggests that more porous soils (lower bulk densities), such as sands or peat, should allow for greater CO_2 exchange (Welles et al., 2001). However, it has been shown that sandy soils have only slightly higher or similar R_{TOT} values as clays (Bouma and Bryla, 2000; Lohila, 2003). It appears that soil texture has a more profound influence on soil moisture which leads to R_{TOT} variability (Davidson et al., 2000; Sinkyu et al., 2003). Similar to soil texture, it appears that factors such as temperature, soil moisture and substrate quality that influence the production and consumption of organic matter are more important in controlling the rate of R_{TOT} than the vegetation itself (Raich and Tufekcioglu, 2000).

2.5.4 Spatial Variability of Soil Respiration

Many studies have explored the spatial variability of R_{TOT} (Bremer et al., 1998; Frank et al., 2002; Norman et al., 1992; Mielnick and Dugas, 2000; Tufekcioglu et al., 2001) for grass dominated ecosystems. Davidson et al. (2000) obtained a mean coefficient of variation of 30% for 8 measurements representing 4 plots (secondary forest, primary forest, degraded cattle pasture and active cattle pasture) in the Brazilian rainforest. The measured R_{TOT} values for clipped grassland plots had a CV of 50%, whereas for bare soil it was only 15% (Dugas et al., 1997). This variability was attributed to the presence of grass roots and residual rhizosphere soil.

Seasonal variability in R_{TOT} was better explained by temperature, whereas, inter-site variability was better explained by soil moisture (Sinkyu et al., 2003). Others have

found that temperature is effective at explaining respiration when soil moisture is sufficient to permit microbial and root respiration (Xu and Qi, 2001). Maestre and Cortina (2003) discovered that soil temperature explained less than 30% of the temporal variability within a semiarid steppe, which supports this hypothesis that R_{TOT} is constrained by soil moisture at higher temperatures. Climatic factors (soil temperature and moisture) are good predictors of the temporal variability of R_{TOT}, whereas soil factors (bulk density, N and TC) seem to be better predictors of the spatial variability of R_{TOT} (Franzluebbers et al., 2002).

2.6 Temporal Variability of Net Ecosystem CO_2 Exchange

Global C models have difficulty balancing the amount of C released from fossil fuel emissions and land-use change with the total amount of C released because of the spatiotemporal variability of terrestrial and oceanic NEE and R_{TOT} (Fan et al., 1998). These spatial and temporal trends can be attributed in some part to the various climatic influences controls (section 2.5) in addition to the dynamics of larger weather events (Suyker et al., 2003). Temperature, through its control on C mineralization and microbial activity (Fang and Moncrieff, 2001; Kane et al., 2003), is considered the primary mechanism that regulates the seasonal variations of R_{TOT} at the plot scale for forest ecosystems (Davidson et al., 1998; Raich, 1998) and grasslands (Suyker and Verma, 2001). However, at the ecosystem scale, soil water content (Davidson et al., 1998), soil substrate quality (Aerts, 1997) and vegetation types (Raich and Tufekcioglu, 2000) also seem to influence C exchange. Despite these numerous controls on C exchange, R_{TOT} has typically been modelled using Q_{10} (exponential, linear or quadratic) models (Fang and Moncrieff, 2001; Rustad et al., 2000). Employing various relationships that fit the data

suggests that the R_{TOT} and NEE response to temperature has more than one explanation, requiring further exploration of the other controlling factors.

2.6.1 Inter-annual Variability of Net Ecosystem CO_2 Exchange

Grasslands have been shown to sequester atmospheric CO_2 during the growing season (May to September) through plant uptake and root storage (Frank et al., 2002). This usually coincides with the timing of the highest leaf area index (LAI), above - ground biomass (Dugas et al., 1999; Frank and Dugas, 2001; Kim et al., 1992). In temperate regions this seasonal timing of maximum NEP and NEE usually occurs in late May or early June and uptake is sustained until the end of August (Hunt et al., 2002) when plant senescence begins. However, inter-annual variability of temperature and moisture regimes can alter this timing (Suyker et al., 2003). Annually, the NEE for grasslands typically range between -300 g C m^{-2} and + 155 g C m^{-2} during the growing season with maximum daily rates ranging from -1 g C m^{-2} d^{-1} and -9.5 g C m^{-2} d^{-1} (Novick et al., 2004). Many factors influence the inter-annual variability of NEE, some of which include the length of the growing season, overall cloudiness, LAI, above-ground biomass, spring temperatures (that affect leaf out) and moisture stress (relating to timing and magnitude of precipitation events) (Sims and Bradford, 2001; Dugas et al., 1999; Griffis et al., 2001a; Law et al., 2002; Suyker and Verma, 2001). However, the key variable seems to be water supply (Meyers, 2001). Water availability severely limits the C acquisition of ecosystems with the result that during a summer drought period net ecosystem productivity (NEP) is closely related to both the frequency and the timing of rainfall events (Frank and Dugas, 20001; Sims and Bradford, 2001). Drier years, or years with severe moisture stress early in the season, have also been shown to exhibit lower

growing season NEE uptake for grassland ecosystems compared to well-watered years (Frank and Dugas, 2001; Meyers, 2001; Suyker et al., 2003). This reduced uptake was attributed a decline in growing season precipitation, above-ground biomass and the photosynthetic surface area, hence lowering growing season fluxes. For example, the growing season fluxes (April 24 to October 26) for a Northern mixed grass prairie ecosystems was 2.6 times larger in 1999 (-130 g C m^{-2}) than in 1998 (-49 g C m^{-2}) although the amount of precipitation was similar for both years (405 and 508 mm during the growing season, respectively) (Frank and Dugas, 2001). However, in 1998, 245 mm of precipitation was received after August 15, which was after the period of greatest biomass production. This suggests that antecedent soil moisture conditions and the timing of precipitation are critical to the establishment of biomass (Scurlock et al., 2002). During a summer drought positive NEE values of 3.1 g C m^{-2} d^{-1} (Kim et al., 1992), 1.0 g C m^{-2} d^{-1} (Ham and Knapp, 1998), and 1.3 g C m^{-2} d^{-1} (Kim and Verma, 1990) have been documented for tallgrass dominated prairies.

Studies thus far, although limited in number, suggest that the inter-annual variability of NEE in grasslands is driven by drought impacts on photosynthesis and subsequent growth (Knapp et al., 1998). Thus, NEP is the key determinant in the inter-annual C balance. However, this is in contrast to forest ecosystems in that R_{TOT} (through exposed surface litter) not photosynthesis, was the primary contributor to the inter-annual C balance among sites (Valentini et al., 2002).

2.6.2 Diurnal Variability of Net Ecosystem CO_2 Exchange

Daily maximum NEE rates often occur between the hours of 10:00 and 14:00 and usually only a 10 - 15% deviation from daily values occurs from 9:00 to 16:00 (daylight

hours) under sunny skies (Hunt et al., 2002; Mielnick and Dugas, 2000). This suggests that chamber methods can approximate daily CO_2 fluxes (within 15%) if the measurements are constrained to midday. However, this daily variability of NEE is governed by cloud cover (control on PAR) (Saigusa et al., 1998), precipitation and wind speeds (Emmerich, 2003), all of which are dynamic and can vary on short timescales. Saigusa et al. (1998) noted that when the photosynthetic photon flux density (quantity of light - photon - that can be utilized in chlorophyll reactions) (Q_P) was less than 35 mol m^{-2} d^{-1} CO_2 fluxes were less than 2.7 g C m^{-2} d^{-1} throughout the growing season. Conversely, when Q_p was larger than 45 mol m^{-2} d^{-1}, the daily NEE increased to values greater than 10.9 g C m^{-2} d^{-1}, which was more pronounced with increasing LAI (i.e. more leaf level photosynthetic capacity). Furthermore, when rain fell at night or early in the morning, daily CO_2 uptake maintained robust values, whereas when it fell during the day CO_2 emissions increased. This increase in emissions is possibly due to rain flushing out CO_2 trapped in soil pores or a combination of both an addition of moisture and high daily soil temperatures stimulating microbial activity (Hunt et al., 2002; Sims and Bradford, 2001).

2.7 Spatial Variability of Net Ecosystem CO_2 Exchange

Spatial variability is encompassed within and between land types, thus, the significance of environmental controls may differ at various sites and scales (Maestre and Cortina, 2003). Most studies that examine NEE usually quantify it over one distinct, apparently homogeneous area using EC or BREB techniques, which is concerned with temporal, rather than spatial variability. To address spatial variability the use of the

chamber method is usually employed. As such, there are only a few studies that have examined the NEE for grasslands using chamber methods (LeCain et al., 2002).

Numerous landscape factors can be related to spatial variability of NEE. Lower topographical features, such as hollows and pools, generally have larger NEE uptake, whereas higher features, hummocks and ridges have lower sink potentials through greater aerobic conditions (Waddington and Roulet, 1996). The tropic and moisture status seem to influence NEE such that nutrient rich species are able to sustain more lucrative plant growth during the summer and were reduced under nutrient limiting conditions (Bubier et al., 1998). One study used EC to spatially examine the NEE of 5 fields (winter wheat, winter barley, spring barley, maize and grass) within an agricultural watershed in Denmark (Soegaard et al., 2003). The average daily NEE from May to July, 2003 was -2.5, -4.7, -3.8, -3.4, and -0.5 g C m^{-2} from winter barley, winter wheat, grass used for hay, spring barley and maize, respectively. The large values for wheat were attributed to higher LAI and later senescence, whereas the lower value for maize is because it is sown later in the season. Furthermore, grass showed larger NEE than both winter and spring barley and was attributed to large CO_2 gains offsetting large respiratory losses (Soegaard et al., 2004). Although most CO_2 studies focus on natural ecosystems (forest and wetlands), it is evident that agricultural and possibly other human modified systems, especially in the mid-latitudes may be strong contributors to the regional CO_2 budgets.

2.8 Grassland Land-Use and Management

Grasslands are often examined to assess the influence of grazing (Bremer et al., 1998; Bremer and Ham, 2002; Knapp et al., 1998), annually burning (Knapp et al., 1998), or harvesting. These practices alter the LAI and above-ground biomass, and as a result,

may reduce the C sink potential. Spring fires have shown to increase the monthly soil CO_2 flux by 20 - 55% relative to unburned sites, and seasonal soil respiration in annually burned sites was 33% larger than in fire exclusion sites (biotic processes in burned sites are limited by additional factors such as soil moisture and available N) (Bremer and Ham, 2002). This was because exposed soils were warmer, which stimulated biological activity. Also, grazed sites respired 30% less CO_2 than ungrazed sites because of lower canopy photosynthesis and reduced C allocation to the rhizosphere and root biomass (Knapp et al., 1998). However, irrigation increased monthly R_{TOT} by 13% in both grazed and ungrazed sites (Knapp et al., 1998). LeCain et al. (2002) found contrasting results and showed that the removal of 60% of the above-ground biomass had only a minor effect on the ecosystem. This was because approximately 80% of the net C fixed above-ground is translocated to the root system (Schlesinger, 1997). After harvesting vegetation responds quickly to growth and can acquire a sink function within days (Dugas et al., 1999).

Riparian areas act as sinks for sediments and nutrients delivered from upland systems to streams (Naiman and Decamps, 1997). Although many studies examine the possible eutrophication of streams within agricultural areas caused by excessive fertilizer applications, an additional issue may be the possible enhancement of CO_2 released as stimulated by accelerated soil biological activity. However, riparian grasses may exhibit greater respiratory CO_2 losses concurrent with enhanced CO_2 uptake. Thus, assessing the spatial variability and obtaining region specific CO_2 fluxes for soil and vegetative components for riparian areas, and the role they play in grassland ecosystems are crucial to examine.

Chapter 3
STUDY AREA

3.1 PHYSIOGRAPHY OF THE STRAWBERRY CREEK WATERSHED

The study was conducted at the Strawberry Creek Watershed (SCW) (80°23′15″W, 43°33′10″N) in Southwestern Ontario. The watershed is located 1 km east of the town of Maryhill, Ontario, approximately 15 km northeast of Waterloo, Ontario. SCW drains a small (2.7 km^2) agricultural basin (Figure 3.1) eastward into Hopewell Creek and eventually into the Grand River, which is one of the largest watersheds in Southern Ontario (6800 km^2) (GRCA, 1998). It is a perennial, first-order stream that is approximately 2 km in length and is typically less than 1 metre wide for most of the year (except during spring melt and short, intensive precipitation events). The basin is divided into an upper and lower portion (Figure 3.1). Many of the fields and agricultural lands, especially those in the upper portion of the basin, are drained by tile systems. These tiles are constructed of clay or plastic, located approximately 0.75 – 1.00 m below the ground surface and are in place to enhance the rate of water drainage from the fields (Harris, 1999). The lower portion of the basin is not tiled, excluding the Harris field (Figure 3.1)..

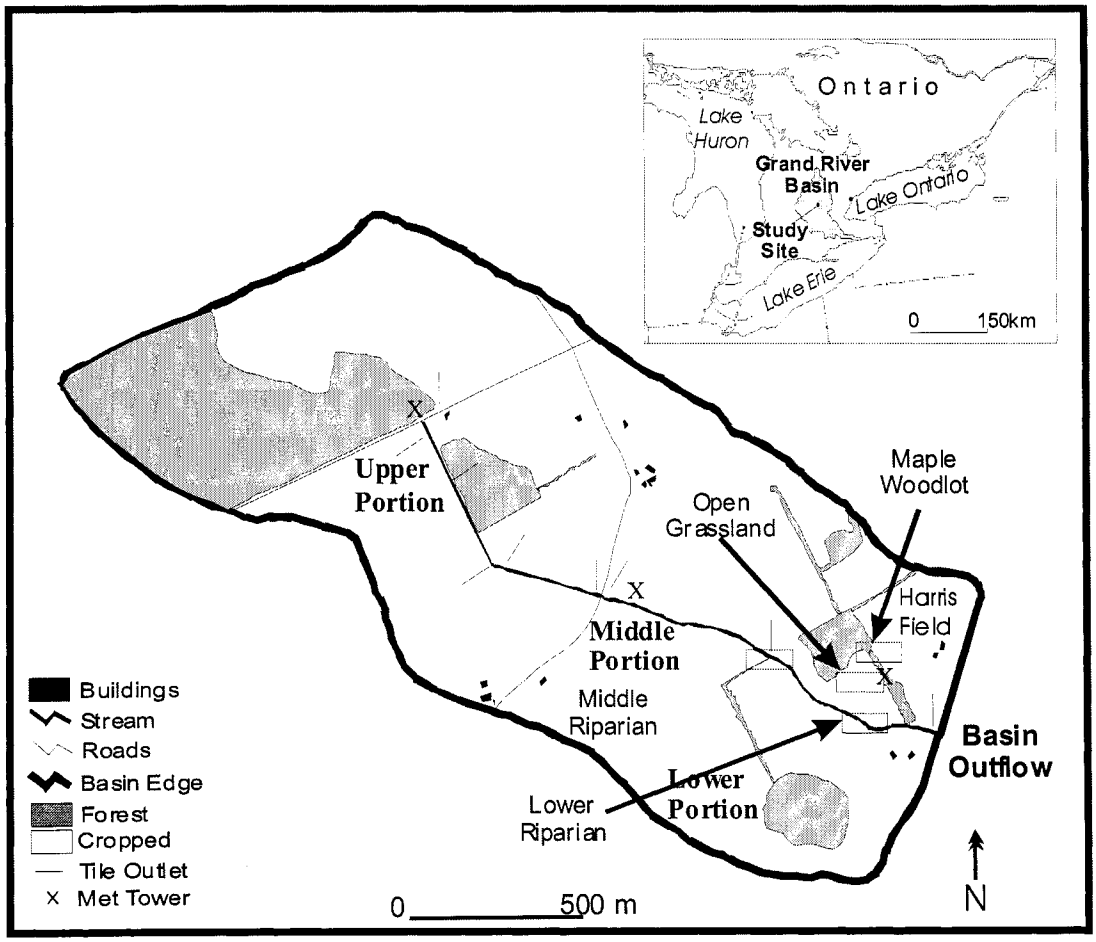

Figure 3.1: Map of Strawberry Creek Watershed, study sites and location relative to Southern Ont. (inset). The watershed perimeter is defined as the area of land that drains to the culvert at the basin outflow. Refer to section 3.3.3 for a more detailed description of the study sites.

3.1.1 Regional Geology and Geomorphology

Strawberry Creek has been shaped primarily by late Quaternary glacial processes and is located towards the western edge of the Guelph Drumlin field (Chapman and Putnam, 1984). Drumlins in this region are low and widely dispersed, with long, east to west axes. Much of the area between the drumlins is relatively flat, generally having relief less than 30 m within 10 km of the study site (Karrow, 1987). Overall, the general topography of SCW is relatively flat with slopes typically less than 0.03 (Harris, 1999).

One notable exception is the Breslau Moraine which rises almost 15 m above the surrounding terrain, forming a large hill towards the western edge of the drainage basin (Karrow, 1987) (figure 3.2). Much of southern Ontario is underlain by stratified glacial tills and bedrock of Silurian origin with the underlying geologic materials in the study area composed primarily of three glacial till units. In much of the SCW, the Port Stanley till sheet comprises the surface material and is typically sandy and silty in texture and generally only a few metres thick (Karrow, 1993). This till matrix has a 50% carbonate content originating from limestone and dolomite (Karrow, 1987). Underlying the Port Stanley till is finer, clay-rich Maryhill till, which is less than 3 m thick (Karrow, 1993). A very compact and stoney Catfish Creek till is situated below the Maryhill till and is about 3 - 7 m thick, below of which is bedrock.

3.1.2 Strawberry Creek Soils

Soils in the region have been created over loamy parent material consisting of 50% sand, 35% silt and 15% clay (Chapman and Putnam, 1984). The soils are classified as Grey Brown luvisols, Melanic Brunisols and Humic gleysols (Presant and Wicklund, 1971). At 2 m, a fine, clay-rich layer is present that acts as an aquiclude between shallow and deep soils. This is the reason many agriculture fields within this region contain tile drainage systems. Surface soils within the riparian areas typically contain an organic layer (0.20 – 0.40 m deep), underlain by a gleyed clay layer up to 0.6 m (greatest depth analyzed). Fine grass roots are concentrated in the upper 0.2 – 0.5 m, but extend to greater depths. Within the shallow soil matrix medium sized stones (<0.2 m wide) were found in the buffer area. Similar findings were observed for the open grassland soil, but the presence of stones was more common. The water table during the summer season in

this area is relatively stationary at 0.6 m below surface at the riparian areas and the grassland (Macrae, 2003). However, the woodlot had an organic layer extending beyond 0.4 m deep, and which depth a water table was encountered in late May, 2003.

3.2 LAND-USE TYPES WITHIN THE STRAWBERRY CREEK WATERSHED

Land-use in the area consists of residential lands (houses and barns), in addition to agricultural cash crops (corn, soybean, winter wheat and strawberries), open grassland fallow, small deciduous woodlots and narrow grass-dominated riparian sites (Figure 3.1 and 3.2). The approximate percent cover of various land-use types are shown in Table 3.1.

Table 3.1: Approximate percent cover of land-use types within the Strawberry Creek Watershed, Maryhill, Ont. (Source: Macrae, 2003).

Land-Use Types	Percentage Cover in the Basin
Croplands (corn, soybean, wheat and strawberries)	60
Open grassland(grasslands)	15
Woodlots and Hedgerows (maple and cedar)	10
Riparian grasses	10
Residential areas	5

Agriculture is, and has been, the principle land-use in the area. Organic (cattle and poultry) fertilizers are applied periodically throughout the year to 40% of the basin (upper portion) (Macrae, 2003). It is estimated that inorganic fertilizers are applied to 35% of the basin (middle and lower portions) at a rate of 1.5×10^5 kg NO_3-N yr^{-1} and 2×10^3 kg P yr^{-1} in the form of manure and fertilizers (Macrae, 2003). These numbers are approximations because it is often difficult to obtain exact quantities of fertilizer use from land owners because of the lack of documentation.

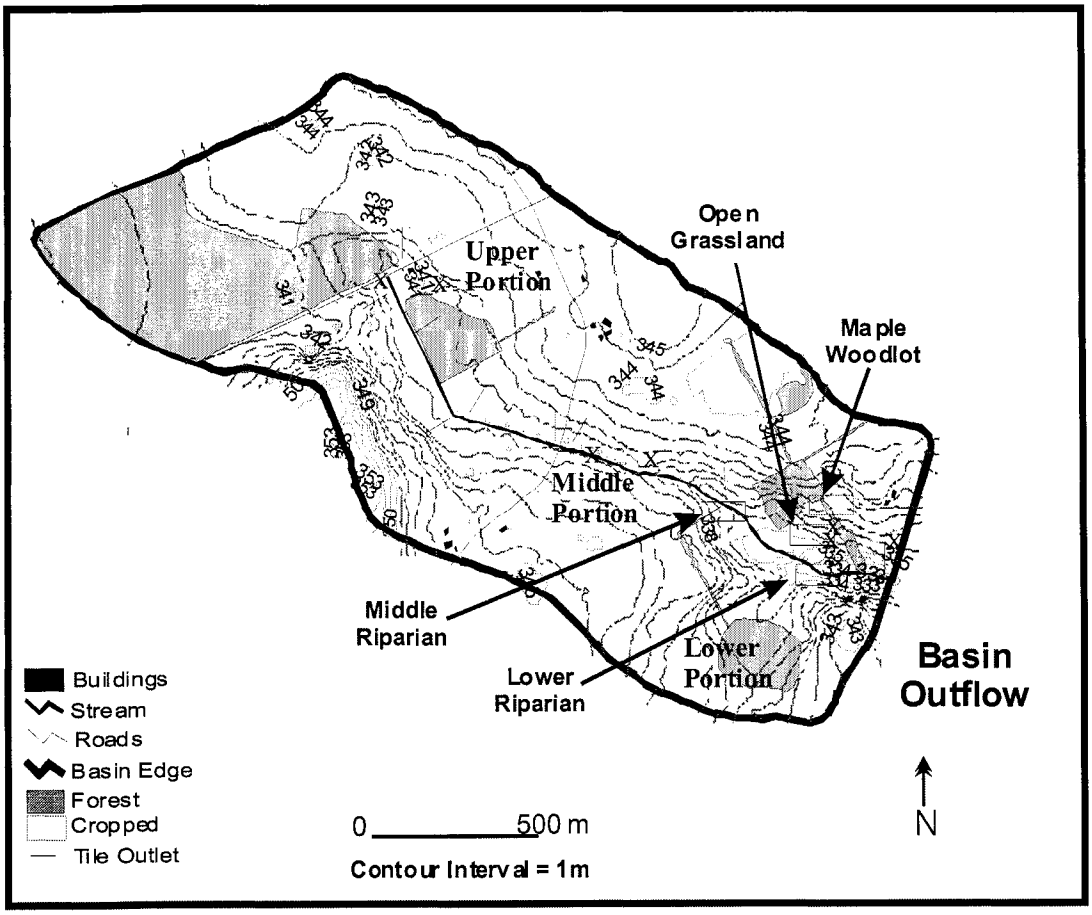

Figure 3.2: Contour map of the Strawberry Creek Watershed, Maryhill Ont.. Catchment boundary, stream, residential buildings, woodlots, cultivated lands and drainage tile locations are shown. See Figure 3.3 for more detailed agricultural land-use and refer to section 3.3.3 for a more detailed description of the study sites.

3.3 VEGETATION SPECIES WITHIN THE STRAWBERRY CREEK WATERSHED

This study basin is unique, such that numerous ecosystem types are represented within a small area (2.7 km^2). These include riparian grasslands, open grassland fallows, deciduous woodlots and several agricultural crops (e.g. corn and soybean).

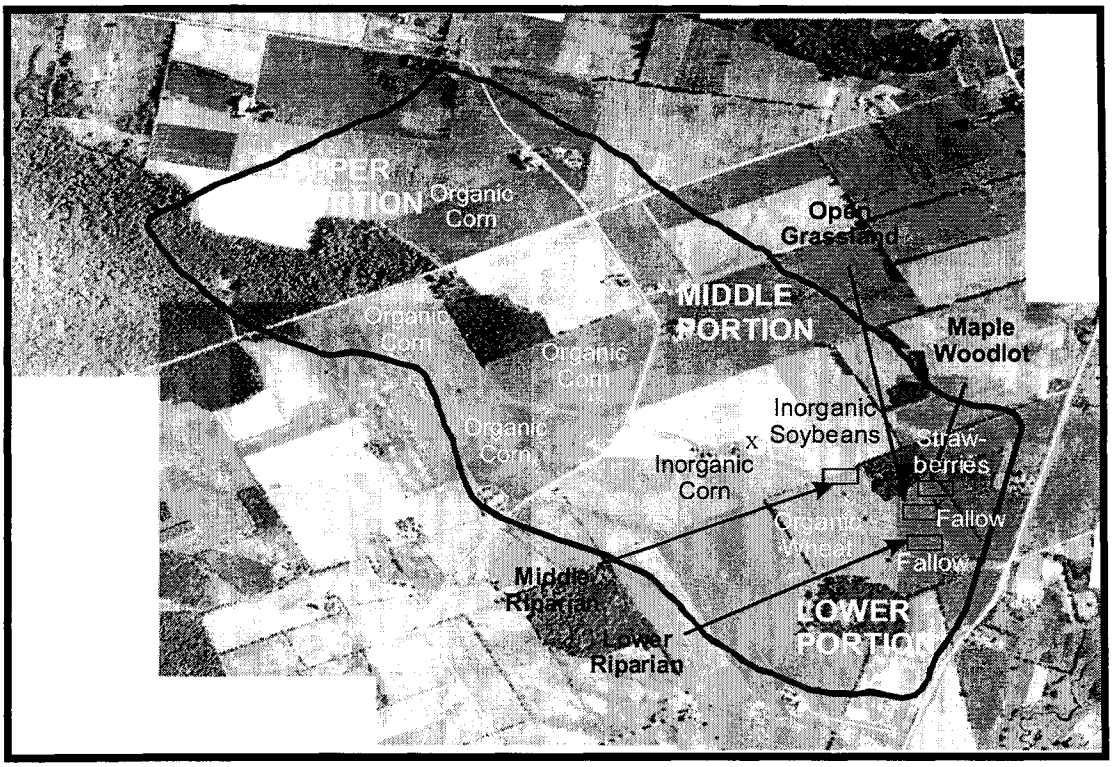

Figure 3.3: Air photo of the Strawberry Creek Watershed, Maryhill, Ont., showing the type of fertilizer and crop grown in each field. Refer to section 3.3.3 for a more detailed description of the study sites. Scale is the same as shown in Figure 3.1 and 3.2.

3.3.1 Riparian Zone Vegetation

A strip of vegetation separates Strawberry Creek from the adjacent land along most of the stream reach. In areas of rapid change in slope, or on poorly drained soils, cultivation is difficult. As a result, these areas are not farmed and it is very probable that the perimeter of these riparian areas represent land which historically has not been cultivated. The riparian zone over most of the SCW is approximately 3 - 10 m wide, on each side of the stream, but is much narrower in some areas. In the lower portion of the basin riparian areas are typically 8 - 10 m wide with a slope of about 0.05. In the upper

section of the basin riparian areas are narrower and steeper (4 - 6 m wide with a slope of 0.10).

The vegetation within the riparian zones is dominated by warm season tall grasses (*Gramineae spp.*) consisting of Big Bluestem (*Andropogon gerardi*), Indian grass (*Sorghastrum nutans*) and Little Bluestem (*Schizachyrium scoparium*), with less amounts of alfalfa (*Medicago sativa*). They also contain non grass herbaceous vegetation (forbs) including Canada Goldenrod (*Solidago canadensis*), Yarrow *(Achillea millefoleum*), Thistle (*Cirsium spp.*), common Milkweed (*Euphorbia corollata*), Queen Anne's Lace (*Daucus carota*) and Common burdock (*Arctum minus*) (Harris, 1999; Kline, 1997). A few trees (*Salix spp.*) are also present in the riparian areas towards the middle-to-low end of the basin. Grasses and forbs comprised of Upland White Aster (*Solidago ptarmicoides*), Field thistle-pink flower (*Cirsium discolor*) and Ticktrefoil species (*Desmodium spp.*) have developed in the fallow fields, but the fallow is dominated by tallgrasses (*Gramineae spp.*) such as those present in the riparian areas.

3.3.2 Woodlot Vegetation

Most of the original forest cover was removed from the area in favour of agriculture. However, small woodlots and hedgerows remain (Figure 3.1). Two woodlots, one in the northern portion, and one in the southern, are located in the vicinity of the study area. In the northeast, the dominant species are Sugar Maple (*Acer saccharum*) with lesser amounts of American Beech (*Fagus grandifolia*), Trembling Aspen (*Populus tremuloides*), White Ash (*Fraxinus americana*) and American Basswood (*Tilia americana*) (Harris, 1999). The southwest woodlot is located on poorly drained, organic

soils and is dominated by Red Maple (*Acer rubrum*) with small amounts of Red Ash (*Fraxinus pennsylvanica*) and Eastern White-Cedar (*Thuja occidentalis*) (Harris, 1999).

3.3.3 Study Site Selection Rationale

Study sites were chosen based on location within the watershed and site history. In particular, riparian zones along two sections of the stream were selected for study and were chosen to determine if grass-dominated riparian areas adjacent to active agricultural land differed in their C dynamics when compared to a riparian area not influenced by such land management. The first reach was located in the southern portion of SCW (called Lower Riparian (LR)) (Figure 3.1). Both sides of the stream are adjacent moderately sloped open grassland that extends about 300 m upland. The riparian area is about 6 - 8 m wide on each bank. The second riparian area is located in the middle of the watershed (called Middle Riparian (MR)), approximately 350 m upstream from the LR site. This riparian area is about 10 - 12 m wide on each bank and is adjacent to agricultural land (soybeans to the east and corn to the west) spanning about 500 m upland and underlain by drainage tiles. In addition, an open grassland (OG) and a maple woodlot (WOOD) were also explored. The OG site had similar vegetation to that of the riparian areas (Section 3.3), was harvested twice during the summer, and was explored as somewhat of a control compared to the riparian areas. The WOOD site was included to assess soil respiration from a land-use type with different vegetation species, that is not dominated by roots, and to complete an upland to riparian transect (Figure 3.1). Within each site, collars were chosen to represent vegetated and soil locations (explained further in section 4.2.2), with vegetative collars primarily consisting of grass species.

3.4 HISTORICAL AND 2003 CLIMATE

The study site is located within a humid continental climatic region with a mean annual temperature of 6.7°C, mean annual precipitation of 909 mm (160 mm as snow) and annual potential evapotranspiration of 590 mm (Environment Canada, 2003). Averaged 2003 summer (May – September) air temperature (T_a) was within 1°C of the 30-year normal (16.5°C and 16.4°C for 2003 and the 30-year normal, respectively (Environment Canada, 2003). However, the summer precipitation was 69% of the 30-year normal (229 mm and 423 mm for 2003 and the 30-year normal, respectively) (refer to Figure 5.2).

Chapter 4
METHODOLOGY

4.1 INTRODUCTION

The field component of this study was conducted between May and October, 2003. CO_2 data from May 28 to September 12 was collected, on average, twice a week along with two nighttime respiration measurements performed on September 29 and October 21. The gap in data collection from May 7 to May 28 was the result of complications with the EGM-1 Infrared gas analyzer (IRGA). The second component of the study, partitioning root from soil CO_2 respiration, was performed in the lab during March and April, 2004.

4.2 FIELD INSTRUMENTATION

Extensive networks of instruments were installed within the SCW to measure plot scale CO_2 exchange and meteorological variables. Land-use, particularly cropped terrains, restricted the placement of most equipment to riparian zones and open grassland fallows, which would minimize impacts on local farmers. Figure 4.1 shows the location of meteorological instruments and CO_2 measurement sites within SCW. Much of the instrumentation and all the study sites were concentrated within the middle and lower portions of the basin, as a result of land accessibility and to utilize the presence of high spatial variability in location of vegetative terrain within a smaller, more isolated area.

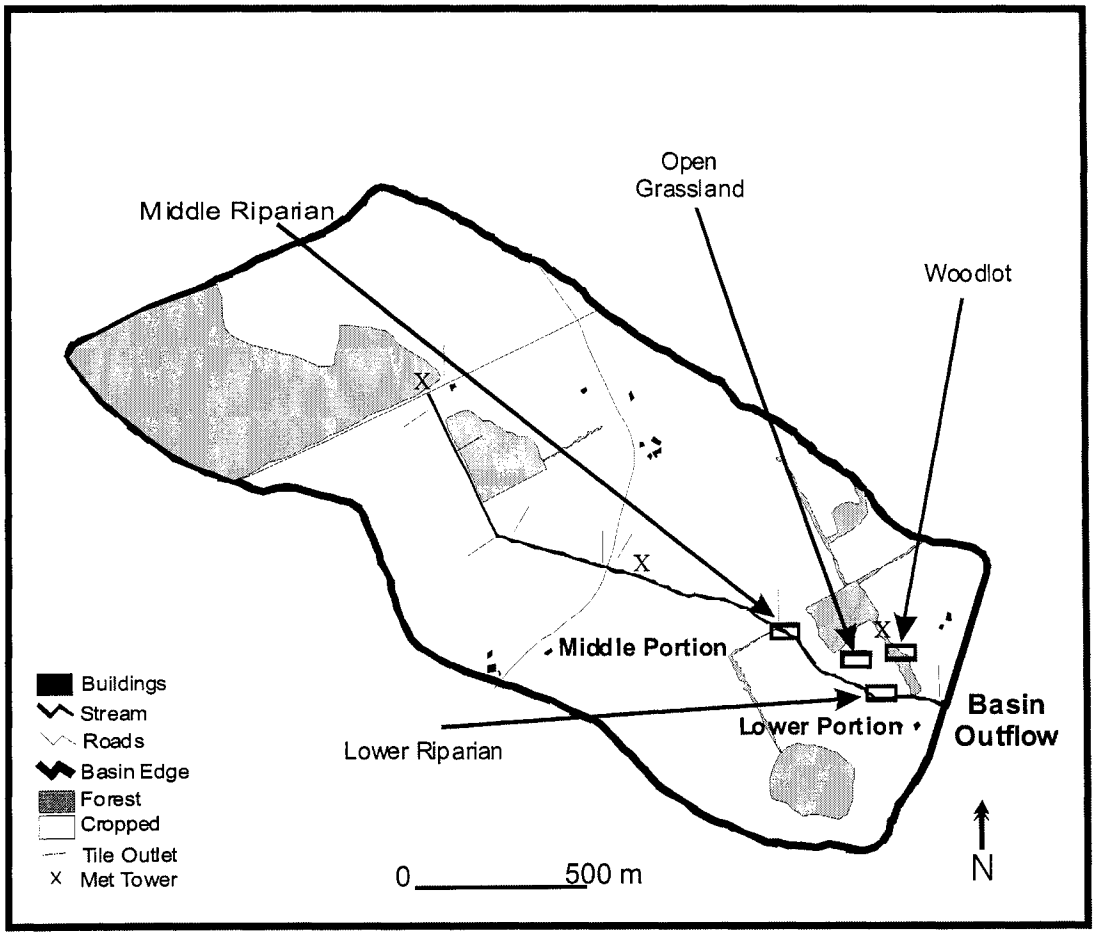

Figure 4.1: Instrument and CO_2 measurement site locations within Strawberry Creek Watershed, Maryhill, Ont., 2003.

4.2.1 Meteorological Instrumentation

Two automated meteorological stations were installed within the middle and lower portions of the basin (Figure 4.1), one within the riparian zone and the other in a maple woodlot. A CR 21X data logger was used to continuously monitor the meteorological variables at both locations during the study (Table 4.1).

Table 4.1: Manufacturer and characteristics of meteorological instruments used. Note: [1] only the meteorological station at the middle riparian area was equipped with a rain gauge and [2] soil moisture was measured at depths of 10 and 50 cm.

Parameter	Instrument and Manufacturer	Scan Rate	Recording rate
Temperature and relative humidity	CS500 (Campbell Scientific)	Every 5 seconds	Averaged half-hourly
Wind speed and direction	Wind Sentry (RM Young)	Every 5 second	Averaged half-hourly
Rainfall [1]	Tipping Bucket (Texas Electronic)	Every 5 seconds	Summed half-hourly
Net radiation	NR Lite Radiometer (Kipp Zonan)	Every 5 seconds	Averaged half-hourly
Soil moisture [2]	TDR probe (30 cm wave guide) CS616 (Campbell Scientific)	Every 5 seconds	Averaged half-hourly
Ground heat flux	HFT03 Heat Transducer (Campbell Scientific)	Every 5 seconds	Averaged half-hourly

4.2.2 Site Preparation and Arrangement of Collars

Study locations for CO_2 measurements were chosen based on proximity to actively farmed land, streams and site history (Section 3.3.3). The number of collars and vegetation types within the collars are shown in Table 4.2. Collars within the two riparian areas, MR and LR, were arranged in matched pairs, representing vegetation and bare soil. These sites were situated approximately 9 and 15 m from the centre of the stream. The spread of the matched pairs was arbitrarily chosen to disperse the collar locations, but not to address the possibility of a distance relationship from the stream. The inclusion of soil plots, although not representative of the agricultural watershed because the majority of the land is covered by grasses, was to assess soil respiration by separating below-ground from above-ground plant respiration (PR). This would permit the examination of whether the variability in CO_2 exchange is influenced more by soil or vegetation dynamics. For the soil plots, which represent soil microbes, root and mycorrhizae respiration (herein referred to as Bare), all the above-ground vegetation was removed 2 weeks prior to the

first sampling date (May 7, 2003) and periodically over the duration of the study to ensure no above-ground growth in the collar. Vegetated plots, which represented ecosystem respiration of both soil and vegetation components (now referred to as Veg), were occasionally clipped to a height of 15 cm.

Table 4.2: Quantity of collars and vegetation contained within collars at each site. Note: each vegetation collar (riparian and open grassland fallow) contained about 10 - 15% alfalfa by weight (data not shown).

Site	Number			
	Soil	Vegetation	Vegetation Type	Adjacent terrain cover
Middle Riparian	4	4	Warm tall grasses	Corn and soybean (inorganic fertilizer)
Lower Riparian	4	4	Warm tall grasses	Grasses
Open Grassland	3	3	Warm tall grasses	Grasses (harvested 2-3 times yearly)
Woodlot	3	0	Soil in maple forest	Soil

Clipping vegetation within 2 - 5 cm of the ground surface reduced soil fluxes from a Minnesota grassland by 10 - 19% through reduced C substrate supplied to roots (Craine et al., 1999). However, the vegetation clipped in this study was minimal (usually no more than 3 cm at one time with standing vegetation height maintained at least 15 cm high). This clipping was performed to allow the chamber to be placed on the collar while minimizing any possible plant stress from vegetation folding within the chamber. Consequently, the removal of a minor portion of the above-ground vegetation should have minimal implications on C allocated below-ground. Clipping also alters microclimates through enhanced soil temperatures and soil moisture loss (Wan et al.,

2002). However, grass vegetation dominated all locations, excluding the woodlot, the altered microclimates and the decreased respiration should be experienced at all sites.

4.3 Acquisition of Field CO_2 Data

In order to relate CO_2 fluxes to environmental controls it is necessary that the measurements made are at the same spatial and temporal scale at which the driving environmental variables change (Davidson et al., 2002). Thus, the use of chambers provides the most direct way to measure NEE and soil R_{TOT} from Bare and Veg plots. This enables the CO_2 budget to be estimated for various mixed ecosystems and allows biotic (C/N, pH, TC) and meteorological (temperature, soil moisture, PAR) controls on the surface-atmosphere CO_2 exchange to be characterized (Rochette et al., 1992b; Lund et al., 1999). The majority of studies examining terrain-scale (plot scale from centimetres to 10's of metres) CO_2 fluxes have relied on chamber techniques (Bremer and Knapp, 1998; LeCain et al., 2002; Maestre and Cortina, 2003; Waddington et al., 1996; Xi and Qi, 2001). This is because chambers are simple to employ, easily constructed and transported between sites (Rochette et al., 1992b). In addition, the chamber technique can overcome the presence of surface vegetation that interferes and complicates EC measurements (Lund et al., 1999). However, the main drawback of the chamber method is that they can disturb and alter the natural environment (pressure, CO_2 gradient and wind velocity), but numerous chamber types are still used because of their above-mentioned advantages and methodological measures have been employed to minimize these disturbances and uncertainties.

4.3.1 Perturbations of Chamber Measurements

When placing chambers, and their associated collars, in the ground, precautions must be taken to minimize ground disturbances and possible CO_2 perturbations. The presence of chambers can induce flux disturbances related to air pressure differences between the chamber headspace and the ambient atmosphere, modify wind speeds, influence the soil-to-air CO_2 gradient and alter the chamber temperature and relative humidity, through evaporation, within the chamber (Davidson et al., 2002; Lund et al., 1999; Welles et al., 2001). Since the chamber remained on the collar for only a few minutes, the modification of temperature, pressure, wind speeds and the CO_2 concentration gradient are usually minimal (Longdoz et al., 2000).

