# CARBON EXCHANGE IN A TEMPERATE DECIDUOUS FOREST IN SOUTHERN ONTARIO

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A Thesis Submitted to the School of Graduate Studies In Partial Fulfillment of the Requirements For the Degree Master of Science

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## ABSTRACT

Continuous measurements of carbon fluxes and meteorological variables were made at a newly initiated flux tower site at an oak-dominant temperate deciduous forest in Southern Ontario, Canada from January to December 2012. Results indicate this forest was a moderate carbon sink in 2012. Annual values of net ecosystem productivity (NEP), gross ecosystem productivity (GEP) and ecosystem respiration (R) were  $263 \pm 30$ , 1192 and 922 g C m<sup>-2</sup>, respectively. An unusual warm period in March caused a strong increase in R. Erratic peaks of daily air temperature in April also increased R. A drought in July and early August reduced NEP rates when soil moisture values reached the lowest point of the year in late July and early August (minimum 0.023 m<sup>3</sup> m<sup>-3</sup>). This decrease in NEP was mostly caused by a decrease in GEP, rather than increased R. Water use efficiency at this deciduous forest was 2.86 g C kg<sup>-1</sup> H<sub>2</sub>O, indicating conservative water use by the forest. Downwelling photosynthetic active radiation (PAR) was a dominant environmental control on photosynthesis, followed by air temperature and vapour pressure deficit, except in extreme dry periods when soil water stress affected carbon uptake. Extremely cloudy days in the growing season resulted in net carbon release due to low photosynthetic uptake values. Results indicate that large climatic fluctuations in this region may cause high instability in photosynthetic carbon uptake and release from soil carbon pools. This study helps to evaluate and quantify the responses of deciduous forests in the Great Lakes region to future climate change and extreme weather events.

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## SYMBOLS AND ABBREVIATIONS

С	Carbon	
$\rm CO_2$	Carbon dioxide	
DBH	Diameter measured at breast height (1.3m)	(cm)
Е	Evapotranspiration	$(mm day^{-1})$
EC	Eddy covariance	
F <sub>c</sub>	Carbon flux	$(\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1})$
GEP	Gross ecosystem productivity	$(\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1})$
LAI	Leaf area index	$(m^2 m^{-2})$
NEP	Net ecosystem productivity	
Р	Precipitation	(mm)
PAR	Incoming photosynthetically active radiation	$(\mu \text{ mol } m^{-2} \text{ s}^{-1})$
R	Ecosystem respiration	$(\mu \mod CO_2 m^{-2} s^{-1})$
RH	Relative humidity	(g C m <sup>-</sup> ) (%)
T <sub>a</sub>	Air Temperature	(°C)
T <sub>s</sub>	Soil Temperature	(°C)
TPD	Turkey Point Deciduous site	
TPFS	Turkey Point Flux Station	
VPD	Vapour pressure deficit	(kPa)
u*	Friction velocity	$(m s^{-2})$
θ	Volumetric soil water content	$(m^3 m^{-3})$

## **CHAPTER 1. INTRODUCTION**

Carbon balance of forest ecosystems is of interest to the scientific community because forests can be large sinks for organic carbon (Houghton et al 1987). The exchange of carbon dioxide (CO<sub>2</sub>) between a vegetated ecosystem and the overlying atmosphere plays an important role in global biogeochemical cycling (Geider et al 2001). Mid-latitude broadleaf and mixed wood forests cover over 3% of the earth's terrestrial surface (Olsen et al 1978) but they store  $119 \pm 6$  Pg of carbon, which accounts for 14% of all carbon stock in forests (Pan et al 2011). During the growing season, temperate deciduous forests absorb CO<sub>2</sub> from the atmosphere through photosynthesis and release CO<sub>2</sub> through autotrophic, and to a lesser extent, heterotrophic respiration (Jarvis and Leverenz 1983). As a major source of mobilizable carbon, temperate forests influence regional climate and the global carbon balance through the rates at which they capture and release carbon (Musselman and Fox 1991).

Changes in climate over the past several decades have altered carbon exchange patterns and carbon budgets of forest ecosystems. Large-scale changes in northern terrestrial ecosystems have been identified, such as the northward shift of the boreal tree-line in North America (Grace et al 2002). A study in the early 1990's found that carbon uptake of mid-latitude temperate forests were notably greater than what had been previously assumed in global carbon studies (Wofsy et al 1993). At this time, it was noted that few eddy covariance studies provided datasets long enough to determine seasonal or annual carbon budgets of temperate forests (Wofsy et al 1993). Since then, research has continued to attempt to quantify carbon uptake and release in temperate forests to

advance understanding of their carbon sink or source potential (Baldocchi 2008, Barr et al 2002, Black et al 2000, Chen et al 1999, Greco and Baldocchi 1996, Lee et al 1999, Schmid et al 2000, Teklemariam et al 2009).

Changes in global average temperatures and occurrence of extreme weather events (IPCC 2012) are causing increased awareness for understanding ecosystem responses. Studies utilizing phenological, satellite and climatological data have concluded indisputable shifts in timing and length of growing season (Keeling et al 1996, Linderholm 2006). Predictions of the response of terrestrial ecosystems to climate warming began by focusing on changes in annual mean temperature, but current literature has found that shifts in annual CO<sub>2</sub> exchange from changes in climate seem to be most pronounced at times when the ecosystem is particularly sensitive, rather than from changes in annual mean temperature (Goulden et al 1996). Specific intervals of the year, such as spring and autumn, are now more often the focus when examining ecosystem responses to climatic change, such as periods of drought or heat stress (Goulden et al 1996, Piao et al 2008).

The phenology of temperate forests is mainly driven by temperature (Farnsworth et al 1995), affecting the timing and duration of the growing season (Kramer et al 2000, Richardson et al 2013). In a study of two deciduous forest stands, one boreal and the other temperate, Barr et al (2001) found that unusually warm spring months caused early leaf out, which led to the early spring rise of gross ecosystem productivity (GEP). Similar results were found by Goulden et al (1996) in a temperate deciduous forest located in

New England, USA. The annual carbon dioxide exchange was particularly sensitive to the length of the growing season, which was regulated by air temperature in spring and early fall. Photosynthesis and respiration were relatively insensitive to the average growing season temperature (Goulden et al 1996). These studies suggest that changes in seasonal patterns have the potential to increase carbon sink strength in temperate deciduous forests by altering growing season length. Apart from spring, changes in the autumn season may also affect carbon uptake in forests (Piao et al 2008). Dragoni et al (2011) found that increased NEP in a temperate deciduous forest in south-central Indiana, USA was attributed to extended photosynthetic periods in autumn, with no significant increase in the duration of carbon capture in springtime.

