

Spatial variability of CO₂ exchange for riparian and open grasslands within a first-order agricultural basin in Southern Ontario

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Abstract

Agriculture is one of the most widespread land-use types in Ontario, Canada, where cultivated lands are often located within small first-order catchments with extensive grass-dominated riparian areas. These grass-dominated areas may be significant to the overall catchment carbon functioning as they are often high in soil organic matter and elevated biological productivity due to the availability of agricultural nutrients. As such, this study examines midday CO₂ exchange between the atmosphere and two grass-dominated riparian areas (one adjacent to a cultivated disk-tilled cornfield, one adjacent to a no-till grassland) and an open area grassland (no-till field) in a predominantly agricultural basin in Southern Ontario using daytime dynamic closed-chamber measurements from May 7 to October 27, 2003. Soils in this catchment are generally comprised of 50% sand, 35% silt and 15% clay, with riparian areas containing an organic layer approximately 0.20–0.40 m deep. The influence of nearby agriculture on riparian areas is apparent, as larger rates of CO₂ exchange were correlated with elevated soil nutrients as well as above ground biomass and canopy height, which were larger in the riparian zone influenced by intensive agriculture (Rip-Corn) than the grassland-influenced riparian area (Rip-Grass) and the adjacent grassland field (Grass). Spatial patterns in soil and vegetation respiration (R_{Tot}), net ecosystem CO₂ exchange (NEE) and gross ecosystem productivity (GEP) for all sites showed strong positive relationships with soil characteristics such as total nitrogen, carbon–nitrogen ratio and above-ground biomass.

Our results show that grass-dominated riparian and non-riparian areas, with similar vegetation that appear to be homogenous, located approximately 250–300 m from one another, may exhibit very different CO₂ fluxes. In general, CO₂ exchange is much greater in riparian areas than in the adjacent upland grasslands, and this is more exaggerated where those upland sites are tilled and receive inorganic fertilizers. Furthermore, our results indicate that the effects of land-use (i.e. agriculture) over-ride the effects of microclimate in controlling spatial patterns in CO₂ exchange in this watershed. This highlights the need to better assess CO₂ fluxes from heterogeneous agricultural landscapes, and emphasizes that estimates based on data grouped solely on soil or vegetation units can be rather conservative and may not capture the inherent spatial variability and small scale processes that drive CO₂ exchange.

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1. Introduction

Thirteen percent of agricultural lands within Canada are located in the temperate zones of Ontario and Quebec (Paustain et al., 1998), where they are characterized by diverse

land-use types. These areas are usually located within a small area (3–6 km²), containing first-order streams neighbored by narrow grass-dominated riparian areas that potentially show high biological activity (Romero et al., 2002). Riparian areas in temperate agricultural basins are composed mainly of grass species, soils that are often high in soil organic matter (SOM) content, and large microbial populations and surface residues (Conant et al., 2001; Frank et al., 2002). Such areas are sinks

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for nutrients from upland agricultural areas (e.g. Hill, 1996). The elevated storage and availability of nutrients in riparian areas may increase the biological productivity of riparian vegetation (Tufekcioglu et al., 2003) and consequently influence the CO₂ exchange dynamics of these areas.

Previous CO₂ exchange studies within agricultural areas have mainly focused on crop management techniques (no-till versus tillage) (Follet, 2001; Paustian et al., 2000) and crop types (corn, soybean, etc.) (Duiker and Lal, 2000; Lohila et al., 2003; Soegaard et al., 2003). However, few studies have examined grass-dominated sites within agricultural watersheds (Bremer et al., 1998; Knapp et al., 1998; LeCain et al., 2002). Also, few studies have explored CO₂ exchange from adjacent riparian areas, although such areas can comprise a large proportion of the land-use in agricultural basins. Furthermore, studies that have explored the carbon (C) dynamics of agricultural riparian areas have tended to focus exclusively on soil respiration, neglecting vegetation dynamics (vegetation CO₂ uptake and respiration) (Griffiths et al., 1997; Groffman et al., 2002; Tufekcioglu et al., 2001) or have been at the scale of micrometeorological techniques making it difficult to capture small scale variability (c.f. Kim et al., 1992; Kim and Verma, 1990; Ham and Knapp, 1998). There is a need to gain a better understanding of ecosystem-specific magnitude, variability and processes controlling net CO₂ exchange (NEE), gross ecosystem productivity (GEP), and ecosystem (soil and vegetation) respiration (R_{Tot}) within smaller landscape units such as upland and riparian grasslands within the context of the larger ecosystem to explore

anthropogenic influences such as the application of fertilizers in adjacent fields (Knapp et al., 1998; LeCain et al., 2002; Bremer et al., 1998).

Thus, the objective of this study is to evaluate the climatic, soil, vegetation and land-use controls on the spatial and temporal variability of CO₂ exchange of grass-dominated riparian vegetation and non-riparian grass vegetation, using a dynamic chamber technique.

2. Materials and methods

2.1. Study site

The study was conducted at the Strawberry Creek Watershed (SCW) (80°23'15"W, 43°33'10"N) in Southwestern Ontario, which is characterized by a humid continental climatic (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)). The watershed is located approximately 16 km northeast of Waterloo, Ontario. The SCW drains a small (<3 km²) agricultural basin (Fig. 1) eastward into Hopewell Creek and eventually into the Grand River, which is one of the largest watersheds in Southern Ontario (6800 km²) (GRCA, 1998). It is a perennial, first-order stream that is approximately 2 km in length and is typically less than 1 m wide for most of the year except during spring melt and large precipitation events.