4.3.2 Field CO_2 Sampling Scheme, Frequency and Chamber Employment

The sampling scheme and interval chosen was aimed at evaluating the change in CO_2 dynamics over the growing season (May - September). Most samples were obtained between the peak growth hours of 10:00 and 16:00 to minimize flux variations caused by the diurnal cycle (Mielnick and Dugas, 2000; Laporte et al., 2002) and to obtain fluxes operating at maximum levels to ensure existing spatial variability is captured. A pseudo-replication process was employed which entailed that each collar was sampled about twice a week, from May 28 to August 19. From August 19 to September 13 sampling was conducted once a week. The sampling scheme was aimed to acquire greater spatial data set over the study period, rather than the more common approach to extensively replicate a few sites, less frequently (Buchmann, 2000; LeCain et al., 2002; Maestre and Cortina, 2003). However, each site contained at least 3 Bare and 3 Veg plots, which partially addressed the issue of site replication. Furthermore, chambers provide only point

measurements and to allow temporal/seasonal comparisons the daily sampling scheme was altered and fluxes were grouped into climatically distinct phenological periods (*cf.* Griffis et al., 2000a; Petrone et al., 2003; Waddington et al., 1998) so that diel variations can be best accounted for. Another drawback to chambers is discontinuous measurements, so that when comparing, or extrapolating results many inferred assumptions must be made, such as flux measurements are representative of daily averages, and fluxes are conservative between sampling dates (Mielnick and Dugas, 2000; Tufekcioglu et al., 2001).

The evolution of CO_2 from Bare and Veg plots were measured using a dynamic closed NEE chamber system similar to that of Waddington and Roulet (2000). Collars were constructed of 19 cm (inside diameter) polyvinylchloride (PVC) plastic pipe and cut to a height of 10 - 20 cm, with perforated grooves etched into the lower 3 - 6 cm of the collars for easier placement into the soil. The chamber was placed in a 3 mm wide groove that was cut into the top of each collar. PVC collars were inserted 2 - 4 cm into the soil, 2 weeks prior to sampling on May 7, and remained permanently in place during the entire study. This was done to allow repeated measurements at a single location, while minimizing soil disturbances (root growth into the soil and under the collar) to better assess temporal influences (Tufekcioglu et al., 2001).

To collect point measurements of CO_2 the enclosures were placed on the collars and the grooves were filled with water to obtain an air tight seal. The chamber enclosure (surface area 0.03 m^2, volume 0.06 m^3) was made of clear Plexiglass, which transmits about 87% of PAR (Waddington and Roulet, 2000). The clear chamber allowed NEE (plant uptake simultaneously with soil and plant respiration), whereas a dark chamber

(surface area 0.03 m^2, volume 0.06 m^3) was used to measure soil and plant respiration. To obtain the chamber volume the adjustment height within the collar was initially measured by averaging the distance between the soil surface and the top of the collar at 4 reference locations. The entire system (Figure 4.2) utilized was closed in that air was circulated through tygon tubing between the chamber and an EGM-1 Infrared Gas Analyzer (PP Systems, Amesbury, MA) and gradient effects were minimized by circulating the air within the chamber.

The CO_2 flux was determined by the rate of increase in CO_2 concentration (ppm) over the 5-minute interval (Lund et al., 1999; Welles et al., 2001). A 30 s equilibrium period passed before the first CO_2 measurement was recorded (t = 0) to allow the soil and/or vegetation to adjust to the initial chamber disturbances. Thereafter, the CO_2 concentration was recorded every minute for 5 minutes.

The temperature and relative humidity (RH) inside the chamber was maintained at ± 2°C and ± 10%, respectively, of initial conditions. This was done by using a cooling system which consisted of a heat exchanger coil, water flow system and a cooling bath. This provided a cold source to reduce water vapour accumulation and regulate temperatures within the chamber. Every 20 minutes (10 minutes on days when the ambient temperature was greater than 25°C) the water in the coil was replaced and between collars measurements the chamber was ventilated by alternating between clear and dark chambers. Air inside the chamber must also be sufficiently mixed to minimize the development of a concentration gradient, but the method of mixing must be accomplished without ventilating the soil surface or creating localized pressure gradients (Welles et al., 2001). Thus, a CPU fan was installed in the chamber and run from a 12 V

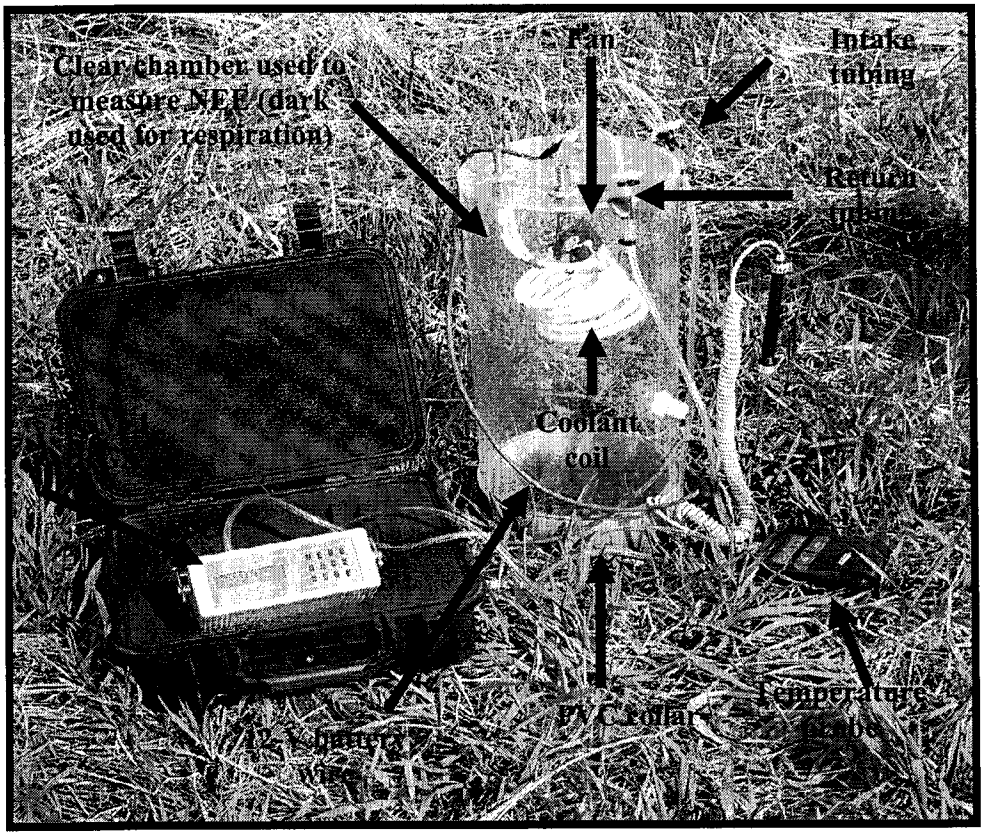

Figure 4.2: Experimental set-up employed to measure the CO_2 evolution. Shown is the clear chamber used to measure Net ecosystem CO_2 Exchange, for MR Bare collar in early May, 2003.

power source during each 5 minute sampling interval. However, the fan may reduce the natural variability of wind speed and alter boundary layer formation. This was likely a minor issue with the short 5 minute sampling interval.

In conjunction with the CO_2 concentration, soil temperature, soil moisture and photosynthetically active radiation (PAR) were also measured at 3 specific locations surrounding each collar that was representative of either the Bare or Veg surface covers. The soil temperature was measured using an HH200A digital temperature probe (Omega,

Quebec) at 4 depths (5, 10, 20 and 30 cm) and soil moisture was integrated to a depth of 12 cm using a portable Hydrosense^{TM} time domain reflectivity (TDR) probe (Campbell Scientific Inc, Utah). PAR was measured at each site using a LiCor Quantum Sensor (LiCor, Nebraska) placed at eye height (about 1.5 m) and held 0.75 m outwards, and an average value was obtained by orienting the PAR sensor in the principle coordinate directions (N, E, S and W).

4.3.3 CO_2 Flux Calculation and Quality Control of CO_2 Data

The CO_2 concentration was sampled over 5 minutes, every minute, to obtain an overall rate of change in CO_2 min^{-1}. This method assumes that the CO_2 evolution is from diffusion rather than advection, or ebullition, and diffusion has been shown to be the dominant mechanism in which CO_2 is transported from the soil (biogenic emissions from soil decomposition and root respiration) to the atmosphere (Welles et al., 2001). Non-linear diffusion occurs during thawing and wetting events (Emmerich, 2003; Sims and Bradford, 2001), which was not encountered in this study. Flux sign directions herein will follow the meteorological convention, such that positive values represent a flux from the biosphere to the atmosphere (CO_2 loss) and negative values a flux from the atmosphere to the biosphere (CO_2 uptake) (Kim et al., 1992).

The concentration of CO_2 was measured in ppm and converted to mg CO_2 m^{-2} hr^{-1} as shown,

$$F = \frac{\Delta \times MM}{N} \times \frac{V}{A} \times CF \qquad (4.1)$$

where F is the gas flux (mg CO_2 m^{-2} hr^{-1}), Δ is the linear change in CO_2 concentration with time (ppm × hr^{-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 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). For example, Figure 4.3 shows the slope of CO_2 change over a 5 minute interval of -6.4 ppm min^{-1} which is approximately 360 mg CO_2 m^{-2} hr^{-1}. Photosynthesis (NEP) was estimated by subtracting gross respiration (R_{TOT}) from NEE as shown in equation 4.2.

$$NEP = NEE - R_{TOT} \quad (4.2)$$

To quality control the CO_2 fluxes, for each daily measurement, the regression slope (change in CO_2 flux over the 5 minute sampling interval) was compared to the original regression slope that was obtained on the first sampling date for each collar. This was done to evaluate the representativeness of each sampling date compared to the original date (Elberling, 2003) and to ensure that CO_2 diffusion was the dominant mode of transport. If the slope comparison ($r^2_{original}/r^2_{sample}$) was below 0.85 then the sample for that day was not used in analysis. This was the case for less than 1% of the data, which is promising and suggests that CO_2 did evolve primarily from diffusion. In addition, the CO_2 concentration during field analysis periodically jumped from 25 - 50 ppm (or 10 – 20% of normal operating CO_2 values) between sampling minutes. If this occurred, a maximum of 10 seconds was allowed to pass for the concentration to readjust and this new, adjusted value was recorded. If this process prevailed over the sampling time, the chamber(s) were reanalyzed. This phenomenon may be attributed to faunal respiration (e.g. earthworms, beetles, etc.), poor distribution of air, or moisture build-up within the chamber (Nay et al., 1994). Although chamber design was constructed to minimize these disturbances chamber re-sampling of occurred less than 2% of the time.

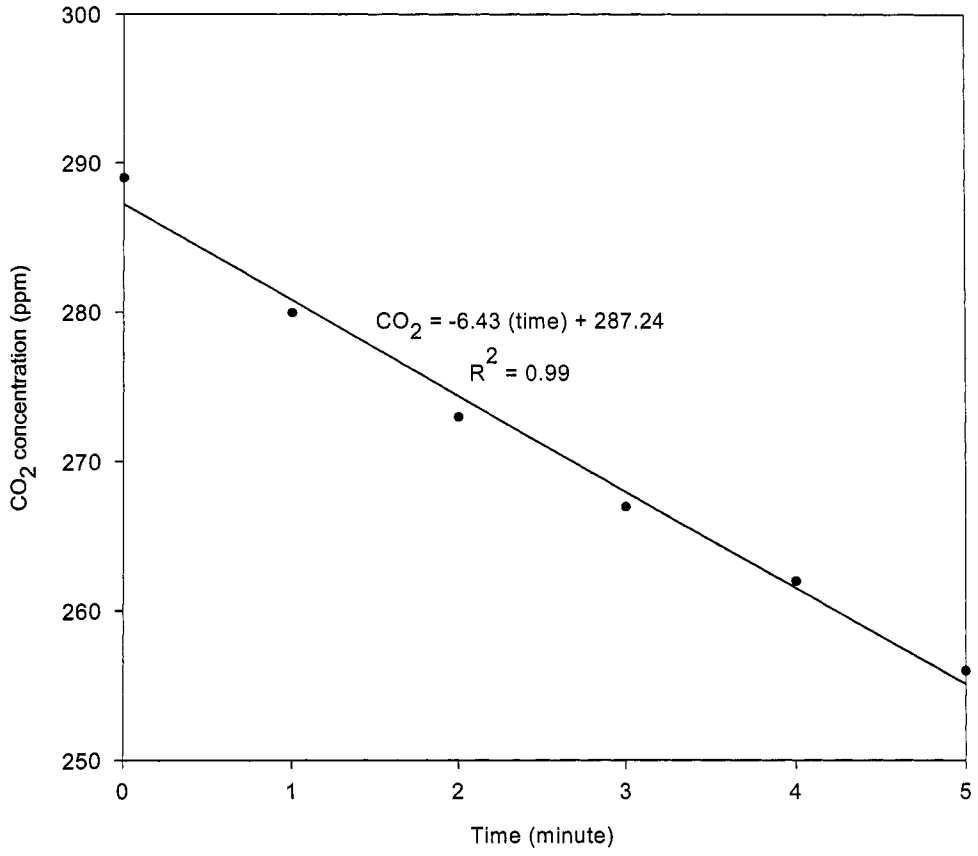

Figure 4.3: Example of the slope-regression process used to measure CO_2 flux. Data is from the MR site, Veg collar for July 8, 2003. The negative slope (-6.4 ppm min^{-1}) represents CO_2 uptake.

4.4 LABORATORY ANALYSIS

The laboratory analysis consisted of examining bulk soil and vegetation properties from the study locations to assess the biospheric determinants of spatial variability.

4.4.1 Soil Characteristics

Soil samples were collected in triplicate from each of the 4 sites and analyzed for bulk density (ρ_b), porosity (ø), soil organic matter (SOM), soil texture, pH and C/ N

ratios. Soil pits were dug 100 cm wide and 60 cm deep and samples were extracted from the vertical side of the pit using soil tins (approximately 9 cm in diameter with a volume of ~490 mL) at depth intervals of 0 - 10, 10 - 20, 20 - 30 and 30 - 40 cm at all 4 locations. However, only data from a depth of 0 - 30 cm was used in analysis because the majority of evolved CO_2, measured at short timescales, originates within the top 30 cm of the surface (Elberling, 2003; Groffman et al., 2002). Prior to analysis, soil samples were oven dried at 105°C for 24 hours. The total carbon (labile organic carbon and carbonate) for all sites was determined through loss on ignition using a muffle furnace and burning samples at 550°C for 45 minutes (Fang et al., 1998).

4.4.2 Vegetation and Root Biomass Analysis

Above-ground green biomass (AGB) was measured at each site, excluding the WOOD, by clipping 3 representative 0.25 m^2 plots on June 4, July 7 and August 5. The green plant material was separated from dead material and straw, oven dried at 80°C for 24 hours, and weighed to obtain total AGB dry biomass (g m^{-2}). No differentiation between speciation of the green material and the amount of hay was made. Root biomass was sampled on two dates, June 24 and August 5 adjacent to the above-ground sample sites. Three cores (56 mm in diameter) to 0.25 m depth were taken at each site. This depth was chosen because 60 - 90% of the total root biomass has been shown to be situated in the upper 0.3 m (Dugas et al., 1999; Frank et al., 2002). Roots were separated from the soil by hand and any remaining rhizosphere soil was removed through elution with water, after which they were oven dried at 80°C for 24 hours. No attempt was made to separate live from dead roots due to the difficulty of differentiating them and the time demand (Sims and Bradford, 2001).

Standing vegetation heights (H_M) at each location, excluding the WOOD site, were measured weekly at three representative (referenced by wooden stakes) locations throughout the study period (May 7 – Sept 12). To compensate for soil compaction, at the beginning of the study a surface reference was marked on each wooden stake (little heaving). Furthermore, when wind and rain toppled the vegetation, the vegetation was pulled and measured against the reference point. Although this may have caused a slight misrepresentation of the height it still allows reasonable relative vegetation heights to be estimated.

4.4.3 C/N Ratios

The C component of soils is comprised of organic carbon (OC) and carbonate (CO_3^{2-}) (Emmerich, 2003), which represents the total soil carbon (TC). However, no separation between organic and inorganic forms was made. The total percent TC (%TC) and nitrogen (N) contents of the soil, for the 4 sites, were determined through dry combustion using a Isochrom - elemental analysis (EA), Carlo-Erba Isotope Ratio Mass Spectrometry, autocombustion carbon - nitrogen analyzer (Micromass UK, Ltd., Environmental Isotope Laboratory, Department of Earth Sciences, Waterloo, Ont.). Approximately 40 mg of soil was weighed for EA analysis to obtain C/N ratios. No differentiation was also made between nitrogen speciation (nitrate, nitrite, ammonia etc.) owing to N's volatile nature and seasonal dependence (Brady and Weil, 1999). Thus, the C/N ratio represents total carbon (TC)/total nitrogen (TN). In addition to the C and N, water extractable phosphorus (EXT-P) from 0 - 20 cm depths were measured (Macrae, unpublished data), which is an indictor of the orthophosphate form directly absorbed by plant cells (McDowell et al., 2001).

4.5 Partitioning of Soil Respiration

The field experiment, during the summer of 2003, examined the daily, point fluxes of CO_2 (NEE, NEP and R_{TOT}) from Bare and Veg plots. Although, the bulk of the basin is vegetated, excluding the WOOD site, the inclusion of soil plots was to further examine the spatial patterns of below-ground CO_2 and determine the magnitude and variations in R_{TOT}, if any, were attributed to plant (above-ground) or soil (below-ground) dynamics. Soil heterotrophic activity is proportionate to the rate of organic decomposition, which is primarily governed by soil temperature and moisture (Fang and Moncrieff, 2001). However, the CO_2 loss from roots and rhizosphere are dependant on the supply of above-ground organics (Hanson et al., 2000). The CO_2 contribution from roots may be independent from the soil C pool and as such, must be explored separately to assess the relative magnitudes and understand the possible responses to climate change (Hanson et al., 2000). However, these two dynamic factors are difficult to separate within a field context (Bouma and Bryla, 2000). Thus, in order to separate the overall contribution of CO_2 respired from roots and soil, a lab experiment was established to isolate these components.

4.5.1 Methods of Partitioning Soil Respiration Components

It is important to evaluate root respiration contributions because ecosystems in which roots and rhizosphere contribute a large proportion of the total CO_2 flux may be the areas which are most sensitive to an increase in soil temperature affecting root and microbial respiration (Boone et al., 1998). Hence, respiration for grasslands and northern ecosystems may be extremely sensitive to temperature increases. To distinguish between hetero- and autotrophic respiration three main methods have been used. These are: 1)

component integration (roots, litter and soils); 2) root exclusion methods; and 3) the application of stable C isotopes.

4.5.1.1 Component Integration and Root Exclusion

The traditional methods for separating the source contributions of soil and root respiration usually involve physical separation and these methods can be broadly categorized as component integration and root exclusion techniques (Hanson et al., 2000). Component integration (CI) involves calculating the individual contributions of each below-ground source of CO_2 (root, soil and litter) and the sum based on subsurface weighted averages (Hanson et al., 2000). Perhaps the biggest disadvantage of the component integration method is that the separation of the roots and litter creates a disturbance to the natural soil structure that will alter soil moisture, microbial species composition, soil texture and gas diffusivity, which can drastically alter the rhizosphere environment (Hanson et al. 2000; Winkler et al., 1996). Furthermore, field and lab experiments which use CI must allow adequate time for roots and soil to equilibrate after the disturbance, but should be analyzed before desiccation or death occurs (Burton et al., 2004).

The root exclusion method (RE) indirectly estimates the root contribution by measuring soil respiration with, and without, live roots (i.e. no direct measurements of bare roots are made) (Hanson et al., 2000). The most common field approach is trenching, which is a straightforward approach to measure R_{TOT} without roots on relatively undisturbed soil. Trenching can be applied to a variety of ecosystems by inserting root growth barriers in the soil to isolate microbial derived respiration (Lohila et al., 2003). Previous studies have assumed that root respiration is a constant proportion of

R_{TOT} throughout the year and the decomposition of the severed roots are not differentiated from soil respiration in the non-root plots (Bowden et al., 1993). If the rate of decay of these roots is higher than soil decomposition rates, these results may misrepresent the total contribution of root respiration. However, some studies have suggested that C in dead roots does not turnover rapidly and are minor contributors to the overall R_{TOT} (Ewel et al., 1987). Thus, the decay of fine roots in the trenched plots would be negligible. Buchmann (2000) compared the respiration of soil plots with recently cut roots and roots that had been dead for up to 6 months and showed that respiration of soil plots with roots cut 24 hours prior to sampling were 20 to 30% higher than ones that were installed 1 to 6 months earlier, and no significant (α = 0.05) was exhibited between collars installed 1 and 6 months earlier. This suggests that higher R_{TOT} rates shortly after the initial disturbance may be the result of high initial SOM decomposition rates from the rhizosphere (including fine roots, mycorrhizae, soil microorganisms and labile organic matter), which continues to contribute to the surface flux shortly after root death (< 1 month) (Buchmann, 2000; Ohashi et al., 2000), but stabilizes within a month. RE can also be done, at smaller scales, within a lab setting utilizing incubation jars in conjunction with an infrared gas analyzer (IRGA) or gas chromatography (Silvola et al., 1996). Some methods disturb the soil from a natural state and extrapolation of individual measurements to the ecosystem scale may not reflect the natural environmental conditions and processes (Hanson et al., 2000). In spite of these spatial and magnitude uncertainties associated with soil and root respiration, relative contributions of roots can be assessed, whereas overall magnitudes contain inherent uncertainty (Dumas, M. Pers. Comm., 2004).

4.5.1.2 Isotopic Methods

The use of isotopic labelling, or stable isotopes of C, to separate R_{TOT} components has an advantage over conventional techniques because it can be done in situ, thus, the disturbance of the root-soil system is avoided (Rochette et al., 1999). The $\delta^{13}C$, the ratio of $^{13}C/^{12}C$, can be used to partition NEE of CO_2 into its component one-way fluxes, photosynthesis and respiration, and determine whether the CO_2 evolved from root-derived C (root respiration, respiration of root exudates) or soil-derived C (soil organic matter) (Bowling et al., 2003). The premise is, photosynthesis removes relatively more of the lighter $^{12}CO_2$ isotope, thus the air becomes enriched (more positive $\delta^{13}C$) as the day progresses (Bowling et al., 2003). Conversely, the total ecosystem respiration (composed of vegetation and soils sources) releases CO_2 back to the atmosphere, which is depleted (more negative $\delta^{13}C$) relative to the air (Bowling et al., 2003).

The major disadvantages of the isotopic method are the complexity of the experimental setup, and the added difficulty and cost of analytical measurements (Hanson et al., 2000). Rochette et al. (1999) found that the ^{13}C isotopic labelling and root exclusion methods produced similar values of root contributions. However, more comparative studies which examine the various methods of assessing the contribution of roots are needed. A discussion of isotopic analysis is beyond the scope of this thesis and is merely presented here to show it is another method that can be utilized to partition R_{TOT}. A more detailed overview of isotopic methods is given in Hanson et al. (2000) and Meharg (1994).

4.5.2 Sample Collection, Preparation and Sampling Scheme

Two soil corers made of PVC and sharpened at both ends (32 cm in high and 12 cm in diameter) were collected from the 4 study locations (MR, LR, OG and WOOD). The corers were placed flush and gently forced into the soil to avoid the compaction of organic material. Soil cores were collected on October 31, 2003 and were refrigerated in the dark at 4°C before analysis in January, 2004. Although 30 cm cores were obtained, only the top 20 cm, which represents the depth containing the majority of the roots, were used for analysis.

The sampling scheme was aimed at examining the CO_2 release from both roots and soil, at two temperature regimes under a gradual change in soil moisture. This should give insight into the overall contribution of root and soil respiration towards the total respiration flux under the two most dominant climatic controls (Fang and Moncrieff, 2001; Mielnick and Dugas, 2000; Kane et al., 2003). To accomplish this, the root extraction method was employed in which samples with roots, soil and symbiotic mycorrhizae (R_{R+S}) were compared to samples devoid of roots (R_S) (Hanson et al., 2000). Cores were removed from refrigeration and cut into subsections of the upper 20 cm and lower 10 cm. The top 20 cm subsection of the cores was divided into six, vertical, 60 – 100 g subsamples (no root separation was performed at this time) and used for soil and root analysis. Thus, each site had 6 matched pairs (12 subsamples) comprised of the R_{R+S} and R_S groupings. One sample from each matched pair was sieved (500 μm) to separate the free and rhizosphere soil from the roots (root size was defined as greater than 500 μm). Any visible remaining roots were removed using tweezers and deionized water and these samples were used to represent R_S. Since these samples were disturbed during the

separation process, all the samples for the R_{R+S} mixture were also disturbed (similar to the disturbance of the R_S soil samples when roots were removed) to allow comparisons to be made. This soil disturbance and warmer lab temperature may lead to an overestimation of CO_2 fluxes (Winkler et al., 1996) and thus magnitudes may not represent field conditions, however, comparisons can still be valid.

Samples were placed in incubation jars (surface area of 0.0095 m^2, volume of 0.0014 m^3), which were half-filled with the R_{R+S} or the R_S mixture. Four sample locations (MR, LR, OG and WOOD) with 2 substrates (R_{R+S} and R_S) at 2 temperatures (refrigerated 8 ± 2°C and room 20 ± 2°C) with 3 replicates, were measured. The moisture influence was assessed gravimetrically between each sampling day and it was assumed that the mass lost due to C decomposition was negligible, thus mass loss was exclusively related to moisture (Winkler et al., 1996).

4.5.3 Acquisition of Laboratory CO_2 Data

R_{R+S} and R_S samples in glass jars remained open to the atmosphere between measurement periods to allow the diffusion of CO_2 and O_2 into, and out of the soil, and placed in the dark to avoid any potential light influences. Two holes were drilled in the cap of the incubation jar (same cap used throughout analysis) and brass fittings were put in place, and sealed with silicon, to allow the IRGA tubes to be connected. The cap was then placed on the incubation jar and the CO_2 evolution was recorded every 30 s over a 3 minute period. The regression determination and calculation of CO_2 are identical to that used to measure the field CO_2 fluxes (Section 4.3) using the linear increase in headspace concentration over the 3 minute time interval. Each sample jar was analyzed for CO_2 every 1 - 3 days for an overall study interval of 30 - 35 days (n = 20). This allowed the

evolution of CO_2 and the respective temperature and moisture influences to be better temporally assessed.

To standardize measurements, soils were dried at the end of the experiment, and the dry soil and total root mass (no differentiation between live and dead roots) was determined for each jar. Each jar was oven dried at 80°C for 24 hours and the total dry soil and root mass were determined. This allowed the relative respiration (R_{R+S} and R_S) and specific root respiration (SRR) to be evaluated using equation (4.3) and (4.4), respectively,

$$R_{R+S} \text{ or } R_S = \frac{Respiration\ mg\ CO_2\ m^{-2}\ hr^{-1}}{weight\ of\ dry\ soil\ (g)} \tag{4.3}$$

$$SRR = \frac{Root\ respiration\ mg\ CO_2\ m^{-2}\ hr^{-1}}{weight\ of\ dry\ root\ (mg)} \tag{4.4}$$

The relative contribution of roots (RC) was assessed as the difference between R_S and R_{R+S},

$$RC = R_{R+S} - R_S \tag{4.5}$$

The EGM-1 IRGA was used to collect the field CO_2 data, however, the WMA-4 IRGA was used for laboratory analysis. This is because the flow rate for the WMA-4 IRGA can be adjusted to 0.4 L min^{-1} (1.6 chamber volumes per minute), whereas, the EGM-1 IRGA flow rate is fixed at 1.0 L min^{-1} (4 chamber volumes per minute). Larger flow rates would drastically disrupt the chambers' CO_2 gradient (Welles et al., 2001).

Chapter 5

RESULTS: SPATIAL AND TEMPORAL RELATIONSHIPS OF GRASSLAND CO_2 EXCHANGE

5.1 INTRODUCTION

This chapter explores the spatial and temporal relationships between the four study locations: MR (adjacent to agricultural areas), LR (adjacent to open grassland fallow), OG (an open grassland fallow) and WOOD (maple woodlot) (Figure 3.1). In addition, terrains types (surface cover) will be denoted by Bare (sites devoid of above-ground vegetation) and Veg (sites with grass-dominated above-ground vegetation intact). The results will be discussed in four sections: 1) the microclimate, biotic and nutrient characteristics among the study sites; 2) the spatial and temporal relationships of carbon (C) fluxes ((net ecosystem exchange (NEE), respiration (R_{TOT}), net ecosystem productivity (NEP) and plant (PR)) for all sites during summer growing season; 3) the partitioning of soil and root respiration contributions towards the overall CO_2 flux; and 4) the temporal and spatial controls on the CO_2 exchange

5.1.1 Phenological Study Periods

In general, respiration tends to show large spatial and temporal variability (Fang et al., 1998; Frank et al., 2002; Maestre and Cortina, 2003), as a result, the community (various sites) fluxes have been grouped into three distinct periods (*cf.* Griffis et al., 2000a; Petrone et al., 2003; Waddington et al., 1998) to better depict the temporal relationships. Period one, the early green (EG), extended from May 1 to June 20

representing the early and rapid growth phase of the vegetation. Period two, green (G), encompassed June 21 through August 4 when the vegetation approached full maturity and the above-ground biomass reached a maximum. Period three, late green (LG), included August 3 to September 12 and the September 29 and October 21 nocturnal measurements. This period generally coincided with vegetation senescence. These groupings were based upon climatic distinctions (air temperature (T_a) and 10 cm depth averaged soil moisture (SM)) that would allow at least 5 - 7 measurements to be included in each period (Table 5.1). This method of grouping creates uncertainties regarding inter-annual comparisons and timing of leaf-out and senescence. However, it does provide an efficient method to compare sites intra-annually using point measurements (Griffis et al., 2000a).

Table 5.1: Number of sample points contained within each phenological period and the study total for each site.

Period	Dates	Site			
		LR	MR	OG	WOOD
Early Green	May 1 – June 20	7	8	6	6
Green	June 21 – August 3	9	8	8	8
Late Green	August 3 – October 21	8	7	7	8
Total		24	23	21	22

5.1.2 Statistical Analysis and Confidence

The literature that pertains to chamber fluxes use standard deviation (σ) (Franzluebbers et al., 2002; Mielnick and Dugas, 2000; Simek et al., 2004) or standard error (SE) (Bremer and Ham, 2002; Craine et al., 1999; Frank et al., 2002; Knapp et al., 1998; Tufekcioglu et al., 2001) to assess the daily uncertainty within and between sites. The σ represents the average of the spread (or variability) of each data point from the

overall sample mean (Kvanli, 1988), and in conjunction with the coefficient of variation (CV), which is defined as the σ divided by the population mean, is useful to describe how spatially variable measurements are at any given site. However, it is somewhat difficult to compare the CV between sites because of the different sample and chamber sizes employed for the various studies (Fang and Moncrieff, 2001). However, within a study CV can be a good indicator of natural site variability (Yim et al., 2003).

The SE is the sample fluctuation (average variability) of individual samples from the likely overall population mean and is useful in describing how confident the reported value is to the probable overall mean (Kvanli, 1988). Both σ and SE can be related to one another via,

$$SE = \frac{\sigma}{n} \qquad (5.1)$$

where n is the number of samples. For this study the SE will be used because it better describes the confidence of the reported mean, rather than the natural variability (which is often high in grasslands) (Ambus, 2001; Simek et al., 2004). However, for completeness the σ, and more importantly the CV, will also be discussed to comment on the general site variability.

5.2 Climate, Soil and Biological Characteristics

5.2.1 2003 Climate

The data indicated that the study period had a similar temperature regime, but lower precipitation than normal (Figure 5.2). Precipitation for May, June, July, August and September were 88%, 68%, 77%, 69% and 49% of the 30-year normal, respectively (Figure 5.2b).

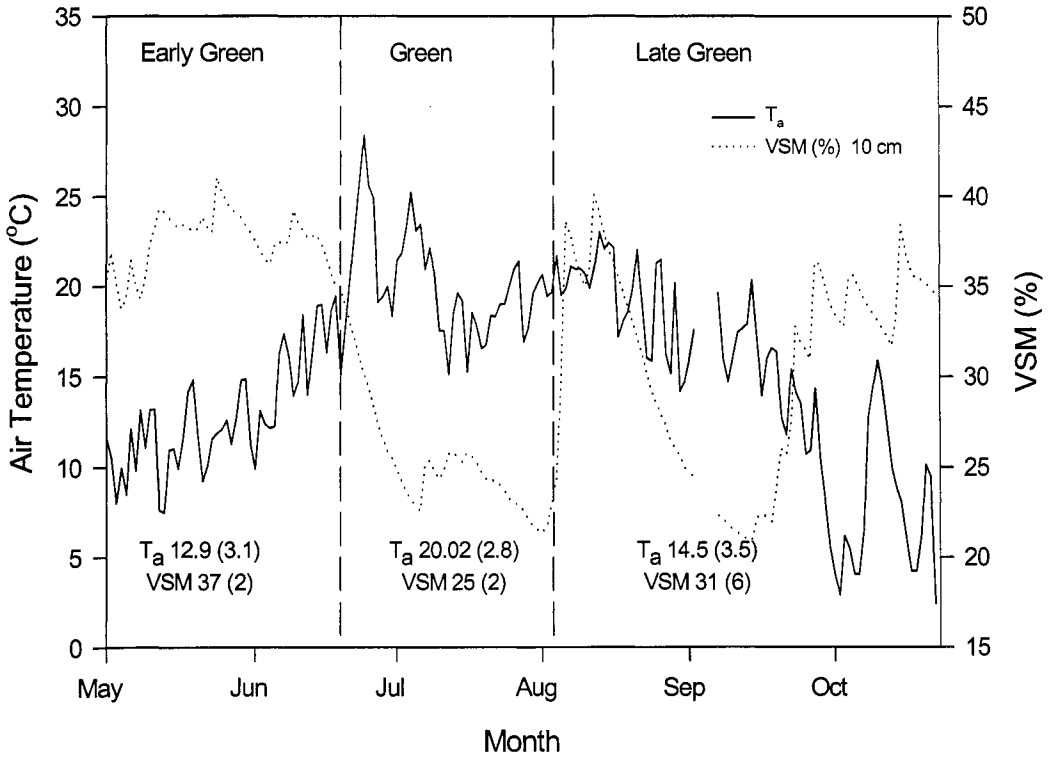

Figure 5.1: Air temperature (T_a) and volumetric soil moisture content (%) (VSM) (10 cm depth averaged) used to separate the growing season at Strawberry Creek, Maryhill, Ont. into 3 phenological periods. Averages and standard deviations (in parenthesis) for each period are indicated on the graph. Period transitions are illustrated with vertical dashed lines.

The warmest temperature during the summer period was 28°C, observed in late June to early July (Figure 5.3a). Two dry periods occurred during midsummer (July 9 –August 4) and late August (August 31 – September 18), at which time the volumetric soil moisture content (VSM) was at, or below, 25% and 34% for 10 and 50 cm depths, respectively (Figure 5.3b). The VSM did not vary greatly at the 10 cm depth (mean = 31%; range 21% - 41%) or the 50 cm depth (mean = 37%; range 30 - 44%) throughout the study period (Figure 5.3b). Although the VSM did drop to levels of 21% at the MR meteorological

station, point measurements as low as 10 - 15% were obtained through manual sampling at the various chamber sites.

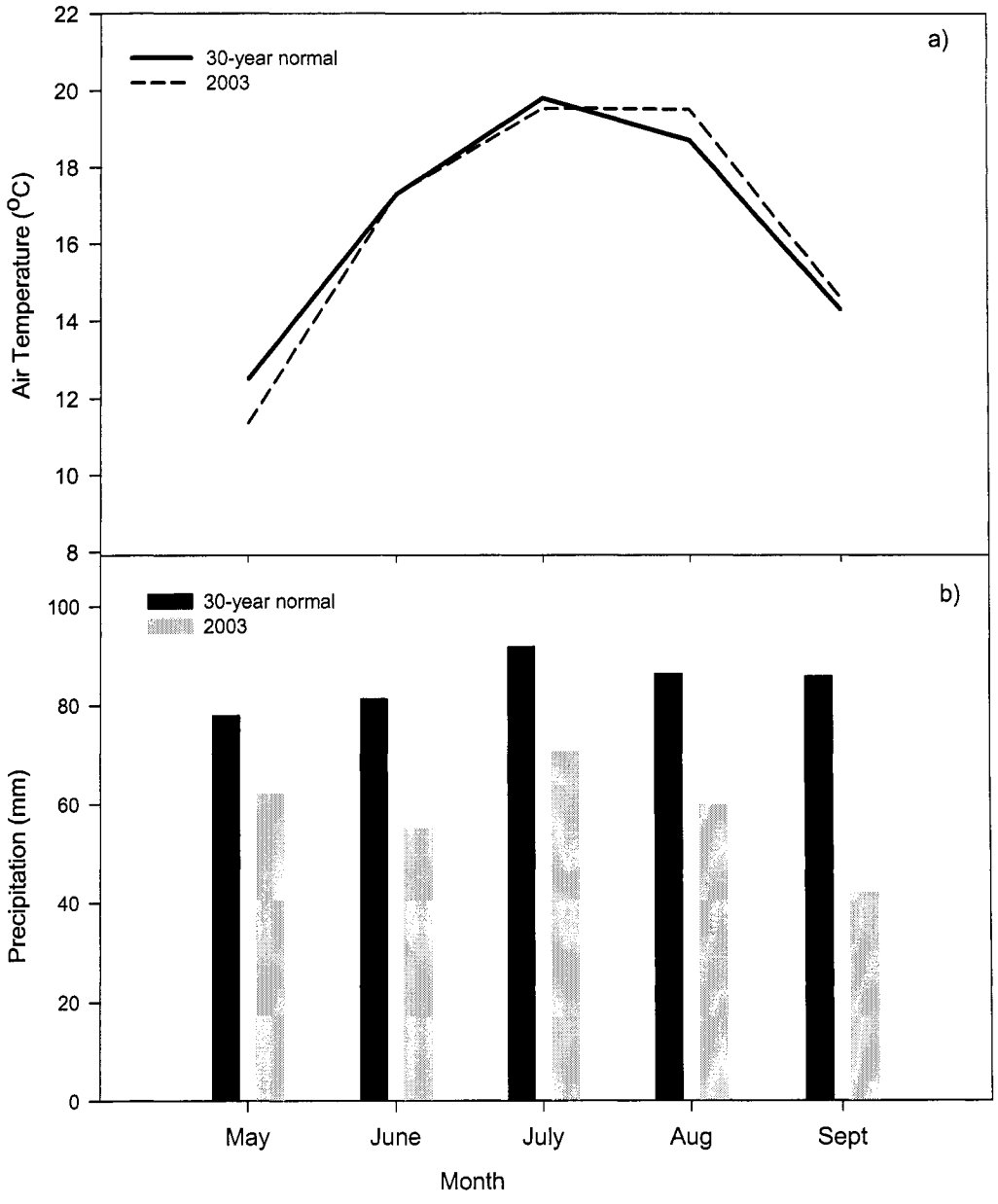

Figure 5.2: Comparison of monthly 30-year normals (1970 - 2000) of a) air temperature (T_a) and b) precipitation (ppt) to the average 2003 values at Strawberry Creek, Maryhill, Ont., 2003. Note: historical 30-year averages are from a government meteorological station at Breslau, Ont. about 6 km south of Maryhill. (Source: 30-year averages Environment Canada, 2003).

Precipitation events were small and generally uniform throughout most of the study period with events (> 0.5 mm d^{-1}) occurring every 4 days on average. There were 4 - 5 precipitation events greater than 5 mm d^{-1} in the months of May through July, with those in July concentrated between July 6 and July 20 (Figure 5.3). This distribution was comparable to the frequency distributions of the 30-year normal precipitation (Environment Canada, 2003). In August, however, the precipitation was primarily concentrated in the first week of the month, during which 40 mm was received comprising 66% of the monthly total (Figure 5.3d).

Both the low VSM and lack of precipitation contributed to the low seasonal discharge observed at the Strawberry Creek (Figure 5.3c). The discharge peaked on May 6 (54 L s^{-1}), May 24 (66 L s^{-1}), June 9 (31 L s^{-1}), August 6 (30 L s^{-1}) and August 12 (35 L s^{-1}) following days with precipitation events greater than 5 mm. In general, the G period was hotter and drier than the EG or LG periods. The heavy rains experienced in mid-July temporarily ended the soil moisture stress (Figure 5.3). However, the dry conditions re-emerged in early August again due to the lack of precipitation.