Estimates of carbon sequestration in North American temperate deciduous forests generally range between 100 and 400 g C m<sup>-2</sup> year<sup>-1</sup> (Barr et al 2002, Dragoni et al 2011, Greco and Baldocchi 1996, Lee et al 1999, Noormets et al 2008, Wofsy et al 1993). Lowest NEP estimates were found in Ontario, Canada with annual carbon uptake of 20 g C m<sup>-2</sup> in a maple-dominant deciduous forest in 1996 and 2000 (Teklemariam et al 2009). Highest reported net carbon flux estimates from a North American eastern deciduous forest came from measurements in Oak Ridge, Tennessee, USA between April 1993 and April 1994, estimating carbon capture of 525 g C m<sup>-2</sup> for the study period (Greco and Baldocchi 1996). The literature suggests that eastern deciduous forests in North America are usually a moderate to strong carbon sink, with variation depending on environmental conditions of the growing season.

Evaluating the effect of climate change in northern temperate forests is complex and will vary among sites and ecosystem types due to the competing influences on NEP brought about by increased temperatures (Barr et al 2002). Warmer springs encourage snowmelt and early leaf-out, increasing the duration of the growing season and therefore increasing GEP (Barr et al 2002, Black et al 2000, Kramer et al 2000). Prolonged warm periods, however, can increase soil moisture stress and vapour pressure deficit, which leads to a decrease in GEP (Barr et al 2002). Increases in ecosystem respiration (R) are also correlated with longer periods of unfrozen soil and warmer ground temperatures. However, periods of low soil moisture are also correlated with reduced soil respiration. The effect of drought on carbon uptake and release is dependent upon drought severity and soil site characteristics and may have opposing effects for each individual extreme weather occurrence. The resultant effect on NEP, which is defined as the difference between GEP and R, is challenging to predict for each ecosystem because of the complexity of the variables in question and the variety of conditions between temperate forests.

Canada is a major forested nation and home to large areas of temperate deciduous forest in southern regions. There is a need to assess the possible impact of climate change and extreme weather events on growth of different Canadian forest types. Carolinian forests are an important ecosystem in the Great Lakes region in North America (Blouin 2001). Further understanding of C sink and source potential in these areas is important in order to evaluate the response of these forests to future climate change.

The main objective of this research is to enhance understanding of carbon exchanges between the soil, vegetation and atmosphere in a temperate deciduous forest ecosystem. Analysis of water vapour and energy fluxes at this site are reported in Khader (2013). This research site expands the coverage of flux tower sites as the first eddy covariance tower in an oak-dominant eastern deciduous forest in Canada, and provides data to allow for cross-biome and within-biome investigations. Documenting the mechanisms of plant response to meteorological and environmental variables would allow insight into the ecosystem functioning of carbon sequestration and permits more accurate parameterization of regional and global-scale models.

The specific objectives of this study are to (a) quantify the carbon sink or source strength of a temperate deciduous forest in Southern Ontario (b) describe seasonal patterns of carbon flux and (c) examine responses of photosynthesis to environmental variables, in particular, extreme weather events.

## CHAPTER 2. METHODOLOGY

### Site description

The study area is located north of Lake Erie, near South Walsingham in Norfolk County, Ontario (42° 38' 7'' N, 80° 33' 27'' W; 214 m above sea level). This area of Southern Ontario is host to the Carolinian forest type within the Eastern Deciduous Forest biome. Carolinian forest in Southern Ontario represents the northern-most range of hardwood deciduous forest that extends along the eastern half of North America from the Carolina states, upwards to Southern Canada (Lauriault 1989, Blouin 2001, Carolinian Canada 2003). Soils in the region are coarse-grained, sandy soils deposited by glacial till (Richart and Hewitt 2008). Topography of the forest land is flat with light undulations ranging no more than a few meters in depth. Historically, vegetation of this region is oak savannah and mixed forest, a transition zone between broadleaf forests and the coniferous evergreens of the boreal forest ecozone of mid-to-northern Ontario.

Widespread agricultural deforestation occurred in the area in the early 1900s, most commonly for tobacco, corn and soybean crops, which caused drastic reduction in forest cover (from 90% to 11%) (Richart and Hewitt 2008). Abandonment of land and government forest regrowth initiatives in the mid-1900's resulted in an increase of forested area. As land was acquired by the Long Point Region Conservation Authority (LPRCA), regeneration of forest patches was encouraged through plantation practices. The forest under study is approximately 90 years old, naturally regenerated on abandoned agricultural land. Predominantly hardwood with a few scattered conifers, this tower location, named Turkey Point Deciduous (TPD) site, is the first temperate broadleaf deciduous site of the Turkey Point Flux Station (TPFS), which previously comprised of an age-chronosequence of four white pine (*Pinus strobus*) plantations (Arain and Restrepo-Coupe 2005). As of 2012, TPD is the most recent addition to the Turkey Point Flux Station where flux, meteorological and biometric data has been collected at four tower sites since 2003. The land is owned and maintained by the Ontario Ministry of Natural Resources (OMNR), in conjunction with stewardship from the LPRCA. Flux measurements at TPD commenced on January 5 2012 and are ongoing.

The dominant tree species is white oak (Quercus alba), with other scattered broadleaf Carolinian species including sugar and red maple (Acer saccharum, A. rubrum), American beech (Fagus grandifolia), black and red oak (Q. velutina, Q. rubra) and white ash (Fraxinus americana). A few scattered conifers, mostly white and red pine (*Pinus strobes*, *P. resinosa*), comprise about 5% of the canopy. Average tree height is 25.7 m with a stand density of  $504 \pm 18$  trees per hectare (Kula 2013). Average tree trunk diameter at breast height (measured at 1.3 m above the ground) is 22.3 cm and basal area, on average per tree, is 0.06 m<sup>2</sup> (approx 29 m<sup>2</sup> per hectare) (Kula 2013). Maximum leaf area index (LAI) measured by a plant canopy analyzer (model LAI2000, LI-COR, Lincoln, Nebraska, USA) and TRAC (Tracing Radiation and Architecture of Canopy, developed by Dr. Jing M. Chen's group at the University of Toronto) is 8.0 m<sup>2</sup> m<sup>-2</sup>. There is extensive and rich understory, including the Canada mayflower (Maianthemum canadense), putty root (Aplectrum hymale), yellow mandarin (Disporum lanuginosum)), and red trillium (Trillium erectum), horsetail (Equistum) and other species. See Table 1 for a concise list of TPD site characteristics.

Climate of the region is cool temperate with warm, humid summers and cold winters. The nearby Lake Erie and other Great Lakes help to moderate cold winter temperatures. Average annual temperature of the area is 7.8°C with total annual precipitation of about 1010mm, which is distributed evenly throughout the year with the exception of relatively dry summer months of July and August. Of the total annual precipitation, about 130mm falls as snow in the winter months, according to 30-year Environment Canada measurements from the Delhi weather station in Norfolk County.

Regional soil is classified as a brunisolic grey-brown luvisol (Present and Acton 1984) with mid-to-coarse grain size. Sandy soil layers can be as deep as 9 m in this region (Present and Acton 1984). The litterfall and organic-rich loamy sand layer is 5 cm to 10 cm thick. Lower layers are over 90% sand, well-drained with low moisture holding capacity (0.10 cm cm<sup>-3</sup>) and less than 2% organic matter. Bulk density of the loosely packed sand was calculated to be 1.15 g cm<sup>-3</sup> with a soil pH of 5.0. See detailed soil chemical composition in Table 2.