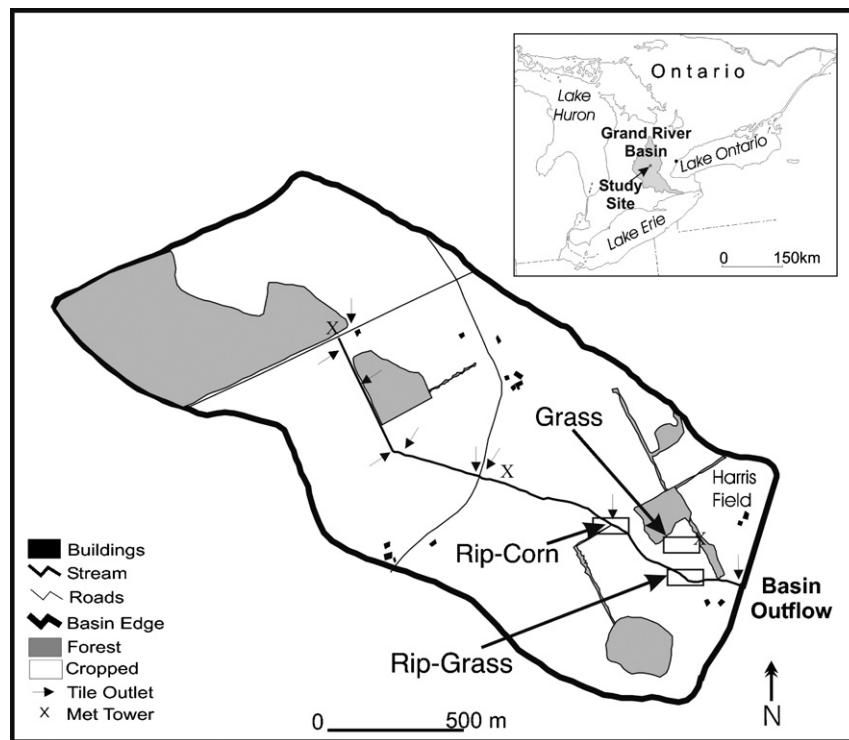


Fig. 1. Map of Strawberry Creek Watershed, study sites and location relative to Southern Ontario (inset). The watershed perimeter is defined as the area of land that drains to the culvert at the basin outflow.

The general topography of SCW is relatively flat with slopes typically less than 0.03. Soils in the region have been created over loamy parent material consisting of 50% sand, 35% silt and 15% clay (Chapman and Putnam, 1984) with soil in the riparian areas containing an organic layer (0.20–0.40 m deep), underlain by a gleyed clay layer up to 0.6 m (greatest depth analyzed). The soils are classified as Grey Brown luvisols, Melaic Brunisols and humic gleysols (Presant and Wicklund, 1971). The entire basin is underlain by a compact layer of Maryhill till at a depth of 2 m (Karrow, 1974) that impedes vertical groundwater flow and causes shallow groundwater to flow laterally from fields through riparian areas into the adjacent stream (Mengis et al., 1999). The water table during the summer in this basin is approximately 0.6 m below surface in the near stream zone and 1.5 m beneath the surface in upland areas.

Land-use in the catchment consists of residential (houses and barns), in addition to agricultural cash crops (corn, soybean, winter wheat and strawberries), open grasslands, small deciduous woodlots and narrow grass-dominated riparian sites. The vegetation within the riparian zones are dominated by warm season tall grasses (79% areal cover) (*Gramineae spp.*) (Big Bluestem (41%) (*Andropogon gerardi*), Indian grass (27%) (*Sorghastrum nutans*), Little Bluestem (3%) (*Schizachyrium scoparium*), and alfalfa (8%) (*Medicago sativa*)), non-grass herbaceous vegetation (21% areal cover) (forbs) (Canada Goldenrod (6%) (*Solidago canadensis*), Yarrow (2%) (*Achillea millefolium*), Thistle (8%) (*Cirsium spp.*) and common Milkweed (5%) (*Euphorbia corollata*)) (Petrone, unpublished data; Harris, 1999). Grass roots (<2 mm wide) are concentrated in the upper 0.2–0.5 m, but often extend to depths greater than 0.75 m. Grasses and forbs comprised of Upland White Aster (18% areal cover) (*Solidago ptarmicoides*), Field thistle-pink flower (16%) (*Cirsium discolor*) and Ticktrefoil species (12%) (*Desmodium spp.*) have developed in the fallow fields, but the fallow is also dominated by tallgrass (53%) (*Gramineae spp.*).

Agriculture is, and has been, the principle land-use in the area. The remainder of the basin is comprised of woodlots and hedgerows, residential properties and fallowing fields (grasslands). Organic (cattle and poultry) fertilizers are applied at a rate of approximately 33 kg N ha⁻¹ year⁻¹ and 9 kg P ha⁻¹ year⁻¹ to 40% of the basin (upper portion) and inorganic fertilizers are applied at a rate of 113 kg N ha⁻¹ year⁻¹ and 25–30 kg P₂O₅ ha⁻¹ year⁻¹ to 35% of the basin (Macrae et al., 2007a). Some of these added nutrients are transported into riparian areas via groundwater flow, and a substantial portion of the applied fertilizers pass into the stream each year via a combination of groundwater and tile drainage (Macrae et al., 2007a,b).