5.2.2 Microclimates of Soil and Ecosystem Plots

Measurements were taken from Bare plots to assess the contribution and spatial variability of below-ground respiration (roots and microbes). This unnatural surface perturbation has been shown to lead to elevated ground temperatures (T_g) and altered water and energy exchange through enhanced evaporation (Wan et al., 2003). However, there were minimal differences exhibited in both the VSM and the 20 cm depth averaged

T_g (Figure 5.4 and 5.5). The VSM for the Bare sites averaged 5.9 %, -0.4% and -0.1% wetter than their accompanying Veg plots for the LR, MR and OG, respectively. For the

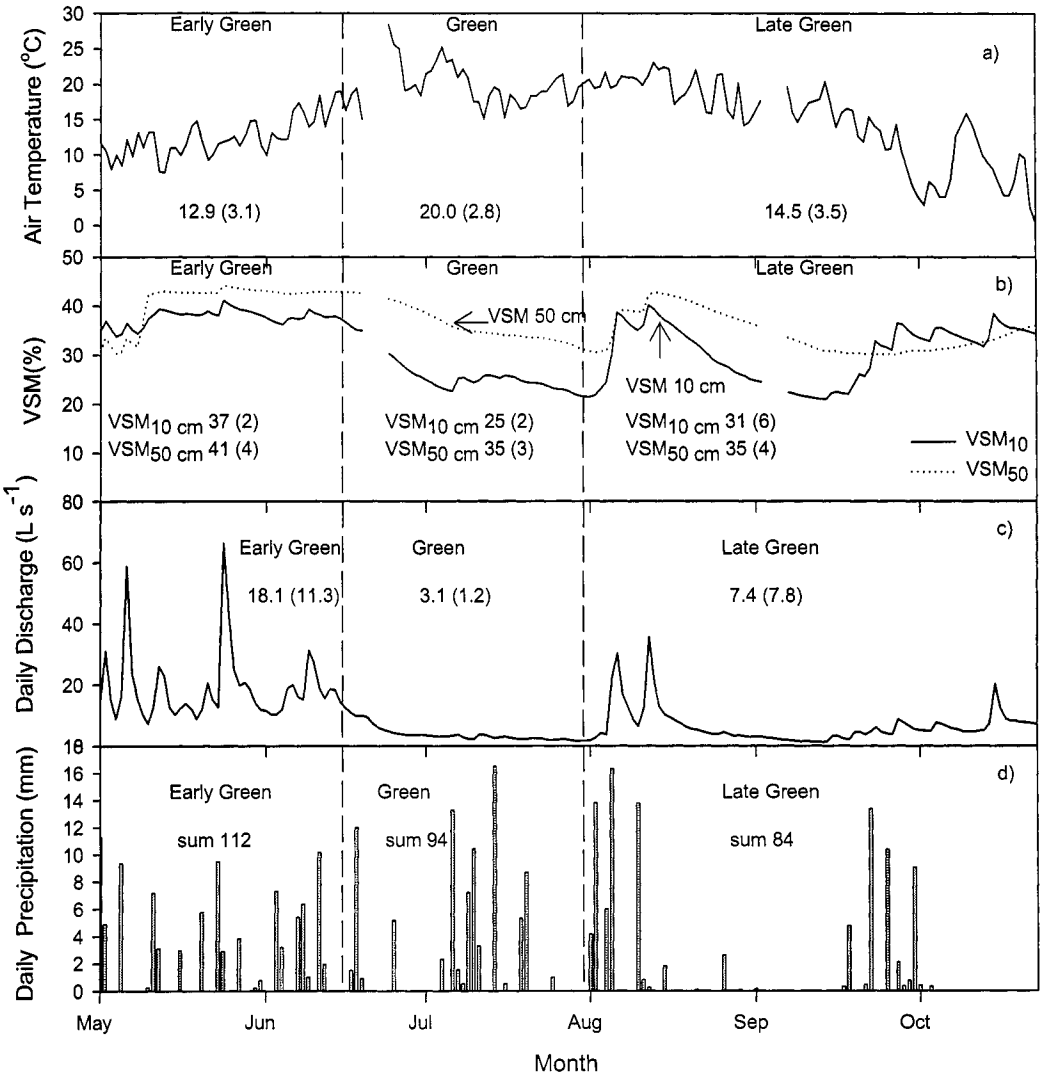

Figure 5.3: Seasonal trends in a) air temperature (T_a), b) volumetric soil moisture content (%) (VSM), c) discharge and d) precipitation at Strawberry Creek, Maryhill, Ont. from May 1 to October 25, 2003. Averages and standard deviations (in parenthesis) for each period are shown on the graph. Period transitions are illustrated with vertical dashed lines.

majority of sample dates there was little difference between the two terrain plots for the MR and OG (Figure 5.4 and Figure 5.5). The largest difference was observed for the LR site, possibly a result of one collar being located on a hummock 8 cm above the surrounding land. During the study period the VSM was mainly within the 10 - 50% range for all the sites, with the largest range observed at the OG and much lower ranges for the riparian grassland communities (Figure 5.4). There was little difference in the T_g between the Bare and Veg plots at the MR, LR and OG sites, with the Veg plots being less than 0.5°C warmer than their accompanying Bare plots (Figure 5.4 and 5.5). However, when plant senescence began to occur in September, temperature differences of up to 2°C were observed (Figure 5.4).

5.2.3 Soil Properties

Table 5.2 summarizes the soil measured soil properties at all study sites. All grass-dominated sites had generally the same soil texture except the LR site, which exhibited lower silt content. The pH for the MR site was below neutral (6.0), whereas the other sites were near neutral (6.5 - 7). The bulk densities (ρ_b) for the two riparian sites (LR and MR) were very similar (~1.1 g cm^{-3}), however, the OG and the WOOD had higher and lower bulk densities, respectively (Table 5.2). As a result, the porosity for the WOOD was the highest (66 ± 5%) and the OG was the lowest (50 ± 5%). Comparing the grass-dominated sites, the TC was slightly higher for the MR site than the LR and the OG site, however, the WOOD site had the largest TC (Table 5.2).

Table 5.2: Soil characteristics for the top 0 - 30 cm for the four study locations at the Strawberry Creek Watershed. Values shown are the mean and standard deviations (in parenthesis) and *n* varies from 4 - 8 depending on the soil variable. Abbreviations are ρ_b (bulk density), ø (porosity) %TC (percent carbon content – organic and inorganic), %TN (percent total nitrogen), C/N (carbon nitrogen ratio) and EXT-P (water extractable phosphorus).

Site	% sand	% silt	% clay	pH	ρ_b (g cm^{-3})	ø (%)	TC (%)	%T N	C/N	EXT-P (mg kg^{-1})
MR	30	41	29	6.0 (0.1)	1.14 (0.07)	58 (1)	6.22 (1.3)	0.52 (0.03)	11.62 (0.2)	18.6 (12.6)
LR	34	34	32	7.3 (0.2)	1.13 (0.06)	60 (2)	4.89 (1.8)	0.34 (0.02)	13.67 (0.2)	1.83 (0.99)
OG	28	47	25	6.5 (0.1)	1.33 (0.11)	50 (4)	5.22 (1.50)	0.24 (0.01)	15.68 (0.5)	1.98 (0.86)
WOOD	28	45	27	6.4 (0.1)	0.83 (0.08)	66 (6)	7.33 (1.6)	0.32 (0.01)	14.10 (0.5)	1.59 (0.35)

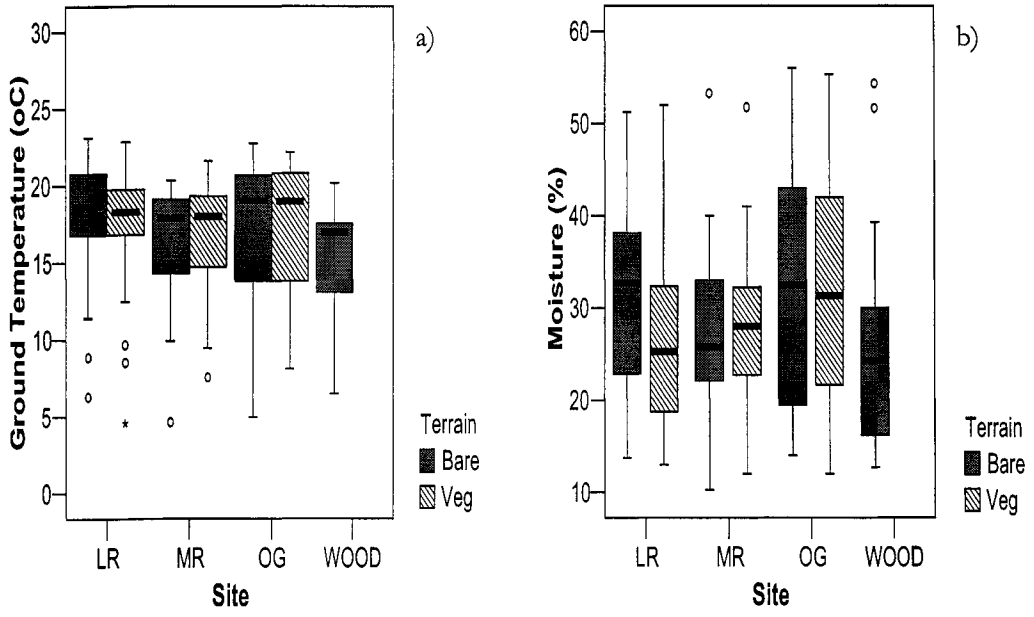

Figure 5.4: The distribution of a) ground temperature (T_g) and b) volumetric soil moisture (%) (VSM) of all sample dates for Bare and Vegetated plots. Solid black line represents the mean and the upper and lower error bars are the 75 and 25% quartile intervals, respectively. The circles represent outliers measured during the nights of September 29 and October 21 at Strawberry Creek, Maryhill, Ont., 2003.

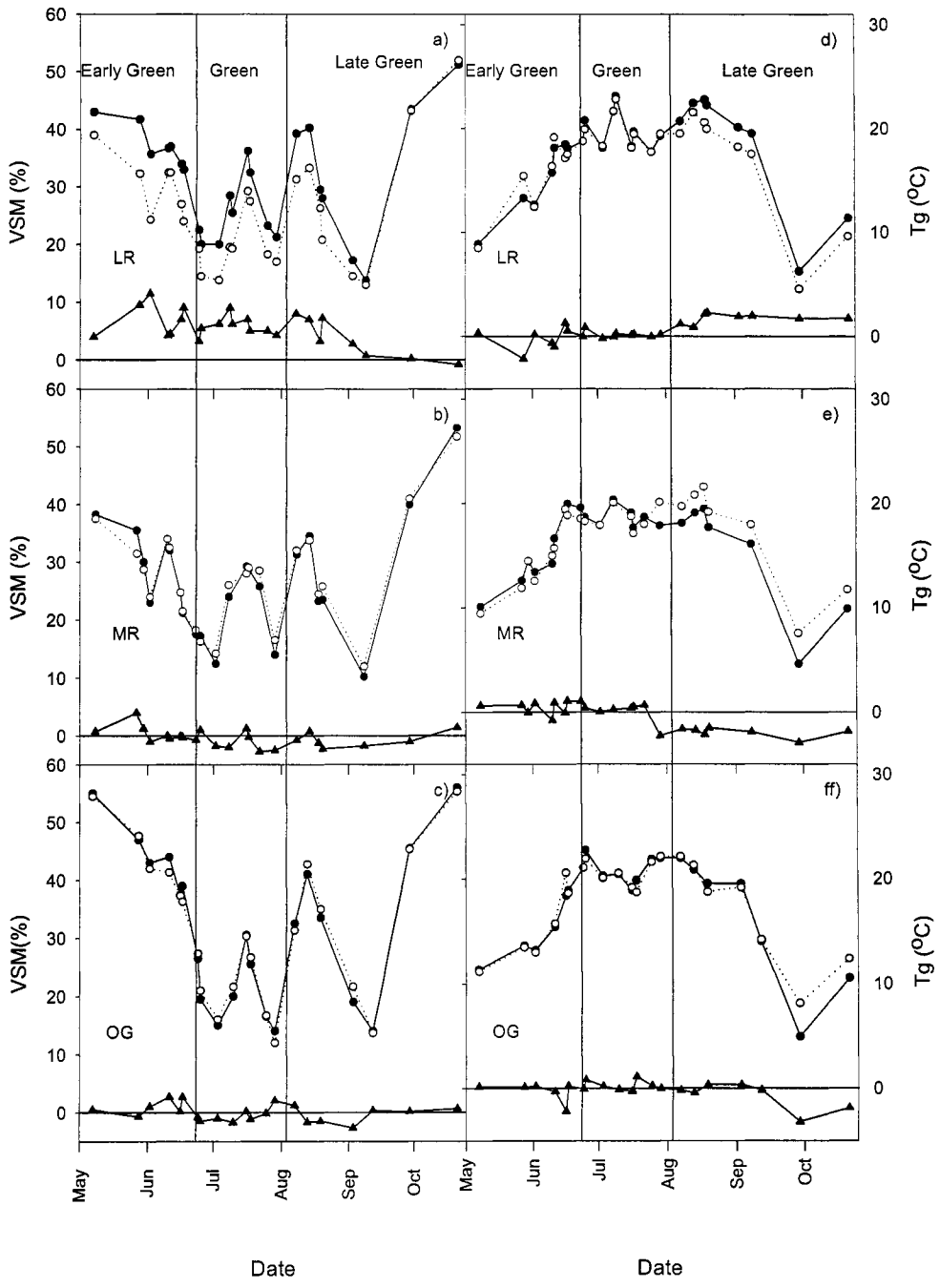

Figure 5.5: Variation in volumetric soil moisture content (%) (VSM) of a) LR, b) MR, c) OG, and 20 cm depth averaged ground temperature (T_g) of d) LR, e) MR and f) OG for Bare (open circles) and Vegetated (closed circles) plots, and Bare - Vegetated difference (triangles) for all sites at Strawberry Creek, Maryhill, Ont., during 2003. Period transitions illustrated with vertical lines.

influenced by fertilizer use. Moreover, the C/N ratio at the LR site was 14% lower than at the non-riparian OG site. The narrow range that was exhibited for the C/N ratios between sites was not shown in the EXT-P data. The EXT-P for the WOOD, LR and OG sites was similar (approximately 2 mg kg^{-1}), whereas the MR location showed values 10-fold larger (about 20 mg kg^{-1}) (Figure 5.6). The %TN, C/N ratio and EXT-P for the WOOD site was comparable to those exhibited at the LR site (Table 5.2). This exemplifies the nutrient inputs from nearby fertilizer application at the MR site, whereas the other sites, the LR, OG and WOOD have adjusted to more 'natural' (climatic and biological) conditions because no fertilizer has been applied in close proximity to these locations within the last 11 years.

5.2.4 Canopy Heights and Above-ground Biomass

All sites exhibited similar ranges in canopy heights and seasonal patterns, with a rapid increase of about 0.75 m which occurred from early May to the middle of June (Figure 5.7). However, the MR site was approximately 0.2 m greater than the LR and OG sites throughout the summer. In July and August the canopy heights stabilized and peaked around August 7 at 1.41, 1.26 and 1.17 m for the MR, LR and OG, respectively.

For every sampling date the MR site showed the largest and the OG the smallest above-ground green biomass (AGB) (Table 5.3). The AGB for the MR, LR and OG sites, were 426 ± 62, 372 ± 60 and 324 ± 37 g m^{-2}, respectively. The percentage increase from June to August for MR, LR and OG were 43, 35, and 46% respectively.

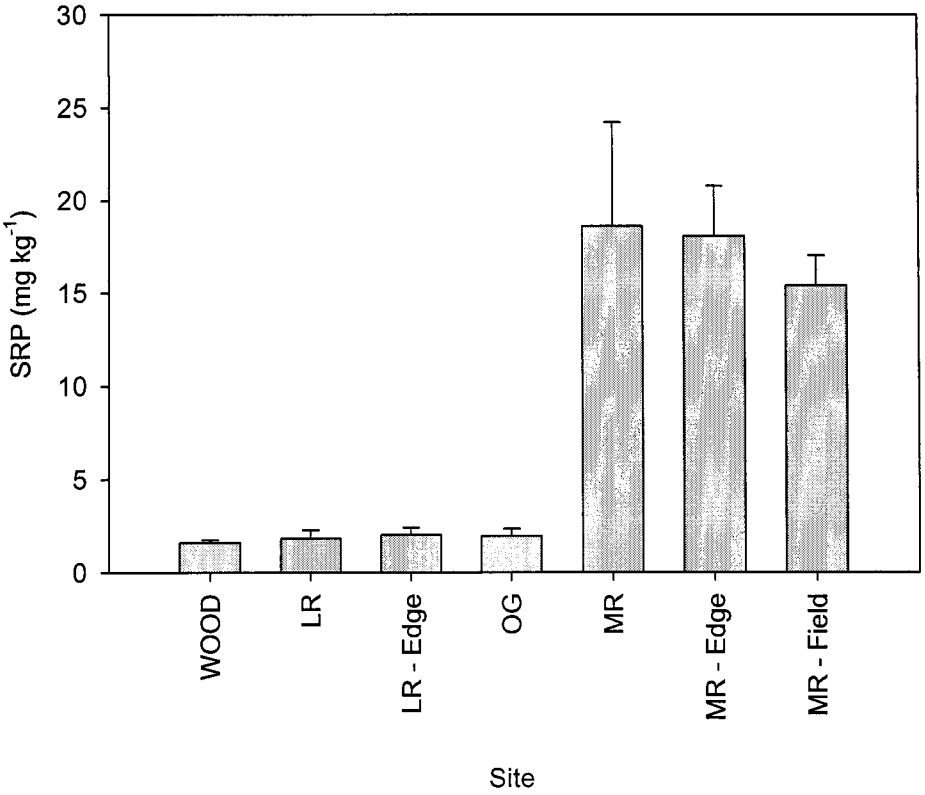

Figure 5.6: Water extractable phosphorus (EXT-P) distribution at Strawberry Creek Watershed, Maryhill, Ont., 2003 at various study locations. Bars are means + SE (n = 5). Edge represents sites at the upland - riparian boundaries, and field sites upland agricultural field locations (Source: Macrae, unpublished, 2003).

The root biomass was similar among the grass-dominated sites averaging 1578 ± 367, 1502 ± 202 and 1518 ± 279 g m^{-2} for the MR, LR and OG sites, respectively. The root biomass for the WOOD site was lower and relatively conservative between sampling dates (ranged 96 g m^{-2}). This was probably a result of the root samples being collected between trees within the top 0.3 cm of the soil. The root biomass was about 4 times larger than the above-ground biomass, with the average below:above-ground biomass ratio being 3.7:1, 4.0:1 and 4.7:1 for the MR, LR and OG sites, respectively.

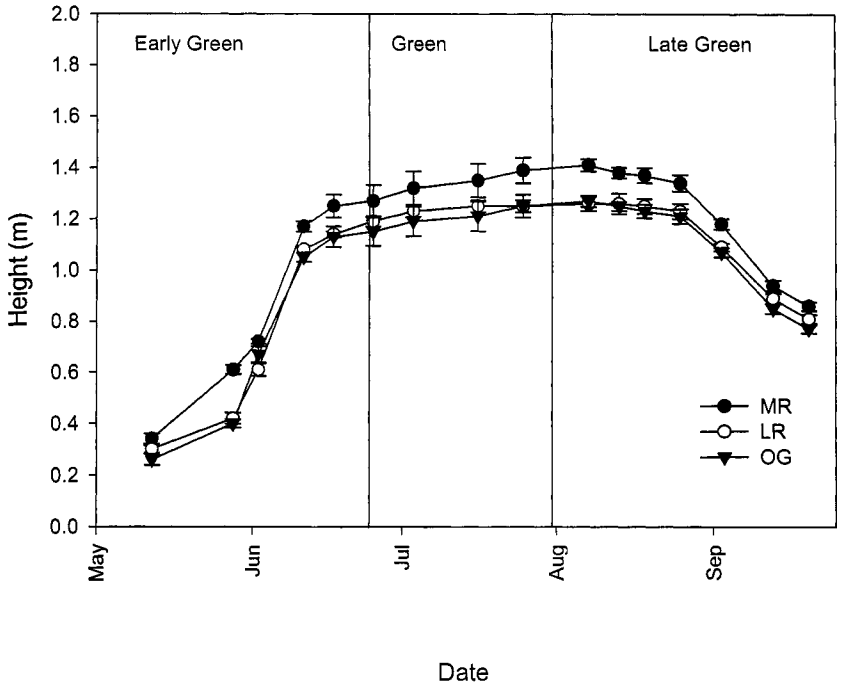

Figure 5.7: Average above-ground biomass heights for the middle riparian (MR), lower riparian (LR) and open grassland (OG) sites at the Strawberry Creek Watershed, Maryhill, Ont., 2003. Values shown are daily averages ± SE with $n = 3$. Canopy absent at WOOD site.

Table 5.3: Above- and below-ground biomass measurements at Strawberry Creek Watershed, Maryhill, Ont. obtained on selected days from June to August, 2003 for $n = 3$. Above-ground biomass absent at the WOOD site.

Site	Date	Above-ground Biomass (g m^{-2} ± S.E.)	% increase	Date	Root Biomass (g m^{-2} ± S.E.)	% decrease
MR	June 4	351 ± 48		June 24	2012 ± 523	---
	July 7	424 ± 67	0.21		---	---
	Aug 5	502 ± 71	0.18	Aug 5	1143 ± 211	-43
LR	June 4	324 ± 47		June 24	1838 ± 193	---
	July 7	353 ± 67	0.09		---	---
	Aug 5	438 ± 61	0.24	Aug 5	1166 ± 211	-36
OG	June 4	257 ± 35		June 24	1989 ± 428	---
	July 7	341 ± 34	0.33		---	---
	Aug 5	374 ± 41	0.10	Aug 5	1047 ± 130	-47
WOOD	June 4	---		June 24	1386 ± 162	---
	July 7	---			---	---
	Aug 5	---		Aug 5	1294 ± 241	-7

5.3 Spatial and Temporal Dynamics in CO_2 Exchange

5.3.1 Soil Net Ecosystem CO_2 Exchange and Soil Respiration Comparisons

Figure 5.8 compares seasonal values for NEE and R_{TOT} for all the Bare soil plots. For the LR, MR and WOOD sites the NEE was about 5 - 20% less than the Bare R_{TOT} during the early green (EG) and green (G) periods (Figure 5.8a, b & d). For the OG site the NEE was similar for the EG and about 20% lower for G period (Figure 5.8c). A shift to larger NEE relative to Bare R_{TOT} began emerging during the LG period in early August at all sites. Consequently, with the reduced level of NEE during the EG and G periods, and the enhanced level during the LG period, the total season averaged NEE and Bare R_{TOT} are similar at all sites. Although some uptake from microbes and roots from nearby grasses growing under the collar may have occurred, these small influences should fall within the range of uncertainty. This is evident in the increase in NEE relative to Bare R_{TOT} as the season progressed owing to root and microbial decay outperforming the lingering affects of C uptake processes (Figure 5.8). Since the Bare NEE is likely confounded by root and microbial uptake it will only be discussed if drastically different from Bare R_{TOT}. Furthermore, NEP is a measure of photosynthetic uptake (Novick, 2004) and thus, the NEP for the Bare sites will be excluded because theoretically the lack of above-ground vegetation should translate to a NEP of zero.

5.3.2 Seasonal Trends in Total Ecosystem Respiration Rates

The temporal trends of R_{TOT} for the Bare and Veg plots are shown in Figure 5.9, and the NEE and NEP for the Veg sites is shown in Figure 5.10. The Bare R_{TOT} for LR, MR, OG and WOOD sites ranged from 140 - 1230, 160 - 1020, 80 - 1680 and 90 - 1290 mg CO_2 m^{-2} hr^{-1}, respectively (Figure 5.9a). The Bare and Veg R_{TOT} had two seasonal

peaks corresponding to plant growth occurring in mid-June, and after frequent precipitation, following the relatively dry month of July (Figure 5.3d). The Veg R_{TOT} for LR, MR and OG sites was about 2 times larger than Bare R_{TOT} and ranged 420 - 2610, 590 - 3230 and 200 - 2080 mg CO_2 m^{-2} hr^{-1}, respectively (Figure 5.9b).

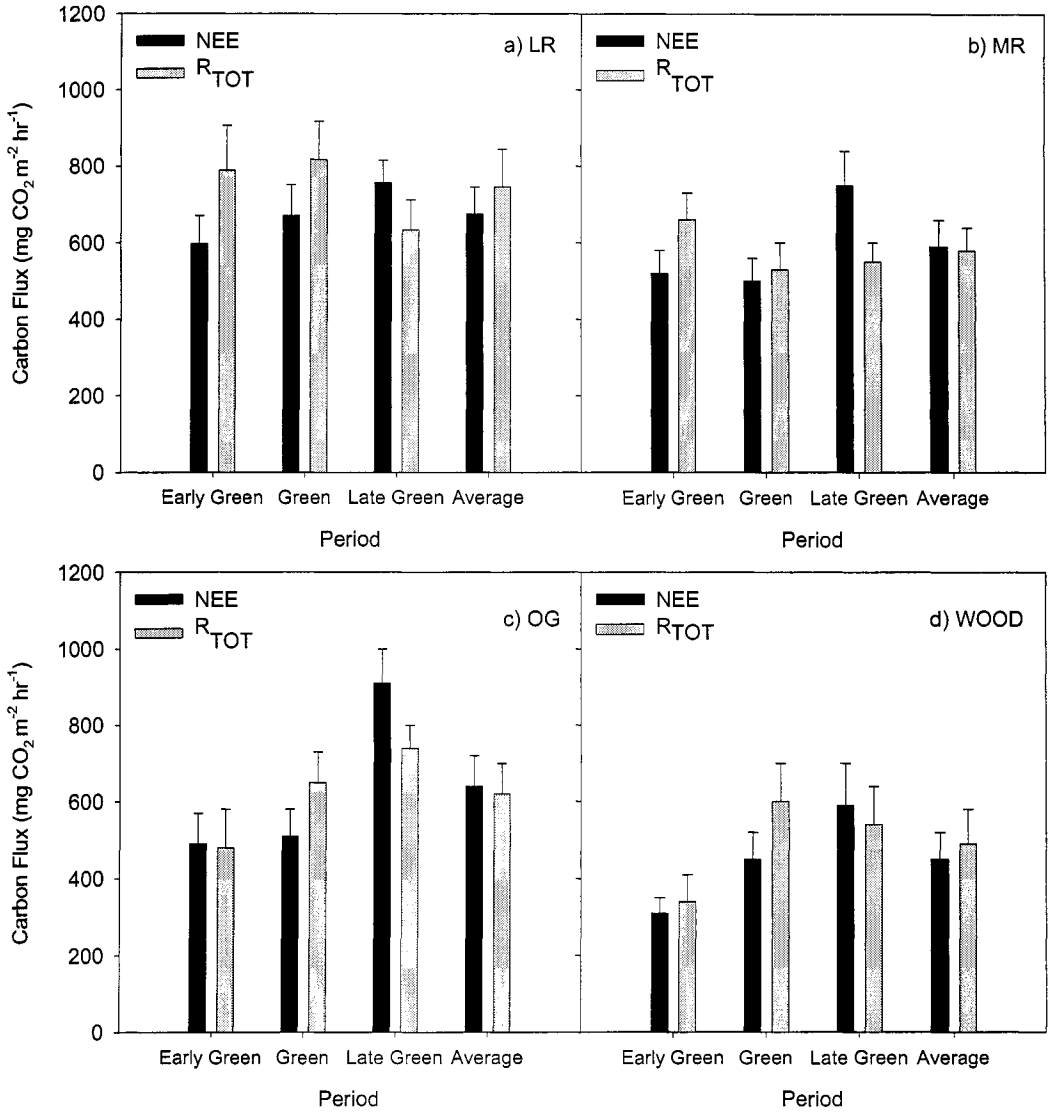

Figure 5.8: Mean ± SE site net ecosystem CO_2 exchange (NEE) and soil respiration (R_{TOT}) for Bare plots for a) lower riparian (LR), b) middle riparian (MR), c) open grassland (OG) and d) woodlot (WOOD) sites by phenological study periods.

For the two riparian sites (MR and LR) the maximum Bare R_{TOT} was observed during mid-to-late June (Table 5.4), which coincided with the period of the most rapid rate of vegetation growth (Figure 5.7). However, comparable values were also observed in mid-August (Figure 5.9). Conversely, the Bare R_{TOT} at the OG site peaked in mid-August, 2 weeks after harvesting, but another large value of 1160 mg CO_2 m^{-2} hr^{-1} was observed in late-June, which may be more representative of the relative timing of peak Bare R_{TOT} in the absence of land management practices (Table 5.4). The WOOD Bare R_{TOT} peaked in late July. For Veg plots, maximum MR, LR and OG Bare R_{TOT} occurred in late-May, mid-June and late-June, respectively. However, values comparable to (within 15%) those of the early season peak values were observed in mid-August (Figure 5.9).

Table 5.4: Magnitude and timing (in parenthesis) of the maximum CO_2 fluxes. Fluxes reported in mg CO_2 m^{-2} hr^{-1} ± SE.

Terrain	Bare			Veg		
Site	NEE	R_{TOT}	NEP	NEE	R_{TOT}	NEP
LR	950 ± 50 (Aug 19)	1230 ± 140 (June 25)	0 [a]	-990 ± 190 (Sept 2)	2610 ± 80 (May 28)	-3230 ± 180 (May 28)
MR	880 ± 80 (Aug 18)	1020 ± 120 (June 17)	0 [a]	-1420 ± 210 (May 27)	3230 ± 280 (June 17)	-4060 ± 130 (Aug 18)
OG	1500 ± 80 (Aug 18)	1680 ± 100 (Aug 19)	0 [a]	-780 ± 220 (Aug 13)	2080 ± 70 (June 25)	-2560 ± 210 (June 25)
WOOD	980 ± 130 (Aug 18)	1290 ± 250 (July 30)	0 [a]	---	---	---

Note: [a] values represent no uptake.

The maximum NEE for all Bare plots occurred in mid-August, and were 24, 14 and 11% lower than the Bare R_{TOT} at the LR, MR and OG sites, respectively. For the Veg plots, maximum NEE occurred in early September for LR, mid-August for OG and at the end of May for the MR site (Table 5.4). Maximum NEP for the LR and MR sites occurred in late-August to early September, whereas harvesting at the beginning of

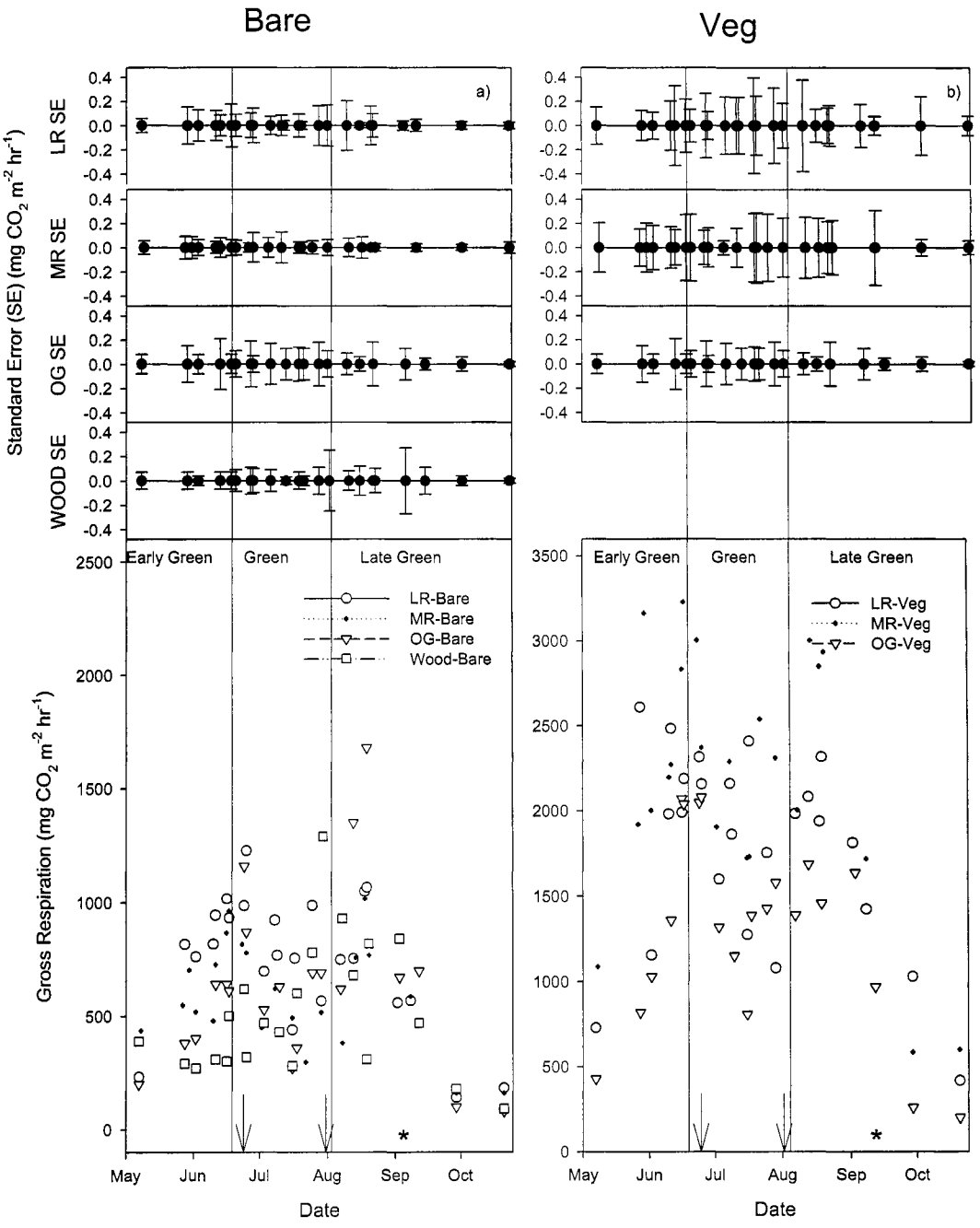

Figure 5.9: Average, hourly fluxes for respiration (R_{TOT}) for a) Bare b) Vegetated plots from May 7 to Oct 21, 2003. Top graphs show relative standard error (SE), whereas bottom graph shows daily site means. Vertical arrows and the star denote harvest (June 25 and July 30) and herbicide application (September 2), respectively for the OG site only. Note: measurements were not all collected on the same days. Period transitions are illustrated by vertical lines. Note the difference in scale for gross respiration between Bare and Veg plots.

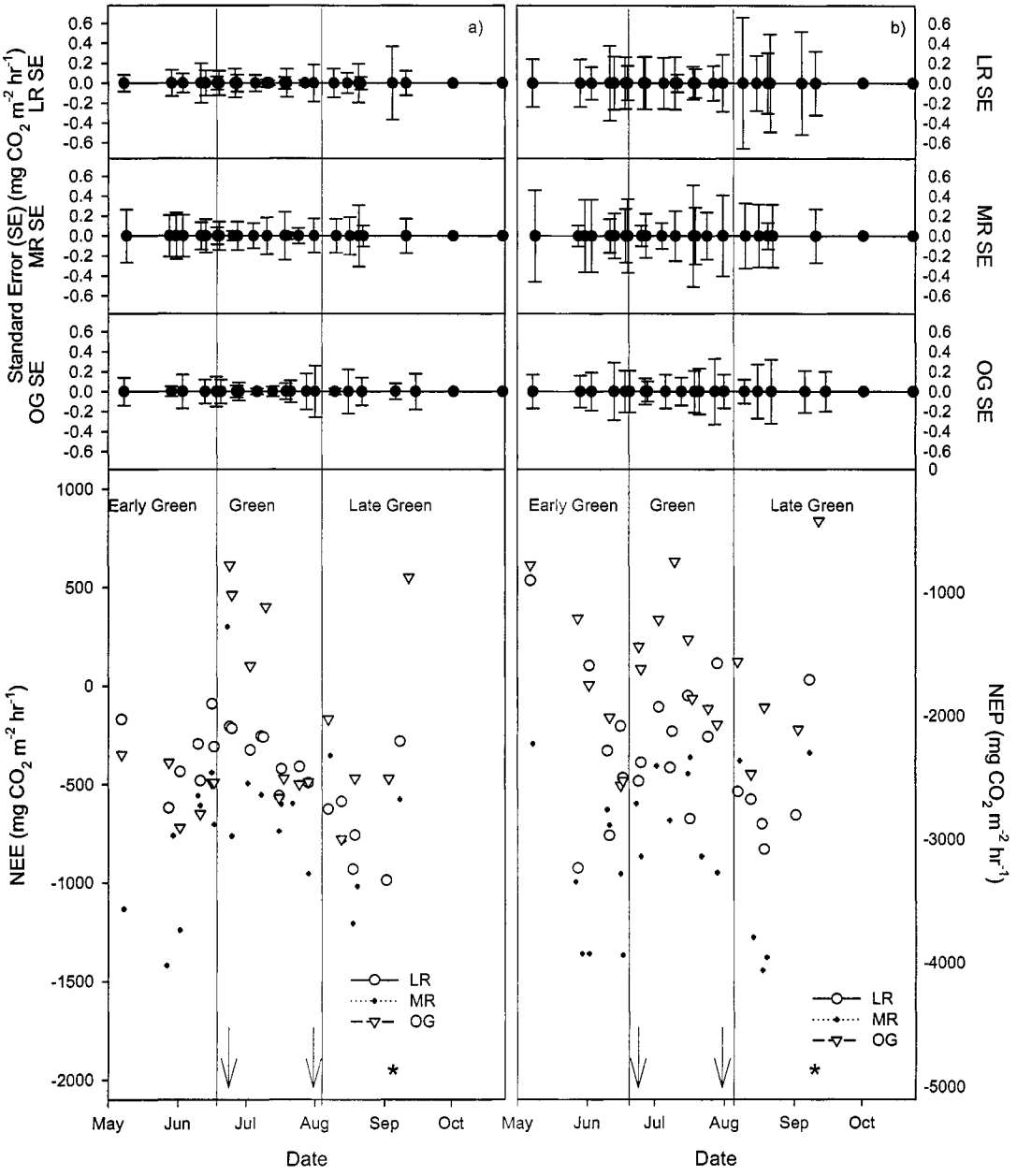

Figure 5.10: Average, hourly fluxes for a) NEE and b) NEP for Vegetated plots from May 7 to September 12, 2003. Top graphs show relative standard error (SE), whereas bottom graph shows daily site means. Vertical arrows and the star denote harvest (June 25 and July 30) and herbicide application (September 2), respectively for the OG site only. Note: all measurements were not collected on the same days. Period transitions are illustrated by vertical lines.

August caused the maximum observable OG NEP to occur in late-June. For all sites comparable large values were observed in late-May to early June and mid-August (Figure 5.10).

5.3.3 Spatial and Temporal Variability of Soil and Ecosystem Respiration, and Net Ecosystem Productivity

The majority of the chamber measurements for this study were taken between 10:00 and 16:00, during the growing season. Therefore higher photosynthetic and R_{TOT} rates may be exhibited than would be expected had the fluxes been continuously monitored and integrated over the entire day, and represented on an hourly basis. However, it is the relative difference in CO_2 exchange among the sites that is the primary interest of this study. Thus, measuring at midday when biological activity is at the greatest rate should capture any spatial C differences.

The variability of R_{TOT} for all the Bare plots, for each phenological period is shown in Figure 5.11. At the LR site the Bare R_{TOT} averaged 750 mg CO_2 m^{-2} hr^{-1} seasonally with a coefficient of variation (CV) of 28% and averaged 790, 820 and 630 mg CO_2 m^{-2} hr^{-1} for the EG, G and LG, respectively (Figure 5.11). The Bare R_{TOT} for the MR site averaged 580 g CO_2 m^{-2} hr^{-1} seasonally, with a CV of 24%, and averaged 660, 530 and 550 mg CO_2 m^{-2} hr^{-1} for the EG, G and LG, respectively (Figure 5.11). The average Bare R_{TOT} at the OG site was 620 mg CO_2 m^{-2} hr^{-1} seasonally with a CV of 26% and averaged 480, 650 and 740 mg CO_2 m^{-2} hr^{-1} for the EG, G and LG, respectively (Figure 5.11) with a CV of 26%. The WOOD site Bare R_{TOT} site averaged 490 mg CO_2 m^{-2} hr^{-1} over the season with a CV of 36% (slightly lower than the grass-dominated sites) and averaged 340, 600 and 540 mg CO_2 m^{-2} hr^{-1} for the EG, G and LG periods, respectively (Figure 5.11).

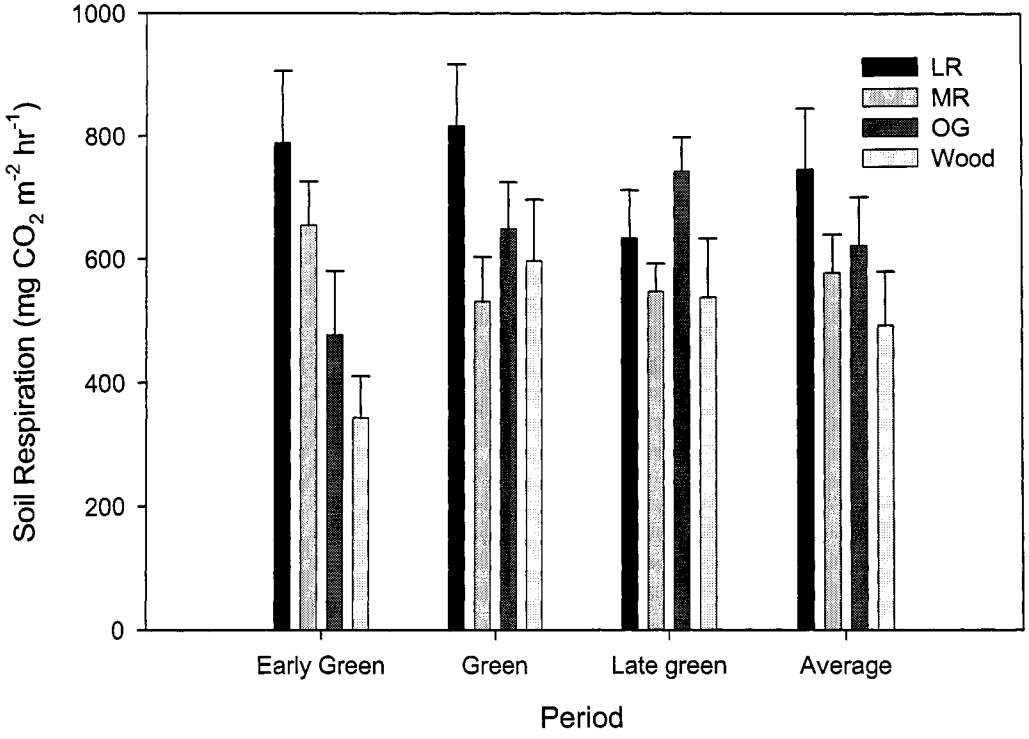

Figure 5.11: Mean + SE soil respiration (R_{TOT}) by phenological study periods for all Bare plots at Strawberry Creek, Maryhill, Ont., during the summer of 2003.