#### **Flux measurements**

The eddy covariance technique measures exchanges of heat, mass and momentum using covariances between vertical wind velocity and the quantity of interest. This method has become popular in measuring the exchange of CO<sub>2</sub> between a plant canopy and the overlying atmosphere because it measures fluxes from an ecosystem on a landscape scale and can be used for time periods of a few hours to many years (Baldocchi 2003). Almost three decades ago, the method was first used in short term studies over agricultural fields (Aubinet et al 2012, Baldocchi 2003). Since then, the technique has been extended to long term studies of almost every major biome, including forests, becoming a valuable tool in measuring carbon fluxes of terrestrial ecosystems (Aubinet et al 2012, Baldocchi 2003, 2008). Flux stations, using the eddy covariance technique, measure turbulent fluctuations of atmospheric carbon dioxide ( $F_c$ ). Using these measurements, the net flux of carbon entering or leaving the atmosphere is calculated, providing a measure of net ecosystem exchange (NEE). In eddy covariance literature, it is assumed that losses or gains of atmospheric carbon are a direct reflection of carbon loss or gain in the underlying ecosystem. Net ecosystem productivity (NEP = -NEE), which is defined as the imbalance between gross ecosystem production (GEP) and ecosystem respiration (R), indicates the magnitude of carbon uptake or release from a (Van Dijk and Dolman 2004). NEP provides a direct estimate of the ecosystem carbon balance (positive values indicate a terrestrial carbon gain and negative values indicate carbon loss to the atmosphere). In this study, the eddy covariance technique was used to measure energy, water and carbon flux at our newly established deciduous forest site.

Half-hourly energy, water vapour ( $H_2O$ ), carbon dioxide ( $CO_2$ ) flux and meteorological measurements commenced on January 5 2012. Flux and meteorological instruments were installed above the canopy on a newly constructed walk-up scaffolding tower. The flux tower is a self-supporting structure of galvanized steel, equipped with interior stairs and a full work platform at the top.

Eddy covariance measurements of carbon dioxide ( $F_c$ ), water vapour ( $H_2O$ ), momentum, sensible (H) and latent heat (LE) fluxes were measured using a closed-path eddy covariance system (CPEC) following Fluxnet-Canada protocol. The instrumentation consisted of a LI-7200 CO<sub>2</sub>/H<sub>2</sub>O gas analyzer with a LI-7550 Analyzer Interface Unit and the 7200-101 Flow Module pump (LI-COR, Lincoln, Nebraska, USA). The flow module generates an airflow of 15 liters per minute (LPM) through the optical path of the infrared gas analyzer (IRGA). A high-speed ultrasonic anemometer (model CSAT3, Campbell Scientific Inc., Logan, Utah, USA) is located adjacent to the gas analyzer. The extended (~1m) gas intake tube connected to the IRGA is placed to avoid interference of CSAT3 measurements but close enough to provide accurate measurements of wind conditions simultaneously between the two instruments. The LI-7200 gas analyzer and CSAT3 sonic anemometer are installed at a height of 35.7m above ground. All flux data is sampled at 20 Hz. Raw digital signals are sent to a field trailer located beside the tower which houses a personal computer upon which data is saved via direct connection to flux instruments. Software developed at the University of British Columbia (UBC, Dr. Andy Black's micrometeorology group) is used to monitor and calculate fluxes. A mid-canopy IRGA (model LI-820, LI-COR) measures mid-canopy CO<sub>2</sub> concentration at 16 m above ground, which is used to estimate CO<sub>2</sub> storage within the forest air column. Year-round flux measurements continue at this site, but measurements made after December 31 2012 are not included in this analysis.

## **Meteorological and Ecological Measurements**

Air temperature ( $T_a$ ) and relative humidity (RH) were measured by an HMP155A probe (Vaisala, Helsinki, Finland), which contains a Platinum Resistance Temperature detector (PRT) and a Humicap capacitive relative humidity sensor. The probe is housed in a compact aspirated shield that protects from solar radiation interference to allow for

more accurate measurement of ambient air temperature and humidity. An energy efficient continuous blower delivers a consistent supply of air to the instrument. The air temperature and humidity sensor is installed atop the tower at a height of 35.3m above ground. Wind speed and direction were measured by a heated 2-axis anemometer without moving parts (model 85004, RM Young Company, Traverse City, Michigan, USA) at 36.6m on the tower. The CSAT3 sonic anemometer associated with flux measurements also measured wind speed and direction at 35.7 m.

Radiation above the canopy was measured by a four dome radiometer (model CNR4, Kipp & Zonen, Delft, Netherlands) which senses incoming (downward) and outgoing (upward) longwave and shortwave radiation with pairs of opposite-facing pyranometers and pyrgeometers at 35.1 m above ground. The shortwave sensors detect ranges of solar radiation from 0.3 µm to 2.8 µm. Longwave radiation, emitted from matter in the atmosphere or the earth, is measured in wavelengths between 4.5 µm and 42  $\mu$ m. Net radiation is the sum of incoming shortwave from the sun, incoming longwave from matter in the atmosphere, outgoing longwave emitted by earth and outgoing shortwave radiation that has been reflected by the earth's surface. The net radiometer is installed at 35.5 m above ground. Incoming and outgoing photosynthetically active radiation (PAR), solar radiation between the wavelengths of 0.4  $\mu$ m to 0.7  $\mu$ m, was measured with two PAR quantum sensors (model PQS1, Kipp & Zonen) above the canopy at 35.1m, facing opposite directions (upward and downward). All radiation sensors on the tower were installed on metal booms to eliminate possible influences of the support structure. An additional PAR sensor was installed on the forest floor, at a

height of 1.7 m, to capture the intensity of radiation penetrating the forest canopy. Atmospheric pressure was measured near the ground using a pressure sensor (model 61302V, Campbell Scientific, Logan, Utah, USA).

Soil moisture ( $\theta$ ) and temperature (T<sub>s</sub>) was measured along a depth profile in two locations selected as representative of the condition of the forest floor. Soil water reflectometers (model CS650, Campbell Scientific) with 30 cm parallel rods measured volumetric water content (utilizing electrical conductivity) and temperature of soil. Additionally, soil matric potential sensors (model 253, Watermark 200, Campbell Scientific) were installed to estimate matric potential in soils. Soil sensors were buried at depths of 5, 10, 20, 50 and 100cm. Four soil heat flux plates (model HFT3, manufactured by Radiation and Energy Balance Systems (REBS), supplied by Campbell Scientific), were buried in various locations at a depth of 3cm. Precipitation was measured by a heated all-weather accumulating rain gauge (model T-200B, GEONOR, Augusta, New Jersev. USA) and an unheated tipping bucket rain gauge (model CS700, manufactured by Texas Instruments Inc, supplied by Campbell Scientific). The rain gauges were located side-by-side in an open field, approximately 20 km from the forest site. Winter precipitation data were not available from the tipping bucket gauge. Depth of snow at this site was measured using a sonic ranging sensor (model SR50a, Campbell Scientific).