2.2. CO₂ flux measurements

Three experimental sites were chosen: (1) a 6–8 m wide riparian area (Rip-Grass) with both sides of the stream

adjacent to a moderately sloped open grassland that extends 300 m upland; (2) a 10–12 m wide riparian area (Rip-Corn) adjacent to tile-drained agricultural land (corn) spanning 500 m upland; and (3) an open grassland field (Grass), with similar vegetation to that of the riparian areas, that is mown and harvested twice during the summer (Fig. 1).

For each experimental site 3–4 collars representing combined soils and vegetation were employed. CO₂ was 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. Collars were inserted 4–10 cm into the soil, and remained permanently in place during the duration of the study 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). A 3 mm wide groove was cut into the top of each collar and filled with water to obtain an airtight seal with the chamber. The chamber enclosure (surface area 0.03 m², volume 0.06 m³) was made of clear Plexiglass, which transmits about 87% of PAR (Waddington and Roulet, 2000). The clear chamber measured NEE (plant uptake simultaneously with soil and plant respiration), whereas the dark chamber was used to measure total ecosystem respiration. The entire system was closed, in that air was circulated through tygon tubing between the chamber and an EGM-1 Infrared Gas Analyzer (PP Systems, Amesbury, MA). To minimize the development of a concentration gradient a CPU fan was installed in the chamber and run from a 12 V power source during each 5 min sampling interval (Welles et al., 2001). The temperature and relative humidity (RH) inside the chamber were maintained within ± 1 K and 6%, respectively, of ambient conditions, using a cooling system (heat exchanger coil, water flow system and a cooling bath).

Measurements were made, on average, twice per week between May and September 2003. Aside from two night time measurements in September and October, all measurements 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 near maximum levels to ensure the largest possible spatial differences. The sampling scheme was aimed to acquire a 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). Although chambers provide only point measurements, to allow temporal/seasonal comparisons, the daily sampling scheme between sites were altered (i.e. sampling order was determined randomly each day) and fluxes were grouped into distinct phenological periods based on visual observations of bud burst, leaf-out and senescence along with the controlling climatic variables (i.e. air temperature and PAR)

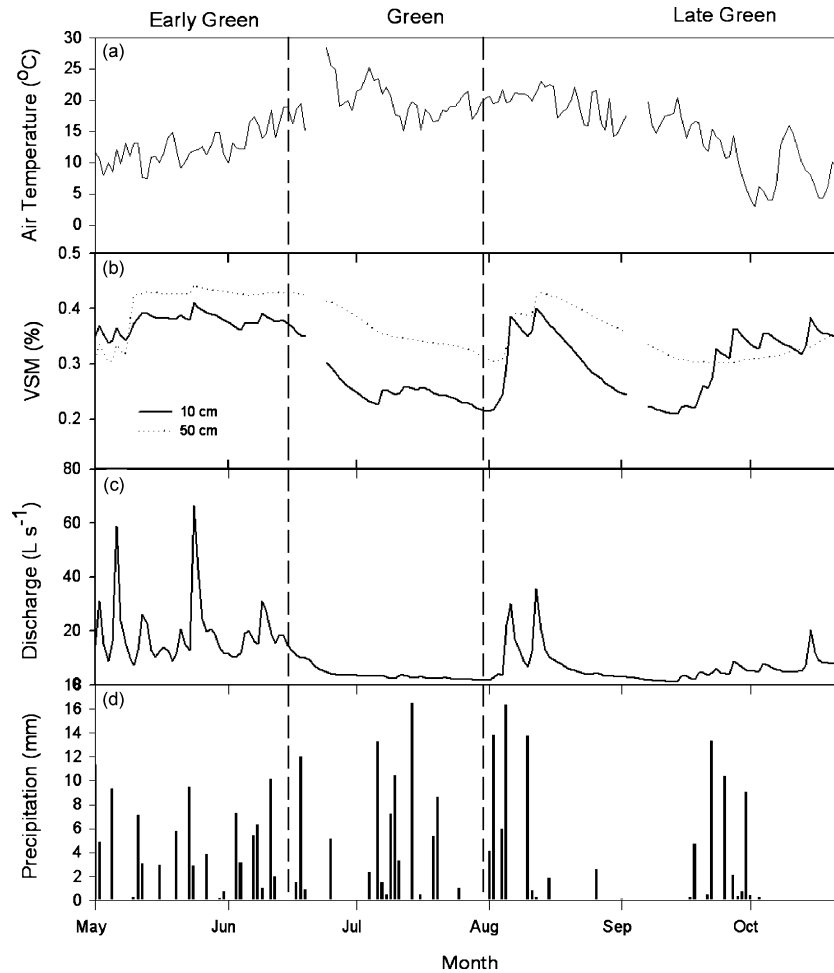


Fig. 2. Seasonal trends in (a) air temperature (T_a), (b) volumetric soil moisture content (%) (VSM), (c) discharge, and (d) precipitation at Strawberry Creek, Maryhill, Ontario from May 1 to October 25, 2003. Averages and standard deviations (in parenthesis) for each period are shown on the graph. Period transitions are illustrated with vertical dashed lines.