Figure 5.12 shows the variability of R_{TOT} and NEP for each phenological period, for all the Veg plots. At the LR site Veg R_{TOT} averaged 1780 mg CO_2 m^{-2} hr^{-1} with a CV of 25%, and slightly decreased with successive periods (Figure 5.12a). Seasonal NEP at the LR site averaged -2350 mg CO_2 m^{-2} hr^{-1} and also showed a CV of 25%, but NEP values slightly increased over the study periods exhibiting -2220, -2200 and -2620 mg CO_2 m^{-2} hr^{-1} for the EG, G and LG periods, respectively (Figure 5.12b). The Veg R_{TOT} at the MR site averaged 2180 mg CO_2 m^{-2} hr^{-1} with a CV of 20%, also decreased over the study period (Figure 5.12a). Seasonal NEP at the MR site averaged -3090 mg CO_2 m^{-2} hr^{-1} with a CV of 18%, with the EG, G and LG averaging -3200, -2790 and -3290 mg CO_2

m^{-2} hr^{-1}, respectively (Figure 5.12b). The OG Veg R_{TOT} averaged 1280 mg CO_2 m^{-2} hr^{-1} with a CV of 18% and averaged 1290, 1480 and 1090 mg CO_2 m^{-2} hr^{-1} during the EG, G and LG periods, respectively (Figure 5.12a). Seasonal NEP at the OG site averaged -1680 mg CO_2 m^{-2} hr^{-1} with a CV of 25% and the EG, G and LG averaged -1800, -1530 and -1700 mg CO_2 m^{-2} hr^{-1}, respectively (Figure 5.12b). Generally, the CV for Veg R_{TOT} sites was larger than that of the Bare sites. R_{TOT} and NEP were of relatively similar magnitude for all time periods likely due to similar vegetation and soil types, and because the study focused primarily on the growing season fluxes.

5.3.4 Spatial and Temporal Variability of Net Ecosystem CO_2 Exchange

Figure 5.13 shows the NEE for Bare and Veg plots. The NEE for all Bare plots, in which the above-ground vegetation was removed, is analogous to Bare R_{TOT}. For comparative purposes, the complimentary Bare R_{TOT} is shown in brackets. The seasonal average for Bare NEE at the LR site was 670 (750) mg CO_2 m^{-2} hr^{-1} with a CV of 22%. The EG, G and LG for NEE at the LR site averaged 600 (790), 670 (820) and 760 (630) mg CO_2 m^{-2} hr^{-1}, respectively (Figure 5.13a). The Bare NEE for the MR site averaged 590 (580) mg CO_2 m^{-2} hr^{-1} seasonally with a CV of 26%. During the EG, G and LG period the

Bare NEE at the MR site averaged 520 (660), 500 (570) and 750 (550) mg CO_2 m^{-2} hr^{-1}, respectively (Figure 5.13b). The NEE for the OG Bare site seasonally averaged 640 (480) mg CO_2 m^{-2} hr^{-1} with a CV 25%. At the Bare site the EG, G and LG period NEE averaged 490 (650), 510 (740) and 910 (620) mg CO_2 m^{-2} hr^{-1}, respectively (Figure 5.13b). Finally, the NEE for the WOOD site averaged 450 (490) mg CO_2 m^{-2} hr^{-1} over the season with a CV of 34%. During the EG, G and LG periods the Bare NEE for the

WOOD site averaged 310 (340), 450 (600) and 590 (540) mg CO_2 m^{-2} hr^{-1}, respectively (Figure 5.13b).

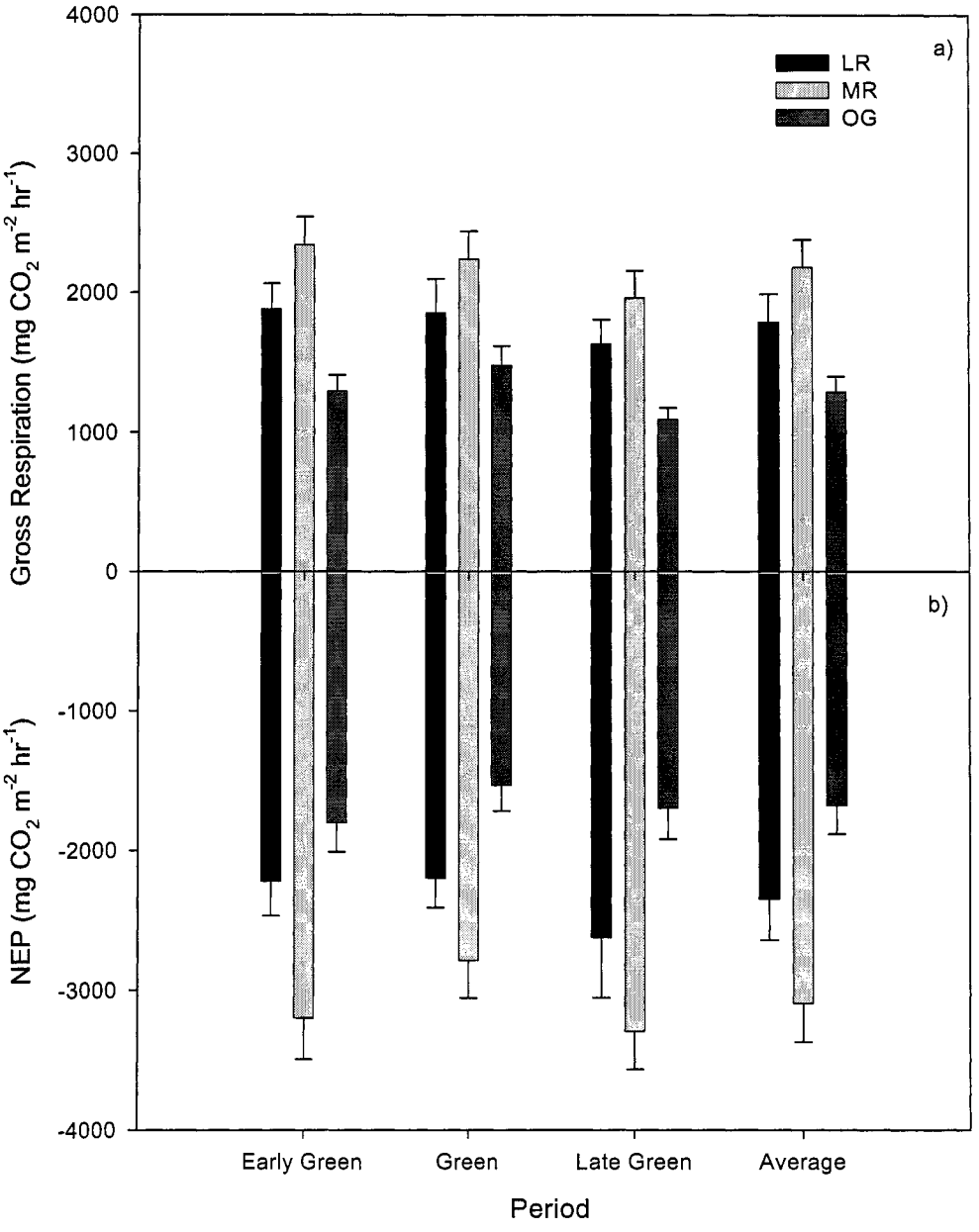

Figure 5.12: Mean + SE a) respiration (R_{TOT}) and b) net ecosystem productivity (NEP) by phenological study periods for all Vegetated plots at Strawberry Creek, Maryhill, Ont., during the summer of 2003.

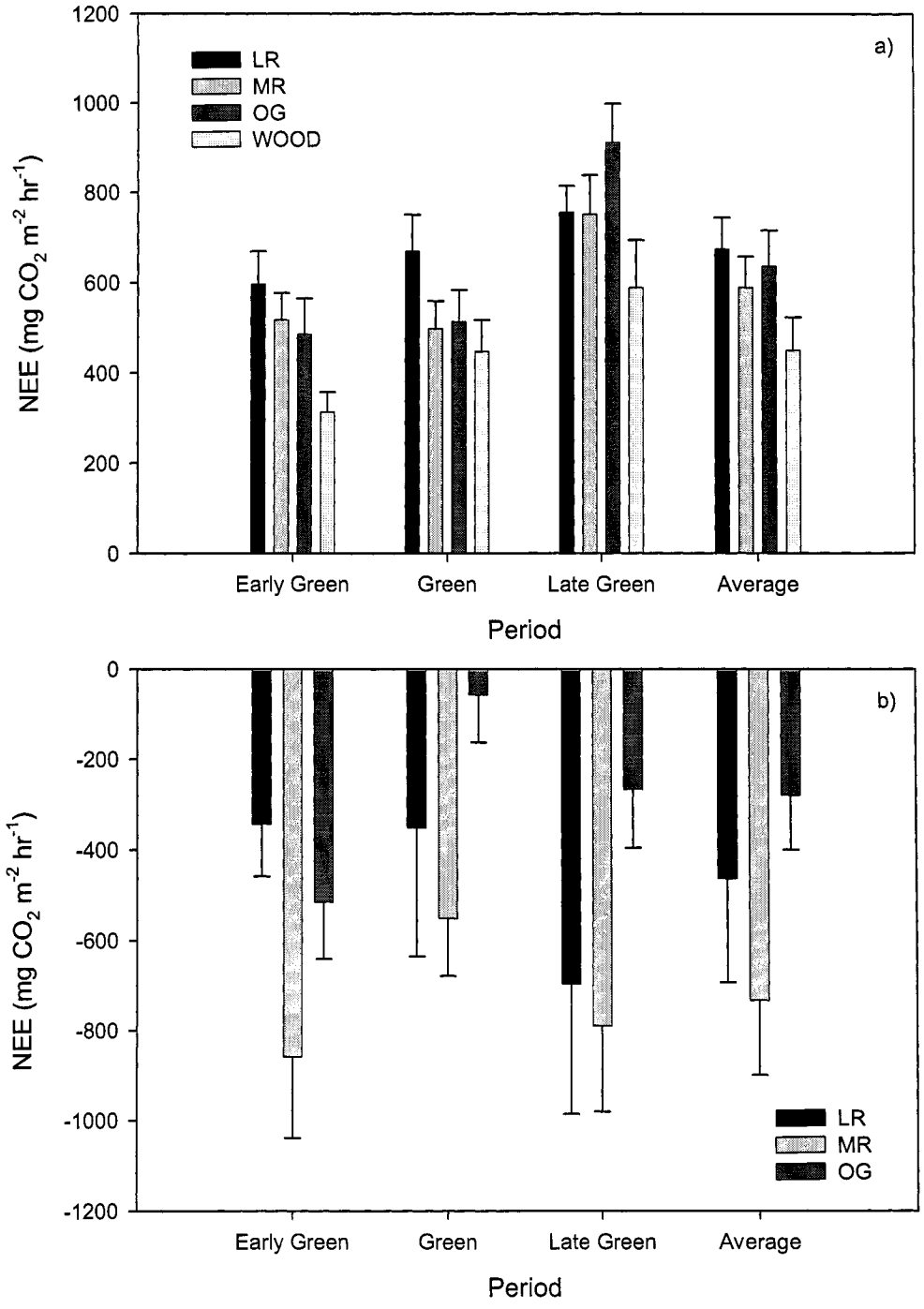

Figure 5.13: Mean + SE net ecosystem CO_2 exchange (NEE) for all a) Bare and b) Vegetated plots by phenological study periods at Strawberry Creek, Maryhill, Ont., during the summer of 2003.

The NEE for the LR Veg site seasonally averaged -460 mg CO_2 m^{-2} hr^{-1} with a CV of 122%. The EG, G and LG NEE averaged -340, -350 and -700 mg CO_2 m^{-2} hr^{-1}, respectively at the LR Veg site (Figure 5.13b). Seasonally the NEE for the MR Veg site averaged -730 mg CO_2 m^{-2} hr^{-1} with a CV of 45%. During the EG, G and LG periods the MR Veg NEE averaged -860, -550 and -790 mg CO_2 m^{-2} hr^{-1}, respectively (Figure 5.13b). The NEE for the OG Veg site averaged -280 mg CO_2 m^{-2} hr^{-1} seasonally with a CV of 42% and averaged -510, -160 and -270 g CO_2 m^{-2} hr^{-1} during the EG, G and LG periods, respectively (Figure 5.13b).

5.3.5 Same Day Carbon Flux Comparisons

All sites could not be measured on the same day because of the time demand and the self-imposed limitation that CO_2 fluxes were collected during the midday period. As a result, CO_2 fluxes were averaged over periods determined by meteorological distinctions to assess temporal relationships in the spatial variability (Section 5.1.1). Such averaging creates a degree of uncertainty in day-to-day climatic variables (T_a, cloud cover, precipitation, etc.). Thus, this section is aimed at comparing sites with fluxes (R_{TOT}, NEE and NEP) collected on the same day (within 4 hours) to explore if group averaged data showed similar spatial trends to data collected on the same day. Again, since Bare NEE has uncertainties in C uptake and NEP is essentially zero, only R_{TOT} for Bare sites and all the fluxes for Veg plots are shown.

The MR Bare R_{TOT} was lower than LR Bare R_{TOT} during the early stages of plant growth (EG and G periods) with no discernable difference after peak growth in late-July (Figure 5.14a). This differs from the group averaged data where the MR was significantly ($\alpha = 0.05$) lower than LR during all periods (Figure 5.11). The Bare R_{TOT} at the MR site

was slightly, but not significantly ($\alpha = 0.05$), larger than the OG Bare R_{TOT} for the EG period (Figure 5.14b), but since the data did not encompass the harvest dates, there was little differences between the MR and OG sites. The MR site exhibited double the Bare R_{TOT} observed at the WOOD site for the EG and G periods, from which point both sites exhibited similar fluxes (Figure 5.14c). This differed from group averaged data such that the MR and WOOD were no different during the G period (Figure 5.11). The LR Bare R_{TOT} was slightly higher than the OG Bare R_{TOT} at the beginning of June, and mid-July, but lower after harvesting in early August (Figure 5.14d) which is identical to the group averaged data (Figure 5.11). Similar to the MR Bare R_{TOT}, the LR Bare R_{TOT} was approximately 1.5 times larger than the WOOD Bare R_{TOT}, especially during the EG and G periods (Figure 5.14e). Finally, the OG and WOOD Bare R_{TOT} were similar throughout the season except after harvesting on June 25 and July 30 (Figure 5.14f) where similar trends were exhibited for the group averaged data (Figure 5.11). For all plots, Bare R_{TOT} measurements made during senescence (September 29 and October 21) followed the trend from largest to smallest LR ~ MR > Wood ~ OG, exemplifying a riparian dominance.

Generally, Veg data exhibited similar trends to the group averaged data. The MR Veg R_{TOT} was about 15% and 35% larger than the LR Veg R_{TOT} and OG Veg R_{TOT}, respectively, with the greatest differences exhibited in June (EG) and August (LG) and converging during the mid-July dry (G) period and plant senescence (Figure 5.15a & b). This was consistent with the group averaged data (Figure 5.12). The LR Veg R_{TOT} was larger than OG Veg R_{TOT} throughout the season (Figure 5.15c). The differences exhibited in Veg R_{TOT} were also observed in Veg NEE and NEP. The MR had 40% larger NEE

(greater uptake) and 15 - 25% larger NEP than the LR and OG sites (Figure 5.16 a - d), whereas the LR and OG sites had similar NEE and NEP (Figure 5.16e & f). This differed from group averaged data that exhibited more consistent trends during all phenological periods (Figure 5.12b and Figure 5.13b). Again, values were largest during plant growth from June to July and converged towards the end of July, during the onset of the dry period.

The Bare MR R_{TOT} was substantially lower than at the LR site during the EG period. Furthermore, the MR showed a greater magnitude of NEP and NEE compared to LR and OG sites, concurrently with larger Veg R_{TOT}. However, the NEE and NEP showed spatial and diel variability for the same day comparisons (Figure 5.16) which resulted in slightly different trends than that observed for the group averaged data (Figure 5.12b and Figure 5.13b).

This suggests that flux measurements made on days between same day comparisons experience different climatic dynamics, such as cloud cover, temperatures, precipitation etc., which may lead to varying CO_2 fluxes. However, the general similarity of the same day comparisons to that of group averaged data indicates that when CO_2 measurements are grouped averaged these dynamic climatic responses are reduced, but the site trends are better quantified by a greater number ($n > 6$) of sample points.

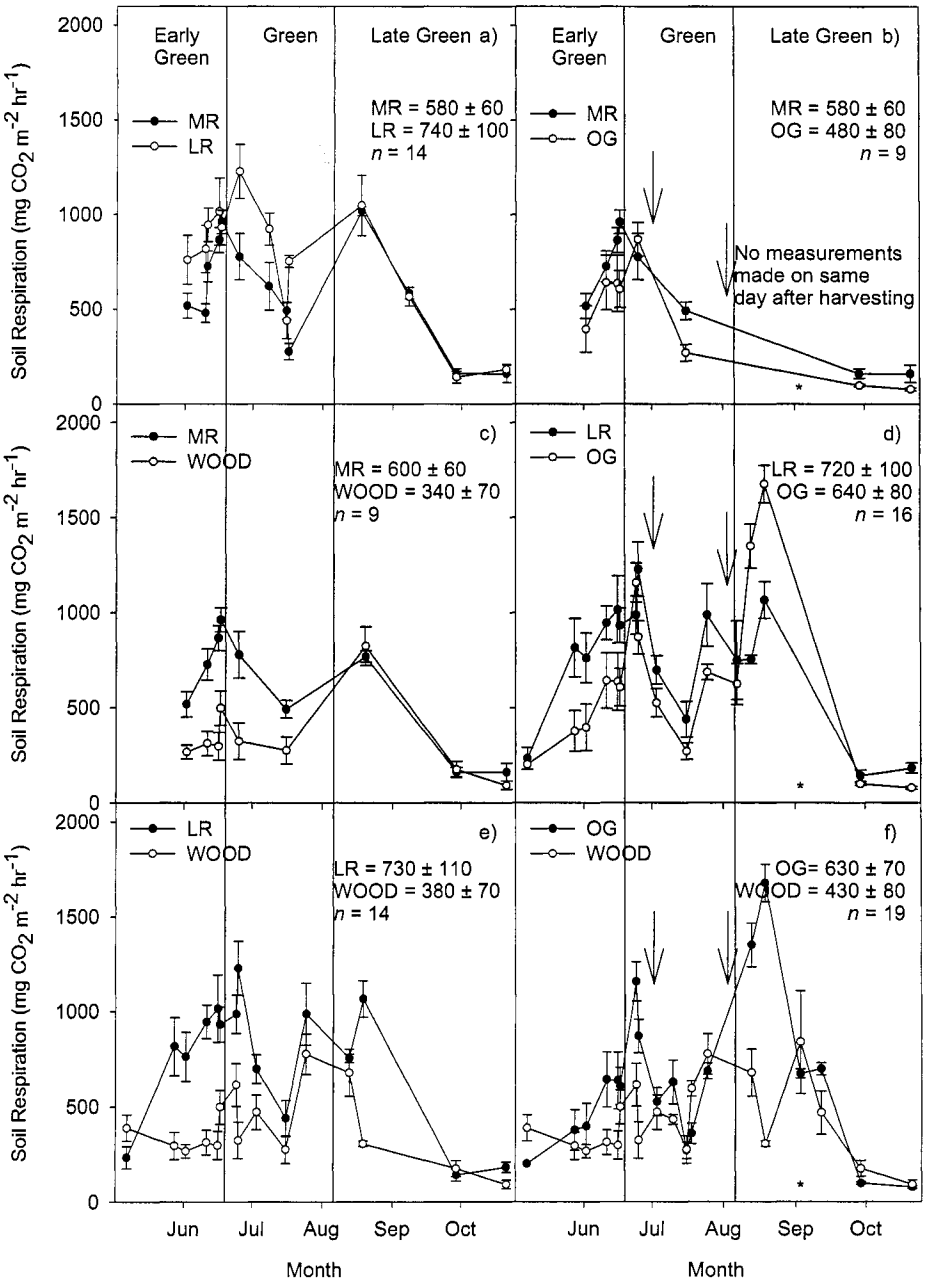

Figure 5.14: Comparison of soil respiration (R_{TOT}) of Bare sites for measurements made on the same sample dates for a) MR and LR, b) MR and OG, c) MR and WOOD, d) LR and OG, e) LR and WOOD, and f) OG and WOOD. Means ± SE are shown. Note: arrows and star denote the date of harvesting (June 25 and July 30) and pesticide application (September 2), respectively. Period transitions are represented by vertical lines.

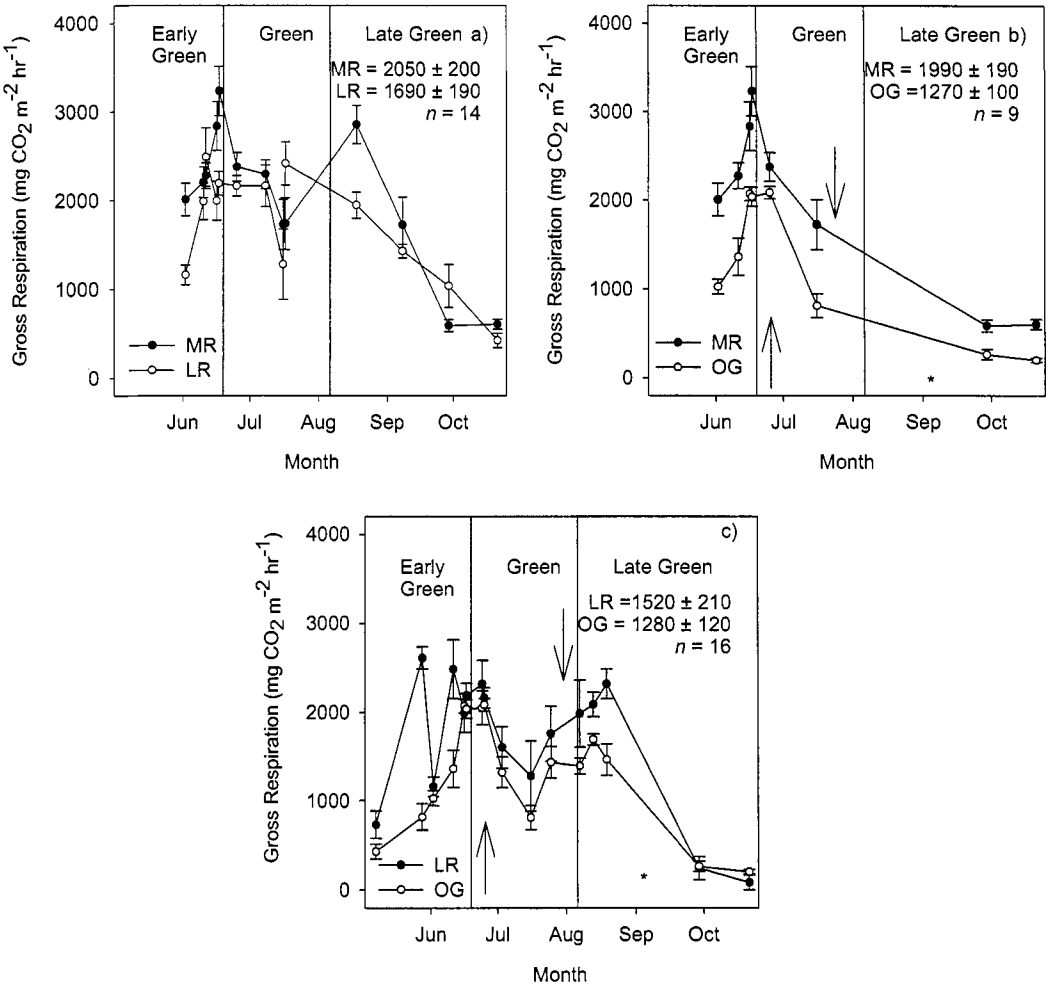

Figure 5.15: Comparison of R_{TOT} of Vegetated sites for measurements made on the same sample dates for a) MR and LR, b) MR and OG, and c) LR and OG. Means ± SE are shown. Note: arrows and star denote the date of harvesting (June 25 and July 30) and pesticide application (September 2), respectively. Period transitions illustrated by vertical lines.

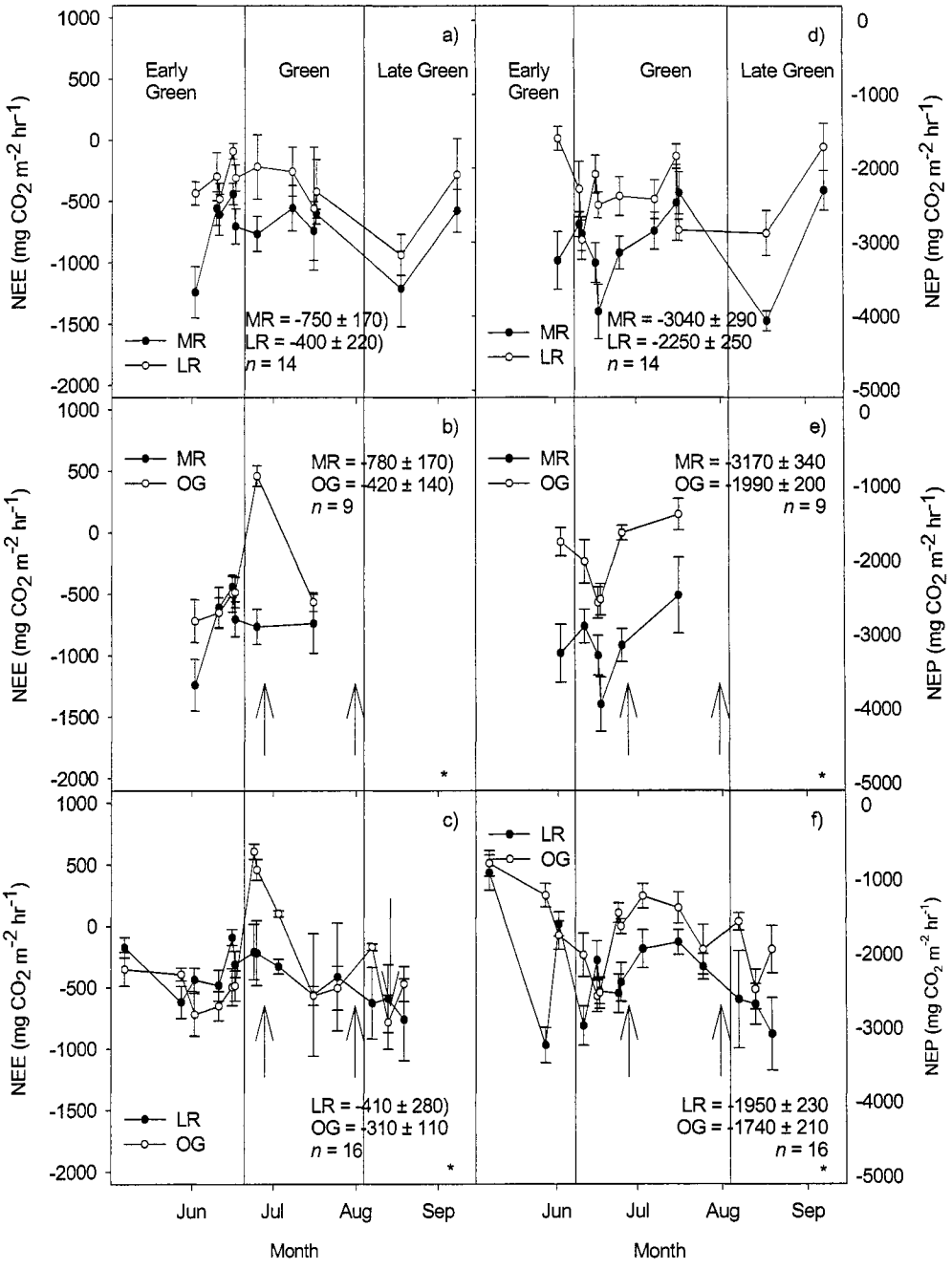

Figure 5.16: Comparison of NEE of a) MR and LR, b) MR and OG, c) LR and OG and NEP of d) MR and LR e) MR and OG and f) LR and OG for Vegetated sites for measurements made on the same sample dates. Means ± SE are shown. Note: arrows and star denote the date of harvesting (June 25 and July 30) and pesticide application (September 2), respectively. Period transitions illustrated by vertical lines.

Seasonally, for the Veg plots, R_{TOT} for the MR site was significantly ($\alpha = 0.05$) larger than that of the LR and OG sites (Table 5.5). Furthermore, NEE and NEP for the Veg sites showed significant differences ($\alpha = 0.05$) with the MR site being greater than the LR site, and both exceeded values at the OG site (Table 5.5). For the Bare R_{TOT} for the MR site was significantly ($\alpha = 0.05$) lower compared to the LR site, larger than the WOOD site and no different from that of the OG site (Table 5.6).

Site	LR-NEE	MR-NEE	OG-NEE	LR-R_{TOT}	MR-R_{TOT}	OG-R_{TOT}	LR-NEP	MR-NEP	OG-NEP
LR-NEE		**0.004**	0.078						
MR-NEE			**0.000**						
OG-NEE									
LR-R_{TOT}					**0.039**	**0.004**			
MR-R_{TOT}						**0.000**			
OG-R_{TOT}									
LR-NEP								**0.000**	**0.000**
MR-NEP									**0.000**
OG-NEP									

Table 5.5: Difference of mean ('P' values) for Veg sites. Test was an unpaired, unequal variance, students' t-test. 'P' value is the probability that the null hypothesis (CO_2 flux from site 1 is no different than the CO_2 flux from site 2), by chance, is true. Bold denotes significance at $p < 0.05$. Abbreviations are: Lower Riparian (LR), Middle Riparian (MR), Open Grassland (OG), Maple Woodlot (WOOD), net ecosystem CO_2 exchange (NEE), respiration (R_{TOT}) and net ecosystem productivity (NEP).

Site	LR-NEE	MR-NEE	OG-NEE	WOOD-NEE	LR-R_{TOT}	MR-R_{TOT}	OG-R_{TOT}	Wood-R_{TOT}	LR-NEP	MR-NEP	OG-NEP	Wood-NEP
LR-NEE		**0.047**	0.391	**0.000**								
MR-NEE			0.555	**0.050**								
OG-NEE				**0.041**								
WOOD -NEE												
LR-R_{TOT}						**0.031**	0.225	**0.005**				
MR-R_{TOT}							0.566	0.330				
OG-R_{TOT}								0.192				
WOOD -R_{TOT}												
LR-NEP										**0.046**	0.463	0.503
MR-NEP											0.267	0.206
OG-NEP												0.931
WOOD -NEP												

Table 5.6: Difference of mean ('P' values) for Bare sites. Test was an unpaired, unequal variance, students' t-test. 'P' value is the probability that the null hypothesis (CO_2 flux from site 1 is no different than the CO_2 flux from site 2), by chance, is true. Bold denotes significance at $p < 0.05$. Abbreviations are: Lower Riparian (LR), Middle Riparian (MR), Open Grassland (OG), Maple Woodlot (WOOD), net ecosystem CO_2 exchange (NEE), respiration (R_{TOT}) and net ecosystem productivity (NEP).

5.4 Climatic and Biological Influences on CO_2 Exchange

The periodic collection of point data precludes a thorough investigation of temporal variability. However, some comments regarding the general controlling factors regulating CO_2 dynamics and spatial variability can be assessed. This section focuses on correlations and controls on the spatial and temporal variability of the CO_2 exchange (NEE, R_{TOT} and NEP). First, meteorological variables (ambient temperature (T_a), 0 - 30 cm ground temperature (T_g), volumetric soil moisture content (VSM), photosynthetically active radiation (PAR), and preceding cumulative 7-day precipitation) will be explored. Secondly, biological factors such as soil properties (total carbon (%TC), total nitrogen (%TN), C/N ratios and water extractable phosphorus (EXT-P)) and vegetative parameters (above-ground green biomass (AGB), below-ground root biomass (RBM) and peak summer vegetation height (H_M)) will be examined. For precipitation influences, weeks receiving less than 5 mm of rain were excluded from analysis, which represented approximately 20 - 30% of the sample dates. These were excluded because the magnitude of water infiltrating to significant depths to affect root zone or microbial activity should be minimal (Laporte et al., 2002). The biological analysis was limited by the periodic measurements of the CO_2 fluxes (n = 21 – 24 over the season), the number of collars per site (at least 3 for Bare and Veg) and the frequency of measurements of the biological variables (2 to 4 location per site and sample dates) (Section 5.2.3 - 5.2.5). The biological relationships are explored between seasonal site-averaged CO_2 fluxes and site-averaged seasonal biological variables.

5.4.1 Thermal Influences on CO_2

A result of collecting data at midday and from sites within 2 km of one another is the lack of spatial variability in the meteorological data. Section 5.3 showed that spatially there were no significant differences between T_a, T_g, VSM and PAR between sites. Even the WOOD site, with differing vegetation and canopy cover, showed little variation in meteorological variables (excluding PAR). As a result, the spatial variability of CO_2 fluxes cannot be attributed to meteorological variables, however, they explain the seasonal patters of CO_2.

Temporal variation in CO_2 exchange during the study season was best represented by an exponential relationship with T_a and T_g (Figure 5.17 a - g). Generally, for all sites and terrain covers (Bare and Veg), excluding the WOOD, T_a explained the greatest amount of the temporal variability in R_{TOT} (63 - 83% for Bare and 77 - 86 % for Veg) and the 20-cm depth-averaged T_g explained 30 - 51% and 48 - 68% of the temporal variability for Bare and Veg sites, respectively (Figure 5.17 a - g).

5.4.2 Field Q_{10} Values

The Q_{10} ratio shows the temperature dependence of R_{TOT} for a 10°C change in soil temperature (Fang and Moncrieff, 2001) and is defined as:

$$Q_{10} = \frac{R_{T+10}}{R_T} \qquad (5.1)$$

where R_T and R_{T+10} are R_{TOT} at soil temperatures of T and $T + 10$, respectively. The first-order exponential equation, which was used in this study adjusts for temperature variations different from 10°C and assumes that Q_{10} is constant over the observed soil

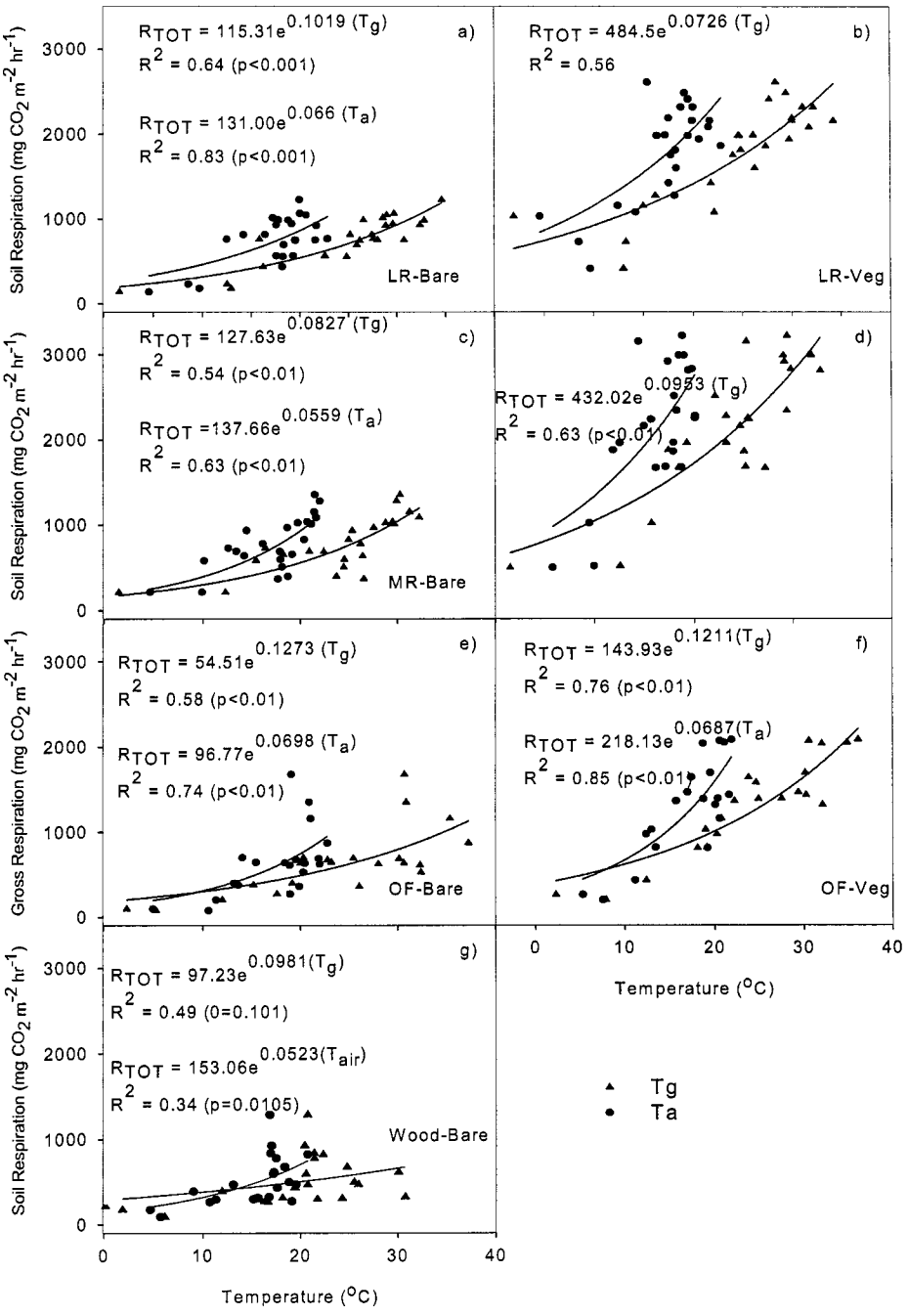

Figure 5.17: Relationship between respiration (R_{TOT}) with air temperature (T_a) and 20 cm depth averaged ground temperature (T_g) for a) LR Bare, b) LR Vegetated, c) MR Bare, d) MR Vegetated, e) OG Bare, f) OG Vegetated and g) WOOD Bare. Each point represents the means of 3 - 4 daily measurements over the 4-month study period.

temperature range (no nonlinear relationships incorporated as temperature rises), thus Q_{10} can be calculated using:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(T_2-T_1)} \qquad (5.2)$$

where R_2 and R_1 are the R_{TOT} for soil temperatures T_2 and T_1 (Fang and Moncrieff, 2001).

The larger the Q_{10} values the more sensitive the reaction (SOM decomposition) is to temperature increases. The Q_{10} value for all of the Bare plots combined ranged from 2.3 to 2.9, with a value of 3.6 for the OG site (Table 5.7). Generally, all sites, except the OG site, exhibited similar Q_{10} responses. This may be related to periodic summer harvesting, which can supply detrital biomass compared to the MR and LR riparian sites (LeCain et al., 2002).

Table 5.7: Q_{10} values for soil respiration (R_{TOT}) derived from the first-order fitted exponential relationship for 20 cm depth averaged ground temperature and ground temperature at 5 cm. [1] value is reduced to 3.0 if 1 data point collected immediately after August harvesting is excluded.

Site	LR	MR	OG	WOOD
Q_{10} - average	2.8	2.3	3.6[1]	2.7
Q_{10} - 5 cm	2.4	2.1	2.9	2.0

5.4.3 Soil Moisture, Precipitation and PAR Influences on CO_2

A moderately strong quadratic relationship exists between VSM and Bare R_{TOT} (*cf.* Davidson et al., 2000; Mielnick and Dugas, 2000) (Figure 5.18). For Bare plots, VSM explained 27 - 52% of the variability, and 27 - 50% for the Veg plots. Utilizing this relationship, maximum fluxes were observed between VSM values of 25 and 30% (water

filled pore space between 50 and 60%). The weakest Bare plot relationship with VSM was found at the OG site. This may be due to the open nature of the terrain and the lack of fetch adjustments from cooler, moister areas, such as water near riparian areas. Rapid changes in wind direction may alter soil evaporation and plant transpiration demands that may have affected the direct influence of soil moisture (Oke, 1987).

Preceding cumulative 7-day precipitation was shown to be negatively related to Bare R_{TOT} (r^2 =0.33 – 0.39, $p<0.01$) and Veg R_{TOT} (r^2 = 0.36 – 0.52, $p<0.01$) (Table 5.8). PAR was also shown to be logarithmically related to plant uptake, eventually reaching a saturation level in which plant activity is operating at a maximum (Griffis et al., 2000). PAR was shown to be positively related to R_{TOT} with regression coefficients stronger for Veg (27 to 65%) than corresponding Bare sites (21 to 49%) (Table 5.8).

NEE and NEP for Veg sites showed weak, but significant ($\alpha = 0.05$), relationships at the MR site with VSM and 7-day precipitation, LR with T_a and PAR, and OG with T_a, PAR and 7-day precipitation (Table 5.8). Generally, poor temporal relationships between the CO_2 uptake fluxes were observed.