All meteorological and soil data were sampled at 5 second intervals and averaged to produce 30 minute averages using a datalogger (model CR3000, Campbell Scientific).

### **Flux Calculations and Gap Filling**

Carbon flux ( $F_c$ ) measured by the IRGA were quality controlled after data collection. Half-hourly  $F_c$  measurements were filtered for outliers using software developed in Matlab (The Mathworks Inc.) such that each half-hourly point was compared to the previous and following point to determine likelihood of extremity based on the general variation within the data. Systematic post-processing criteria also involved the calculation of moving-window means and variances. Large, brief departures from the mean were examined and filtered by a spike threshold determined as a multiple of the standard deviation. A spike is noted if the fluctuation from the mean is greater than the determined threshold and the duration is too brief to likely be a physical event. After one iteration, the means and variances are recalculated to reject previously identified outliers and the process is repeated.

CO<sub>2</sub> storage flux within the air column below the eddy covariance sensors was calculated using the difference between current and previous half-hourly CO<sub>2</sub> concentration measurements made at two heights, at mid-canopy at 16 m and at the top of the tower at 35.7 m. For times when mid-canopy CO<sub>2</sub> measurements were not available, storage flux within the forest was calculated using the difference between current and previous half-hourly carbon concentration values of the eddy covariance sensors at 35.7 m height (see equation 1). A study of the eddy covariance measured carbon balance of a Douglas fir forest in British Columbia, Canada found good agreement between this method of estimating storage flux when compared to a four-level profile measurement system (Morgenstern et al 2004).

$$S_{CO_2} = \frac{CO_{2_t} - CO_{2_{t-1}}}{\Delta t}$$
(1)

Net ecosystem exchange (NEE) is determined by calculating the sum of the measured carbon flux ( $F_c$ ) and carbon storage flux within the air column ( $S_{CO2}$ ).

$$NEE = F_c + S_{CO2}$$
<sup>(2)</sup>

 $(\mathbf{n})$ 

Net ecosystem productivity (NEP), carbon uptake by ecosystem vegetation, is assumed to be the inverse of net ecosystem exchange (NEE), which is the carbon dioxide gain or loss to the atmosphere. The two terms differ in the direction in which positive carbon movement is indicated. Positive NEP indicates carbon uptake by the forest, that is, net movement of carbon downwards into the ecosystem. No corrections were applied to NEE data for closure of the ecosystem energy balance.

$$NEP = -NEE \tag{3}$$

At times of low turbulence, for example on calm nights with weak wind and stable boundary layer conditions, eddy covariance measurements may underestimate fluxes. To resolve issues of flux underestimation, a threshold of friction velocity, the u-star threshold (u\*<sup>Th</sup>), is used to identify and remove questionable periods of flux measurements. The u\*<sup>Th</sup> value of 0.225 used at this site was determined following the change-point detection method newly proposed by Barr et al (2013) and Brodeur (2013). The simpler approach of determining an appropriate u\*<sup>Th</sup> value by regressing half-hourly nighttime NEE values against the corresponding measured friction velocity value to find

a point of plateau also indicated a threshold value of 0.225. F<sub>c</sub> values that did not pass the friction velocity threshold criteria were rejected for use in determining NEP values.

Daytime ecosystem respiration was estimated using nocturnal measurements of NEE at times of high turbulence ( $u^* \ge 0.225$ ). At night, with no radiation to drive photosynthesis, or outside of the growing season when the trees are leafless, all carbon flux detected by the IRGA is assumed to be due to respiration. Respiration was modeled using a logistic function parameterized by soil moisture and soil temperature (Barr et al 2002).

$$R = \frac{a_1}{1 + \exp \left[a_2 \left(a_3 - T_s\right)\right]} a_w(t)$$
(4)

This model is a non-linear regression (NLR) where  $a_1$ ,  $a_2$  and  $a_3$  are empirically fitted parameters,  $T_s$  is soil temperature and  $a_w(t)$  is a moving-window time-varying parameter to correct for biases that may arise from autocorrelation in modeled respiration values. Estimates from this model were used to fill nocturnal CO<sub>2</sub> fluxes when friction velocity was less than 0.225 and to calculate respiration rates throughout daylight hours during the growing season.

Gross ecosystem productivity (GEP), defined here as carbon uptake by forest vegetation via photosynthesis, was estimated as the sum of measured NEP and daytime R.

$$GEP = NEP + R \tag{5}$$

These values were used to parameterize a rectangular hyperbolic function to fit halfhourly GEP values data during rain-free, turbulent periods (Brodeur 2013, Peichl 2010).

$$GEP = \frac{\alpha \cdot PAR \cdot A_{max}}{\alpha \cdot PAR + A_{max}} p_w(t)$$
(6)

Where  $\alpha$  is the increase in photosynthesis per unit quanta PAR (quantum yield), and A<sub>max</sub> is the maximum photosynthetic flux at saturated PAR levels (photosynthetic capacity). The time-varying parameter p<sub>w</sub>(t) corrected for sustained bias in model output.

Rejection of certain flux values during quality control causes gaps in NEP data (in addition to instrument malfunction, power failure, maintenance, etc) that must be filled in order for estimation of total annual NEP of the site. The parametric models of GEP and R, as described above, generate filled estimates of these component carbon fluxes, which in turn, allow for gap-filling of NEP using NEP = GEP – R.

Gaps in meteorological data may also arise due to instrument malfunction or power failure. Missing data of shorter durations (a couple hours or less) was filled by linear interpolation. Larger gaps in meteorological data was filled with the aid of meteorological sensors at the other sites comprising the Turkey Point Flux station, all within 20km of each other. Existing TPD data for the meteorological variable requiring filling was regressed against each other site to identify the site with the greatest fit. Gaps were filled using the slope of the linear regression between the two data sets. Due to the close proximity of sites, meteorological data between TPFS sensors usually had high linear correlation. Gaps in precipitation data were also filled using data from rain gauges at the nearby flux tower sites.

## CHAPTER 3. RESULTS

#### **Meteorological measurements**

Figure 1 shows the annual course of daily mean values of selected soil and meteorological variables for the study period. Seasonal values of key meteorological variables are shown in Table 3. Maximum values for incoming photosynthetically active radiation (PAR), air and soil temperature occurred in the summer months, which provided optimal conditions for high rates of photosynthesis and respiration. Incoming PAR reached maximum levels in June and early July, with the greatest value of daily mean PAR occurring on June 13. Large variation in daily mean PAR, as observed by large, frequent downward spikes in Figure 1a was due to heavily cloudy days. Extreme dips in daily average PAR coincide with large rain events.