(cf. Griffis et al., 2000; Petrone et al., 2003; Waddington et al., 1998) so that diel variations and temporal variability could be better examined (Fig. 2). Period one, early green (EG) (May 1 to June 20) represents the early and rapid growth phase of the vegetation. Period two, green (G) (June 21 through August 4) represents the period when vegetation approached full maturity and the above-ground biomass reached a maximum. Period three, late green (LG) (August 5 to September 12 and September 29 and October 21 nocturnal measurements) generally coincided with vegetation senescence. These groupings were based upon climatic distinctions (air temperature (T_a) and 10 cm depth averaged soil moisture content) that would permit at least 6–9 measurements to be included in each period (Fig. 2). Although this method of grouping creates uncertainties regarding inter-annual comparisons related to the timing of leaf-out and senescence, it does provide an efficient method to compare sites intra-annually using point measurements (Griffis et al., 2000).

In conjunction with CO_2 measurements, soil temperature, volumetric soil moisture content and photosynthetically active radiation (PAR) were also measured at 3 locations

surrounding each collar. The soil temperature was measured using an HH200A digital temperature probe (Omega, Quebec) at 4 depths (5, 10, 20 and 30 cm) and soil volumetric moisture content was integrated to a depth of 12 cm using a portable HydrosenseTM time domain reflectivity (TDR) probe (Campbell Scientific Inc, Utah). PAR was measured at each site using a LiCor Quantum Sensor (LiCor, Nebraska) placed at 1.5 m.

The CO_2 flux was determined by the rate of increase in CO_2 concentration (ppm) (which was recorded every minute) over the 5 min interval (Lund et al., 1999; Welles et al., 2001). Flux sign directions herein will follow the plant physiology or ecosystem science convention, such that negative values represent a flux from the biosphere to the atmosphere (CO_2 loss) and positive values a flux from the atmosphere to the biosphere (CO_2 uptake).

The concentration of CO_2 was measured in ppm and converted to $\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ via,

$$F = \frac{\Delta \times \text{MM}}{N} \times \frac{V}{A} \times \text{CF} \quad (1)$$

where F is the CO_2 flux ($\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), Δ is the linear change in CO_2 concentration with time ($\text{ppm} \times \text{h}^{-1}$), MM is the molar mass of CO_2 ($44,010 \text{ mg mol}^{-1}$), 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 ($1 \text{ ppm} = 10^{-6} \text{ mol}$). Photosynthesis (GEP) was estimated by subtracting ecosystem respiration (R_{Tot}) from NEE.

$$\text{GEP} = \text{NEE} - R_{\text{Tot}} \quad (2)$$

Quality control of CO_2 data, for each daily flux measurement, calculated the Pearson product moment correlation coefficient (r^2) using the regression slope (Δ) of the CO_2 concentration and the linear regression slope of the time interval for each sampling date at each collar (Elberling, 2003; Waddington and Roulet, 2000). If the r^2 was below 0.85 then the concentration samples for that period were not used in the analyses. This was the case for less than 1% of the data, which suggests that CO_2 did evolve primarily from diffusion (Welles et al., 2001).

2.3. Soil sampling and laboratory analysis

Soil samples were collected in triplicate from each site from soil pits dug 100 cm wide and 60 cm deep. Samples were extracted from the vertical side of the pit using soil tins (9 cm in diameter with a volume of $\sim 490 \text{ mL}$) at depth intervals of 0–10, 10–20 and 20–30 and analyzed for bulk density (ρ_b) (oven dried at 105°C , 24 h), porosity (ϕ), soil organic matter (SOM) (Loss on Ignition, 550°C , 45 min.), soil texture and pH. Total carbon (TC) and nitrogen (TN) contents of the soil, for the 3 sites, were also determined through dry combustion using an 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, Ontario), using approximately 40 mg of soil. Water extractable phosphorus (WEP) from 0 to 20 cm depths was also measured, which is an indication of the orthophosphate form directly absorbed by plant cells (McDowell et al., 2001). WEP was obtained by adding 25 ml of deionized water to 1 g of soil and shaking the solution for 1 h (Pote et al., 1996). Samples were subsequently centrifuged at 20,000 g for 10 min and passed through $0.45 \mu\text{m}$ pore size filters. Samples were immediately analyzed for soluble reactive phosphorus using Ammonium molybdate–stannous chloride reduction techniques (Environment Canada, 1979).

Above-ground living biomass (AB) was measured at each site by clipping 3 representative 0.25 m^2 plots on June 4, July 7 and August 5 during the 2003 growing season. The green plant material was separated from dead material and straw, oven dried at 80°C for 24 h, and weighed to obtain total AB dry biomass (g m^{-2}). No differentiation among species of the green material was made. Root biomass (RB) was sampled on two dates, June 24 and August 5, 2003 adjacent to the above-ground sample sites. Three cores were

taken at each site (56 mm in diameter) to 0.25 m depth, where 60–90% of the total root biomass has been shown to be situated (Dugas et al., 1999; Frank et al., 2002). Roots were physically separated from the soil and any remaining rhizosphere soil was removed through elution with water, after which they were oven dried at 80°C for 24 h. No attempt was made to separate live from dead roots due to the difficulty of differentiating between them (Sims and Bradford, 2001). Standing vegetation heights (H_M) at each location were measured weekly at three representative locations throughout the study.