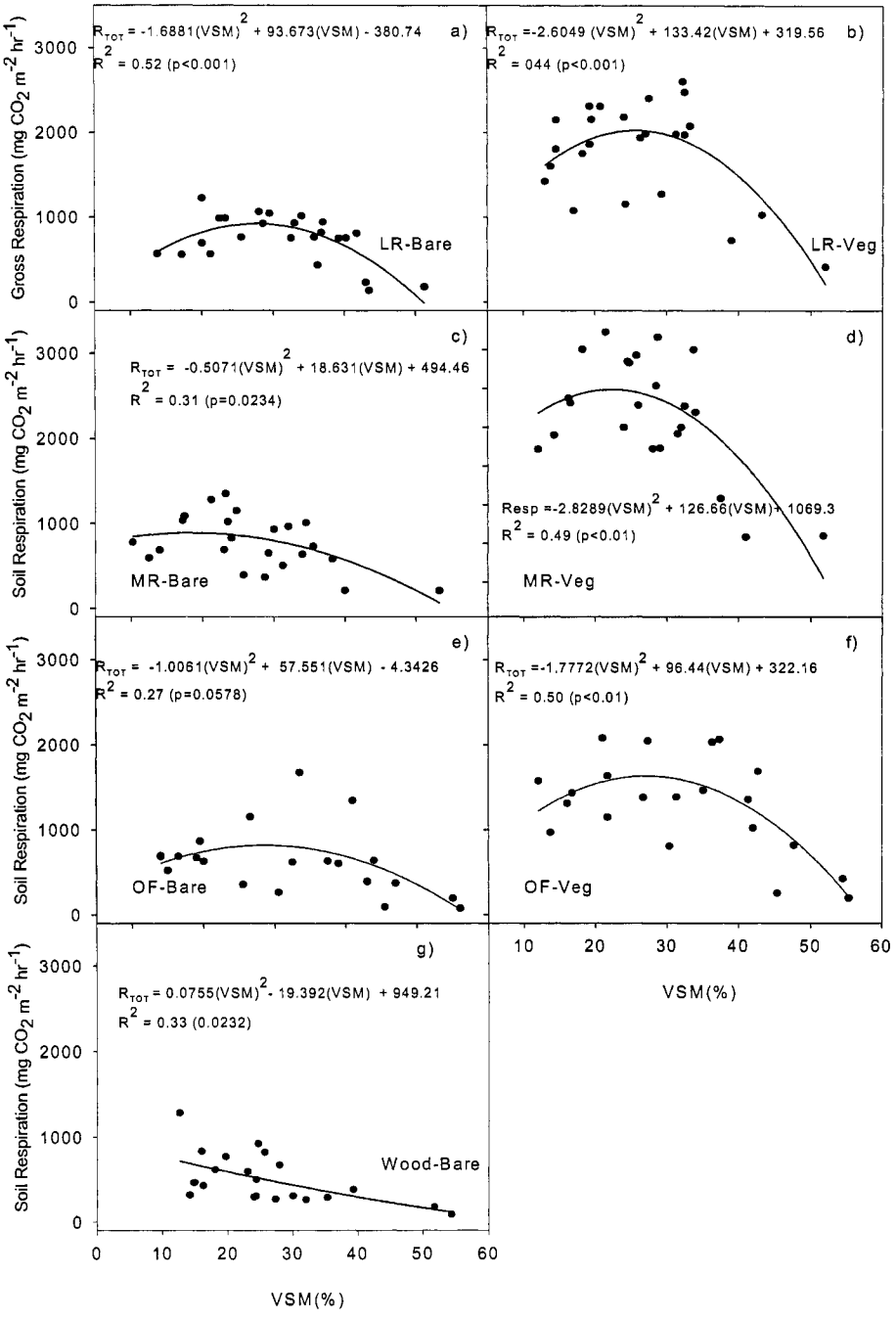

Figure 5.18: Relationship between volumetric soil moisture content (%) (VSM) and respiration (R_{TOT}) for a) LR Bare, b) LR Vegetated, c) MR Bare, d) MR Vegetated, e) OG Bare, f) OG Vegetated and g) WOOD Bare. Each point represents the means of 3 - 4 daily measurements over the 4-month study period.

Site	Terrain	Carbon Flux	*N*	T_a (°C)		T_g (°C)		VSM (%)		Par (W m^{-2})		7-day precipitation
Curve Type				**linear**	**exponential**	**linear**	**Exponential**	**linear**	**quadratic**	**linear**	**logarithmic**	**linear**
LR	Bare	R_{TOT}	23	**0.77****	**0.83****	**0.49****	**0.65****	**0.18***	**0.52*****	**0.55****	**0.49****	**0.39****
MR	Bare	R_{TOT}	24	**0.57****	**0.63****	**0.51****	**0.55****	**0.22***	**0.32****	**0.34****	**0.21****	**0.39****
OG	Bare	R_{TOT}	21	**0.50****	**0.74****	**0.34****	**0.58****	0.10	**0.27***	**0.22***	**0.26****	**0.33****
WOOD	Bare	R_{TOT}	22	0.16	**0.40****	**0.30****	**0.49****	**0.32****	**0.33*****	<0.1	<0.1	<0.1
LR	Veg	NEE	21	<0.1	<0.1	<0.1	0.06	<0.1	<0.1	<0.1	<0.1	0.20
MR	Veg	NEE	22	**0.25***	0.20	**0.20***	**0.19***	<0.1	<0.1	**0.24***	**0.25****	<0.1
OG	Veg	NEE	19	<0.1	<0.1	<0.1	0.03	**0.24***	0.24	<0.1	<0.1	<0.1
LR	Veg	R_{TOT}	23	**0.70****	**0.64****	**0.52****	**0.61****	0.14	**0.44****	**0.65****	**0.65****	0.16
MR	Veg	R_{TOT}	24	**0.71****	**0.77****	**0.54****	**0.63****	**0.27***	**0.49****	**0.36****	**0.27***	**0.45***
OG	Veg	R_{TOT}	21	**0.86****	**0.86****	**0.68****	**0.76****	**0.24***	**0.50****	**0.69****	**0.65****	**0.52****
LR	Veg	NEP	21	**0.59****	**0.52****	**0.36****	**0.36****	<0.1	0.20	**0.50****	**0.55****	<0.1
MR	Veg	NEP	22	0.15	0.15	<0.1	<0.1	<0.1	**0.29***	<0.1	<0.1	**0.36***
OG	Veg	NEP	19	**0.25***	**0.25***	0.15	<0.1	<0.1	0.23	**0.34****	**0.36****	**0.37***

Table 5.8: Variation explained for single regressions between carbon fluxes: respiration (R_{TOT}), net ecosystem CO_2 exchange (NEE) and net ecosystem productivity (NEP) with air temperature (T_a), 20 cm depth averaged ground temperature (T_g), volumetric soil moisture content (%) (VSM), photosynthetically active radiation (PAR) and cumulative 7-day precipitation. Significant regressions are in bold with ($P < 0.01$) and ($P < 0.05$) denoted by, ** and *, respectively. Note: Bare the NEE and NEP was omitted (refer to section 5.3.2).

5.4.4 Biological, Soil and Vegetative Influences

The seasonal relationships between site averaged R_{TOT}, NEE, NEP and %TC, %TN, C/N and EXT-P, for Bare and Veg sites, are shown in Figure 5.19. The lack of large inter-site variability for Bare R_{TOT} produces weak trends, for all soil variables (Figure 5.19 d, g, j,) and biological indicators (Figure 5.20 a, d, g,). The only evident relationship for Bare R_{TOT} was a negative relationship with %TC (Figure 5.19a). This seems counterintuitive, however, is related to microbial influenced and will be further discussed in Section 6.3.1. The NEE and NEP for Veg sites showed strong positive (greater uptake) relationships with %TN and C/N ratios (Figure 5.19 e - f, h - i). However, no strong relationships were found between EXT-P and any CO_2 flux. Strong relationships between AGB, RBM H_M were exhibited for Veg R_{TOT}, NEE and NEP (Figure 5.20). This indicates more uptake and release with greater above-ground biomass.

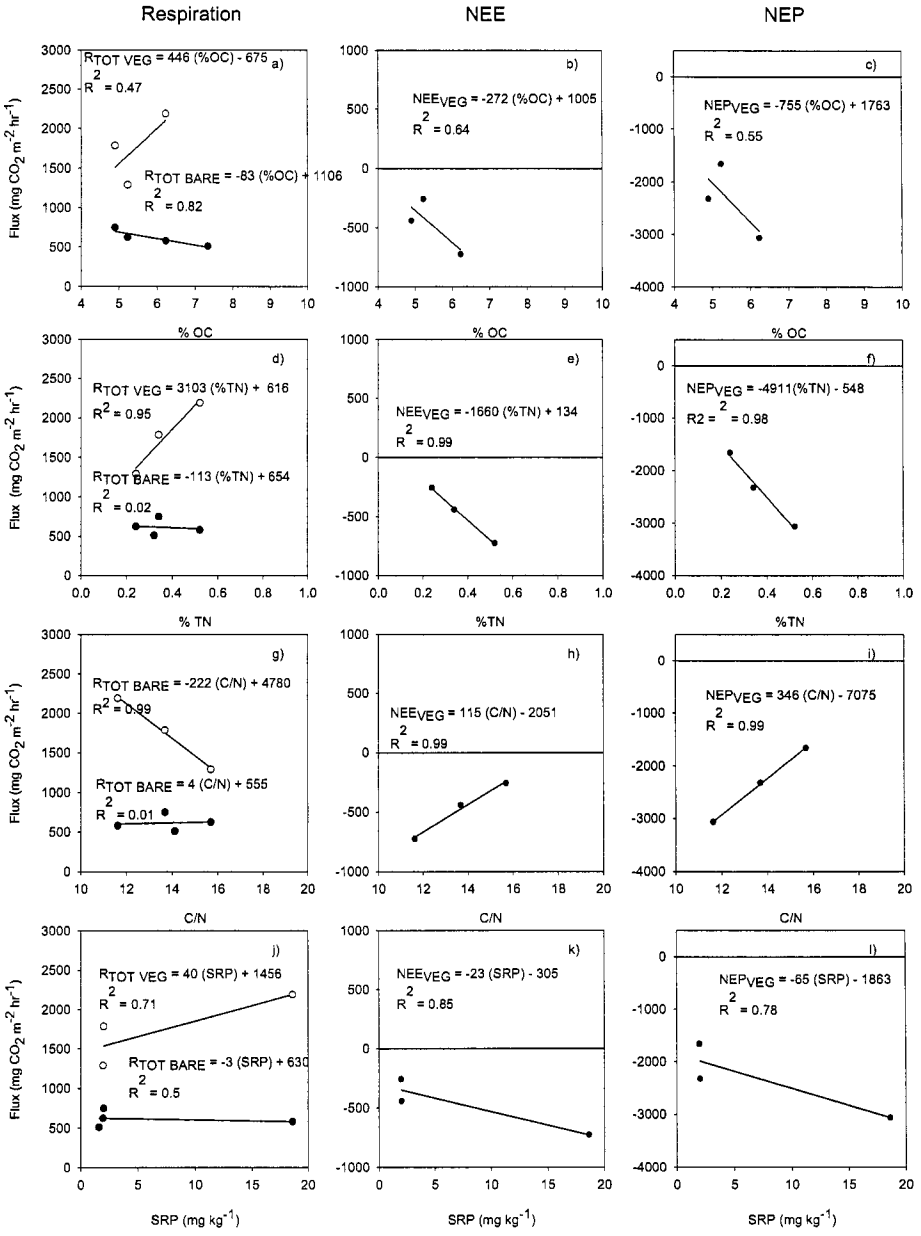

Figure 5.19: Relationships between a) respiration (R_{TOT}) and percent organic carbon (%TC), b) net ecosystem CO_2 exchange (NEE) and %TC, c) net ecosystem productivity (NEP) and %TC, d) R_{TOT} and total nitrogen (%TN), e) NEE and %TN, f) NEP and %TN, g) R_{TOT} and carbon/nitrogen ratio (C/N), h) NEE and C/N, i) NEP and C/N, j) R_{TOT} and water extractable phosphorus (EXT-P), k) NEE and EXT-P and l) NEP and EXT-P for Bare and Vegetated plots.

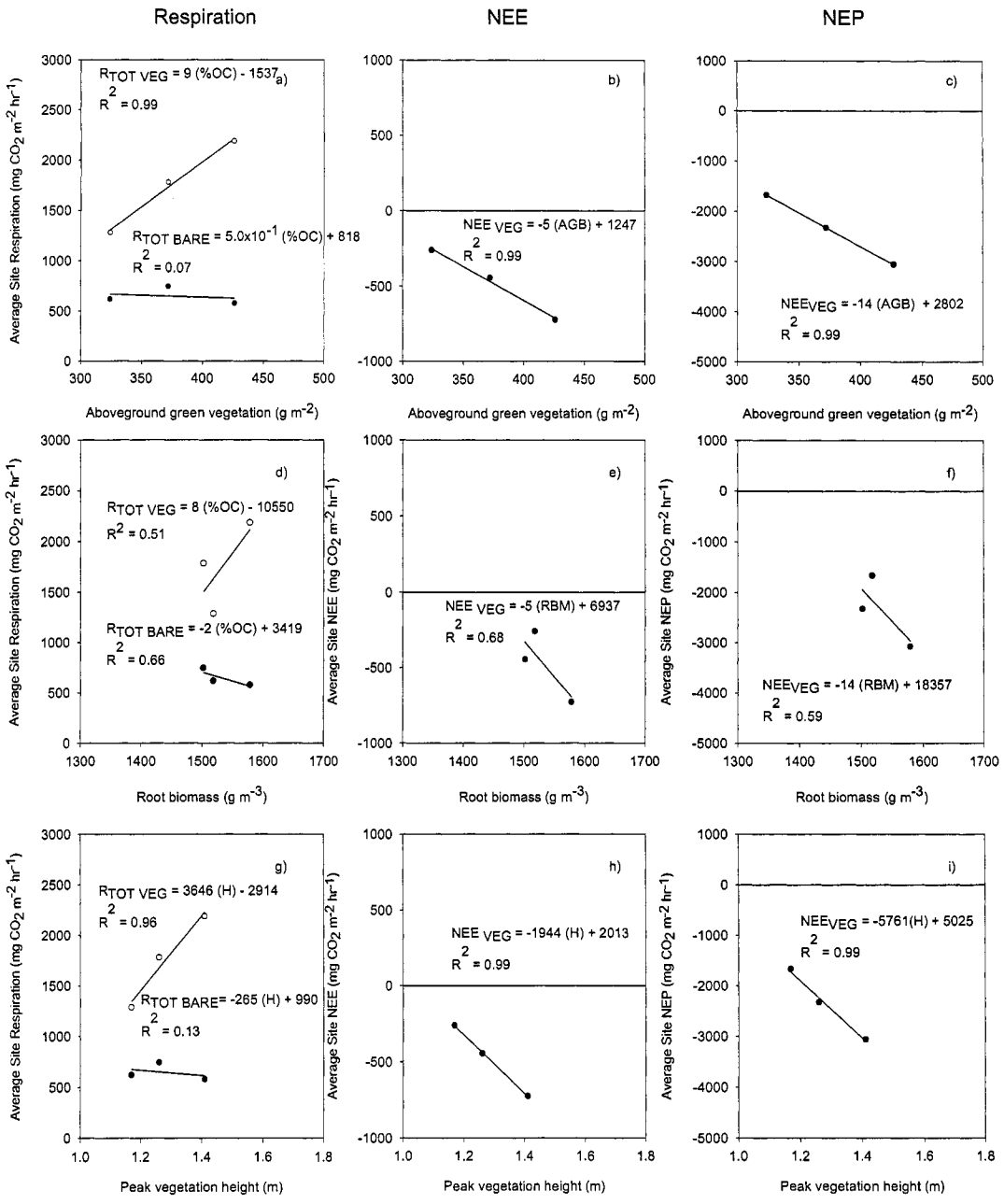

Figure 5.20: Relationships between a) respiration (R_{TOT}) and above-ground green biomass (AGB), b) net ecosystem CO_2 exchange (NEE) and AGB, c) net ecosystem productivity (NEP) and AGB, d) R_{TOT} and root biomass (RBM), e) NEE and RBM, f) NEP and RBM, g) R_{TOT} and peak vegetation height (H_M), h) NEE and H_M and i) NEP and H_M for Bare and Vegetated plots.

5.5 PARTITIONING TOTAL RESPIRATION

5.5.1 The Contribution of Plant Respiration

The Veg R_{TOT} losses in this study were 2.1, 3.7 and 1.9 times greater than the accompanying Bare R_{TOT} for the LR, MR and OG sites, respectively. This value compares favourably to the estimated plant respiration (PR) (Veg R_{TOT} – Bare R_{TOT}) being 2 times greater than the Bare soil R_{TOT} (Raich and Tufekcioglu, 2000). The Veg R_{TOT} losses at the MR site were almost 4 times larger than Bare R_{TOT} and with the incorporation of active root respiration the Veg R_{TOT} losses would likely be smaller than Bare R_{TOT} (Craine et al., 1999).

PR was estimated as the daily difference between the average Veg R_{TOT} and Bare R_{TOT} for each individual site. For all sites, the percent contribution of PR to the overall R_{TOT} was relatively conservative for all periods and throughout the season, with the only exception of the OG site during the LG period (Figure 5.21a). The relative (average ± SE) contribution of PR followed the trend MR (72 ± 5%) greater than LR (59 ± 5%) and OG (52 ± 6%). The relative contribution of PR at the OG site was lower during the LG period (38 ± 7%) due to the vegetation harvesting in late July (Figure 5.21b). Overall, the PR for the MR site was the greatest with values of 1650 ± 60, 1690 ± 80, 1380 ± 80 and 1570 ± 70 mg CO_2 m^{-2} hr^{-1} for the EG, G, LG periods and seasonal average, respectively (Figure 5.21b). The LR site also exhibited large magnitude contributions of 1110, 1030 and 980 mg CO_2 m^{-2} hr^{-1} compared to the OG site with values of 800, 830 and 380 mg CO_2 m^{-2} hr^{-1} for the EG, G and LG periods, respectively.

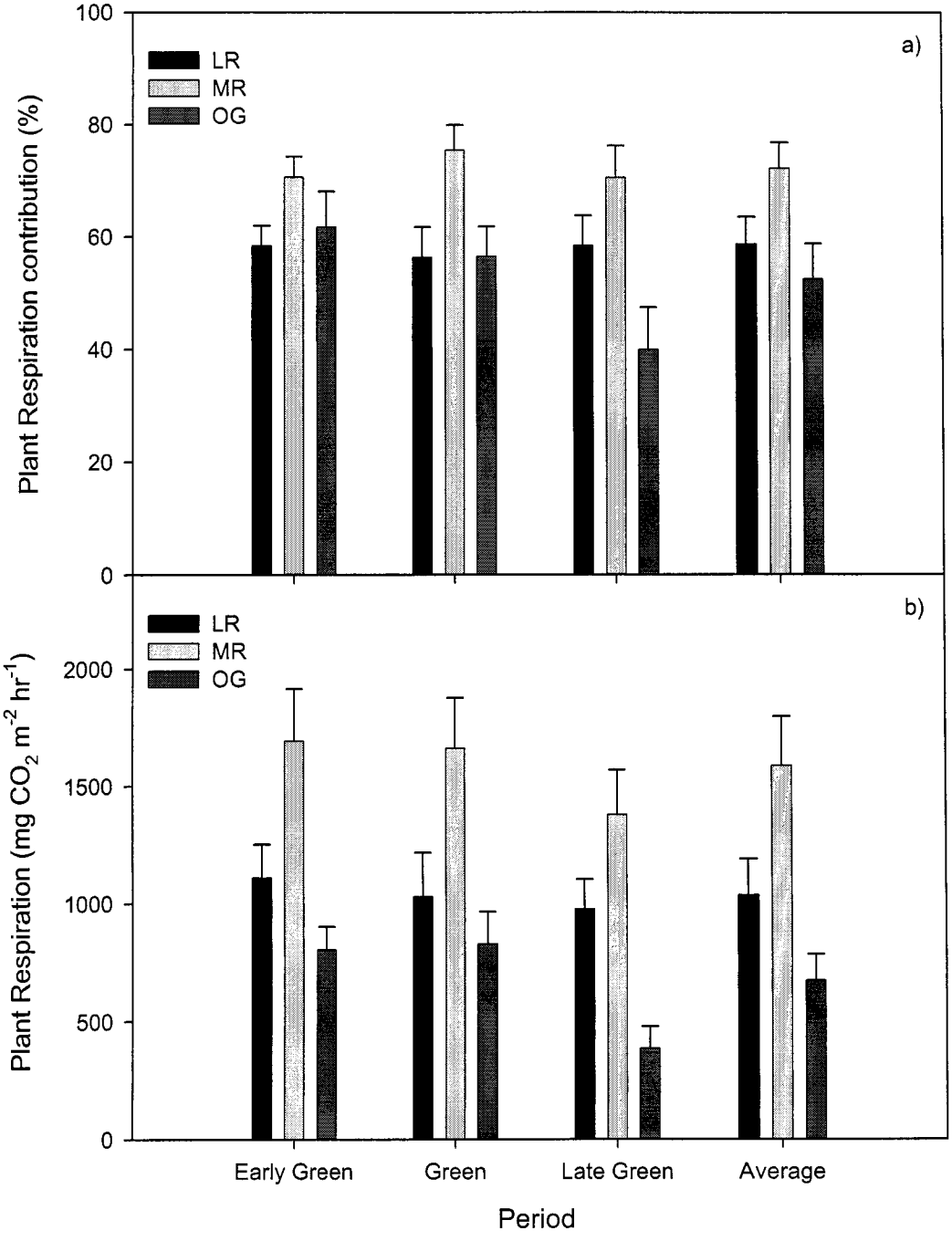

Figure 5.21: Seasonal plant respiration (PR) for a) percent contribution and b) overall magnitude for the Middle Riparian (MR), Lower Riparian (LR) and open grassland (OG) sites. Means ± SE are shown. (n = 5 - 8).

5.5.2 Laboratory Experiment: Root Contributions to Overall Soil Respiration

5.5.2.1 Temporal Variability of Root and Soil Respiration

Roots can contribute a substantial component towards the overall R_{TOT}, thus understanding their magnitude and variability should shed some insight into root functions (Hanson et al., 2000). The temporal trends over the duration of the experiment were similar for all sites (Figure 5.22). Generally, prior to day 10 when soils were wet, (VSM > 85%) fluxes were low. After day 10, at 20% VSM, loss through evaporation (E) from larger pores (Brady and Weil, 1999) rapidly increased the fluxes by 20 - 60% and 20 - 45% for the 20 ± 2°C (now referred to as the 20°C) and 8 ± 2°C °C (now referred to as the 8°C) treatments, respectively. Rapid flux increases have been related to the high quality of dissolved organic C from microbes killed by freezing or other related substrate conditions that may enhance microbial respiration (Elberling et al., 2003). The high fluxes were maintained until about day 30 between VSM losses of 25 and 40% (Figure 5.22) and then after water drained from pore spaces and gaseous exchange of O_2 in, and CO_2 out of, the soil were allowed to proceed. A sudden decrease in fluxes, for all sites under both temperature regimes occurred around day 30. This may be attributed to the labile C from SOM, C from microbial death and/or nutrient levels becoming exhausted (Sjögerten and Wookey, 2002). At the 20°C treatment, the prolonged fluxes towards the end of the experiment reflected soil organic C content, such that the maintained fluxes were largest at the WOOD site and smallest at the OG (Figure 5.22 a & c).

Large CVs of 50 - 60% occurred within the first 10 days of the experiment and towards the end, between days 35 and 55, when average fluxes were relatively low. Maximum daily CVs for all sites were around 65 - 75%. When fluxes were the largest,

between days 10 and 30, CVs were approximately 20 - 35%. The large CVs can be explained by the differential rate of water drainage from pores and the variability in substrate availability between sample jars (Winkler et al., 1996). During the experiment two temperature anomalies occurred, one for each temperature regime (20°C and 8°C). First, on day 17 the ambient room temperature declined to approximately 16°C in response to the building's air conditioning system being activated, thus a decline in root and soil (R_{R+S}) and soil devoid of roots (R_S) was exhibited for the 20°C treatment. Second, the refrigerator thermostat accidentally was reduced to 4°C on day 10 which reduced respiration fluxes.

5.5.2.2 Spatial Variability of Root and Soil Respiration

Over the 55 day incubation period there were significant ($\alpha = 0.05$) differences between the time average R_{R+S} and R_S, between among the four sites under 20°C treatments (Figure 5.22 and Table 5.9). However, there were minor variations that occurred during the middle portion of the experiment. Between day 12 and 30 the MR R_{R+S} was 24% lower (6.2 ± 0.8 mg CO_2 m^{-2} hr^{-1}/ g dry weight (wt) soil) than that at the LR site (8.3 ± 0.8 mg CO_2 m^{-2} hr^{-1}/ g dry wt of soil) and 51% less (1.4 ± 0.3 mg CO_2 m^{-2} hr^{-1}/ g dry wt soil) relative to the LR site (2.9 ± 0.2 mg CO_2 m^{-2} d^{-1}/ g dry wt of soil) under the 20°C and 8°C treatments, respectively. For the R_S at 20°C there were no significant differences between the sites. However, at 8°C the MR site was significantly (α=0.05) lower (0.66 ± 0.16 mg CO_2 m^{-2} hr^{-1}/ g dry wt of soil) than the LR site (1.19 ± 0.66 mg CO_2 m^{-2} hr^{-1}/ g dry wt of soil), which may be accounted for by the large fluxes

exhibited at the LR site from days 22 to 30 (Figure 5.22). The large fluxes at the LR site may be the result of the slower

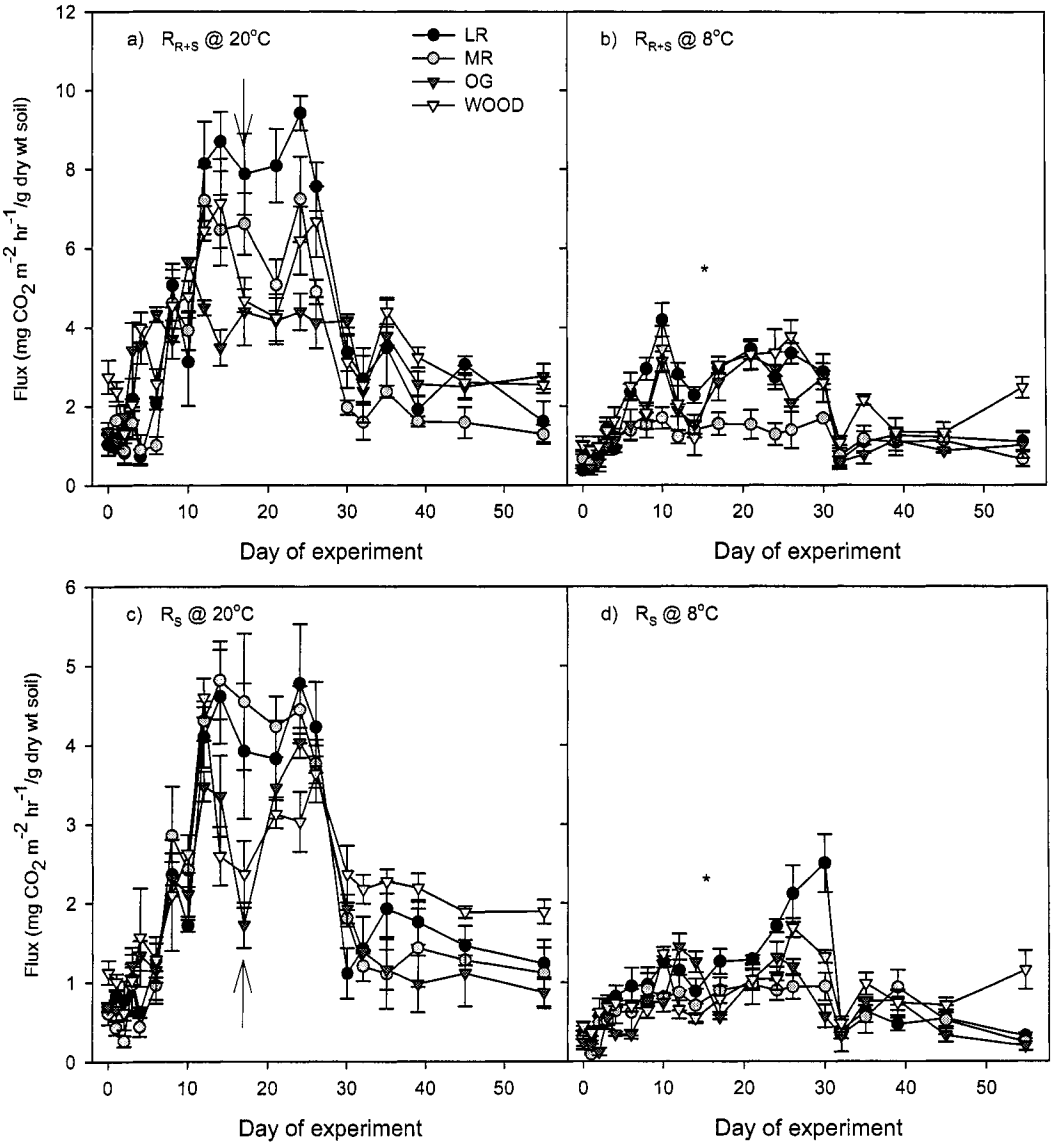

Figure 5.22: Respiration rates of a) roots and soil (R_{R+S}) at 20°C , b) R_{R+S} at 8°C, c) soil (R_S) at 20°C and d) R_S at 8°C for all sites over the 55 day duration of the laboratory experiment. Mean, hourly values (mg CO_2 m^{-2} hr^{-1}/g dry weight (wt) of soil) ± SE are shown, n = 3. Note: arrow and star denote a decline in room temperature to 16°C and refrigerator temperature to 4°C, respectively (see text for further explanation) and the different scale for a) & b) compared to c) & d).

decline in VSM for the LR site compared to the MR site (slightly more clay at the LR site – Table 5.2), which may have favoured greater dissolution of soil bound nutrients (Brady and Weil, 1999). As a result of the lower R_{R+S} and R_S, the flux from roots (R_R) was also lower at the MR site (Table 5.9).

5.5.2.3 Overall Root Contributions

Figure 5.23 and 5.24 show the R_{R+S} and R_S for the 20°C and 8°C treatments with the difference between the two representing an indirect estimate of root respiration (R_R). The average root R_R (percent in parentheses) at the 20°C treatment was 1.91 (47%), 1.04 (33%), 1.54 (45%) and 1.73 (44%) mg CO_2 m^{-2} hr^{-1}/ g dry wt of soil for the LR, MR, OG and WOOD sites, respectively (Table 5.9). At the 8°C treatment, the R_R averaged for the LR, MR, OG and WOOD were 0.99, 0.54, 0.95 and 1.24 mg CO_2 m^{-2} hr^{-1}/ g dry wt of soil, respectively. The approximate increase in R_R from 8°C to 20°C was 48%, 48%, 38% and 28% for the LR, MR, OG and WOOD sites, respectively showing distinctive trends for both riparian sites. Each site exhibited a large range in percent root contribution (%RC) of 28 - 53% (Table 5.9) in response to the dynamic change in VSM, nutrient availability and soil aeration. The %RC for the 20°C treatment for the LR, OG and WOOD sites were no different. However, the MR site exhibited significantly ($\alpha = 0.05$) lower %RC and R_R fluxes than the other three sites. At the 8°C treatment the two riparian sites (LR and MR) showed lower %RC than the OG and WOOD sites (Table 5.9).

The specific root respiration (SRR) at the LR site was 4 times greater than that at the MR, and 3 times larger than the OG and WOOD sites at 20°C treatment (Table 5.10). At the 8°C treatment, the SRR at the LR site was 6 times greater than at the MR, 3 times

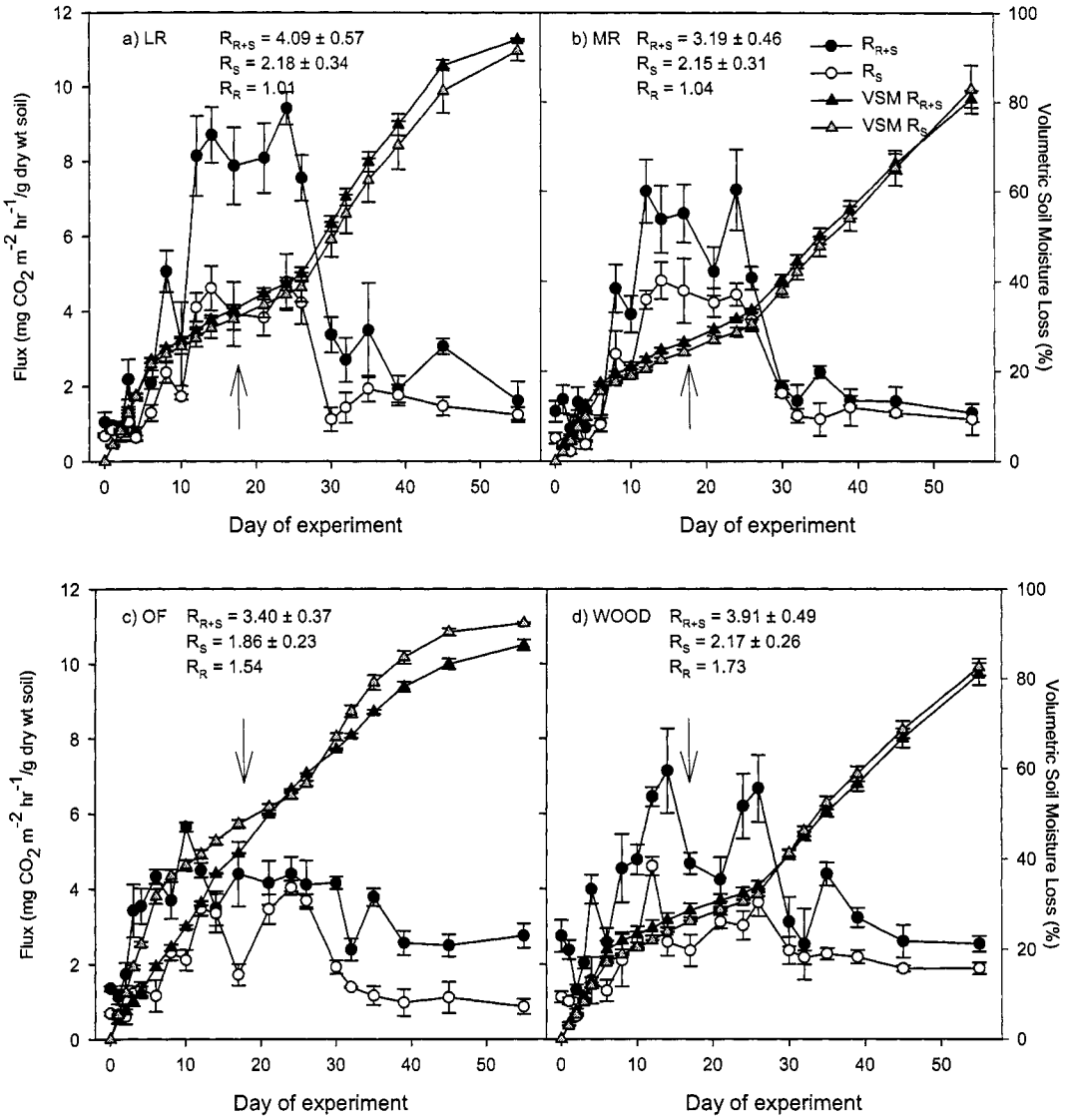

Figure 5.23: Respiration rates of root and soil (R_{R+S}) and soil (R_S) and accompanying volumetric soil moisture content (%) (VSM) loss at 20°C treatment over the duration of the 55 day laboratory experiment for a) LR, b) MR, c) OG and d) WOOD. Mean, hourly flux (mg CO_2 m^{-2} hr^{-1}/g dry weight (wt) of soil) ± SE are shown, n = 3. Note: arrows denote a decline in room temperature to 16°C (see text for further explanation).

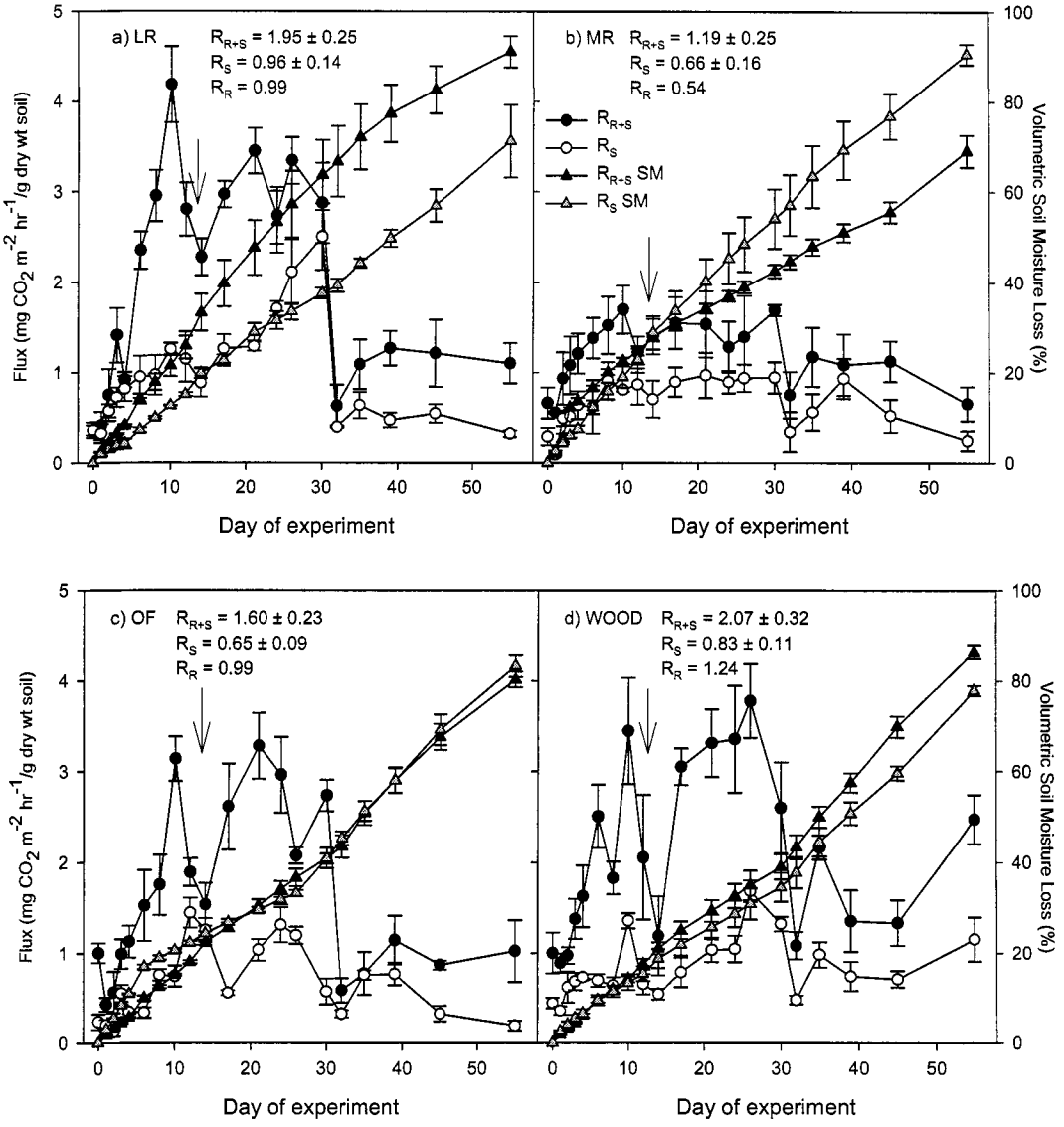

Figure 5.24: Respiration rates of root and soil (R_{R+S}) and soil (R_S) and accompanying volumetric soil moisture content (VSM) loss at 8°C treatment over the duration of the 55 day laboratory experiment for a) Lower Riparian (LR), b) Middle Riparian (MR), c) Open Grassland (OG) and d) Maple Woodlot (WOOD). Mean, hourly flux (mg CO_2 m^{-2} hr^{-1}/g dry weight (wt) of soil) ± SE are shown, n = 3. Note: arrows denote a decline in refrigerator temperature to 4°C (see text for further explanation).

greater than at the OG, and 1.25 times larger than that observed at the WOOD site. For all sites the SRR decreased from the 20°C to 8°C treatments by 48, 60, 52 and 11% for the LR, MR, OG and WOOD, respectively, however, roots contributed a greater amount towards the total R_{TOT} at lower temperatures (Table 5.10) likely through reduced microbial respiration (Hanson et al., 2000; Maier and Kress, 2000).

Table 5.9: Study averaged respiration fluxes for roots and soil (R_{R+S}), soil (R_S), roots (R_R) and percent root contribution (%RC) under the 20°C and 8°C laboratory treatments. Values in mg CO_2 m^{-2} hr^{-1} / g dry weight (wt) of soil ± SE. $R_R = R_{S+R} - R_S$ and %RC is determined by study averaged R_{R+S} / R_S. Test was an unpaired, unequal variance, students' t-test and all data passed the Kolmogorov-Smirnov goodness of fit normality test. Means within each column and treatment followed by a different letter are significantly different ($\alpha = 0.05$).