Air temperature follows similar trends of increase and decrease as PAR (Figure 1b). The warmest day occurred on July 7 with a mean daily temperature of 28.5 °C. Conversely, the coldest day of the year was January 15 with a mean temperature of -11°C. The hottest half-hourly average temperature recorded at the site was 33.7°C on July 6 and the coldest half-hourly average temperature was -16°C on January 14. Air temperature reached its maximum in late July, while maximum radiation occurred in June. Mean annual air temperature was 11.8 °C, which is quite warm as compared to the 30 year mean value of 7.8 °C.

Soil temperature followed general air temperature trends with dampened extreme values (Figure 1b). In winter months of January and February, mean soil temperature in

the uppermost 30cm soil layer generally remained between 0.5 °C and 2°C. Snow cover also usually provides additional insulating effects but there were few snow events in the winter of 2012 large enough to produce consistent ground cover. Snow cover data from the on-site snow depth sensor and from the Environment Canada Delhi weather station indicated intermittent ground snow in January, with persistent snow cover only at the end of the month following a fairly large snowfall. Another large snow event in February caused a 14 day ground cover of snow in the middle of the month, but thickness of snow was reduced shortly after the snowfall. The presence of snow cover resulted in the stability of soil temperatures. At times when ground snow was absent, soil temperatures showed greater oscillations in temperature following changes in air temperature. The mean temperature for the 30cm soil layer in the presence of snow remained constant at about 1°C. Without snow, soil temperatures showed large variation between 1.5°C and 4°C because of warmer winter temperatures in 2012. Consistent soil thaw, as indicated by shallow soil temperatures consistently above 4°C, occurred in the middle of March as the area experienced abnormally warm air temperatures. Maximum soil temperature at 30cm depth was reached on August 6 at 21 °C.

Annual peak specific humidity occurred later in the year than maximum PAR, reaching greatest values in July and early August (Figure 1c). The highest half-hourly measurement of humidity occurred on August 5 with a specific humidity value of 20.3 g kg<sup>-1</sup>. Mean daily specific humidity rarely exceeded 5 g kg<sup>-1</sup> in the winter months. At the beginning of the year (Jan – May) mean soil moisture in the upper 30 cm layer remained fairly consistent due to small, frequent precipitation events that replenished subsurface

moisture (Figure 1d). In these months, soil moisture did not fall below 0.1 m<sup>3</sup> m<sup>-3</sup>. A large precipitation event (45 mm) occurred on June 1<sup>st</sup>, preceding a two month dry period in June and July and early August (from June 2 to August 11) in which only 184 mm of precipitation fell in small rainfall events. These few small precipitation events did not succeed in replenishing steadily declining soil water content. The dry period reached its climax with a minimum volumetric water content of 0.023 m<sup>3</sup> m<sup>-3</sup> on August 4<sup>th</sup> and ended on August 11<sup>th</sup> after a rain event. The largest rainfall of the year (50 mm in a day) occurred on September 8<sup>th</sup>. Additional large precipitation events in September and October replenished soil moisture to levels above 0.1m<sup>3</sup>m<sup>-3</sup>. The total annual accumulated precipitation for the 12 month study period was 1001 mm, which is similar to the 30-year mean value of 1010 mm in the area.

## **Carbon fluxes**

Annual values of net ecosystem productivity (NEP), gross ecosystem productivity (GEP) and ecosystem respiration (R) for 2012 are  $263 \pm 30$ , 1192 and 922 g C m<sup>-2</sup>, respectively. Corresponding seasonal values are given in Table 3. In 2012, daily average values of NEP became positive (signifying greater carbon uptake than release by respiration) in the 2<sup>nd</sup> week of May and continued to be positive until mid-October (Figure 2a and 3a), suggesting a growing season of 173 days (from April 30<sup>th</sup> to October 18<sup>th</sup>). Rapid springtime increases in NEP in May indicated the occurrence of significant photosynthesis resulting from developing leaves. Midday peak NEP values in the first few weeks of the growing season were typically between 5 to 10 µmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>.

Maximum carbon sequestration occurred in July, with midday peak carbon uptake values usually between 20 to 30  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>.

The least productive day of the growing season, June 1, coincided with one of the largest rainfall events of the year, in which downwelling PAR was extremely low throughout the day. June and July were the most productive months (Figure 3a). The maximum daily total NEP of 8.5 g C m<sup>-2</sup> was observed on July 14. The three most productive days of the year were all in the month of July. Late July and early August were the times of lowest soil moisture following a prolonged dry period with only a few small precipitation events, as mentioned earlier (see Figure 3a, c). Although soil moisture values started to decline rapidly in early June with the start of the dry period, NEP values did not show a persistent decline until after the second week of July, when soil water values reached their lowest point at 0.023 m<sup>3</sup> m<sup>-3</sup>. At this time, daily NEP values showed slow but persistent decline until early August, when a 33 mm precipitation event on August 11 ended the dry period (Figure 1e; Figure 3a,d). During the peak of drought in the last week of July and first week of August, when soil water content was at its lowest, daily NEP values were among the lowest of the growing season, as indicated by a large dip in the time series of NEP in Figure 3a. After the end of the dry period, NEP increased to values of about 2.5 to 4.0 g C day<sup>-1</sup> within a few days. As leaf senescence began in early October, NEP declined rapidly, becoming negative in mid-October and reaching lowest autumn values in the last week of October, indicating a large emission of carbon (Figure 3a).

## Warm periods outside of growing season

Outside of the growing season, warm periods in the spring months of March and April caused pronounced increased in respiration-related release of carbon (Figure 3a,b). Spring of 2012 in this region was unique because of the occurrence of extreme warm temperatures in the late winter period. At this site, monthly mean  $T_a$  was 7.2 °C in March 2012, which is much warmer than the mean monthly  $T_a$  of 0.2 °C for the past 30 years (measured at Environment Canada's weather station at Delhi, Ontario). The lowest 30-year mean monthly temperature of March was -4.1 °C in 1984 and the highest was 4.4 °C in 1973. Large, erratic peaks in  $T_a$  in March and April of 2012 caused pronounced decreases in daily total NEP, indicating increase in respiratory losses from this forest (see Figure 3).

From March 17 to 23, maximum half-hourly T<sub>a</sub> exceeded 20.5 °C every day, reaching a maximum half-hourly value of 26 °C on March 23, which is very rare in the region during this time of year. Mean daily T<sub>a</sub> on that day was 20 °C and total daily NEP fell to -3.65 g C m<sup>-2</sup> (negative values indicating carbon loss). Prior to this warm period, daily total NEP generally oscillated between -0.2 and -1.2 g C m<sup>-2</sup> day<sup>-1</sup>. A steady decline of NEP began on March 10 (daily total NEP was 0.33 g C m<sup>-2</sup>) and continued to decrease as warm temperatures persisted until culmination on March 23. Similar drops in NEP occurred twice in April when daily average temperatures jumped to 19.2 °C and 18.1 °C on April 16 and April 2. Daily total NEP for these days were -2.55 g C m<sup>-2</sup> and -3.14 g C m<sup>-2</sup>, respectively.