2.4. Statistical analyses

The literature that pertains to chamber fluxes use standard deviation (σ) (Franzuebbers et al., 2002; Mielnick and Dugas, 2000; Simek et al., 2004) or standard error (S.E.) (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 is given by,

$$\sigma = \sqrt{\frac{\sum(x - \bar{x})^2}{n - 1}} \quad (3)$$

where x is the sample CO_2 concentration, \bar{x} is the mean CO_2 concentration of the measurements at a site, and n is the total number of measurements at that site. The coefficient of variation (CV) is a measure of the dispersion that creates variation in some measure (e.g. CO_2 flux), and is given by,

$$\text{CV} = \frac{\sigma}{\bar{x}} \quad (4)$$

Thus, σ in conjunction with the CV 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 Moncreiff, 2001). However, within a study CV can be a good indicator of natural site variability (Yim et al., 2003). The S.E. 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), The S.E., which describes the standard deviation of a reported mean concentration is then obtained via,

$$\text{S.E.} = \frac{\sigma}{\sqrt{n}} \quad (5)$$

For this study the S.E. 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 et al., 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.

3. Results and discussion

3.1. Seasonal water balance

Warmest temperatures in the study basin occurred during the midsummer ‘green’ (G) period, with an average maximum temperature of 29 °C, warmer than the 30-year average daily maximum for the same period of 24.7 °C (Environment Canada, 2003) (Fig. 2). The study period was drier (289 mm of precipitation for May–September) than the 30-year average for this region (423 mm of precipitation for May–September) (Environment Canada, 2003), with the precipitation events fairly regularly distributed throughout the study period (Fig. 2). However, seasonal discharge from the study basin (28 mm) was similar to what is typically exported from the study basin (based on a 10 year data set) (Fig. 2). Further, average evapotranspiration (ET) from the riparian areas in SCW was 3.4 mm/d (Petrone et al., 2006), very similar to the 3.6 mm/d reported by Brown et al. (1980). Although the summer of 2003 was slightly drier than long-term averages, it is unlikely that this had a strong effect on soil moisture status because of the presence of a layer of compact till in the SCW, which restricts vertical groundwater flow and assists in maintaining moist conditions in the rooting zone within the riparian zone.

3.2. Net ecosystem CO₂ exchange

As expected, CO₂ was taken up (e.g. positive fluxes) by vegetated surfaces at all three sites. However, the data show that there is substantial spatial variability in land–atmosphere CO₂ exchange in the 3 adjacent grassed sites. Seasonal mean midday net ecosystem exchange (NEE) was largest at the Rip-Corn site ($x = 0.73 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$; CV = 45%) and smallest at the Grass site ($x = 0.28 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$; CV = 42%) (Fig. 3). NEE was much lower at the Grass site during the G and late green (LG) periods (0.16 and 0.27 $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) due to reduced above-ground biomass following a mowing of the grassland in July. If these values are extrapolated in order to provide daily averages, our data (ranging from 5.1 to 9.3 $\text{g C m}^{-2} \text{ d}^{-1}$) are comparable to what has been reported for grazed and ungrazed shortgrass steppe pastures in Colorado (5.0 to 8.6 $\text{g C m}^{-2} \text{ d}^{-1}$, LeCain et al., 2002) and a tallgrass prairie in Manhattan, Kansas (4.8 $\text{g C m}^{-2} \text{ d}^{-1}$, Ham and Knapp, 1998). However, values presented in this study should be treated with caution as they are based on midday CO₂ fluxes, which are when peak uptake is expected to occur, and are thus likely an overestimation of true daily fluxes.

3.3. Contribution of production and respiration in CO₂ exchange

The spatial variability in NEE is a product of variability in both photosynthesis and respiration. Gross ecosystem production (GEP) was greater than respiration (R_{Tot}) at all

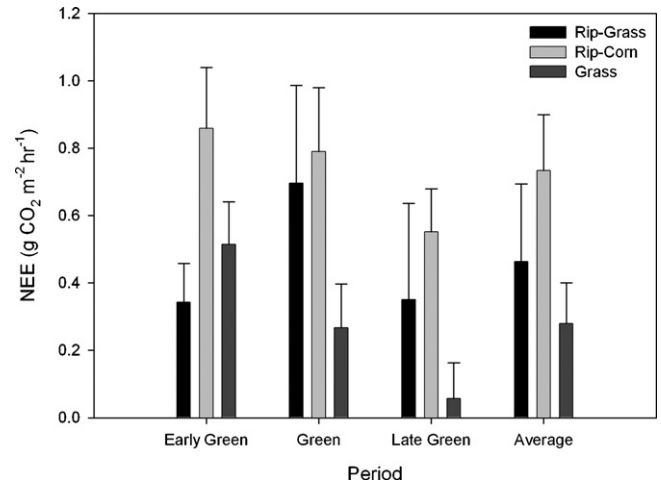


Fig. 3. Mean and Standard Error of the Mean (S.E.) net ecosystem CO₂ exchange (NEE) for all sites by phenological study periods at Strawberry Creek, Maryhill, Ontario, during the summer of 2003.

sites resulting in net CO₂ uptake (Table 1). GEP was consistently largest at the Rip-Corn site, averaging 3.1 $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ (CV = 18%), with the EG, G and LG periods averaging 3.2, 3.3 and 2.8 $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, respectively (Fig. 4). Similarly, R_{Tot} was also largest at the Rip-Corn site averaging $-2.2 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ (CV = 20%). In contrast, GEP at the Grass site was consistently smaller than at other sites (1.7 $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, CV = 25%), with the EG, G and LG periods averaging 1.8, 1.7 and 1.5 $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, respectively (Fig. 4). The seasonally averaged R_{Tot} at the Grass site was also smallest, averaging $-1.3 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ (CV = 18%) and averaging -1.3 , -1.5 and $-1.1 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ during the EG, G and LG periods, respectively (Fig. 4). Thus, in this study GEP and