	20°C				8°C			
Site	**R_{R+S}**	**R_S**	**R_R**	**RC (average)**	**R_{R+S}**	**R_S**	**R_R**	**RC (average)**
LR	4.09 ± 0.57[a]	2.18 ± 0.34[a]	1.91[a]	28 – 60 (47)[a]	1.95 ± 0.25[a]	0.96 ± 0.14[a]	0.99[a]	35 – 63 (51)[a]
MR	3.19 ± 0.46[a]	2.15 ± 0.31[a]	1.04[b]	10 – 49 (32)[b]	1.19 ± 0.25[b]	0.66 ± 0.16[b]	0.54[b]	13 – 66 (45)[a]
OG	3.40 ± 0.37[a]	1.86 ± 0.23[a]	1.54[a]	31 – 57 (45)[a]	1.60 ± 0.23[a]	0.65 ± 0.09[b]	0.95[a]	46 – 69 (59)[b]
WOOD	3.91 ± 0.49[a]	2.17 ± 0.26[a]	1.73[a]	29 – 57 (44)[a]	2.07 ± 0.32[a]	0.83 ± 0.11[a]	1.24[a]	46 – 70 (60)[b]

The Q_{10} values calculated for the incubation experiment are presented in Table 5.11. These values were approximated using the study averaged fluxes ($R_{20°C}$ /$R_{8°C}$) for each soil component (R_{R+S}, R_S and R_R). For the entire incubation period there were no significant ($\alpha = 0.05$) differences between the sites for each component. However, the Q_{10} for the MR site was slightly larger, and the WOOD slightly smaller than the remaining

sites. The Q_{10} for R_S was the largest, whereas the Q_{10} for the R_R was the smallest (Table 5.11).

Table 5.10: Study averaged specific root respiration (SRR) under the 20°C and 8°C laboratory treatments. Values are reported in mg CO_2 m^{-2} hr^{-1} / mg dry weight (wt) of root ± SE. Test was an unpaired, unequal variance, students' t-test and all data passed the Kolmogorov-Smirnov goodness of fit normality test. Means within each column and treatment followed by a different letter are significantly different ($\alpha = 0.05$).

	SRR	
Site	**20°C**	**8°C**
LR	37.2 ± 7.0^{b}	19.4 ± 3.5^{a}
MR	8.4 ± 1.5^{a}	3.4 ± 0.3^{c}
OG	12.4 ± 1.8^{c}	6.0 ± 1.1^{b}
WOOD	14.0 ± 1.9^{c}	15.6 ± 1.9^{a}

Table 5.11: Approximate Q_{10} values for all sites using the study averaged laboratory flux ($R_{20°C}$ /$R_{8°C}$) obtained over the 55 day incubation period. Study averaged (dimensionless) ± SE are shown.

	Q_{10}		
Site	R_{R+S}	R_S	R_R
LR	2.1 ± 0.3	2.3 ± 0.4	1.9 ± 0.5
MR	2.7 ± 0.5	3.3 ± 0.6	1.9 ± 0.7
OG	2.1 ± 0.3	2.9 ± 0.3	1.6 ± 0.4
WOOD	1.9 ± 0.4	2.6 ± 0.4	1.4 ± 0.5

5.5.3 Within Site Variability of CO_2 Fluxes

The seasonal averaged CV for Bare and Veg R_{TOT} ranged from 22 - 35% (22 – 26% for grass dominated sites) and 17 - 23%, respectively (Table 5.12). The CV for the

Veg NEP was comparable to R_{TOT} fluxes. Conversely, the CV for Veg NEE was very large especially for the LR site. This can be explained by one collar being situated at a higher topographical location (8 cm higher) than surrounding land, which increases the surface area for aeration and decomposition. However, excluding this plot still results in a high CV of 64%. The comparable CV for the Veg R_{TOT} and NEP was an artifact of the large R_{TOT} fluxes which seemed to dominate NEP (Figure 5.25). The narrow range and low CV for R_{TOT} was somewhat surprising given the number of sample plots at each site (n = 3 - 4), and natural variability exhibited in other ecosystems (Griffis et al., 2000a; Simek et al., 2004; Xi and Qi, 2001). This may be the result of the study year being drier than normal, possibly reducing the range (especially maximum values) of exhibited CO_2 fluxes. In these grasslands the distribution of grass clumps was more uniform than that of a shortgrass prairie where SOM enrichment under the clumps can lead to greater site heterogeneity (for Veg R_{TOT} CV $\approx$ 70% for Czóbel et al. (2002) and CV $\approx$ 25 for this study).

The similar magnitude in CV exhibited at all sites, and for all CO_2 fluxes, suggests that the number of plots chosen is adequate enough to capture meaningful comparative values. However, more collars may be required to get an estimate that is closer to the actual mean flux (Yim et al., 2003). The estimate of the number of collars required to obtain fluxes within 20% of the reported mean (we will assume that the mean reported for each site is the actual mean C flux) can be obtained by using a statistical analysis provided by Yim et al. (2003). It appears that 5 - 10 collars would be required to be within 20% and 15 – 30, to be within 10% of the actual mean, respectively. However, the time demand of doing so would either require fewer sites to be explored or require

more individual's conducting measurements. This exemplifies the difficulty and considerable time required to obtain accurate flux measurements at the plot scale (Obrist et al., 2003).

Table 5.12: The coefficient of variation (%) (CV) for the carbon (C) fluxes for Bare and Vegetated plots at all sites. Abbreviations: net ecosystems CO_2 exchange (NEE), overall respiration (R_{TOT}), net ecosystem productivity (NEP), plant respiration (PR). Bare NEE was similar to R_{TOT}, and Bare NEE theoretically should be zero because of lack of vegetation, thus were omitted

Site	Bare R_{TOT}	Veg R_{TOT}	Veg NEE	Veg NEP	PR
LR	26	23	99	25	30
MR	22	18	45	18	26
OG	25	17	86	24	29
WOOD	35	---	---	---	---

5.5.4 Within Season Variability of CO_2 fluxes

Throughout the season, and between phenological periods, all sites generally exhibited a CV within 15 - 20% for Bare R_{TOT}, Veg R_{TOT}, PR and NEP (Figure 5.25). The only exception was OG and WOOD sites for Bare R_{TOT}, and the OG site for PR which reflected the greater patchiness of these sites and the periodic harvesting at OG. The relatively conservative nature of CV for R_{TOT} and PR can be attributed to measurements made during the summer, at midday, when vegetation had a chance to adjust to daily meteorological conditions (LeCain et al., 2002). The CV for Veg NEE was very large (CV 45 - 100%), which may be due to the smaller seasonal magnitude exhibited by NEE (about 30% of that of NEP). Thus, similar changes in magnitude R_{TOT} would create larger differences in NEE. In addition, the NEE is comprised of plant

photosynthetic uptake (NEP) and respiratory losses (R_{TOT}) which may have different controlling factors that operate at varying scales (Law et al., 2002).

Annually, it has been shown that the CV for R_{TOT} is largest during the spring and summer when plants are actively photosynthesizing (Lohila et al., 2003), and at higher fluxes (Xu and Qi, 2001). However, since the measurements were confined to the growing season the CV was generally similar. In addition, it appears that there were moderate climatic controls on the observable CV for Bar R_{TOT}, Veg R_{TOT} and PR. Weak, negative linear relationships (r^2 = 0.11 - 0.44, $P< 0.05$) were found between T_a and CV of R_{TOT} for all Bare and Veg sites, excluding the OG and WOOD sites, whereas T_g, VSM and PAR showed little influence on the magnitude of the CV. The most influential measured variable on the CV of R_{TOT} was the preceding, cumulative 7-day precipitation which showed positive linear relationships (r^2=0. 25 – 0.46, $P<0.05$), (r^2= 0.42 – 0.50, $P<0.01$) and (r^2= 0.24 – 0.43, $P< 0.05$) with CV for Bare R_{TOT}, Veg R_{TOT} and PR, respectively.

Although point data was collected, the dynamics of two vegetative processes were revealed. First, T_a has been shown to be a function of evapotranspiration leading to a larger CV, although evaporative losses were not measured, (Law et al., 2002). This was likely related to enhanced moisture stress and possibly reduced stomatal conductance to conserve water, subsequently diminishing the CO_2 loss (Grace et al., 1998; Meyers, 2001). When this occurs, the microsite variability of microorganisms, soil nutrients and soil water that lead to the spatial variability of CO_2 uptake and release may have been

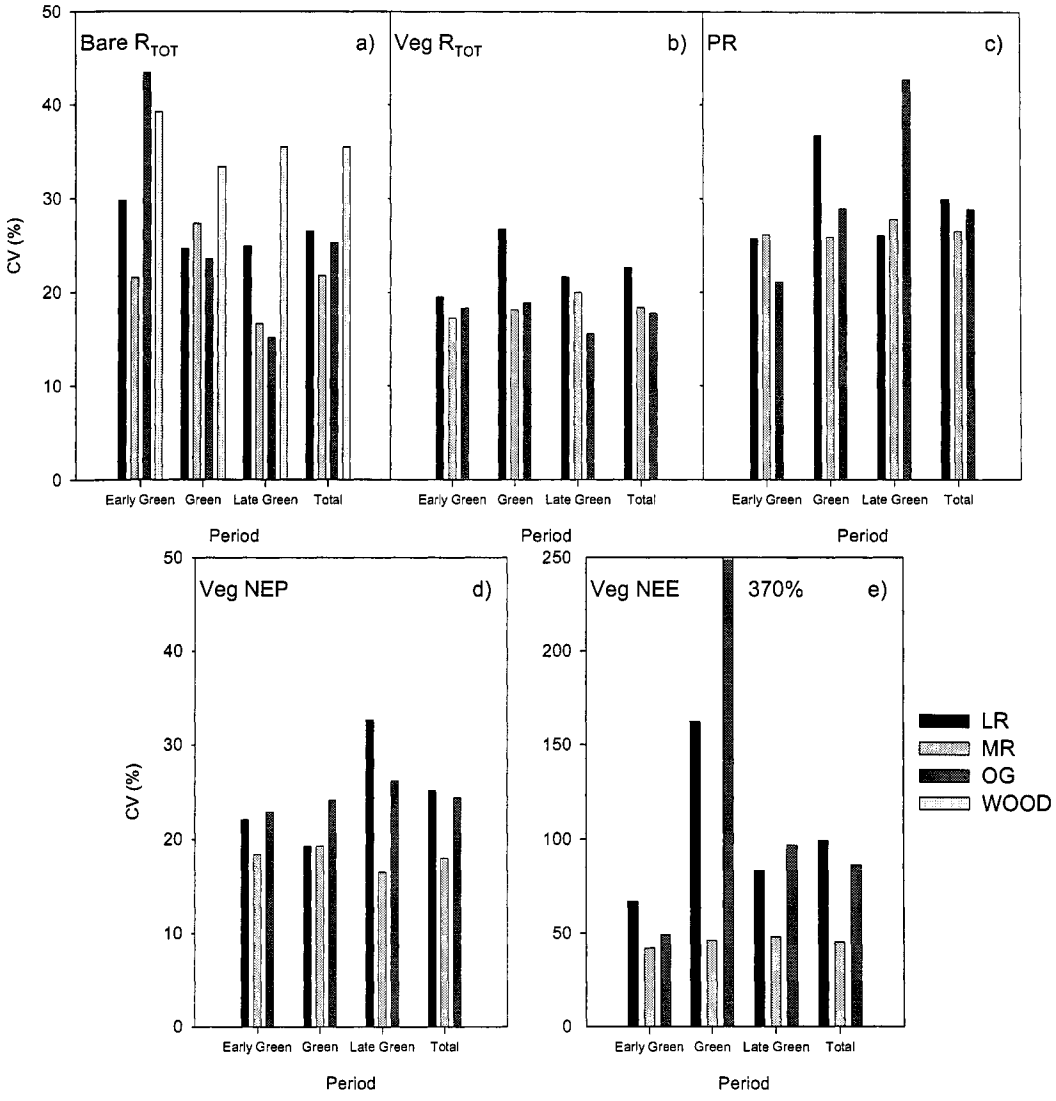

Figure 5.25: The coefficient of variation (%) (CV) of the carbon (C) fluxes for a) Bare, b) Vegetated, c) plant respiration (PR), d) Vegetated net ecosystem productivity (NEP) and e) Vegetated net ecosystem CO_2 exchange (NEE) for all sites. Note the different scale for e).

diminished through plant acclimation to increased stress, thus, the gap in CV narrowed (Grayston et al., 2001). For Bare plots, the observed decrease in the CV at a higher T_a may be the response of microbes approaching a maximum rate of activity.

Secondly, the influence of precipitation has been shown to be both positively related to the uptake and loss of CO_2 (Frank and Dugas, 2001; Kane et al., 2003, Laporte et al., 2002). Precipitation can have two influences, through directly providing plants with water, and a mechanism to transport nutrients to accessible areas for roots and microorganisms (Franzluebbers et al., 2002). As a result, when water is made available, photosynthesis and R_{TOT} are stimulated from the influx of spatially derived nutrients. This will lead to enhanced spatial variability through microbial exploitation of new available resources.

High spatial variability indicates a need for large sample sizes in order to get a representative value of the CO_2 fluxes. However, this requires intensive field sampling over a limited time period because of the diel and seasonal changes exhibited for C fluxes (Xu and Qi, 2001). In more patchy environments the use of larger chambers, greater than 1 m in diameter, would aid in accounting for spatial variability, but chambers of this size are impractical. Thus, it appears that to obtain more representative results, more chambers at fewer locations need to be employed.

5.6 Integration of Seasonal Carbon Fluxes

For seasonal comparisons the cumulative CO_2 exchange over the growing season (May 7 to October 21), encompassing 167 days, was estimated following the method of Mielnick and Dugas (2000) using linear interpolation between successive flux

measurements. The midpoints between flux measurements were used as the beginning and end points of an integration period represented by the flux measurement contained within each interval. For example, an integration period from midday June 16 to midday June 20, represented by a Bare R_{TOT} of 930 mg CO_2 m^{-2} hr^{-1} (section labelled 1 on Figure 5.26) would be multiplied by 96 hrs (4 days), to equal approximately 90 g CO_2 m^{-2} emitted over the four day period.

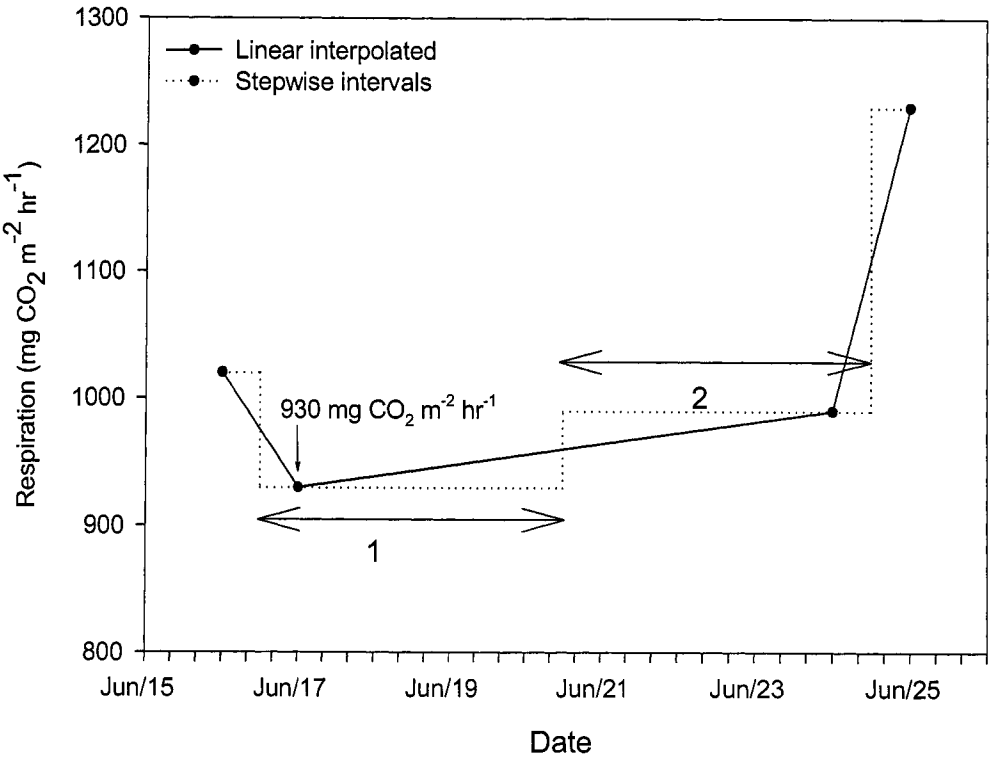

Figure 5.26: Method used to estimate seasonal carbon (C) fluxes. Data for Bare plot soil respiration (R_{TOT}) of Lower riparian (LR) from June 16 to June 25, 2003 is shown. Horizontal dotted lines constrain a flux interval represented by vertical dotted lines. Labels 1 and 2 are examples.

Although the exact time of flux measurements was not always midday (fluxes measured between 10:00 – 16:00), for simplicity midday was used as the daily transition period between flux intervals. Cumulative fluxes were integration over the whole sample period to estimate summer seasonal fluxes. The integration method was used rather than using seasonal regression relationships with influential determinants (e.g. T_a or T_f) because such continuous data was not available.

This integration period only applies to R_{TOT} for Bare plots and is commonly used to estimate seasonal site CO_2 losses when chambers are employed (Mielnick and Dugas, 2000; Frank and Dugas, 2001; Tufekcioglu et al., 2001). The CO_2 fluxes for this study were reported on an hourly timescale to better represent the narrow time window during which data was collected. Thus, when necessary, for comparative purposes, fluxes were converted to daily timescales and units of g C m^{-2} d^{-1} as,

$$F_D = F \times MC \times T \qquad (5.9)$$

where F_D is the daily carbon flux (mg C m^{-2} d^{-1}), F is the hourly flux (mg CO_2 m^{-2} hr^{-1}), MC is the ratio of molar mass of C to CO_2 (dimensionless) and T is the time conversion (24 hr = 1 d). Although this artificial extrapolation creates some uncertainty, in assuming that hourly fluxes are conservative diurnally and midday fluxes are representative (which has been shown to be within 20% of daily averages) (Mielnick and Dugas, 2000; Frank et al., 2002) this method does provide an efficient means to compare sites.

5.6.1 Estimating Seasonal Carbon Fluxes

The dormant season fluxes were not measured in this study, but can be estimated by assuming an average value of 0.76 g C m^{-2} d^{-1} as reported for a tallgrass prairie in

Kansas (Bremer et al., 1998) with winter soil temperatures (as low as -12°C). For this study the dormant period spanned approximately January 1 to April 30 and October 22 to December 31, 2003 encompassing 190 days. If all sites exhibited dormant season soil fluxes at similar ratios to summer fluxes (LR is 1.3 times MR, 1.2 times OG and 1.5 times WOOD) then the estimated dormant season fluxes are 144, 111, 120 and 96 g C m^{-2} for the LR, MR, OG and WOOD sites, respectively (Table 5.13).

Table 5.13: Seasonal, estimated carbon (C) fluxes. Growing season represents May 1 - October 21 (175 d) and dormant season represents January 1 – April 30 and October 22 – December 31 (190 d). All values reported in g C m^{-2}.

Site	Growing Season	Dormant Season	Total
LR	670	144	814
MR	540	111	651
OG	620	120	740
WOOD	520	96	616

5.7 Respiration and Carbon Use Efficiency

Respiration use efficiency (RUE) is defined as the ratio of respiratory CO_2 losses to CO_2 uptake (R_{TOT}/ NEP) (Law et al., 2002) and can be obtained from the slope of the R_{TOT} and NEP relationship (Figure 5.27). The average RUE for all sites combined is 0.68 (Figure 5.26a). Individually, the RE for the LR, MR and OG was 0.78, 0.76 and 0.53, respectively (Figure 5.27b). A compiled data set provided by Law et al. (2002) showed grasslands typically have RUE values of 0.74 compared to 0.85 for deciduous and coniferous forests. This trend is attributed to grasses having less investment in respiring tissues compared to that of forests (Law et al., 2002).

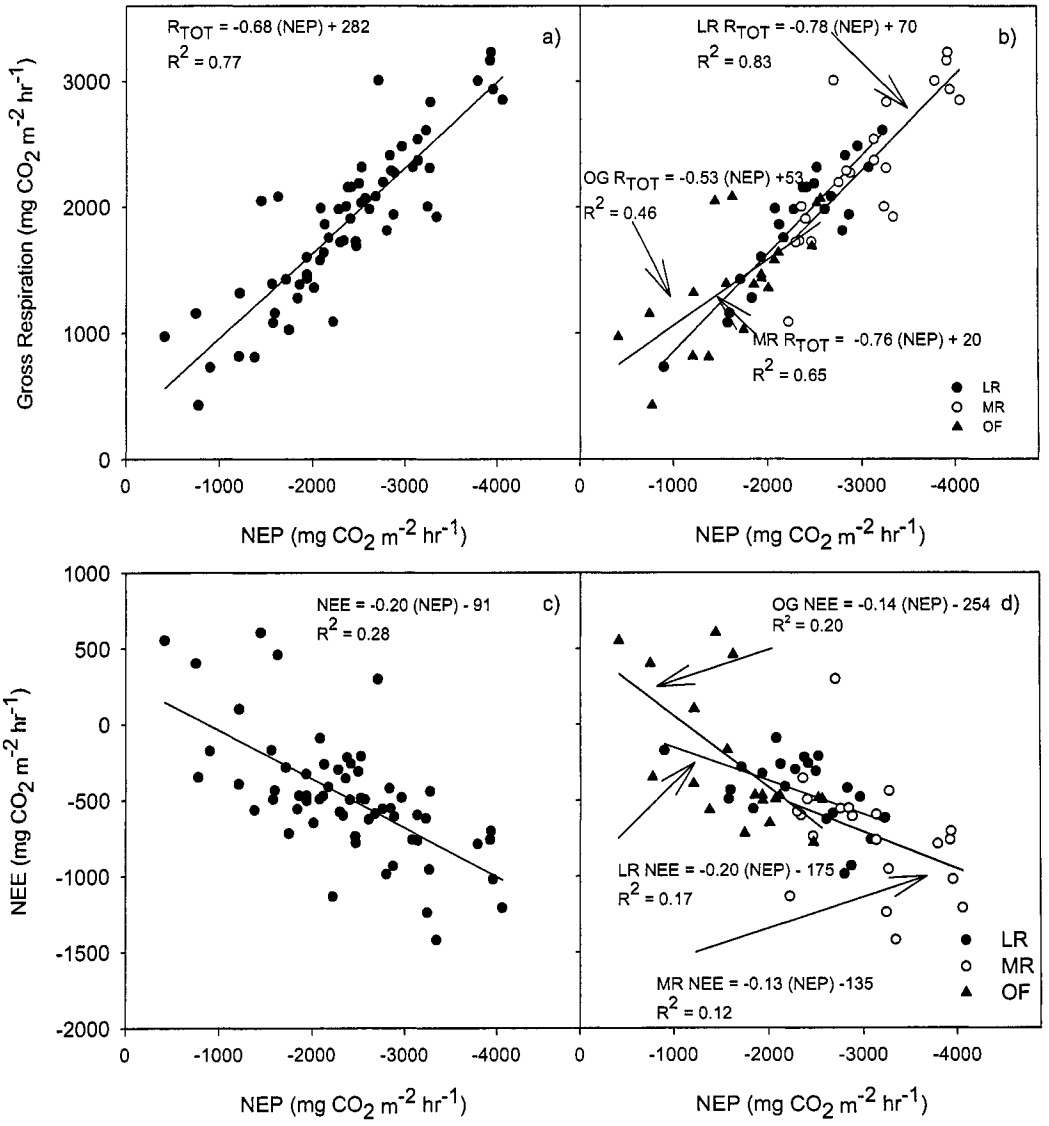

Figure 5.27: Relationship for respiration use efficiency (RUE) for a) all sites combined, and b) individual sites; and carbon use efficiency (CUE) for c) all sites combined, and d) each individual site.

The slope of the relationship between NEE and NEP was 0.20 for all sites combined (Figure 5.27c), and 0.20, 0.13 and 0.14 for the LR, MR and OG, respectively (Figure 5.27d). This ratio was similar to the carbon use efficiency (CUE), which is

defined as NPP/GEP and represents the C utilization by vegetation (Law et al., 2002). This value emphasizes that large uptake values coincide with large respiratory losses, thus mitigating large CO_2 gains by the ecosystem. Large RUE ratios reveal that the Veg sites in this study showed large seasonal CO_2 uptake, but concurrently have large respiratory CO_2 losses. As a result, the CUE is smaller and range in NEE fluctuated less than, and was more stable compared to NEP and R_{TOT}.

5.8 Summary of Ecosystem CO_2 Dynamics

Figure 5.28 and Table 5.14 summarize the overall C exchange contributions from the various study locations. Generally, the Bare R_{TOT}, vegetative PR and overall combined R_{TOT} from largest to smallest followed the trend LR > OG > MR > WOOD, MR > LR > OG and MR > LR > OG, respectively. The NEE and NEP were more stable with largest uptake values for MR and lowest for OG. These data suggest that the observed spatial variability appears to be dominated by vegetation dynamics, rather than soil processes.

Table 5.14: Seasonal average midday CO_2 exchange rates for all study sites Bare and Vegetated plots at Strawberry Creek, Maryhill, Ont. from May 7 to October 21, 2003. All units are in mg CO_2 m^{-2} hr^{-1} and means are the study averaged CO_2 ± SE. (n = 21 - 24).

Terrain	Bare			Veg			
Site	**NEE**	**R_{TOT}**	**NEP**	**NEE**	**R_{TOT}**	**NEP**	**PR**
LR	670±70	750±100	0[a]	-460±230	1780±200	-2350±290	1030±150
MR	590±70	580±60	0[a]	-730±170	2180±200	-3090±280	1590±210
OG	640±80	620±80	0[a]	-280±120	1280±110	-1680±200	670±190
Wood	450±70	490±90	0[a]	---	---	---	---

Note: [a] values represent no uptake.

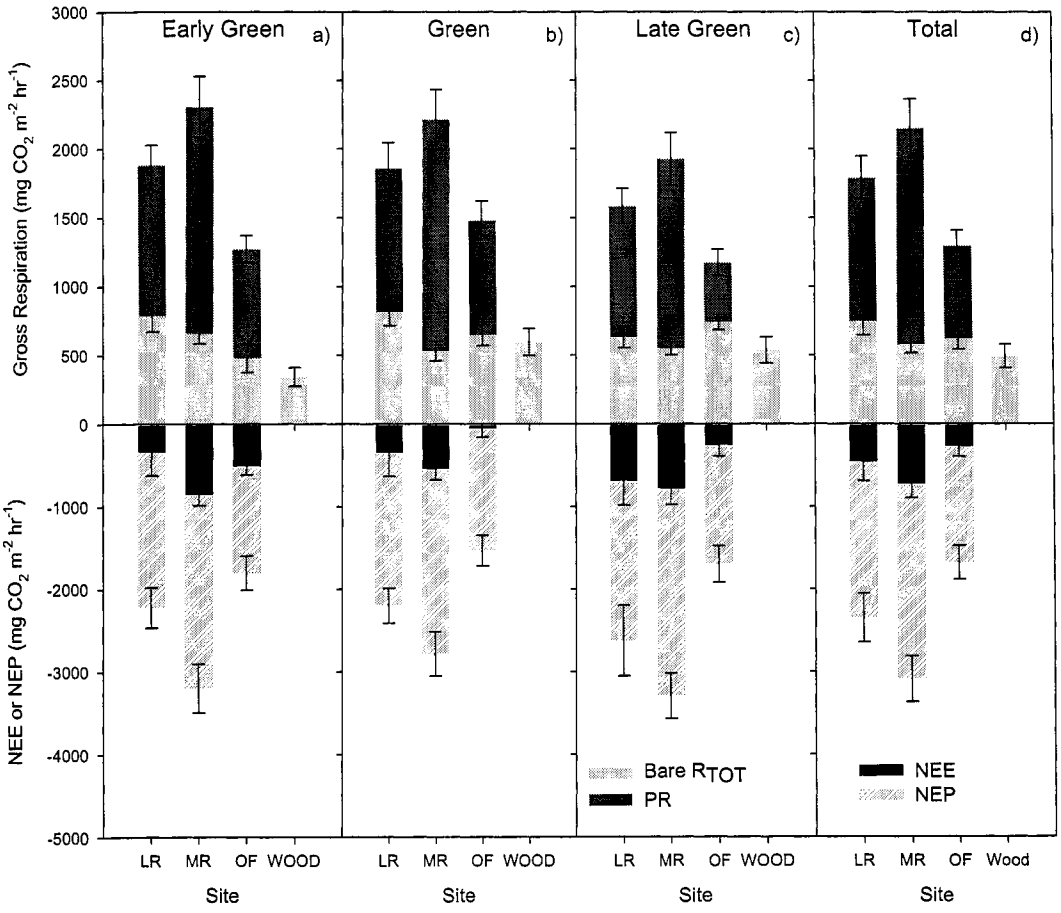

Figure 5.28: Summary of carbon (C) fluxes (Bare and Vegetated overall respiration (R_{TOT}), net ecosystem CO_2 exchange (NEE), net ecosystem productivity (NEP) and plant dark respiration (DR) (DR = Veg R_{TOT} - Bare R_{TOT}) for all sites during phenological periods from May 7 to October 21, 2003 from Strawberry Creek, Maryhill, Ont., during 2003. Error bars represent ± SE (n = 6 - 8 for each period). Root contribution estimated from laboratory experiment is approximately 30 - 60% of soil R_{TOT}. Note that OF = OG.

Chapter 6
DISCUSSION

6.1 SEASONAL CARBON FLUX COMPARISONS

6.1.1 Soil Respiration Comparisons

The averaged daily Bare (soil) fluxes from this study were 4.9, 3.8, 4.1 and 3.3 g C m^{-2} d^{-1} for the LR, MR, OG and WOOD sites, respectively. These values compare favourably in magnitude to other vegetation types, even though fluxes were exclusively measured during midday, with no dormant season measurements. They are similar to the 4.5 g C m^{-2} d^{-1} for a riparian mixed grass and 3.7 g C m^{-2} d^{-1} for a riparian switchgrass in Iowa, measured using static chambers and the soda-lime technique (Tufekcioglu et al., 2001); the 2.5 - 4.6 g C m^{-2} d^{-1} for a tallgrass prairie in Texas using dynamic chambers (Mielnick and Dugas, 2000); 3.5 g C m^{-2} d^{-1} for a non-grazed prairie, 4.3 g C m^{-2} d^{-1} for a grazed prairie and 4.0 g C m^{-2} d^{-1} for a winter wheat grass in North Dakota using dynamic chambers (Frank et al., 2002). Values for this study are slightly lower than the growing season range of 5.1 - 8.6 g C m^{-2} d^{-1} obtained using dynamic chambers for a Colorado shortgrass steppe, which was historically grazed by bison at rates of 20 and 60% (LeCain et al., 2002). This may be the result of added soil fertility from the N in bison excrement and the warmer, drier climate of Colorado. However, values are much lower than the 8.3 g C m^{-2} d^{-1} for a tallgrass prairie in Flint Hills, Kansas (Knapp et al., 1998) and 9.4 g C m^{-2} d^{-1} for a tallgrass prairie in Manhattan, Kansas (Ham and Knapp, 1998), both of which were burned annually and measured using dynamic chambers. The larger Kansas values

may be the result of annual burning accelerating the supply and turnover of detrital mass for microbial populations, in addition to increased soil surface temperatures (Ham and Knapp, 1998; Knapp et al., 1998). Furthermore, some of the inherent variations are likely attributed to the methodologies (static chamber, site spatial variability and seasonality (Fang et al., 1998).

Maximum daily Bare R_{TOT} for the dissimilar managed grasslands and woodlot sites averaged 8.1 g C m^{-2} d^{-1}, 6.7 g C m^{-2} d^{-1}, 11.0 g C m^{-2} d^{-1} and 8.5 g C m^{-2} d^{-1} for the LR, MR, OG and WOOD sites, respectively. The maximum values are similar magnitude, but slightly larger, than the 5.8 g C m^{-2} d^{-1}, 6.9 g C m^{-2} d^{-1} and 6.1 g C m^{-2} d^{-1} for a non-grazed prairie, grazed prairie and a winter wheat grass, respectively, in North Dakota measured using dynamic chambers (Frank et al., 2002), and the 6.2 g C m^{-2} d^{-1} for a riparian mixed-grass and 6.0 g C m^{-2} d^{-1} for a riparian switchgrass in Iowa, using static chambers and the soda-lime technique (Tufekcioglu et al., 2001). The larger values reported in the present study may be the result of: 1) the grasslands being riparian in origin; 2) the higher total TC content at this site; and 3) the more frequent sampling during the growing season which may have captured larger fluxes than observed by Frank et al. (2002) and Tufekcioglu et al. (2001) whom only measured every 20 - 30 days, annually.

Integrated fluxes were 670, 540, 620 and 520 g C m^{-2} $season^{-1}$ and annual totals were 814, 651, 740 and 616 g C m^{-2} yr^{-1} for LR, MR, OG and WOOD sites, respectively (Table 5.13). These values compare favourably with annual soil CO_2 fluxes of 1.45 kg C m^{-2} for a tallgrass prairie (Mielnick and Dugas, 2000), 0.4 - 0.5 kg C m^{-2} globally averaged fluxes (Raich and Schlesinger, 1992), and the 1.3 to 2.1 kg C m^{-2} measured for

an annually burned tallgrass prairie in Kansans (Bremer et al., 1998; Knapp et al., 1998). The values reported here are likely lower because no dormant season fluxes were actually measured and the summer study season was drier than the aforementioned studies. The lack of growing season precipitation has been shown to reduce LAI, biomass and NEE, all of which will have a negative effect on R_{TOT} (Meyers, 2001; Suyker et al., 2003). Thus, the development of roots and accompanying mycorrhizal populations may have been reduced (Gärdenäs et al., 2000).

6.1.2 Ecosystem Respiration Comparisons

Few studies have measured fluxes with vegetation intact (Dong et al., 2000; Franzluebbers et al., 2002; Kucera and Kirkham, 1978; Norman et al., 1997). Average measured Veg (ecosystem) R_{TOT} fluxes for this study (May 7 to September 12) were 11.6, 14.3 and 8.4 g C m^{-2} d^{-1} for LR, MR and OG, respectively. These average values are comparable to the 5.0 - 11.2 g C m^{-2} d^{-1} for meadow steppes and grasslands in Inner Mongolia, measured using dynamic chambers (Dong et al., 2000); much larger than the 2.6 to 3.1 g C m^{-2} d^{-1} for a tallgrass prairie in Manhattan, Kansas, obtained with static chamber and soda-lime technique (Franzluebbers et al., 2002); and the 2.5 g C m^{-2} d^{-1} for a tallgrass prairie in Missouri measured with static chambers and soda-lime (Kucera and Kirkham, 1978). The larger values reported here are also likely due to the grasses being of riparian origin, higher TC and more frequent sampling for this study. Maximum daily R_{TOT} for the dissimilar managed grasslands averaged 15.9 g C m^{-2} d^{-1} for LR, 21.2 g C m^{-2} d^{-1} for MR and 13.6 g C m^{-2} d^{-1} for OG.

Integrated summer season Veg R_{TOT} was 1.59, 1.97 and 1.18 kg C m^{-2} $season^{-1}$ for the LR, MR, OG and WOOD sites, respectively. These values are similar to the 1.30 kg C m^{-2} yr^{-1} for a mixed-grass field in North Carolina (Novick et al., 2004); much larger than the 1998 - 2000 annual average of 0.27 kg C m^{-2} yr^{-1} for a moist-mixed grass in Alberta (Flanagan et al., 2002); the 0.52 kg C m^{-2} yr^{-1} for a tallgrass prairie in Oklahoma (Suyker et al., 2003), all utilizing EC. The large values for summer Veg R_{TOT} in this study are the result of artificially extrapolating large midday values to seasonal timescales, which would overestimate vegetation contributions.

Although, the vegetative plots contained mainly mixed grasses, some inherent uncertainty may be attributed to the presence of minor quantities of alfalfa. Wichern et al. (2004) reported average alfalfa fluxes of 2.34 g C m^{-2} d^{-1}, for 7 days following an irrigation event in Oman. Using this value as representative of temperate alfalfa fluxes and assuming that 30% of the plot coverage was alfalfa yields a daily flux of 0.7 g C m^{-2} d^{-1}. If the remaining 70% of the coverage are grasses and the average daily vegetation flux was 11.4 g C m^{-2} d^{-1} (seasonal daily average of the 3 study sites), then 7.98 g C m^{-2} d^{-1} would be emitted by the grasses. As a result, the 0.7 g C m^{-2} d^{-1} would represent less than 10% of the overall flux. This crude estimation suggests that alfalfa was likely only a small contributor to the overall Veg fluxes.

6.1.3 Net Ecosystem CO_2 Exchange and Productivity Comparisons

Average seasonal NEE for the LR, MR and OG sites were -6.5 g C m^{-2} d^{-1}, -9.3 g C m^{-2} d^{-1} and -5.1 g C m^{-2} d^{-1}, respectively. These values are larger than the -4.8 g C m^{-2} d^{-1} for a tallgrass prairie in Manhattan, Kansas obtained with dynamic chambers (Ham

and Knapp, 1998), and the -5 to -6.5 g C m^{-2} d^{-1} for a tallgrass prairie in Temple, Texas using the BREB approach (Dugas et al., 1999). However, these results are comparable to the 1997 - 1999 average of -7.5 to -9.5 g C m^{-2} d^{-1} for a tallgrass prairie in Shidler, Oklahoma using EC (Suyker et al., 2003) and the -5.0 to – 8.6 g C m^{-2} d^{-1} range over 3-years for grazed and ungrazed shortgrass steppe pastures in Colorado (LeCain et al., 2002).

Maximum NEP for the LR, MR and OG sites was -21.1 g C m^{-2} d^{-1}, -26.6 g C m^{-2} d^{-1} and -16.8 g C m^{-2} d^{-1}, respectively. These values are larger than the -4.5 to -9.0 g C m^{-2} d^{-1} collected from 1998 to 2000 for a moist-mixed grassland in Lethbridge, Alberta using EC (Flanagan et al. 2002) and the -9.5 g C m^{-2} d^{-1} for a tallgrass prairie in Manhattan, Kansas measured using chambers (Ham and Knapp, 1998).

Chambers have been shown to underestimate EC fluxes by 15 - 30% (Davidson et al., 2002; Griffis et al., 2000b) and BREB by 10 - 20% (Angell et al., 2000) through depressed CO_2 concentration gradients and enhanced chamber temperatures that may lead to stomatal closure (Angell et al. 2001). As a result, the reported values here may be larger. However, tower and chamber measurements have been shown to be similar during midday when photosynthesis operates at maximum rates (Griffis et al., 2000b). In this study, the conversion of midday, hourly fluxes to daily timescales artificially enhances reported values and may be the reason that estimated NEE and NEP are larger. Furthermore, tower measurements integrate daily NEE continuously, such that positive nocturnal NEE may offset a portion of the daytime CO_2 gains (negative fluxes). If diurnal losses are a $\frac{1}{3}$ to $\frac{1}{2}$ of the reported daily fluxes (Grace et al., 1998; Kim et al., 1992; Suyker et al., 2003), then values from this study would be more similar to reported

values. Integrating NEE and NEP to meaningful seasonal estimates is difficult because of the sporadic point data on differing days and the fact that plant response to daily climatic variability is more dynamic than that of soil (Falge et al., 2002). Thus, the integration period approach does not adequately represent seasonal plant functions. The only possible way to obtain meaningful comparative values is from PAR response curves, using chamber shrouds with varying emissivities (Suyker and Verma, 2001; Wilsey et al., 2002).

6.2 Soil Respiration and Net Ecosystem CO_2 Relationships

Clipping vegetation did create some unnatural perturbations to the soil environment and this was shown through Bare NEE and R_{TOT} comparisons. The lack of above-ground vegetation suggests that dark and clear chamber fluxes should be similar. However, this was not the case. The observed lower Bare NEE (less of a CO_2 loss) during the EG and G period may be from the lingering affects of the remaining roots and the associated microbial activity, or root undergrowth into the collar from nearby grasses, both of which contribute to CO_2 uptake through reduced nutrient competition with dead roots (Buchmann, 2000). The data here suggests that the shift began emerging during the LG period, some time in early August (Figure 5.8) when NEE values became larger (more C release) than R_{TOT}. At this point, vegetation growth and supply of root exudates are declining (Sims and Bradford, 2001) and the presence of labile C, such as dead roots may have provided a favourable source of decomposable material (Bowden et al., 2004; Franzluebbers et al., 2002). However, it is difficult to determine if the decrease in Bare NEE is from reduced decomposition of dead roots or a decline in CO_2 uptake by roots

from the undergrowth of nearby grasses. Nonetheless, with the reduced level of NEE during the EG and G periods, and the enhanced level during the LG period, the total seasonal Bare NEE and R_{TOT} for each site was no different, except for a slightly lower NEE at the LR site. It appears that the initial disturbance of the vegetation clipping and the influence of dead roots adjusted by August. As a result, measurements made in subsequent years, at the same plots, would better represent soil respiration, in the absence of roots. It has also been shown that trenching shallow roots following collar insertion can increase R_{TOT} by 20-30% for the following month in a spruce forest (Buchmann, 2000). However, in this study, collars were inserted one month (in early April) prior to the first measurements, but, the shallow root system is more extensive in grasslands, so the influence of dead roots appeared to be prolonged. This phenomenon should be experienced at all sites and since spatial variability is the prime importance, only absolute, rather than comparative values would be affected.