Nearing the end of the growing season, daily total NEP steadily decreased throughout the month of October (Figure 3). Shortly after the end of the growing season, daily total NEP reached an autumn low of -2.95 g C m<sup>-2</sup> (carbon loss) on October 26<sup>th</sup> when leaf senescence was its maximum, then increased and stabilized at ranges of -0.4 g C m<sup>-2</sup> to -1.6 g C m<sup>-2</sup> for the rest of autumn and winter. One day in early December shows an outlier of daily total NEP of -2.35 g C m<sup>-2</sup> which coincides with an abnormally warm day with a daily average temperature of 12.8 °C.

## **Response of fluxes to environmental variables**

The response of daily total GEP to daily PAR showed a general increase of photosynthesis with increased light intensity. GEP increased almost linearly up to PAR of about 600  $\mu$ mol m<sup>-2</sup> day<sup>-1</sup> followed by a gradual decrease in GEP with increasing PAR (Figure 4). The value of  $\alpha$ , which represents increase in photosynthesis per unit PAR was 0.039 and A<sub>max</sub> (photosynthetic capacity) was 27.6  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. Relationship of daily total GEP with mean daily VPD is shown in Figure 5. On a daily basis, total photosynthesis peaks on days with daily mean VPD values ranging from 1.0 to 1.5 kPa. GEP values start to decline when VPD values exceed a 1.75 kPa threshold. Interestingly, the response of GEP to daily mean  $\theta$  shows a decreasing linear trend that indicates greater GEP at lower levels of soil moisture (Figure 6). When examining this trend in conjunction with levels of cloudiness, a pronounced pattern of sunny days coinciding with lower soil moisture is observed at this site. Cloudy days have a chance of precipitation and greater soil moisture, at the expense of sunlight intensity which is

required for photosynthesis. This shows that PAR was a dominating control on GEP at this site, especially compared to  $\theta$ .

To investigate statistical significance of environmental variables as driving influences of carbon uptake and release in our forest, a linear multivariate analysis was conducted over the growing season with NEP, GEP and R as dependent variables. Independent variables used for each analysis were downward PAR,  $T_a$ ,  $T_s$ , VPD, and  $\theta$ for 30 cm soil layer. The reader is cautioned of a certain degree of autocorrelation between the independent variables in this analysis, due to the interconnected nature of the climate system. For NEP, results indicated t-scores of 117.03, -15.50, -9.65, 3.53 and -0.26 for PAR, VPD,  $\theta$ , T<sub>a</sub> and T<sub>s</sub>, respectively and r<sup>2</sup> = 0.7095. Using a significance threshold of 0.05, all independent variables were significant for NEP except  $T_s$  (refer to Table 4a for full test results of NEP analysis). For GEP, all environmental variables were significant (Table 4b) with t-score values of 54.14, -16.55, 15.89, 2.71 and 2.47 for PAR, VPD, T<sub>s</sub>, T<sub>a</sub> and  $\theta$ , respectively, and r<sup>2</sup>=0.5375. Similarly, for R, all variables were significant but  $T_a$  and VPD had the lowest significance while  $\theta$  and  $T_s$  had the highest significance (Table 4c). Resulting t-score values for R were 67.87, 67.38, -5.28, 2.34 and 2.21 for  $\theta$ , T<sub>s</sub>, PAR, T<sub>a</sub> and VPD, respectively and r<sup>2</sup>=0.61. Results of R analysis are summarized in Table 4c.

Independent variables were standardized with a mean of 0 and standard deviation of 1 to allow for comparison between parameter estimates. The variables share similar ranges of distribution, facilitating comparison of relative impact on the dependent

variable through examination of the parameter estimate. The greatest parameter estimate in NEP analysis is 7.5 for PAR, indicating a 7.5 unit increase in NEP for a standard deviation increase in NEP. The next greatest parameter estimate indicates a 1.34 unit decrease in NEP per standard deviation increase in VPD. In analysis of R, the two greatest variable coefficients were  $\theta$  and T<sub>s</sub>, with approximately the same values, 67.87 and 67.38, respectively. This indicates a 67 unit increase in respiration per standard deviation increase in  $\theta$  or T<sub>s</sub>. The environmental variable with the greatest parameter estimate for GEP is incoming PAR, with a 5.57 unit increase in GEP per standard deviation increase of PAR. In contrast, the smallest parameter estimate for GEP is  $\theta$ .

The inclusion of a half-hourly lag in the linear multivariate analysis of NEP resulted in an increase in model fit. The  $r^2$  value increased from 0.71 to 0.82 with the inclusion of the half-hour time lag. Addition of an hourly lag was also significant but caused minimal increase in the goodness of fit. Addition of a 1.5 hour lag was not significant.

#### Water use efficiency

The relationship between GEP and evapotranspiration (ET), which includes loss of water to the atmosphere from both plants and soil, is shown in Figure 6. Low water loss corresponds with low GEP. As evapotranspiration increases, GEP increases, until a point of plateau at about 3.5mm day<sup>-1</sup>. Overall, the water use efficiency curve indicates approximately 2.86 g of carbon sequestered for each kilogram of water lost in this growing season. GEP vs ET relationships for the spring, summer and fall season follow a similar trend when all data were pooled together over the full growing season (Figure 6).

## CHAPTER 4. DISCUSSION

#### Annual carbon uptake in eastern North American forests

This oak-dominated temperate deciduous forest was a moderate carbon sink in 2012 with a net carbon sequestration of  $263 \pm 30$  g C m<sup>-2</sup>. An early study at the Harvard forest, a mixed deciduous forest in Massachusetts, USA, found an annual net uptake of carbon of 370 g C m<sup>-2</sup> year<sup>-1</sup> (Wofsy 1993). A few years later, Greco and Baldocchi (1996) found carbon sequestration rates even greater (525 g C m<sup>-2</sup> year<sup>-1</sup>) in a similar forest type in Tennessee, USA. Results from the first full year of measurements in the Morgan-Monroe State Forest in Indiana, USA indicated carbon sequestration of 2.4 t C ha<sup>-1</sup> year<sup>-1</sup> (Schmid et al 2000). After a decade of continuous flux measurements at this site, a follow-up paper reported an annual increase in forest productivity of about 0.1 t C ha<sup>-1</sup> between 1998 and 2008, with annual NEP estimates ranging between 3.0 and 4.4 t C ha<sup>-1</sup> year<sup>-1</sup> in that decade (Dragoni et al 2011). The closest deciduous flux tower site to this study site, a successional mixed deciduous forest with predominantly maple, ash and aspen in Borden, Ontario, estimated annual net carbon uptake of 60, 240 and 170 g C m<sup>-2</sup> year<sup>-1</sup>, in 1996, 1997 and 1998, respectively (Barr et al 2002). Annual NEP estimates similar in range to the annual NEP value at our site, have been published for flux tower

sites in Indiana, Ohio, and Massachusetts, USA (Dragoni et al 2011, Noormets et al 2008, Wofsy 1993).