Table 1

Relationships between gross respiration (R_{Tot}), net ecosystem CO₂ exchange (NEE) and net ecosystem productivity (GEP) with percent total carbon (%TC), total nitrogen (%TN), carbon nitrogen ratio (C/N), water extractable phosphorus (WEP), above ground biomass (AB), root biomass (RB), and peak vegetation height (H_M) for all bare and vegetated collars

	R_{Tot}	GEP	NEE
%TC	446TC–675 $r^2 = 0.47$	–755TC + 1763 $r^2 = 0.55$	–272TC + 1005 $r^2 = 0.64$
%TN	3103TN + 616 $r^2 = 0.85$	–4911TN–548 $r^2 = 0.98$	–1660TN + 134 $r^2 = 0.99$
TC/TN	–222C/N + 4780 $r^2 = 0.99$	346C/N–7075 $r^2 = 0.99$	115C/N–2051 $r^2 = 0.99$
WEP	40WEP + 1456 $r^2 = 0.71$	–65WEP–1863 $r^2 = 0.78$	–23WEP–305 $r^2 = 0.85$
AGB	9AGB–1537 $r^2 = 0.99$	–14AGB + 2802 $r^2 = 0.99$	–5AGB + 1247 $r^2 = 0.99$
RBM	8RBM–10,550 $r^2 = 0.51$	–14RBM + 18,357 $r^2 = 0.59$	–5RBM + 6937 $r^2 = 0.68$
H_M	3646 H_M –2914 $r^2 = 0.96$	–5761 H_M + 5025 $r^2 = 0.99$	–1944 H_M + 2013 $r^2 = 0.99$

Data are grouped according to experimental site.

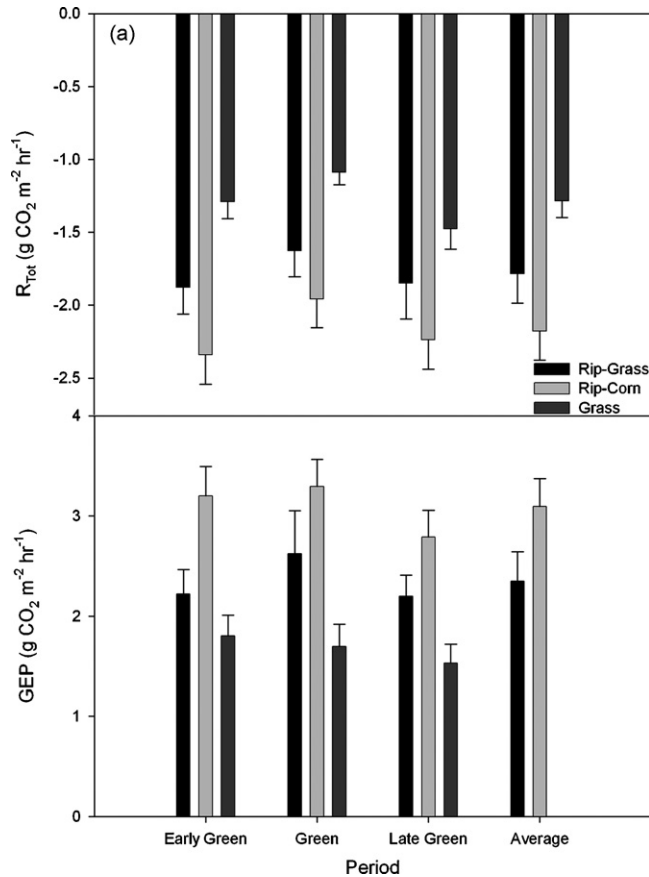


Fig. 4. Mean and Standard Error of the Mean (S.E.) in (a) gross respiration (R_{Tot}) and (b) gross ecosystem productivity (GEP) by phenological study periods for all sites at Strawberry Creek, Maryhill, Ontario, during the summer of 2003.

R_{Tot} showed the same trends, with largest rates of CO_2 cycling occurring at the Rip-Corn site and smallest rates of CO_2 cycling occurring at the Grass site suggesting that some biotic–abiotic interaction is occurring here despite similarities in hydrologic conditions. The tight coupling between enhanced rates of photosynthesis and respiration are expected because increases in labile C and root respiration from recently fixed CO_2 may lead to increased decomposition rates (Law et al., 2002; LeCain et al., 2002).