6.3 Variability in Community (Various Sites) Scale CO_2 Exchange

Overall, there were inter- and intra-annual differences in Bare R_{TOT} between the various grassland types and the maple woodlot (figure 5.11). Overall, the Bare MR site exhibited a similar season averaged R_{TOT} to the OG site, but significantly (α=0.05) lower and higher than the Bare LR and WOOD sites, respectively. This result is somewhat surprising given that the microclimates and vegetation types are similar at all sites (there is a lack of an extensive understory at the WOOD site) and the %TC was highest at the WOOD and MR sites. The regulation of T_g through canopy shading likely constrained Bare R_{TOT} from the WOOD site irrespective of larger TC. Furthermore, the amount of

AGB has been shown to be related to Bare R_{TOT} through the supply of labile C (Raich and Schlesinger, 2000), which is related to larger fluxes exhibited at the LR site compared to the OG and WOOD sites.

The MR and LR sites, both riparian sites, differed in their Bare R_{TOT}, (22% lower Bare R_{TOT} at the MR site) which may be the result of higher N values at the MR site. Inorganic N applications at moderate levels (~6 g N m^{-2} yr^{-1}) for grassland ecosystems (Verburg et al., 2004) have been shown to enhance Bare R_{TOT} during the first few years after application and suppress it for subsequent years. Although N was never purposely applied to the riparian areas (applied when tractors are tilling the edge of the cropped fields), the application of inorganic fertilizer to the adjacent agricultural land may have indirectly influenced the C dynamics at the MR site and the fertilizer influence was related to higher N and EXT-P at the MR site (Table 5.2).

The reduced Bare R_{TOT} at the MR site may be caused by a number of root (reduced RBM and root turnover rate) and microbial (reduced mycorrhizae contributions, supply of root exudates and microbial activity) related factors (Burton et al., 2004). The RBM was not different between the grass dominated sites (Table 5.3) suggesting that the root content itself was not the reason for the lower observed R_{TOT} at the MR site. However, an increase in root lifespan in response to greater N levels at the MR site could lead to a lower annual root turnover, and thus, a reduction in the amount of labile root litter C inputs and a subsequent decline in Bare R_{TOT} (Bouma and Bryla, 2000). Burton et al. (2004) suggest that the decrease in root turnover for a sugar maple dominated forest could account for the 15% observed reduction in N elevated (3 g N m^{-2} yr^{-1}) plots. However, in grasslands ecosystems, where root biomass can account for up to 80% of the

total C biomass (Dugas et al., 1999; Frank et al., 2002; Ripley and Saugier, 1978) (75% for this study), a small reduction in root turnover could drastically reduce Bare R_{TOT}. Determining root turnover rates and magnitudes is a formidable task requiring image processing and analysis, which is a time-consuming and an expensive endeavour (Burton et al., 2004) especially for grasslands, so physically determining whether root turnover was the reason for lower Bare R_{TOT} at the MR site was not feasible in this study. Furthermore, reductions in the amount of AGB supplied as litter inputs could decrease R_{TOT} (Raich and Tufekcioglu, 2000) but, the AGB at the MR site was the greatest (Table 5.3) so this is an unlikely possibility. As a result, reduced Bare R_{TOT} for MR Bare site is likely attributed to altered microbial activity, rather than root and vegetation influences.

It is assumed that the total amount of below-ground C utilized by mycorrhizae is generally 22% (McDowell et al., 2001) and if this relative magnitude was assumed for all grasslands then there would have to be almost a complete reduction (elimination) to account for the 22% lower observed R_{TOT} at the MR site relative to LR site. Thus, it seems unlikely that mycorrhizae alone can account for the observed decrease. However, N additions have been shown to alter the infectious rate of mycorrhizal fungi (fewer in magnitude with less competition and need for nutrients), thereby altering nutrient availability, which can affect root exudation (Burton et al., 2004; Dakora and Phillips, 2002). As a result, reduced mycorrhizae and root exudation (nutrient rich substances release into the rhizosphere soil by healthy roots) may have both contributed to some portion of the decline in observed R_{TOT}, but further exploration is required.

A more likely explanation is reduced microbial respiration, either through depressed rates and/or decreased microbial biomass. The addition of inorganic forms of

N have been shown to decrease soil microbial biomass (Saviozzi et al., 2001; Thirukkurman and Parkinson, 2000) for forest ecosystems, however, these influences are from direct N application. Indirect N influences from fertilizer applications at the MR site for this study should have much less of an impact, but the chronic nature of fertilizer application over that past 20 years may have altered the long-term C cycling. Nonetheless, if a reduction in microbial biomass causes a proportionate decline in R_{TOT} and roots account for 20 - 40% (soil 60 – 80%) of the Bare R_{TOT} in grasslands (Kucera and Kirkham, 1971; Buyanovsky, et al., 1987) then an observed decline of 20% in microbial biomass, could account for a 12 - 16% decline in R_{TOT}, which is similar to the 22% lower Bare R_{TOT} at the MR compared to the LR site. The uncertainty as to whether the observed 40% larger N at the MR site was the direct contributor to alter the CO_2 dynamics at the MR site requires further study, but results tend to agree with field studies using direct N applications (Burton et al., 2004; Verburg et al., 2004).

6.3.1 Spatial and Temporal Variability in Soil CO_2 Dynamics

A closer examination of within season variability, through the delineation of distinctive periods (early green (EG), green (G) and late green (LG)) suggests that differences were not uniformly distributed throughout the 2003 study season. During the EG period, the trend from greatest to smallest for Bare R_{TOT} followed LR > MR > OG > WOOD, during the G period followed LR > OG ~ WOOD > MR and OG > LR > MR ~ WOOD for the LG period (Figure 5.28).

At the onset of vegetation growth (the EG period) the soil nutrient status is usually the greatest owing to the winter melt supplying the soil matrix with nutrients and

labile root and detrital organic matter from the previous year preserved by cooler temperatures (Schlesinger, 1997; Stoyan et al., 2000). For the MR site, adjacent to actively cropped land, the fertilizer application in the preceding year(s) and current spring may have been the reason for elevated N (Process outlined in Figure 6.1).

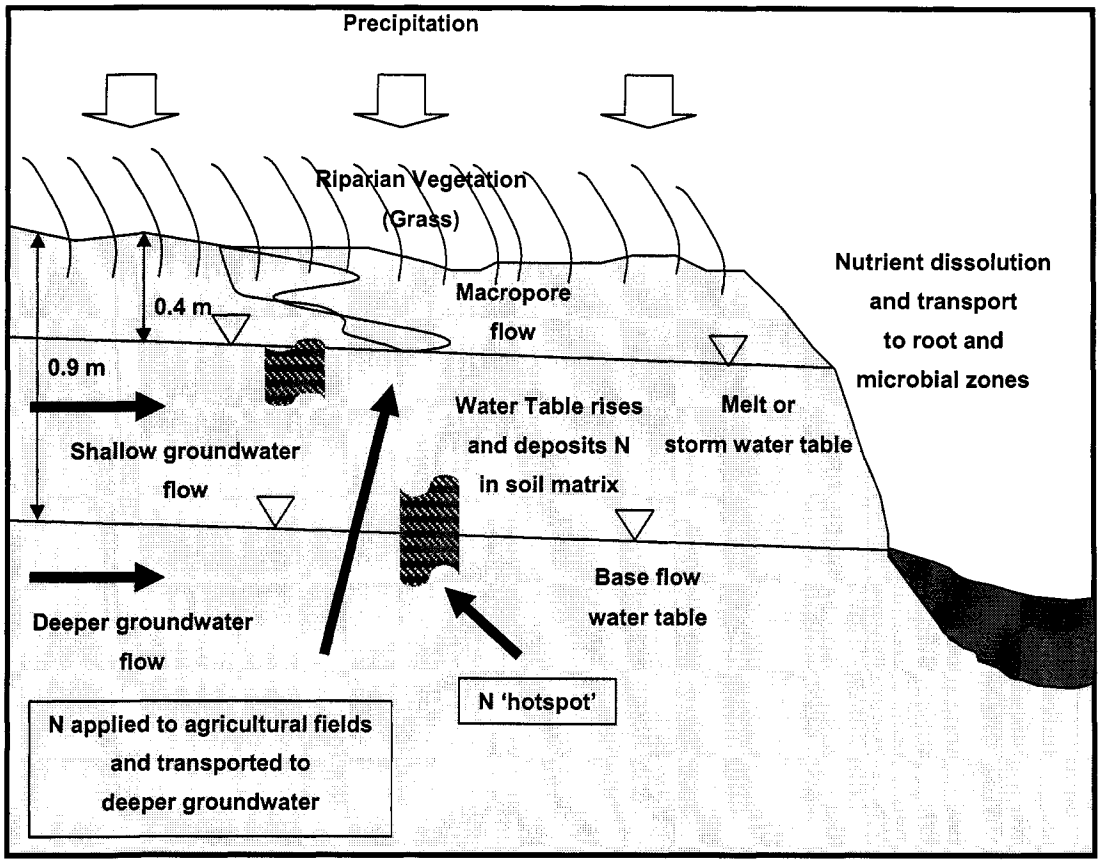

Figure 6.1: A conceptual diagram outlining the possible mechanism responsible for the transport and storage of N within the near surface (unsaturated) zone of the soil matrix. The elevated N can be 'activated' by root growth and precipitation and utilized by vegetation and soil microbes during the summer season.

Although the water table rarely intersects the land surface during the summer and directly deposit nutrients in the soil matrix from upland agriculture, surface nutrients may

have been transported with melt water, retarded and stored within the soil. As vegetation growth proceeds, these stored nutrients are accessed by root growth into nutrient rich areas within the soil, and by dissolution from precipitation (Schlesinger, 1997). Furthermore, the aeration in this near surface oxic zone provides favourable conditions for NO_3^- formation, the form of N preferred by plants and microbes (Brady and Weil, 1999). As a result, the soil may act as a reservoir for nutrients (N and P) which are available, in larger amounts, to plants and microorganisms at the beginning of the growth period. Water is directed and drained to Strawberry Creek, thus transporting dissolved constituents through riparian areas. This may partially account for the reason that sites closer to the stream (LR and MR) showed larger Bare R_{TOT} relative to the OG and WOOD sites (Figure 5.28). The WOOD site had the lowest Bare R_{TOT} during the EG period probably through a delay in surficial warming regulated by the maple tree canopy (Oke, 1987).

During the G period, when soil microorganisms are operating at high rates and the shoot elongation period stimulates intensive nutrient uptake, Bare R_{TOT} may be dominated by mycorrhizal activity and should thrive where nutrients and TC are abundant (Gärdenäs et al., 2000; Lohila et al., 2003). The LR site exhibited the largest Bare R_{TOT}, during the G period followed by OF and WOOD sites, with the MR site being the lowest. Both the OG and WOOD sites exhibited increased soil activity in the EG period through enhanced vegetative growth and warmer temperatures (Angell et al., 2001), but the MR site experienced even lower Bare R_{TOT}. This is in accordance with the Cheng (1999) substrate utilization model for fertile soils in which microbes preferentially exploit labile root derived C and exudates, rather than soil derived C, resulting in

decreased SOM decomposition, whereas if nutrients are limited, nutrient rich SOM is exploited (Martin-Olmedo et al., 2002). Thus, the need for microbes to mineralize SOM and obtain N to create amino acids and perform growth functions, subsequently releasing CO_2 as a by-product, is not as necessary (Bowden et al., 2004; Groffman et al., 2002; Verburg et al., 2004). This reduction in R_{TOT} agrees with the greater %TC observed at the MR site relative to the LR site. For the LG period, the Bare R_{TOT} for the OG site was the largest through harvesting and enhanced detrial supply of labile root C (Bremer et al., 1998; Ham and Knapp, 1998) similar to the phenomena shown for Bare NEE plots. The Bare R_{TOT} at the LR site deceased as vegetation growth began to subside and the MR and WOOD R_{TOT} were of comparable values. Generally, the Bare R_{TOT} for the WOOD site was equal to, or below, that exhibited by the grasslands because no C is allocated to wood production thus, grasses have more photosynthetic material available to allocate below-ground (Raich and Schlesinger, 2000). This seemed to outweigh the larger %TC at the WOOD site suggesting a substantial contribution of root respiration, and hence, lower below-ground C allocation.

6.3.2 Spatial Variability in Ecosystem CO_2 Dynamics

Veg R_{TOT} showed greater spatial variability among sites than Bare R_{TOT}, but trends were similar in the direction and magnitude differences throughout the season, and for all phenological periods (Figure 5.28). For all periods the trend from greatest to smallest followed soil N levels such that Veg R_{TOT} MR > LR > OG.

CO_2 fluxes (both uptake and release) have been related to biological factors, such as %TC (Maeste et al., 2003; Tufekcioglu et al., 2001), N content (Tufekcioglu et al.,

2001), above-ground biomass (Flanagan et al., 2002; Zhang et al., 2003), root biomass (LeCain et al., 2000; Watts et al., 2000) and C/N ratios (Tufekcioglu et al., 2001). However, TC content is thought to be the dominant factor controlling in situ respiration (Franzluebbers et al., 2002) because it is the source of nutrients utilized by microbes for decomposition (Conant et al., 1998). Thus, the greater %TC and labile C should result in larger soil CO_2 fluxes (Schlesinger, 1997). The TC was largest for the WOOD and the MR sites, however, the Bare R_{TOT} was lowest at the MR site. Thus, the C/N ratio is a good indicator of nutrient status, and at narrower (lower) ranges of the C/N ratio general purpose decay and plants can operate at greater capacity, thus showing higher rates of CO_2 release (Brady and Weil, 1999). Although the C/N ratios for all sites are similar in magnitude (11.6 – 15.7) the slightly lower C/N ratio at the MR site suggests that both nutrients (C and N) required for decomposition may be available at more sufficient amounts.

Although the Bare MR R_{TOT} was suppressed, the Veg MR R_{TOT} was enhanced, suggesting a differential response by the soil and plants. This may be the result of the higher AGB at the MR site, which had a 15 - 20% greater AGB, for stomatal activity and CO_2 exchange (Suyker et al., 2003). The NEP showed identical trends to Veg R_{TOT} (MR largest and OG smallest) with little variation throughout the season (Figure 5.28). Positive relationships between NEP and R_{TOT} have been shown for numerous ecosystems (Law et al., 2002; LeCain et al., 2002), suggesting that an increase in labile C and root respiration from recently fixed CO_2 leads to increased decomposition. Although, microbial respiration seemed to be suppressed by elevated N, it appears that plant growth was enhanced. Enhanced N has been accompanied by AGB vegetative growth without a

similar response in root biomass because the below-ground C inputs (roots) most likely experienced a concurrent increase in the production and decomposition of rhizodeposits (nutrient rich organic compounds transported by plant roots in the soil, which include water soluble sugars, amino acids, and polymeric carbohydrates, etc.) that microbial communities favour (Bowden et al., 2004; Verburg et al., 2004). This may the reason why the root biomass at the MR site was comparable to the LR and OG sites. Furthermore, since the Bare R_{TOT} contributed a small fraction compared to Veg R_{TOT} (35%) a considerable amount of active root and shoot respiration during the growing season more than compensated for the suppressed soil heterotrophic R_{TOT}. Thus, the contribution of root activity out performed microbial activity.

The NEE for all Veg sites (Figure 5.13b) showed considerable variation and amounted to about 30 - 35% of the NEP values (Figure 5.27c &d). During the EG, the NEE was largest for MR, likely in response to an abundant soil N supply. The hypothesis is, after nutrients become exhausted, the NEE was more comparable to the LR site reflecting the similar vegetative species and riparian origin. The NEE for the OG site declined substantially, even shifting to midday site C losses, from the EG to the G period, in response to the dry summer (Figure 5.10). This was not exhibited for the MR and LR sites and no significant differences in T_g, VSM, ρ_b or soil texture could account for this. The only observed difference that may explain the observed decline of NEE at the OG site is reduced AGB, following harvesting, which would lower the available area for photosynthesis (Meyers, 2001).

Some uncertainty exists as to the cause of suppressed R_{TOT} at the MR site because the contribution of mycorrhizal R_{TOT}, exudate R_{TOT} and SOM decomposition in the field

was not performed, but these components (Craine et al., 1999). Moreover, the lack of continuous data and point measurements creates uncertainty in the strengths of the temporal relationships. However, the comparative data on the same day (Section 5.3.5) seems to make sense theoretically and compare favourably to the group-averaged data. The most crucial determinant and uncertainty is whether the 40% larger soil N at the MR site is directly from fertilizer use and if this amount is sufficiently high to alter microbial activity. It may be that the observed difference of C dynamics are controlled by other soil constituents (Ca^{2+}, Mg^{2+}, O_2, etc.), thus there is a need for a more thorough soil analysis.

6.4 Partitioning Soil and Root Contributions to Soil Respiration

The amount of C loss was determined using,

$$\%\ Carbon\ Loss = \frac{ICL}{\rho_b \times TC \times V_S} \times 100 \qquad (6.1)$$

where ICL is the integrated C loss over the study period (g C m^{-2} $study^{-1}$), ρ_b is the bulk density (g m^{-3}), TC is the soil organic carbon content (dimensionless) and V_S is the estimated volume of soil (m^3) in the incubation jar, with a surface area of 2.1×10^{-3} m^2 and a height of 0.07 m ($V_S = 1.3 \times 10^{-4}$ m^3). Using equation (6.1) it was estimated that over the duration of the experiment < 5% and < 2% (SCL averaged 7-10 g C m^{-2} $study^{-1}$) of the total SOM was respired under the 20°C and 8°C treatments, respectively. Thus, the temporal trends and different respiration rates, exhibited in the lab experiment, for the sites are unlikely due to the TC becoming exhausted (it is estimated that 10% of the SOM is labile TC (Eswaran et al., 1993)).

6.4.1 Root and Soil Respiratory Flux Relationships

The approach to measuring root respiration (R_R) assumes that ex situ measurements show approximately the same relative differences and comparative trends as in situ values. In terms of magnitudes, this is unlikely the case because of soil disturbances and the artificial soil heating, both of which lead to enhanced CO_2 losses. Since these aberrations are experienced for all the sites comparisons are still valid. However, certain soil processes may have been altered and will be discussed later.

The highest respiration fluxes of root, soil and symbiotic mycorrhizae (R_{R+S}), soil (R_S) and R_R were exhibited for the LR and WOOD sites. The WOOD site has the highest %TC of 7.2 and was expected to have large fluxes. The LR site had similar flux values to the WOOD site, but 25 - 30% larger fluxes than the MR site. The larger R_{R+S} and R_S fluxes at the LR site implies that there may be a higher TC present, either from greater rates of root turnover and/or microbial death, both of which increase the amount of easily decomposable C (Eswaran et al., 1993; Schlesinger, 1997). Furthermore, there may be a more efficient or active decomposing community at the LR site compared to the MR site, for example (Sjögerten and Wookey, 2002). The rates and magnitudes of root turnover, labile C supply and microbial biomass were not directly measured in this study, thus these phenomena need further exploration. Similar to the field R_{TOT} at the MR site had lower microbial activity relative to the MR site and may be related to higher N levels (Bowden et al., 2004; Burton et al., 2004; Frey et al, 2004; Maier and Kress, 2000).

The laboratory experiment showed that there were generally no discernable differences between R_{R+S} and R_S for all sites under the 20°C treatment. At the 8°C treatment the MR and OG R_S were similar, but the R_{R+S} , R_S and R_R were lower at the

MR site relative to the LR site. Complicating matters is what size (diameter) roots are respiring? Maier and Kress (2000) showed that fertilized plots had larger course (> 15 mm) and smaller fine (< 5 mm) root biomass, thus the differences in R_R may be vary for aggregated root classes (i.e. as a lump sum), as opposed to measuring each class separately (Sjögersten and Wookey, 2002).

The less pronounced difference at the 20°C treatment is likely the result of the continuous high temperatures which maintained high respiratory fluxes compared to the 8°C treatment. Fitter et al. (1998) note that above 25°C soil microbes and roots begin to acclimate to their surrounding temperatures, thus as temperature reaches the acclimation point, respiration begins to level, diminishing marked differences. It is possible that the 20°C treatment is close to the acclimation temperature, resulting in less observable differences between the sites. Laboratory incubations were somewhat unrealistic because incubation jars were allowed to be heated in all directions and there was no reduction of soil temperatures that would represent nighttime cooling. These biases may be dramatic because temperature is considered a primary regulator of soil respiratory and microbial activity (Elberling, 2003; Fang and Moncrieff, 2001; Raich and Tufekcioglu, 2000). When temperature is held relatively constant other factors, such as nutrient status can play a more dominant role (Fang and Moncrieff, 1998).

6.4.2 Root Contributions

At the 8°C treatment the MR site had the lowest %RC, and at the 20°C treatment the %RC for the riparian sites (LR and MR) were significantly ($\alpha = 0.05$) lower than the OG and WOOD sites (Table 5.9). The averaged %RC during the study for all sites ranged

32 - 47% and 45 - 60% at the 20°C and 8°C treatments, respectively. This is larger than the 17 - 40% for northern grasslands (Kucera and Kirkham, 1971; Buyanovsky et al., 1987), and compares to the 30 - 50% for broad-leaved forests (Bowden et al., 1993) and the global average of 48% for non-forested areas (Hanson et al., 2000). However, values for this study were lower than the 50 – 93% found in cold, northern regions (Billings et al., 1997) and 62 - 89% in boreal forests (Ryan et al., 1997). This is because cooler temperatures can limit microbial decomposition while the root respiration of grasses, larger trees and certain plants can still operate (Law et al., 2002), thus contributing a larger proportion towards the total respiration. The data for this study demonstrates this, where the cooler incubation temperature of 8°C exhibited a 4 – 16% increase in %RC (Table 5.9).

The range in SRR for this study was approximately 8.4 - 37.3 and 3.4 - 19.4 mg CO_2 m^{-2} hr^{-1} / mg dry wt of root (Table 5.10) for the 20°C and 8°C treatments, respectively. These values are within the range of 10 - 48 mg CO_2 m^{-2} hr^{-1} / mg dry wt of root for three grassland species in the northern Pennies, UK (Fitter et al., 1998) and are lower than the 60 - 100 mg CO_2 m^{-2} hr^{-1} / mg dry wt of root for citrus trees (Bryla et al., 2001). The larger values reported by Fitter et al. (1998) are likely the result of the annual precipitation at their study sites being approximately 20 - 30% greater than that at SCW that would support greater biomass development (Suyker et al., 2003). The higher values showed by Bryla et al. (2001) can be attributed to the coarser roots and greater uptake potential of the tree root systems.

The root control is evident by the SRR at the MR, which is 4 and 6 times lower than at the LR site for the 20°C and 8°C treatments, respectively (Table 5.10). The

decrease in temperature from 20°C to 8°C reduced SRR by 50% for the three grassland sites (LR, MR and OG) with little change observed at the WOOD site. This may be because the coarser roots at the WOOD site continued to respire at similar rates to soil heterotrophic activity even at cooler temperatures (Bekku et al., 2003).

It is difficult to measure SRR because of soil disturbances and small soil samples (75 – 100 g per sample). However, the SRR was measured by solving for R_R as the residual of $R_{R+S} - R_S$ and dividing by root content (equation 4.4). The root content ranged from 100 to 700 mg dry weight. Thus, a small error in the measured root content may cause a large bias in the reported SRR. For example, a difference in measured root content of 100 mg could create a 16% deviation of SRR for a soil sample of 700 mg.

There were clear methodological and measurement constraints that could introduce error and make it difficult to extrapolate magnitudes to field conditions. These include: 1) the unnatural soil disturbance when roots were physically removed that would alter soil texture, porosity and enhance water loss, aeration and C decomposition; 2) the mineralization products of decomposition and decay remained in situ within the incubation jars, and thus had the potential to affect the dynamics of decomposer metabolism, composition and turnover (Bouma and Bryla, 2000); 3) the lack of nutrient replenishment and supply of root exudates can reduce microbial activity and biomass (Winkler et al., 1996); 4) removal of roots may deactivate microbes; 5) the uncertainty of the rate of root decay, which may lead to overestimated R_{R+S} and R_R; 6) the indirect assessment of R_R through the difference in R_{R+S} and R_S, which assumes that processes influencing R_R are similar to R_{R+S} and R_S; and 7) the underestimation and lack of

capturing summer microbial and rhizosphere activity, including mycorrhizae processes arising from the timing of core collection in autumn.

Plant growth occurred in some of the incubation jars which indicated that some below-ground plants remained alive, but it is safe to assume that some of the fine roots, as well as the mycorrhizae, may have died during the refrigeration and storage process (Sjögersten and Wookey, 2002). Hence, the R_S mainly reflects the resilient decomposer community (fungi and bacterial autotrophs and heterotrophs). Furthermore, respiration was expressed per gram dry root at the end of the experiment although there was some plant regrowth after the 55 day measurement period. This simplification of including new root growth has been shown to be negligible, especially when studying process such temperature and drying cycles with rapid temporal dynamics (Bryla et al., 2001).

The issue of extrapolating laboratory data to a natural environment is difficult because percentage contributions show seasonality with large respiratory fluxes in late May and June when nutrient uptake is intensive and root growth and turnover are rapid (Hanson et al., 1993; Lohila et al., 2003) and during senescence when roots allocate C below-ground and microbial decomposition is still occurring (Yazaki et al., 2004). The data illustrates the potential risk of purely field or laboratory-based investigations (Sjögersten and Wookey, 2002). Thus, the results must be interpreted cautiously since they do not reflect all process and magnitudes of the soil respiration.

6.4.3 Laboratory Q_{10} Values

The study averaged Q_{10} values for R_S were slightly larger than the Q_{10} for bulk soil (R_{R+S}) mainly arising from soil disturbance. Roots have been shown to be responsive

to temperature increases, showing higher Q_{10} values (4.6 for roots compared to 3.5 for bulk respiration) (Bowden et al., 1993). The low Q_{10} of roots for this experiment (1.4 ± 0.5 – 1.9 ± 0.7) are comparable to the global average of 2.4 (Raich and Schlesinger, 1992), the 1.7 - 1.9 for a mixed temperate forest in North Carolina, USA (Winkler et al., 1996) and the 1.8 for citrus tree roots in Florida (Bryla et al., 2001). The high inherent variability can be attributed to: 1) lack of active R_R and dynamic climatic conditions controlling R_R, thus fluxes were more sensitive to substrate amounts and availabilities, which differ between samples; 2) the indirect estimation of R_R and resultant additive uncertainties of R_{R+S} and R_S; and 3) the soil disturbance, which may have lead to the oxidation of a large proportion of labile root matter prior to the onset of the lab experiment.

The reduced Bare R_{TOT} at the MR site exhibited in the field may be manifested in reduced R_{R+S}, R_S, and R_R as shown at the lower temperature regime 8°C. This suggests that heterotrophic decomposers (R_S) and the symbiotic relationship of roots, soils and mycorrhizae (R_{R+S}) are suppressed at the MR site compared to the other sites. Although it is quite possible that the phenomenon exhibited in the laboratory experiment is similar to that displayed in the field, the controlled environment (temperature, moisture, lack of nutrient replenishment and active microbial and root functions) underscores that field analysis is crucial. Nonetheless, nutrient (N in particular) supply can have a dramatic role in determining the magnitude and direction of C fluxes.

6.5 Temperature and Environmental Relationships With CO_2 Fluxes

6.5.1 Thermal Influences on CO_2 Fluxes

Uncertainties still exist when modelling the temperature dependence on soil R_{TOT}. In some circumstances linear (Fang et al., 1998) or quadratic (Maestre and Cortina, 2003) relationships fit well, however, most studies represent temperature (T_g in particular) and R_{TOT} using exponential relationships (Davidson et al., 1998; Fang and Moncrieff, 2001; Mielnick and Dugas, 2000). This exponential relationship suggests that microbial activity increases at an accelerated, non-linear rate, as temperature rises. Furthermore, temperature correlates well on daily and weekly timescales, but performs poorly on seasonal or yearly scales (Law et al., 2002), which complicates temperature-based predictions.

For this study, T_a explained most of the temporal variability in R_{TOT} (Section 5.6.1). This was unexpected, but may be explained by the presence of grasses that can exceed heights of 1.3 m (Figure 5.7) and modify surficial warming and subsequently T_g (Oke, 1987; Wan et al., 2002). This is suggested through the similar strength of relationships exhibited for all grassland sites. Although T_a exerted the strongest influence on the temporal variability of all measured variables, sporadic and dynamic cloud cover and wind gusts can limits the reliability of T_a. As such, other researchers have found weak relationships between T_a and R_{TOT} (Frank et al., 2002). It may be that the inter-relatedness with PAR and T_g, and the fact that measurements were made during the summer at midday, when strong relationships with T_a were observed. Thus, T_g is often used to describe the temporal variability in R_{TOT} (Buchmann, 2000; Frank et al., 2002).

The 30 cm depth averaged T_g relationships found here ($r^2 = 0.58 - 0.77$, $p < 0.01$) (Figure 5.17) are higher than the $r^2 = 0.46$ for a tallgrass prairie in Texas (Mielnick and Dugas, 2000). The R_{TOT} was related stronger to T_g at a depth of 5 cm than the 30 cm depth average, suggesting that most of the CO_2 released came from near surface roots and microbial activity, which has been shown by other researchers (Buchmann, 2000; Groffman et al., 2000; Winkler et al., 1996). Generally, the strength of the temporal variability in surficial CO_2 diminished as the depth of the measured temperature increased. However, for the OF site, the strength of the relationship remained similar up to a depth 20 cm, suggesting a more isothermal soil structure and a slightly differing thermal regime compared to the LR and MR sites. Davidson et al. (2000) suggests that the C response of an ecosystem is governed by the most limiting and dynamic variable. Thus, one possible reason for the high correlation R_{TOT} fluxes and temperature is that for most of the study period VSM was not limiting (below 20%) except during late June to mid-July, and early September, when moisture values dropped below 15%. Therefore, it appears that for most of the study period VSM was at sufficient levels to not hinder R_{TOT}.

Half-hourly averaged diurnal NEE measurements (Suyker and Verma, 2001) have been related to T_g, but most often there is a poor relationship. This poor relationship is because of the non-linear response to various soil and meteorological variables that are more often secondary in importance to PAR (Flanagan et al., 2002; Saigusa et al., 1998). Poor relationships between T_g and NEE and NEP for all sites, suggests that temperature was not the controlling temporal factor. It appears that the temporal acquisition of climatic variables was not suitable to capture the dynamics of plant uptake processes.

6.5.2 Field Q_{10} Values

The estimated Q_{10} from the fitted exponential relationships ranged from 2.3 - 3.6 and 2.0 - 2.9 for 20 cm depth averaged and at a depth of 5 cm, respectively. This is similar to the 2.5 reported for other grasslands (Raich and Schlesinger, 1992; Raich and Potter, 1995; Mielnick and Dugas; 2000). 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). 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). A possible drawback from using a first-order exponential relationship is that it is sensitive to low temperatures, when R_{TOT} rates are too low to reflect the actual response of respiration to temperature (Fang and Moncrieff, 2001). Thus, if we assumed that R_{TOT} has smaller Q_{10} values at lower temperatures, a first-order exponential trend, with a fixed Q_{10}, may underestimate temperature influences. Furthermore, Q_{10} has been shown to be larger at higher temperatures, suggesting that microbial activity is reduced through deactivation of enzymatic functions (Bekku et al., 2003). Q_{10} can also vary spatially and seasonally (Davidson et al., 2000) and is related to VSM distribution. That is, higher Q_{10} values have been reported for wetter soils at the same temperatures and decrease with a decline in VSM suggesting that soil CO_2 flux is less sensitive to temperature under low moisture conditions (Conant et al., 2004; Yukiko et al., 2003). With all the above-mentioned uncertainties, values in this study were still comparable to the literature.

6.5.3 Soil Moisture, PAR and Precipitation Influences on CO_2 Fluxes

VSM has been shown to be negatively related to R_{TOT} (Kang et al., 2003; Wichern et al., 2004). However, these studies sample monthly, year-round, and thus obtain a more distinctive, temporal VSM control, whereas measurements made herein are limited to the growing season. Over small ranges of seasonal VSM variability, where the majority of measurements are either at the 'wet' (above 35%) or 'dry' (below 20%) ends of the spectrum a linear model can suitably explain the temporal variability (Simek et al., 2004; Xu and Qi, 2001). However, when the range experiences both 'wet' and 'dry' conditions a quadratic relationship is more representative (Davidson et al., 1998; Mielnick and Dugas, 2000). VSM explained 27 - 50% of the variability in R_{TOT} and strengths were greater for Veg plots (Figure 5.18). This is likely due to the lack of disturbance and vegetative cover mitigating artificially enhanced water losses. Strengths were similar to that found between VSM and R_{TOT} ($r^2 = 0.34$) for a ryegrass in the Czech Republic (Simek et al., 2004), and ($r^2 = 0.26$) for a tallgrass prairie in Texas (Mielnick and Dugas, 2000).

Although there is much scatter in the VSM data, it does however suggest that root and microbial respiration can be limited at dry (limited available nutrients) and wet (diffusion of gaseous CO_2 out of the soil) conditions (Davidson et al., 2000; Franzluebbers et al., 2002). One possible reason for the large scatter between R_{TOT} and VSM may be because the depth of 12 cm at which VSM was measured may have been too shallow to adequately represent the potential deep-rooting of the grasses. Thus, wetter soil at greater depths may buffer the effects of near surface soil water deficits (Mielnick and Dugas, 2000). Furthermore, R_{TOT} has shown little response at high T_g (25°C) for

water filled pore space (WFPS) less than 0.4 m^3 m^{-3} (or VSM of 0.2), but were influenced when WFPS was larger than 0.6 m^3 m^{-3} (VSM of 0.3) suggesting that limited moisture suppressed R_{TOT} (Franzluebbers et al., 2002). When WFPS was increased at low (5°C) and moderate (15°C) temperatures, little change was exhibited for R_{TOT}. Since the maximum T_g during the study was at, or below, 20°C, it is possible that moisture was non-limiting throughout the season, hence reducing the importance of VSM as a predictor variable.

PAR showed a relatively strong control (r^2 = 0.27 - 0.66) on Veg R_{TOT}. Schlesinger (1997) suggests that 50% of the C fixed is lost during plant metabolism and the observed trends may be the result of increasing PAR stimulating NEP and enhancing R_{TOT} losses through root and plant metabolism. However, a more rational conclusion is the interrelatedness of PAR with T_a / T_g (r^2 = 0.60 - 0.80) resulting from the majority (>75%) of the measurement days being partly sunny.

Precipitation has been shown to be negatively associated with R_{TOT} (Kane et al., 2003), whereas some researchers have shown positive relationships on an annual basis (Suyker et al., 2003) and at shorter timescales (Meyers, 2001). This suggests that more available water can supply nutrients to areas where microbes and vegetation can utilize them, thus enhancing decomposition and R_{TOT} (Bekku et al., 2003). However, in this study R_{TOT} showed a moderate negative relationship to 7-day cumulative precipitation (Table 5.10). This may be the result of a lag in microbial response to the supply of nutrients and that CO_2 was evolved at depth, thus the surface signal was reduced because of changing soil diffusivities with moisture content (Kabwe et al., 2002). Moreover, microbial activity has shown quick, less than 24 hr, response to wetting which was likely

missed (Hunt et al., 2002). Thus, the release of R_{TOT} begins after precipitation and declines as nutrients and moisture become exhausted.

NEE and NEP have been linked to PAR (Flanagan et al., 2002; Suyker et al., 2003; Valentini et al., 1995) at half hourly and daily timescales. However, in this study poor relationships were found (Table 5.11), which may be attributed to: 1) fluxes measured at midday when PAR is high; and 2) point measurements that may not reveal plant acclimation and the response of soil and vegetation to dynamic weather conditions may not be represented by daily averages (Kim et al., 1992). This suggests that there are a multitude of other controlling factors that operate, possibly in lag to R_{TOT}. Hunt et al. (2002) showed that an early reduction in R_{TOT} within a few days of rainfall in conjunction with enhanced prolonged NEP maintained NEE for a longer period than that dictated by R_{TOT} alone. Since NEP was indirectly derived from NEE and R_{TOT}, various factors, such as moisture storage and T_g may have been operating at different timescales and exerting varying controls on the CO_2 flux dynamics.

Environmental controls on CO_2 cycling are often difficult to define because CO_2 fluxes from plant and microbial activity are difficult to separate, and the controlling factors are often interrelated (e.g. soil temperature shows co-linearity with PAR and soil moisture) (Franzluebbers et al., 2002). Attempting to extrapolate data within an ecosystem may result in errors from a limited frequency of data collected, observations made exclusively in the summer and at certain times of the day during active vegetation growth, or through techniques that may disturb the natural environment, such as vegetation removal.

6.6 Representativeness of Study Site and Year

Most of the Waterloo-Wellington area within the southern Ontario region is underlain by similar stratigraphy, but soil type varies (till moraine at SCW, sand and clay soil in the Niagara Haldimand and limestone soils in the Kingston area (Chapman and Putman, 1984)). Soils (types and properties) influence plant development and contribute large quantities towards the CO_2 fluxes (Mielnick and Dugas, 2000). Thus, extrapolating CO_2 flux dynamics from SCW to other temperate sites may be problematic, unless soil types are similar. However, SCW is generally representative of a typical temperate agricultural basin in terms of land-use (cropped fields), vegetation (grassland and woodlots) and local infrastructure.

Climatologically, the summer of 2003 was drier than the 30-year normal (Figure 5.2). Thus, the lack of available water has shown to limit the seasonal vegetation growth (LAI and AGB), which can reduce NEP and R_{TOT} (Meyers, 2001; Suyker et al., 2003). A wetter, cooler year (such as the summer of 2004), may provide favourable conditions for vegetative growth, and thus R_{TOT}, NEE and NEP may be larger than observed in 2003. Inter-annual climate regimes have been shown to exert a strong control on CO_2 dynamics. For example, Kim et al. (1992) reported that a tallgrass prairie site in the Central Great Plains of Canada fixed 750 g CO_2 m^{-2} from May to October, 1987, but only 250 g CO_2 m^{-2} from late June to August, 1989. Vegetation speciation is also intimately related to climatic conditions. Optimal temperatures for C_4 and C_3 plants can be as great as 40°C and 25°C, respectively (LeCain et al., 2002), thus, cool and wet years may favour C_3 grasses and forbs, whereas during hot and drier year's, warm season C_4 grasses may be favoured. Although grasses in this study are mainly C_4, this C fixation pathway is less

conducive to hot, drier conditions, because of an extra enzymatic step required to fix CO_2 (Schlesinger, 1997) compared to the one step CO_2 fixation of C_3 plants. This would alter the growth and possibly reduce the productivity of C_4 plants. It appears that a plant species' response to inter- and intra-annual variability underscores the need for long-term measurements encompassing a variety of climatic conditions to validate whether relationships found in one year are similar to a climatically different year.

Chapter 7
CONCLUSIONS AND RECOMMENDATIONS

7.1 SPATIAL VARIABILITY OF CO_2 EXCHANGE AMONG AGRICULTURAL GRASSLANDS

Few studies have explored the CO_2 exchange from riparian areas, thus it is important to assess these areas to: 1) enhance our understanding of terrain- specific fluxes, and to better quantify and represent the role of riparian grasslands within the context of agricultural greenhouse gas emissions and 2) evaluate whether these near stream zones uptake and release larger quantities of CO_2 than surrounding areas, and whether nutrients from adjacent agricultural practices influence the dynamics of CO_2 exchange. Also, examine whether the CO_2 response of soil and vegetation are similar.

This study showed that grass-dominated species, with similar vegetation, located approximately 250 - 300 m from one another displayed very different CO_2 exchange dynamics, explained primarily by location within the watershed. A conceptual diagram which summarizes the study averaged CO_2 fluxes and outlines the important processes is shown in Figure 7.1. Fertilizer application seems to have a dual effect of increasing above-ground biomass, thus ecosystem (vegetative) CO_2 dynamics (vegetated R_{TOT}, NEE and NEP) and reducing soil and microbial respiration (Bare R_{TOT}).

The influence of the adjacent agricultural land was related to elevated total nitrogen (%TN) and water extractable phosphorus (EXT-P), which were 40 and 1000% larger, respectively, at the MR site compared to the other sites. The MR site showed 22%

lower seasonal averaged soil respiration than the LR site and similar values (within 8%) to the OG site (Figure 7.1). The WOOD site, with the lack of an extensive root system exhibited the lowest respiration. Through laboratory incubations root free soil (R_S) and soil, roots and symbiotic mycorrhizae (R_{S+R}) showed that reduced R_{TOT} at the MR site may be attributed to lower soil autotrophic and symbiotic microbes and mycorrhizae respiration. However, caution should be exercised when translating these rates and patterns to field conditions because of changes of the physical, chemical and biological conditions incurred during the collection, storage and construction of samples, especially the likelihood of increased root respiration through enhanced root decay.