The oldest white pine (*Pinus strobus*) plantation forest (currently 74 years old), which is part of the Turkey Point Flux Station, located about 20 km east of this deciduous forest, had a net carbon uptake of 148, 120 and 177 g C m<sup>-2</sup> in 2006, 2007 and 2008, respectively, with a mean annual NEP of 148 g C m<sup>-2</sup> over this period (Peichl et al 2010). Arain and Restrepo-Coupe (2005) earlier reported net carbon uptake of 196 g C m<sup>-2</sup> for June 2002 to May 2003 at this coniferous site.

Given a similar regional environment, the growing season of a coniferous forest is longer in duration than a deciduous forest because time is not required for leaf emergence and development at the beginning of the growing season, nor for leaf senescence concluding the season. Deciduous forests, in contrast, demonstrate more intense levels of photosynthetic activity throughout the growing season (Baldocchi and Vogel 1996). Peak NEP at the conifer site in 2012 was 5.3 g C m<sup>-2</sup> day<sup>-1</sup> on June 24, while maximum NEP at the deciduous site occurred later, on July 14, with a more intense level of carbon capture at 8.5 g C m<sup>-2</sup> day<sup>-1</sup>. In 2012, the growing season duration at the deciduous site was 173 days, which falls within the lower range of growing season lengths reported for an eastern deciduous forest in Indiana between 1998 and 2008 (Dragoni et al 2011), as expected for a similar forest situated at a more northern latitude. Of these growing season days, 154 days had a positive net carbon uptake. In contrast, at the coniferous site, photosynthesis occurred for 281 days in 2012. Within these days,

carbon sequestration exceeded respiratory carbon releases for 169 days of the year. Annual NEP at our conifer site in 2012 was 153 g C m<sup>-2</sup> year<sup>-1</sup>.

As mentioned earlier, annual values of GEP and R at this deciduous forest site in 2012 were 1191 and 922 g C m<sup>-2</sup>, respectively, as compared to 1509 and 1350 g C m<sup>-2</sup> at the conifer forest site, which was thinned in February and March of 2012, having approximately 30% trees selectively removed. Annual NEP of 153 g C m<sup>-2</sup> in 2012 at the conifer site indicated that despite thinning, the annual carbon uptake was similar to earlier reported mean values (e.i. 148 g C m<sup>-2</sup>) (Peichl et al 2010). Therefore, our analysis indicates that despite a shorter growing season and few days of net carbon intake, the deciduous site was a stronger carbon sink than the coniferous site (263 vs 153 g C m<sup>-2</sup>) year<sup>-1</sup>) due to intensive photosynthesis within the relatively short growing season. However, the reader is cautioned when comparing annual values of carbon fluxes among these deciduous and conifer forest sites.

## Seasonal patterns of carbon flux

The summer of 2012 in Southern Ontario, as previously mentioned, experienced a dry period from June to early August, and overall 2012 was a warm year, compared to the 30 year normal values. NEP values at the deciduous site did not show any persistent decline until after the second week of July, when soil water content was depleted to its lowest annual ranges. After this, NEP persistently declined until the first week of August, when the dry period ended with heavy rainfall. At the conifer site, NEP values showed a similar trend, falling from high values of 3 to 5 g C m<sup>-2</sup> day<sup>-1</sup> in the third week of June to

about 0 to -3 g C m<sup>-2</sup> day<sup>-1</sup> by the end of the drought in early August. This drastic drop in carbon sequestration indicates conservative water loss in response to extended soil moisture stress in both forests. However, during this sustained dry period, the deciduous forest demonstrated higher productivity compared to the conifer site. In an experimental drought study by MacKay et al (2012) at the conifer site, transpiration started to decline when  $\theta$  dropped below 0.068 m<sup>3</sup> m<sup>-3</sup> and the forest took approximately 54 days to respond after drought initiation on April 1<sup>st</sup>. A similar response was observed at the deciduous site in 2012 when NEP showed a persistent decline after mid-July, while the drought period started in early June.

Evapotranspiration rates for forests in this region can reach as high as 6.5 mm day<sup>-1</sup> (Arain & Restrepo-Coupe 2005). Maximum observed evapotranspiration at our deciduous site was 3.8 mm day<sup>-1</sup> (Khader 2013), suggesting conservative water loss from forest vegetation, with an estimated water use efficiency of 2.86 g C kg<sup>-1</sup> H<sub>2</sub>O, which is similar to an observed water use efficiency of 2.5 to 3.5 g C kg<sup>-1</sup> H<sub>2</sub>O at the coniferous site. Mean growing season soil moisture between 2006 and 2008 at the conifer site was similar to soil moisture trends observed at the deciduous site, despite variation in precipitation between years (Peichl et al 2010).

## Lags in carbon flux responses

In a multivariate analysis of carbon fluxes and environmental variables, the inclusion of a half-hour temporal lag greatly increased the model coefficient of determination for NEP. This indicates a certain degree of temporal auto-correlation

within NEP measurements on a half-hourly basis; that is, a carbon flux measurement at one half hour is correlated to the carbon flux measurement at a previous or following half hour. Addition of an hourly lag caused a slight increase in model fit, and a 1.5 hour lag was found to be insignificant. These results fit the current understanding of photosynthetic response times of trees to environmental conditions.

Photosynthetic rates are directly related to stomatal aperture and activity (Gregory and Pearse 1937) through the transfer of CO<sub>2</sub> from mesophyll cell walls to chloroplasts, where photosynthetic reactions occur (Holmgren et al 1965). Generally, environmental conditions affecting photosynthesis do not change drastically from one half-hour to another half-hour, and stomata respond gradually to changes in environmental conditions (Brun 1962). PAR impinging on a leaf is not consistent as clouds pass or nearby covering foliage moves with wind. The time required for a tree to reach equilibrium stomatal resistance following a change in illumination varies depending on the tree species, the magnitude of change of intensity, and whether the stomata are opening or closing. Opening to a constant leaf resistance takes less time than closing (Woods & Turner 1971). Oak species required 20 minutes to close to a constant leaf resistance, but other species may take as long as 36 minutes, depending on tolerance to shade (Woods & Turner 1971).

It has been shown that temperature can play a role in stomatal response time, with greater temperatures resulting in slower responses (Brun 1962). It has been postulated that the cause may be linked to the depletion of respiratory substrates within the leaf.

Stomatal opening time also varies depending on the length of time a leaf has been exposed to darkness (Brun 1962). Varying photosynthetic response times to influencing environmental factors cause a delay in carbon uptake, creating a half-hour to hourly lag in which measured carbon flux values at one point in time will be partially correlated to the following half hour, as stomata gradually open or close.