3.4. Control of soil nutrient status and biomass on CO_2 exchange

Spatial patterns in CO_2 exchange (site-averaged, seasonal means) are a function of soil nutrient levels (%TC, %TN, TC/TN ratios, WEP), as well as above-ground biomass and vegetation height (Tables 1 and 2). Strong relationships were found between R_{Tot} , NEE and GEP and above ground biomass, root mass and vegetation height, suggesting that the greater rates of CO_2 uptake and release were caused by enhanced plant growth and productivity. Strong positive relationships were also found between NEE, GEP and R_{Tot} and soil nutrient levels (%TN, TC/TN ratios and WEP). Together these data indicate that greater nutrient levels in soils are associated with enhanced plant growth, which results in greater rates of both GEP and R_{Tot} , and a greater uptake of CO_2 (NEE). CO_2 fluxes (both uptake and release) in other systems have also been related to biological factors, such as %TC (Maestre and Cortina, 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., 2002) and C/N ratios (Tufekcioglu et al., 2001). Previous studies in the SCW have shown that nutrients are transported in both groundwater and surface runoff from upland fields into adjacent riparian areas and are subsequently discharged to the adjacent stream (e.g. Mengis et al., 1999; Harris, 1999; Macrae et al., 2007a,b). This long-term transfer of nutrients from cultivated uplands into riparian areas may consequently be enriching riparian areas with nutrients (Solondz, 2005), accelerating CO_2 exchange at these sites. The enhanced CO_2 exchange at the Rip-Corn site is likely caused by a higher quality substrate (lower CN ratios, higher TN and TP content) at this site relative to the other sites (Table 2). These substrate differences have resulted in a 22% increase in seasonally averaged CO_2 exchange at the Rip-Corn site relative to the Rip-grass site. The differences in substrate are unlikely to be linked to variable patterns in the delivery of nutrients to the respective riparian zones as the direction and magnitude of groundwater flow between uplands and riparian areas do not differ significantly between the Rip-grass and Rip-corn sites (Macrae, unpublished data). However, the land management practices used in upland areas do differ between the two

Table 2

Soil characteristics for the top 0–30 cm for the three study locations at the Strawberry Creek Watershed. Values shown are the mean and standard deviations (in parentheses) and n varies from 4 to 8 depending on the soil variable

Site	% Sand	% Silt Clay	pH	ρ_b (g cm ⁻³)	ϕ (%)	%TC	%TN	TC/TN	WEP (mg kg ⁻¹)	AB (g m ⁻²)	RM (g m ⁻²)	
Rip-Corn	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)	1.86 (1.3)	426 (62)	1578 (367)
Rip-Grass	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)	0.18 (0.1)	372 (58)	1502 (202)
Grass	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)	0.20 (0.09)	324 (37)	1518 (279)

Abbreviations are ρ_b (bulk density), ϕ (porosity) %TC (percent carbon content—organic + inorganic), %TN (percent total nitrogen), C/N (carbon nitrogen ratio) and WEP (water extractable phosphorus). Above- (AGB) and below-ground biomass (RBM) measurements at Strawberry Creek Watershed, Maryhill, Ont obtained on selected days from June to August, 2003 for $n = 3$ are also shown.

riparian sites. The elevated nutrient levels and enhanced vegetation growth at the Rip-Corn site relative to the other two sites likely result from the close proximity of this riparian area to an intensively cultivated, tilled, tile-drained field that receives inorganic fertilizer inputs (Solondz, 2005). Although the grassland also receives nutrient inputs, these are in the form of manure and this grassland is not tilled or tile-drained. Any one or a combination of these differences in land management practices may be contributing to the observed differences in nutrient levels between the sites. This paper has shown that small differences in nutrient levels can lead to substantial differences in land-atmosphere CO₂ exchange. That is, the enhanced inorganic fertilizer applications in the corn field that drains through the Rip-Corn site enhance the vegetation and microbial productivity within the riparian zone (Solondz, 2005; Petrone et al., 2006). These findings are relevant as variable land management practices as well as climate change may alter soil nutrient status and in doing so may also alter the carbon balance of portions of the landscape.

3.5. Microclimatic controls on CO₂ fluxes

Our data suggest that spatial patterns in CO₂ exchange are not a function of microclimatic variables. There was little difference in soil moisture or soil temperature between the different sites during the study period (Table 2). There was also little difference in soil texture (Table 2) indicating that differences between sites were not due to site disturbance or soil properties. There was also no difference in canopy characteristics or root biomass between the sites, with the exception of the Rip-Corn site, which had grasses 0.2 m taller than the other sites.

Although microclimatic variables did not explain spatial variability in CO₂ exchange, they did explain temporal trends. R_{Tot} appears to be a function of temperature and to a lesser degree, soil moisture. Temporal patterns in R_{Tot} are best represented by an exponential relationship with air and soil temperatures (Table 3). Generally, for all sites air

temperature explained the greatest amount of the temporal variability in R_{Tot} (77–86%) and the 20-cm depth-averaged soil temperature explained 48–68% (5-cm depth explained 60–78%—data not shown). The fact that air temperature explained most of the temporal variability in R_{Tot} may be explained by the presence of grasses that can exceed heights of 1.3 m and modify surficial warming and subsequently soil temperature (Oke, 1987; Wan et al., 2002). Further, although it can vary within the averaging period of the flux measurements, which may make relations with biological processes less clear, air temperature showed the strongest correlation with the temporal variability of all measured variables (notably PAR and RH). Other researchers have often found weak relationships between air temperature and R_{Tot} (Frank et al., 2002), and often use soil temperature to describe the temporal variability in R_{Tot} (Buchmann, 2000; Frank et al., 2002). The 30 cm depth averaged soil temperature relationships found here ($r^2 = 0.58–0.77$, $p < 0.01$) are higher than the r^2 of 0.46 reported for a tallgrass prairie in Texas (Mielnick and Dugas, 2000). However, the R_{Tot} was more strongly related to soil temperature at a depth of 5 cm than the 30 cm depth average, suggesting that most of the CO₂ released came from near surface roots and microbial activity, which has also been shown by other researchers (Buchmann, 2000; Groffman et al., 2002; Winkler et al., 1996). This may also suggest that R_{Tot} here is actually better correlated with air temperature ($r^2 = 0.61–0.69$, $p < 0.01$) as observed in other studies on a seasonal basis (Janssens et al., 2001; Atkin et al., 2005; Tjoelker et al., 2001). However, studies with stronger correlations with air temperature are generally in species that are fast growing (cf. Albrizio and Steduto, 2003), or those with much larger above ground biomass (cf. Xu et al., 2001; Adu-Bredu et al., 1997), unlike the vegetation types found in this riparian zone.