Patterns were different, but seasonally similar during the summer, for ecosystem vegetative dynamics. The MR site showed larger vegetative R_{TOT} than the LR and OG sites. Concurrently, the trends were similar for NEE and NEP, with MR showing 36 – 60% and 23 – 45% greater C uptake than the LR and OG sites, respectively. This suggests that higher soil N status, likely from nearby agriculture, suppressed soil CO_2 production and enhanced plant activity. Thus, the spatial variability was attributed to soil (C/N ratios and %TN) and vegetative (above-ground vegetation) properties, whereas climatic variables, ambient and ground temperature, and volumetric soil moisture control temporal patterns of CO_2 respiration (Figure 7.1).

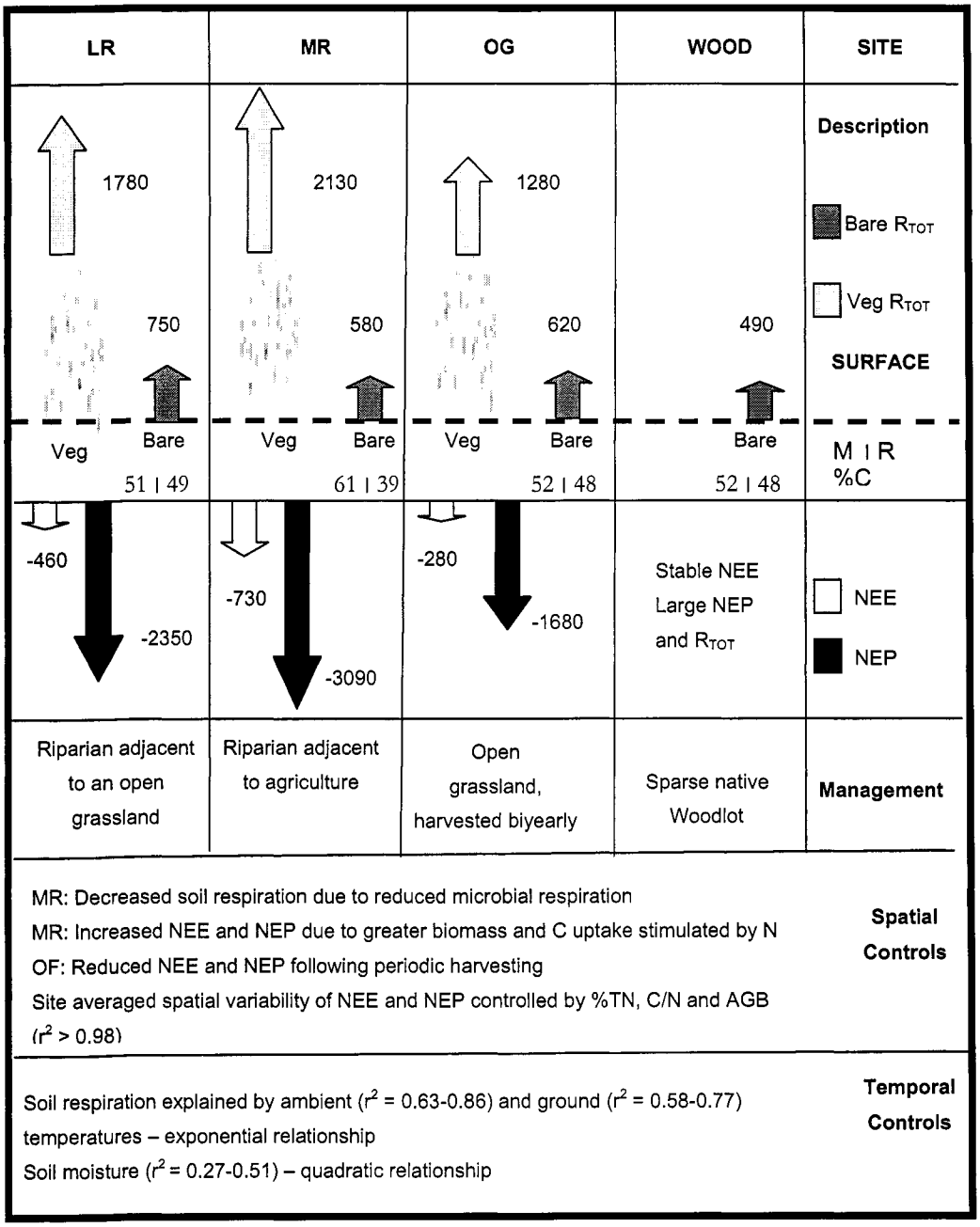

Figure 7.1: Conceptual summary of CO_2 exchange magnitude, processes and spatiotemporal controls from the various land types studied at Strawberry Creek Watershed, Maryhill, Ont., during the summer of 2003. Values in mg CO_2 m^{-2} hr^{-1}. M I R %C is microbial I root percent contributions to the overall soil flux. Refer to Table I for descriptions of acronyms and abbreviations.

Ambient temperature (T_a) was the best predictor of the temporal variability of ecosystem and soil R_{TOT} for all grass-dominated sites (exponential relationships $r^2 = 0.63 - 0.86$, $p < 0.01$) followed by soil temperature (T_g) at a depth of 5 cm ($r^2 = 0.58 - 0.77$, $p < 0.01$). T_g however, was the best predictor of the temporal variability of R_{TOT} for the WOOD site. Volumetric soil moisture content (VSM) also exerted substantial temporal control following a quadratic relationship ($r^2 = 0.27 - 0.51$, $p < 0.01$). Weak relationships were found between T_a, T_g and VSM with NEE and NEP ($r^2 = < 0.25$, $p < 0.01$). Spatially, study averaged R_{TOT}, NEE and NEP for the vegetated plots showed strong positive relationships ($r^2 > 0.98$, $p < 0.01$) with site averaged total soil nitrogen, C/N ratios and above-ground vegetation ($r^2 > 0.99$, $p < 0.01$).

The large magnitude of soil and vegetated fluxes measured for these three different grasslands and the maple woodlot under various land-use regimes highlights the importance of the spatial variability in both soil and vegetative fluxes for features that appear to be homogenous. Hence, there is a need to better assess CO_2 fluxes from heterogeneous agricultural landscapes and it emphasizes that estimates based on soil or vegetated areas, or using micrometeorological approaches, may not attain the spatial.

7.2 Global Carbon Cycle and Land Management

Riparian zones within agricultural areas act as a sink for sediments and nutrients (Hill et al., 1996; Tufekcioglu et al., 2001) and much of the land management within these basins is focused on quantifying and assessing the effectiveness of riparian areas to reduce non-point source pollutants (N and P in particular) originating from fertilizer use and exported to nearby water bodies (Groffman et al., 2002; Hill et al., 1996). These

types of studies are emphasized because of the concern of health impacts (contaminated drinking water) and eutrophication caused by elevated stream concentration of N and P (McDowell et al., 2001). While these types of studies are invaluable in determining when, where and the amount of fertilizer that should be applied the enhanced nutrient supply to these riparian areas have the potential to alter plant activity, and therefore the C balance of these systems.

Land management influenced study averaged CO_2 dynamics, such that periodic harvesting reduced plant uptake and enhanced R_{TOT}, and elevated N suppressed soil R_{TOT} and enhanced plant R_{TOT}, NEE and NEP. A common management practice, such as fertilization, may shift both the above- and below-ground CO_2 exchange processes. That is, root respiration increases may offset microbial decreases (Gough and Seiler, 2004; Maier and Kress, 2000). More importantly, a compromise between fertilization that reduces C losses (enhances CO_2 uptake), and the amount of N transported to streams and converted to N_2O needs to be established. Since agriculture is a chief contributor of N_2O, accounting for approximately 70% of the global N_2O emitted, it may be that from a management perspective the CO_2 release is not an overwhelming concern (Brady and Weil, 1999; IFA and FAO, 2001) because of the small areal coverage that can be influenced by fertilizer applications. However, integrating farm woodlots, riparian strips and grass water ways into the overall land management and farm policy programs could improve water quality and indirectly promote a positive response to global C change.

From a CO_2 exchange perspective characterizing all ecosystems is vital to enhance the reliability of models. Regional scale model estimates of NEE and R_{TOT} are designed to scale plot measurements to model grids based on area averaging pixels to

assess the global C budgets (Falge et al., 2002). These data usually employ temporal predictors, such as temperature and moisture, to obtain a yearly flux (IPCC, 2001). Thus, models that encompass these areas and grouped with similar parameterization may misrepresent the heterogeneity that exists within the ecosystem. Including these differences will undoubtedly lead to an improvement of the predicative capacities of these models. However, the financial costs of obtaining such field information must be weighed against the potential improvement of these models to determine if quantifying the dynamics of these ecosystems is a worthwhile endeavour.

7.3 Study Limitations

The limitations of this study, and most field studies, are confined to the temporal and spatial frequency of measurements. Speculation on the spatial variability of CO_2 exchange based on this study may be limited due to the spatial (3 to 4 plots per site) and temporal coverage (confined to one summer May – October). However, within this limitation, the data does suggest that agricultural areas do have an indirect affect on above- and below-ground C dynamics. The time constraints and diurnal variability of climatic characteristics (PAR and temperature) make measuring and commenting on temporal variability difficult. It is possible that the strength and relative spatial differences exhibited in CO_2 exchange may not be robust throughout the day. Thus, the use of limited CO_2 measurements between 10:00 and 16:00, over differing days allowed spatial variability during peak daylight hours to be addressed at the expense of dawn, dusk and diurnal measurements. Further confounding the temporal resolution is the uncertainty of daily climatic fluctuations. Moreover, all comparative data were not

collected on the same day (data collected on subsequent days were within 20%, which is similar to the midday range in fluxes and less than the overall CV of 25 – 30% for this study), but an effort was made to collect data on the following day, thus the disparities revealed between sites may be somewhat attributed to different sampling dates. However, data which were collected on the same date showed similar trends to the group averaged and data.

Site preparation may have also influenced results. In order to assess soil respiration, vegetation was removed prior to the study, so the interplay between the presence of decaying roots and the lack of respiring live roots may have created unnatural below-ground CO_2 dynamics. For the laboratory experiment, the unnatural conditions (temperature soil disturbance, etc.) and the lack of estimating root decay may have overestimated root and soil, and root contributions.

7.4 Future Research Directions

Future research that may stem from this project can be focused on three themes: 1) exploration of C and N interactions; 2) improvement of spatial and temporal resolution; and 3) further examination of process based controls. The N from fertilizer applications seemed to have an indirect affect on CO_2 dynamics through reduced R_{TOT} and enhanced NEE and NEP, which regulated the spatial variability exhibited within this ecosystem. However, to further verify this it would be useful to conduct a matched pair study by applying N to certain plots and determine whether direct applications have a lesser, greater, or no influence on the respiratory C loss or gain. Studies such as this have focused on forest ecosystems (Bowden et al., 2004; Burton et al., 2004) with fewer on

grassland ecosystems (Verburg et al., 2004). However, the larger below-ground biomass and subsequent mycorrhizae fungi populations (Griffiths et al., 1997) in grasslands may respond differently than in forests. This should be monitored under short (1 to 2 years) and longer (greater than 5 years) timescales to determine the spatiotemporal response of root and/or microbial dynamics. Furthermore, the relationship between soil respiration and the frequency and intensity of fertilizer applications remains uncertain and, along with the timing of measurement following fertilization applications, may explain some of the inconsistencies among reports in the literature (Gough and Seiler, 2004; Maier and Kress, 2000). Thus, in the context of land management, it is unclear whether annually repeated fertilization provides greater suppression of microbial activity and therefore soil R_{TOT}, than a single fertilizer event. Moreover, examining others factors that can influence the rate of organic matter decay such as the leaf and root N contents, root biomass, DOC, microbial community composition and types, as well as soil recalcitrant C, and other major cations and anions would further shed insight and possibly reveal more predictors of above- and below-ground soil processes.

Spatially, this study focused on the lower portion of one basin and thus represents only a small fraction of the watershed area. Thus, the natural progression is to expand the study area and evaluate other sites within this watershed and representative areas within other agricultural basins to explore similarities or disparities in CO_2 exchange processes. Areas such as the cropped (corn and soybean), other transects along the riparian areas, especially the riparian areas in the upper portion of the basin where organic fertilizer (chicken excrement) is applied, would provide more information of land management practices that may influence C exchange. In addition to increasing the number of sites

analyzed, it would be useful to examine the possibility of a distance from stream relationship, and evaluate whether these changes can be related to denitrification and microbial dynamics. However, the differences may be 'masked' given the CV variability of plot scale fluxes within grassland ecosystems.

As well as increasing the sampling frequency, it is important to examine how soils and vegetation are affected by seasonality, biological cycles and the soil physical environment (Gärdenäs et al., 2000). Thus, analysis encompassing a wide array of climatic conditions (especially during the shoulder seasons - spring and fall), over numerous years, and evaluate the dormant season and mid-winter thaw fluxes, would further reveal process based interactions. Also, to further explore the contribution of root respiration, trenching would give insight into the seasonality of the contribution of root respiration and the symbiotic activity of mycorrhizae within a field context.

Methodologically, chambers are suitable to evaluate CO_2 dynamics at the plot scale. However, this method limits the areal extent and resolution of temporal variability that can be measured. As a result, the use of micrometeorological techniques (eddy correlation or BREB methods) should provide a more integrated temporal analysis to assess the transient CO_2 responses, and in conjunction with chamber measurements should provide a larger more detailed data set for temporal comparisons.

It is vital that both field and lab studies are performed to assess and delineate various soil and vegetative dynamics. Measurements and analysis such as these are crucial in understanding how processes in various ecosystems are regulated and shift with climatic and management changes. Attempting to understand, and quantify all the mechanisms influencing CO_2 exchange alone is a formidable task. However, studies that

combine microbial, hydrological and micrometeorological processes are vital, but are difficult to implement both financially and logistically.

Carbon studies have focused mainly on natural (forest or wetland) ecosystems. However, it is evident that agricultural and human manipulated systems, especially in temperate regions, are strong contributors to regional CO_2 budgets. Agricultural landscapes differ from most in terms of homogeneity, whereas the surface seem homogenous at the stand scale (for example each crop) it is more heterogeneous with respect to mosaic of fields and surface types when viewed at the ecosystem level (Soegaard et al., 2003).

These agricultural ecosystems are heavily influenced by humans through harvesting, fertilizer applications and crop rotations. It is probable that the management of these areas could have a greater impact on productivity and C cycling than that of climate change. This is because grasslands are resilient to climate variations due to a large amount of the total NPP (above 75%) being partitioned below-ground (Owensby, 2000). Nonetheless, quantifying the CO_2 variability of region-specific ecosystems (riparian areas) is important to further explore process based dynamics, better represent the terrestrial ecosystem in global C models and it may lead to the development of improved land management policies with regards to C sequestration.

Chapter 8

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APPENDIX A: STUDY AVERAGED DESCRIPTIVE STATISTICS FOR SITE CARBON FLUXES AND MEASURED BIOTIC AND ABIOTIC VARIABLES

Table A: Descriptive statistics of the tested variables for correlation analysis, n = 21 - 24 sampling occasions. Volumetric soil moisture content (%) (VSM), ambient temperature (T_a), ground temperature (T_g), photosynthetically active radiation (PAR), overall respiration (R_{TOT}), net ecosystem CO_2 exchange (NEE) and net ecosystem productively (NEP). Sites are lower riparian (LR), middle riparian (MR), open grassland (OG), maple woodlot (WOOD), and terrain cover is Bare (vegetation removed) and Veg (vegetation intact). [a] Kolmogorov-Smirnov goodness of fit normality test, [b] ground temperature averaged from 0-20 cm, measured at 5, 10, 20 cm; [c] cumulative rainfall in the preceding 7-days (weeks with fewer than 5 mm of rain were omitted), [d] Bare NEE is similar to Bare R_{TOT}, thus not included and [e] Bare NEP has no vegetation, therefore NEP ~ 0 and omitted. Table headings adopted from Simek et al. (2004).

Variable	Site	Units	Mean	Standard Deviation	Standard Error	CV (%)	Min	Max	Median	[a] Normality
VSM (LR)	Bare	%	31.41	9.59	4.79	30	13.75	51.25	32.75	Y
VSM (MR)	Bare	%	27.12	9.90	4.95	37	10.52	53.25	25.75	Y
VSM (OG)	Bare	%	32.12	13.53	6.76	42	14.00	56.00	32.50	Y
VSM (WOOD)	Bare	%	25.92	11.28	5.64	44	12.67	54.33	24.33	Y
VSM (LR)	Veg	%	26.00	9.9	4.95	38	13.00	52.00	25.25	Y
VSM (MR)	Veg	%	27.48	9.14	4.57	33	12.00	51.75	28.00	Y
VSM (OG)	Veg	%	32.18	13.13	6.56	41	12.00	55.33	31.33	Y
T_a (LR)	Bare	°C	24.7	7.7	3.9	31	1.6	34.6	27.0	Y
T_a (MR)	Bare	°C	23.8	7.2	3.6	30	1.5	32.2	25.3	Y
T_a (OG)	Bare	°C	23.7	9.4	4.7	40	2.3	37.3	25.5	Y
T_a (WOOD)	Bare	°C	19.8	6.8	3.4	34	1.9	30.7	20.7	Y
T_a (LR)	Veg	°C	24.4	7.6	3.8	31	1.9	34.3	26.2	Y
T_a (MR)	Veg	°C	23.6	7.1	3.6	30	1.5	32.8	25.2	Y
T_a (OG)	Veg	°C	23.7	8.8	4.4	37	2.3	36.1	24.6	Y
[b] T_g (LR)	Bare	°C	17.9	4.4	2.2	25	6.3	23.1	18.6	Y
[b] T_g (MR)	Bare	°C	16.3	4.0	2.0	24	4.6	20.3	17.9	Y
[b] T_g (OG)	Bare	°C	17.4	4.7	2.3	23	5.0	22.8	19.0	Y
[b] T_g (WOOD)	Bare	°C	15.4	3.6	1.8	23	6.5	20.2	17.0	Y

Table A cont.										
Variable	**Site**	**Units**	**Mean**	**Standard Deviation**	**Standard Error**	**CV (%)**	**Min**	**Max**	**Median**	**[a] Normality**
[b] T_g (LR)	Veg	°C	17.3	4.4	2.2	25	4.6	22.8	18.3	Y
[b] T_g (MR)	Veg	°C	16.7	3.8	1.9	23	7.5	21.6	18.0	Y
[b] T_g (OG)	Veg	°C	17.6	4.1	2.1	24	8.1	22.2	19.0	Y
PAR (LR)	Bare	W m^{-2}	324.6	126.2	63.1	39	58.5	461.8	326.8	Y
PAR (MR)	Bare	W m^{-2}	319.0	112.9	56.4	35	55.9	488.8	352.9	Y
PAR (OG)	Bare	W m^{-2}	321.8	157.3	78.6	49	45.9	497.3	392.7	Y
PAR (WOOD)	Bare	W m^{-2}	15,2	13.5	6.8	89	3.5	53.0	9.5	N
PAR (LR)	Veg	W m^{-2}	316.2	131.7	65.9	42	57.3	466.8	356.2	Y
PAR (MR)	Veg	W m^{-2}	317.4	126.9	63.4	40	75.5	484.3	348.4	Y
PAR (OG)	Veg	W m^{-2}	304.0	148.7	74.3	49	71.7	474.6	360.0	Y
[c] Rainfall (LR)	Bare/Veg	mm	14.08	11.81	2.41	84	0.00	40.22	14.21	Y
[c] Rainfall (MR)	Bare/Veg	mm	14.77	11.56	2.41	78	0.00	40.22	14.4	Y
[c] Rainfall(OG)	Bare/Veg	mm	14.24	12.00	2.62	84	0.00	40.22	14.4	Y
[c] Rainfall (WOOD)	Bare/Veg	mm	13.67	12.01	2.56	88	0.00	40.22	14.4	Y
[d] NEE (LR)	Bare	---	---	---	---	---	---	---	---	---
[d] NEE (MR)	Bare	---	---	---	---	---	---	---	---	---
[d] NEE (OG)	Bare	---	---	---	---	---	---	---	---	---
[d] NEE (WOOD)	Bare	---	---	---	---	---	---	---	---	---
NEE (LR)	Veg	mg CO_2 m^{-2} hr^{-1}	-440	240	120	54	-90	-990	-420	Y
NEE (MR)	Veg	mg CO_2 m^{-2} hr^{-1}	-730	370	190	51	300	-1420	-700	Y
NEE (OG)	Veg	mg CO_2 m^{-2} hr^{-1}	-260	450	260	174	610	-780	-470	Y
R_{TOT} (LR)	Bare	mg CO_2 m^{-2} hr^{-1}	750	290	140	38	140	1230	760	Y
R_{TOT} (MR)	Bare	mg CO_2 m^{-2} hr^{-1}	770	320	160	41	210	1360	730	Y
R_{TOT} (OG)	Bare	mg CO_2 m^{-2} hr^{-1}	630	390	230	62	80	1680	630	Y
R_{TOT} (WOOD)	Bare	mg CO_2 m^{-2} hr^{-1}	510	290	170	57	90	1290	450	Y
R_{TOT} (LR)	Veg	mg CO_2 m^{-2} hr^{-1}	1500	610	310	41	420	2430	1670	Y
R_{TOT} (MR)	Veg	mg CO_2 m^{-2} hr^{-1}	2180	740	370	34	590	3230	2270	Y

Table A cont.										
Variable	**Site**	**Units**	**Mean**	**Standard Deviation**	**Standard Error**	**CV (%)**	**Min**	**Max**	**Median**	**[a] Normality**
R_{TOT} (OG)	Veg	mg CO_2 m^{-2} hr^{-1}	1280	570	330	44	200	2080	1390	Y
[e] NEP (LR)	Bare	---	---	---	---	---	---	---	---	---
[e] NEP (MR)	Bare	---	---	---	---	---	---	---	---	---
[e] NEP (OG)	Bare	---	---	---	---	---	---	---	---	---
[e] NEP (WOOD)	Bare	---	---	---	---	---	---	---	---	---
NEP (LR)	Veg	mg CO_2 m^{-2} hr^{-1}	-2030	680	340	33	-680	-3250	-1920	Y
NEP (MR)	Veg	mg CO_2 m^{-2} hr^{-1}	-3060	610	310	20	-2220	-4060	-3140	Y
NEP (OG)	Veg	mg CO_2 m^{-2} hr^{-1}	-1660	610	350	36	-420	-2560	-1750	Y

APPENDIX B: SELECTED SUMMARY OF GRASSLAND NET ECOSYSTEM CO_2 EXCHANGE AND NET ECOSYSTEM PRODUCTIVITY FROM THE LITERATURE

Table B: Growing season/summer net ecosystem exchange CO_2 exchange (NEE), maximum daily NEE and NEP from various grasslands, sagebrush and agricultural ecosystems. Method of measuring carbon exchange is Eddy Correlation (EC), Bowen Ratio Energy Balance (BREB) and chambers. (Flux sign convention is: positive (biosphere to the atmosphere) and negative (atmosphere to the biosphere). Note: values were all converted to g C m^{-2} d^{-1} using (*1x 10^{-3} mg CO_2 m^{-2} s^{-1} = 22.7 µmol CO_2 m^{-2} s^{-1})* and *(1 g C = 12.01 g C x (44.01 g CO_2)$^{-1}$)*. --- denotes data not available (Source: modified from Novick et al. 2004).

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1]Growing Season/ Summer NEE (g C m^{-2})	[2]Reported carbon units for maximum NEE	[2] Maximum NEE (g C m^{-2} d^{-1})	Max NEP (g C m^{-2} d^{-1})	Reference(s)
Matador, SK., CAN	Mixed-grass prairie	1970	BREB	Clay-soils	Native	---	---	-2.7	-4.9	Ripley and Saugier (1974; 1978) Redman (1978)
		1971	Chambers	Clay-soils	Native	---	---	-6.2	-7.8	
Woodward, OK., USA	Mixed-grass prairie	1995 (driest)	BREB	Mixed, sandy soils	Native, grazed	-118	-0.21 mg CO_2 m^{-2} s^{-1} (-0.07)	-4.9[a] (-1.63)	---	Sims and Bradford (2001)
		1996				-13	-0.14 mg CO_2 m^{-2} s^{-1}(-0.01)	-3.3[a] (-0.2)	---	
		1997 (wettest)				-199	-0.25 mg CO_2 m^{-2} s^{-1}(0.13)	-5.5[a] (-2.76)	---	
Mandan, ND., USA	Northern mixed-grass prairie	1996	BREB	Silt-clay loam	Native	-113[b]	-4.9 g C m^{-2} d^{-1} (-0.61)	-4.1 (-0.61)	---	Frank and Dugas (2001)
		1997 (driest)				-85[b]	-4.6 g C m^{-2} d^{-1} (-0.46)	-4.6 (-0.46)	---	
		1998 (dry May)				-49[b]	-3.7 g C m^{-2} d^{-1} (-0.26)	-3.7 (-0.26)	---	
		1999 (wettest)				-129[b]	-4.9 g C m^{-2} d^{-1} (-0.69)	-4.9 (-0.69)	---	

Table B cont.

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1]Growing Season/ Summer NEE (g C m^{-2})	[2]Reported carbon units for maximum NEE	[2] Maximum NEE (g C m^{-2} d^{-1})	Max NEP (g C m^{-2} d^{-1})	Reference(s)
Walnut Gultch, AZ., USA (Kendall)	Mixed-grass	1997	BREB	Coarse-loamy	Rangeland	-86[c]	-0.16 mg CO_2 m^{-2} s^{-1}	-3.8	---	Emmerich (2003)
		1998				---	-0.20 mg CO_2 m^{-2} s^{-1}	-4.6	---	
		1999				---	-0.23 mg CO_2 m^{-2} s^{-1}	-5.5	---	
		2000				---	-0.16 mg CO_2 m^{-2} s^{-1}	-3.8	---	
Lethbridge, AB., CAN	Moist-mixed grassland	1998 (wetter)	EC	Clay loam	Native	-146[d]	- 14 µmol m^{-2} s^{-1}	-5 (-0.95)	-9	Flanagan et al. (2002)
		1999				-56[d]	- 8 µmol m^{-2} s^{-1}	-3.2 (-0.37)	-5.5	
		2000 (drier)				-23[d]	- 5 µmol m^{-2} s^{-1}	-2.4 (-0.15)	-4.5	
Duke Forest, NC., USA	Mixed-grass field	April 2000-April 2001	EC	Silty loam	Mowed annually	+23[e](-2[f])	-2.8 g CO_2 m^{-2} d^{-1} (0.02)	-2.8 (0.02)[f]	-7.6	Novick et al. (2004)
Manhattan, KN., USA	Tallgrass Prairie (C_4)	1996[g]	BREB	Silty clay loams	Annually burned and not grazed	+217[g]	-17.8 g CO_2 m^{-2} d^{-1}	-4.8 (-2.2)	-9.5	Ham and Knapp (1998)
Temple, TX., USA	Tallgrass Prairie	1993	BREB	Clay loam	Grazed (no fertilizer applied)	---	-18.3 g CO_2 m^{-2} d^{-1}	-5	---	Dugas et al. (1999)
		1994 (wetter)				---	-23.8 g CO_2 m^{-2} d^{-1}	-6.5	---	

Table B cont.

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1]Growing Season/ Summer NEE (g C m^{-2})	[2]Reported carbon units for maximum NEE	[2]Maximum NEE (g C m^{-2} d^{-1})	Max NEP (g C m^{-2} d^{-1})	Reference(s)
Tsukuba, Japan	Grass field (C_3 and C_4 grasses)	1993	BREB	Volcanic ash soil	Mowed once a year in late autumn	---	-45.8 g CO_2 m^{-2} d^{-1}	-12.5	---	Saigusa et al. (1998)
		1994 (drier)		Silty, clay loam		---	-52.0 g CO_2 m^{-2} d^{-1}	-14.2	---	
Shidler OK., USA	Tallgrass Prairie	1989	EC		Native	-68[h]	---	---	---	Kim et al. (1992)
Shidler, OK., USA	Tallgrass Prairie (C_4)	1997	EC	Silty, clay loam	Burned in the spring	-446[i]	-9.5 g C m^{-2} d^{-1} (2.08)	-9.5 (-2.08)[j]	---	Suyker and Verma (2001); Suyker et al. (2003)
		1998				-204[i]	-7.5 g C m^{-2} d^{-1} (0.95)	-7.5 (-0.95)[j]	---	
		1999				-300[i]	-8.5 g C m^{-2} d^{-1}(1.40)	-8.5 (-1.40)[j]	---	
Mackenzie Basin, NZ	Tussock grassland	1998-1999	EC	Fluvial glacial origin (stony soils)	Lightly grazed	---	-5 µmol CO_2 m^{-2} s^{-1}	-1.9[k]	-5.2	Hunt et al. (2002)
Jasper Ridge, CA, USA	Serpentine grassland	July 1990 - July 1991	EC	Loamy	Native	---	---	-1.9	---	Valentini et al. (1995)
Dubois, ID, USA	Sagebrush-steppe[l]	1997	Closed chamber and IRGA	Coarse-to-fine sandy loam	Ungrazed	---	-0.64 mg CO_2 m^{-2} s^{-1}(-0.47)	-15.1(-11.8)[m]	---	Angell et al. (2001)
Dubois, ID., USA	Sagebrush-steppe	1996	BREB	Coarse, sandy loam	Native	-77[n]	---	---	---	Gilmanov et al. (2003)
		1997				-112[n]	---	---	---	
		1998				-203[n]	---	---	---	
		1999 (wet)				-301[n]	---	---	---	

Table B cont.

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1]Growing Season/ Summer NEE (g C m^{-2})	[2]Reported carbon units for maximum NEE	[2] Maximum NEE (g C m^{-2} d^{-1})	Max NEP (g C m^{-2} d^{-1})	Reference(s)
Woodward, OK., USA	Sagebrush	1995 (driest)	BREB	Mixed, sandy soils	Native grazed	-74	-0.11 mg CO_2 m^{-2} s^{-1}	-2.7[a]	---	Sims and Bradford (2001)
		1996 (dry May/June)				+31	0.09 mg CO_2 m^{-2} s^{-1}	-2.2[a]	---	
		1997 (wettest)				+26	0.20 mg CO_2 m^{-2} s^{-1}	-4.6[a]	---	
Walnut Gultch, AZ., USA (Lucky Hills)	Mixed-shrub (Brush)	1997	BREB	Coarse-loamy	Rangeland	+26[c]	-0.03 mg CO_2 m^{-2} s^{-1}	-0.8	---	Emmerich (2003)
		1998				---	-0.11 mg CO_2 m^{-2} s^{-11}	-2.7	---	
		1999				---	-0.11 mg CO_2 m^{-2} s^{-1}	-2.7	---	
		2000				---	-0.11 mg CO_2 m^{-2} s^{-1}	-2.7	---	
Western Denmark	Winter Wheat	April 1998-March 1999	EC	Sandy Loam	Cropped	-432[o]	-12 g C m^{-2} d^{-1} (-4.7)	-12.0 (-4.7)	---	Soegaard et al. (2003)
	Winter Barley			Sandy Loam	Cropped	-230[o]	-9.0 g C m^{-2} d^{-1} (-2.5)	-9.0 (-2.5)	---	
	Spring Barley			Sandy Loam	Cropped	313[o]	-10.5 g C m^{-2} d^{-1} (-3.4)	-10.5 (-3.4)	---	
	Maize			Sandy Loam	Cropped	-350[o]	-9.0 g C m^{-2} d^{-1} (-3.8)	-9.0 (-3.8)	---	
	Grass			Sandy Loam	Hay Feed	-46[o]	-10 g C m^{-2} d^{-1} (-0.5)	-10 (-0.5)	---	

Table B cont.

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1]Growing Season/ Summer NEE (g C m^{-2})	[2]Reported carbon units for maximum NEE	[2] Maximum NEE (g C m^{-2} d^{-1})	Max NEP (g C m^{-2} d^{-1})	Reference(s)
Chickasha, OK., USA	Mixed-grass rangeland	1995	EC	Clay loam	Grazed pasture	-196[p]	-4.5 g C m^{-2} d^{-1} (-1.59)	-4.5(-1.59)	---	Meyers (2001)
		1996				-41[p]	-4 g C m^{-2} d^{-1} (-0.30)	-4(-0.3)	---	
		1997				-188[p]	-5 g C m^{-2} d^{-1} (-1.52)	-5(-1.52)	---	
		1998 (drought)				+155[p]	-1 g C m^{-2} d^{-1} (1.26)	-1 (1.26)	---	
Rodonia, Brazil	C_4 Pasture	May, 1993	EC		Grazed pasture		---	-1.9[q]	-8.0[q]	Grace et al. (1998)

[1] Growing season is considered when NEE is negative and ends when NEE changes and remains positive for the following 10 days
[2] Study average values given in parentheses
[a] Growing season and measurement days varied among years, so 72 days was used to obtain study averaged NEE
[b] 185 days from April 24 - October 26
[c] Annual daytime average over the 4 years
[d] 183 days from April 1 - August 31
[e] 250 days from April 1 - December 6
[f] 90 days from May 30 - August 28
[g] DOY 220 - 320 (transition from autumn sink to source)
[h] May - October 1987
[i] 214 days (April - October) when NEE was negative
[c] Calculated based on a 214 day growing season
[k] 212 days during a summer drought
[l] Plots included shrubs
[m] 4 dates May 17, June 17, July 7 and July 31, 1997 (6-7 times a day)
[n] Length of growing season varies yearly between 105 and 140 days
[o] 92 days from May - July
[p] 123 d growing season May - August
[q] Net daily flux for an 11 day period in May 1993

APPENDIX C: SELECTED SUMMARY OF ECOSYSTEM RESPIRATORY CO_2 FLUXES FROM THE LITERATURE

Table C: Daily average overall CO_2 respiration fluxes from various grasslands, riparian and crop ecosystems measured using chamber methods. (Flux sign convention is: positive (biosphere to the atmosphere) and negative (atmosphere to the biosphere). Note: values were all converted to g C m^{-2} d^{-2} using (*1x 10^{-3} mg CO_2 m^{-2} s^{-1} = 22.7 µmol CO_2 m^{-2} s^{-1})* and *(1 g C = 12.01 g C x (44.01 g CO_2)$^{-1}$)*. --- denotes data not available.

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1] Average soil flux with reported C units for the study	[1] Average soil flux (g C m^{-2} d^{-1})	Reference(s)
NB., USA	Tallgrass prairie	August	Chambers	Silty Loams	Native	---	6.3	Norman et al. (1992)
	No clipping					---	7.1	
	Full clipping					---	5.8	
	Early season clipping					---	5.4	
Manhattan, KN., USA	Tallgrass Prairie (C_4)	1996[a]	Closed chamber and IRGA	Silty, clay loams	Annually burned and not grazed	-0.4 mg CO_2 m^{-2} s^{-1}	9.4	Ham and Knapp (1998)
Flint Hills, KN., USA	Unburned Tallgrass prairie (C_4 grasses)	May 94- May 96[b]	Dynamic chamber and IRGA	Silty clay loams	Bison grazing	4 µmol CO_2 m^{-2} s^{-1} (10.3)	4.1 (10.7)	Knapp et al. (1998)
	Annual burned Tallgrass Prairie (C_4 grasses)	June 94- May 96[b]			Bison grazing	9 µmol CO_2 m^{-2} s^{-1}(15.1)	8.3 (15.7)	

Table C cont.

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1] Average soil flux with reported C units for the study	[1] Average soil flux (g C m^{-2} d^{-1})	Reference(s)
Inner Mongolia	Meadow steppe[X]	1998	Dynamic chamber and IRGA	Sandy loam	Native	1304.3 mg CO_2 m^{-2} hr^{-1}	8.5	Dong et al. (2000)
	Meadow steppe[X] farmland			Sandy loam	Cultivated	1707.9 mg CO_2 m^{-2} hr^{-1}	11.2	
	Grassland 1[X]			Sandy loam	Native	1471.2 mg CO_2 m^{-2} hr^{-1}	9.6	
	Grazing land 1[X]			Sandy loam	Grazed	1046.6 mg CO_2 m^{-2} hr^{-1}	6.9	
	Grassland 2[X]			Sandy loam	Native	895.6 mg CO_2 m^{-2} hr^{-1}	5.9	
	Grazing land 2[X]			Sandy loam	Grazed	1081.3 mg CO_2 m^{-2} hr^{-1}	7.1	
	Dry steppe[X]			Sandy loam	Cultivated	1180.3 mg CO_2 m^{-2} hr^{-1}	7.7	
Temple, TX., USA	Tallgrass prairie	1993-1998	Dynamic chamber and IRGA	Fine, clay loam	Grazed	1.0 - 2.1 kg C m^{-2} yr^{-1}	2.5 - 4.6 (over 5 years)	Mielnick and Dugas (2000)
Planted Vegetation IA, USA	Mixed-grass (Riparian	1996-98			Established	4.55 g C m^{-2} d^{-1} (6.2)	4.55 (6.2)	Tufekcioglu et al. (2001)
	Switchgrass (Riparian)	1996-98	Soda-Lime	Fine-loamy	Established	3.70 g C m^{-2} d^{-1} (6.0)	3.70 (6.0)	
	Soybean	1996-98			Cropped	2.70 g C m^{-2} d^{-1} (4.2)	2.70 (4.2)	
	Corn	1996-98			Cropped	2.40 g C m^{-2} d^{-1} (3.8)	2.40 (3.8)	

Table C cont.

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1] Average soil flux with reported C units for the study	[1] Average soil flux (g C m^{-2} d^{-1})	Reference(s)
ND., USA	Non-grazed, mixed-grassland	1996-2000[c]	Dynamic chamber and IRGA	Loam to silt loam	Native	3.5 g CO_2-C m^{-2} d^{-1} (5.8)	3.5 (5.8)	Frank et al. (2002)
	Grazed mixed-grassland					4.3 g CO_2-C m^{-2} d^{-1} (6.9)	4.3 (6.9)	
	Grazed western-grass	1996-1998[c]				4.0 g CO_2-C m^{-2} d^{-1} (6.1)	4.0 (6.1)	
Ceske, Budejovice, CZ	Ryegrass	1998	Gas chromatography	Sandy loam	Native	159.81 mg CO_2 m^{-2} hr^{-1} (425.23)	1.05[d]	Simek et al. (2004)
	Clover					119.11 mg CO_2 m^{-2} hr^{-1} (345.12)	0.78[d]	
	Grass + Clover					146.00 mg CO_2 m^{-2} hr^{-1}(340.23)	0.96[d]	
Xilim River Basin, Nei Mongol	Semi-arid steppe	2001	Soda-Lime	Loam	Native	1349.6 mg C m^{-2} d^{-1} (1738.9)	1.35 (1.74)[e]	Zhang et al. (2003)
	Wet Meadow					785.9 mg C m^{-2} d^{-1} (2235.6)	0.79 (2.24)[e]	
San Pedro River, AZ., USA	Mesquite	October 2002 to May 2003	Gas chromatography	Loam	Native	241.99 mg CO_2 m^{-2} hr^{-1} (310)	1.58 (2.02)[f]	Martens and McLain (2003)
	Mesquite-Sacaton					240.62 mg CO_2 m^{-2} hr^{-1} (310)	1.58 (2.02)[f]	
	Open					224.9 mg CO_2 m^{-2} hr^{-1} (300)	1.46 (1.96)[f]	

Table C cont.

Site	Ecosystem Type	Year/Study Period	Method	Soil Type	Site History	[1] Average soil flux with reported C units for the study	[1] Average soil flux (g C m^{-2} d^{-1})	Reference(s)
ON., Canada	Barley	69 d in summer of 1990	Soda-Lime	Loamy	Cultivated	---	3.94	Rochette et al. (1992a)
	Open Fallow				Native	---	5.20	
ON., Canada	Deciduous Forest	1992 Growing Season	Soda-Lime	Loamy	Native	---	2.33	Lessard et al. (1994)
	Corn				Cultivated		1.00	
Akhdar, Mountains, Oman	Fallow	2002	Dynamic chamber and IRGA	Loamy and Rocky	Cultivated	27.4 mg C m^{-2} hr^{-1} (136.4)	0.65 (3.3)[g]	Wichern et al. (2004)
	Wheat					45.5 mg C m^{-2} hr^{-1}(98.2)	1.01 (2.35)[g]	
	Alfalfa					97.5 mg C m^{-2} hr^{-1} (201.8)	2.34 (4.84)[g]	
Northeastern, CO., USA	Shortgrass steppe (C_4 grasses)	1995-1997	Dynamic chamber and IRGA	Fine, sandy loam	60% grazing	5.06 -8.24 µmol CO_2 m^{-2} s^{-1}	5.3-8.6	LeCain et al. (2002)
	Shortgrass steppe (C_4 grasses)				20% grazing	4.90 - 7.65 µmol CO_2 m^{-2} s^{-1}	5.1-7.9	
	Shortgrass steppe (C_4 grasses)					5.15 - 8.08 µmol CO_2 m^{-2} s^{-1}	5.3-8.4	
Aigues de Busot, Spain	Shrub grass	Feb - July, 2001	Dynamic Chamber and IRGA	Silty	Native	49.15 mg CO_2 m^{-2} hr^{-1} (90)	1.18 (2.16)	Maestre and Cortina (2003)

[X] Vegetation present when measurements made (vegetation respiration included)
[l] Maximum study values given in parentheses
[a] Measurements made every 7 -10 d during the growing season
[b] Monthly measurements
[c] Measurements made every 20 - 30 days
[d] 13 measurements from March - November
[e] Measurements made every 10 d from June 5 - October 15
[f] Weekly measurements from July - September and monthly from October - March
[g] Measurements made 12 days following irrigation
[h] 6 - 11 growing season measurements from 1995 - 1997