It was expected that soil moisture content would exert a greater influence on CO₂ fluxes than temperature. However, Davidson et al. (2000) suggest that the carbon response of an ecosystem is governed by the most limiting and dynamic variable. Thus, one possible reason for the high correlation

Table 3

Variation explained for single regressions between carbon fluxes: gross respiration (R_{Tot}), net ecosystem CO₂ exchange (NEE) and net ecosystem productivity (GEP) with air temperature (T_a), 20 cm depth averaged soil temperature (T_g), volumetric soil moisture content (%) (VSM), photosynthetically active radiation (PAR) and cumulative 7-day precipitation

Site	Carbon flux	<i>n</i>	T_a (°C)		T_g (°C)		VSM (%)		PAR (W m ⁻²)		7-day precipitation	
			Linear	Exponential	Linear	Exponential	Linear	Quadratic	Linear	Logarithmic	Linear	
Rip-Grass	NEE	21	<0.1	<0.1	<0.1	0.06	<0.1	<0.1	<0.1	<0.1	<0.1	0.20
Rip-Corn	NEE	22	0.25*	0.20	0.20*	0.19*	<0.1	<0.1	0.24*	0.25**	<0.1	<0.1
Grass	NEE	19	<0.1	<0.1	<0.1	0.03	0.24*	0.24	<0.1	<0.1	<0.1	<0.1
Rip-Grass	R_{Tot}	23	0.70**	0.64**	0.52**	0.61**	0.14	0.44**	0.65**	0.65**	0.16	0.16
Rip-Corn	R_{Tot}	24	0.71**	0.77**	0.54**	0.63**	0.27*	0.49**	0.36**	0.27*	0.45*	0.45*
Grass	R_{Tot}	21	0.86**	0.86**	0.68**	0.76**	0.24*	0.50**	0.69**	0.65**	0.52**	0.52**
Rip-Grass	GEP	21	0.59**	0.52**	0.36**	0.36**	<0.1	0.20	0.50**	0.55**	<0.1	<0.1
Rip-Corn	GEP	22	0.15	0.15	<0.1	<0.1	<0.1	0.29*	<0.1	<0.1	<0.1	0.36*
Grass	GEP	19	0.25*	0.25*	0.15	<0.1	<0.1	0.23	0.34**	0.36**	0.37*	0.37*

Note: Significant regressions are in bold with ($P < 0.01$) and ($P < 0.05$) denoted by, ** and *, respectively.

between R_{Tot} fluxes and temperature is that for most of the study period soil moisture content 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, despite the fact that 2003 was a dry year compared to long-term normals, soil moisture content was at sufficient levels to not dramatically hinder R_{Tot} . This may be a result of the surficial geology of the SCW, which maintains shallow groundwater flow close to the surface. Soil moisture content explained 27–50% of the variability for R_{Tot} with a quadratic relationship. Utilizing this relationship, maximum fluxes were observed between soil moisture content values of 25 and 30% (water filled pore space between 50 and 60%).

Temporal variability in NEE and GEP was correlated with microclimatic variables within a given site (e.g. photosynthetically active radiation (PAR), air temperature, soil moisture content); however, the controlling variables differed among sites (Table 3). NEE and GEP have been linked to PAR (Flanagan et al., 2002; Suyker et al., 2003) in other studies. However, in this study poor relationships were found, which may be attributed to: (1) fluxes being measured at midday when PAR is high and the plants are at their photosynthetic capacity and (2) daily averages of point measurements that do not represent plant and soil acclimation to dynamic weather conditions (Kim et al., 1992).

4. Conclusions

This study showed that grass-dominated areas, with similar vegetation, located approximately 250–300 m from one another displayed very different CO_2 exchange dynamics. Both spatial and temporal trends in CO_2 exchange are apparent in this landscape because controlling variables differ. Our results indicate that temporal variability in CO_2 exchange is related to microclimatological variables, most notably temperature and soil moisture. In contrast, spatial variability in CO_2 exchange and its components are driven by soil nutrient status as well as above ground biomass and canopy height. These variables in turn are related to landuse (agricultural) in adjacent areas. This suggests that management practices in upland areas can have a strong effect on CO_2 dynamics in agricultural riparian zones. That is, the effects of landuse (i.e. agriculture) within the catchment over-ride the effects of microclimate in controlling spatial patterns in CO_2 exchange in this watershed even if this landuse change is not directly in the landscape unit being considered.

Therefore, it is apparent that humans through harvesting, fertilizer applications and crop rotations heavily influence the productivity and carbon cycling within non-cropped ecosystems within an agricultural catchment such as riparian zones. Such areas behave differently than fields in their CO_2 dynamics. Thus, quantifying the CO_2

variability of region-specific ecosystems (both riparian areas and fields) is important to further explore process-based dynamics, and better represent the terrestrial ecosystem in global C models that may lead to the development of improved land management policies with regards to C sequestration.

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