### Influence of changing climate

Changing patterns in air temperature over the past several decades has been noted around the globe (Nicholls et al 1996). In particular, the northern hemisphere has experienced significant increases in temperature over the past century (Nicholls et al. 1996, Vitasse et al 2009). The effect of increased biospheric activity in response to increasing temperatures has contradicting effects on possible carbon uptake in forest ecosystems (Garrity et al, 2011). On one hand, increased growing season length may result in greater carbon sequestration by lengthening the duration of the photosynthetically active season (Black et al 2000, Menzel and Fabian 1999, Myneni et al 1997, Randerson et al 1999, Richardson et al 2010). However, increased air temperatures lead to increased soil temperatures, which is the driving force behind heterotrophic respiration in forest soils (Davidson et al 1998, Niu et al 2012).

At our site, greatest carbon release to the atmosphere outside the growing season occurred during an abnormal warm period in March. As daily mean air temperatures climbed over the course of 10 days, reaching a peak at 20°C, soil temperature consistently increased to a peak daily mean temperature of 13°C in the top 30cm soil layer. Despite

the effects of early warm temperatures causing increased carbon release through accelerated heterotrophic respiration, it is possible that the general warm spring temperatures encouraged an earlier than normal emergence and development of deciduous leaves that resulted in greater annual carbon sequestration. In analysis of four years of carbon flux and meteorological measurements in a deciduous aspen forest in Saskatchewan, Black et al (2000) found strong correlation ( $r^2 = 0.99$ ) between total annual carbon capture and spring air temperature. However, forests of this region often have maximum NEP values in the spring, unlike Southern Ontario which generally experiences greatest carbon sequestration in mid-summer. Differing seasonal growing patterns between these forests may cause the positive effect of warm spring temperatures on carbon uptake in the western aspen forest to be extraneous in analysis of eastern deciduous forests.

Results from a temperate deciduous forest in eastern North America (Indiana, USA), the Morgan Monroe State Forest (MMSF), indicate that increased net productivity associated with a longer vegetated season is mainly due to an extension in vegetative activity nearing the end of the growing season, in autumn (Dragoni et al 2011). Results from the annual carbon fluxes at our deciduous forest support this suggestion, however, prolonged drought periods in late summer may cause a decline in net carbon uptake, as observed in late July and early August at our site. Noormets et al (2008) found that their temperate deciduous forest accumulated 40% less carbon in 2004 due to a drought during the leaf expansion period. They suggest that decrease in NEP was caused by decreased GEP due to drought rather than suppression of R. The growing season at our site

persisted well into the autumn season. Average observed trends at the MMSF site indicate an increase in growing season duration of 30 days over the past decade, with a shift in timing of senescence from early to late October (Dragoni et al 2011). It is likely that these trends are also occurring at TPD, due to the close proximity and general similarities in forest structure and growing patterns.

The average annual air temperature in the Great Lakes region is expected to increase only by 0.8°C in next 50 years (McBean and Motiee 2008). However, this apparently small increase masks larger inter-annual changes. Seasonal temperatures and diurnal temperatures are expected to have greater fluctuations, resulting in much warmer winter temperatures and increases in total annual precipitation (McBean and Motiee 2008).

Winter of 2012 at the deciduous site and surrounding region saw abnormal precipitation patterns with very few snowfall events and several rainfalls. Soils exposed during winter because of lack of snow cover may result in lower carbon release through decreased heterotrophic respiration due to deeper soil freezes. However, deep soil freeze may have adverse effects on tree roots and subsequent growth (Boutin and Robitaille 1995). In contrast, above-zero air temperature may cause higher release of carbon in winter. Mariko et al (2000) found that in a cool temperate forest, winter carbon release was heightened by the insulating effects of snow, which caused soil profile temperatures to be notably higher than air temperature. The snowpack caused a decoupling of temperatures between soil and the overlying air, which created ideal warmer temperatures

for the acceleration of microbial activity in unfrozen soil. The occurrence of warm periods in winter, especially without a blanketing layer of soil, would lead to the direct thawing of uncovered soil, causing a large increase in R values (DeForest et al 2009), as has been observed at our temperate forest site.

Large fluctuations in seasonal temperatures, as expected for this region, will cause high instability of the soil carbon pool. While colder temperatures in winter may cause increase in total annual NEP through a decrease in winter R, equivalent or greater warm temperatures in winter months may contradict the positive photosynthetic effects of an increased growing season. Piao et al (2008) found that spring warming increased photosynthesis greater respiration, but autumnal warming resulted in greater respirationrelated carbon releases than photosynthetic uptake. The annual measurements of this study suggest that early warm periods and increased summer and autumn carbon uptake have generally balanced carbon release, causing this forest to be a moderate carbon sink.

### CHAPTER 5. CONCLUSION

Understanding the role of deciduous forests in the global carbon balance requires data related to the interaction between climate variability and the forest ecosystem. This analysis reports the first year of eddy covariance flux measurements with associated meteorological and soil measurements of an oak-dominated temperate deciduous forest in the Carolinian forest zone of Southern Ontario. The forest was a moderate net carbon sink in 2012 with a net carbon intake of  $263 \pm 30$  g C m<sup>-2</sup> year<sup>-1</sup>. Gross ecosystem productivity

(GEP) and respiration (R) were estimated to be 1188 and 896 g C m<sup>-2</sup> year<sup>-1</sup>, respectively. The growing season at this forest in 2012 was 173 days long, beginning on April 29 and ending on October 18.

A sustained 12 day warm period in later winter (March), before leaves had emerged, caused a large increase in release of carbon into the atmosphere. Erratic peaks of daily soil temperature in April also increased respiration, following variations in air temperature. A dry period in June, July and early August strongly negatively impacted photosynthetic rates when soil moisture values reached the lowest point of the year in late July and early August. Water use efficiency at this deciduous forest was 2.86 g C kg<sup>-1</sup> H<sub>2</sub>O, indicating conservative water loss. Incoming PAR was a dominant control on photosynthesis, followed by air temperature and vapour pressure deficit. Extremely cloudy days in the growing season resulted in net carbon release, as well as water stress in a late summer dry period.

Large climatic fluctuations in this region may cause high instability in soil carbon pools. The effect of changing temperature patterns may encourage carbon sequestration in deciduous forests by widening the growing season earlier in spring and later into autumn. However, carbon release encouraged by warmer temperatures, especially erratic peaks when deciduous trees are dormant in winter, may offset these gains.

## REFERENCES

- Arain, M.A. and Restrepo-Coupe, N. 2005. Net ecosystem production in a temperate pine plantation in poutheastern Canada. Agriculture and Forest Meteorology, 128 (3-4), 223-241.
- Aubinet, M., Vesala, T. and Papale, D. 2012. Eddy covariance: a practical guide to measurements and data analysis. Springer Atmospheric Sciences. pp.1-433.
- Baldocchi, D.D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Global Change Biology, 9, 479-492.
- Baldocchi, D.D. 2008. 'Breathing' of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. Australian Journal of Botany, 56(1), 1-26.
- Baldocchi, D.D. and Vogel, C.A. 1996. Energy and CO<sub>2</sub> flux densities above and below a temperate broad-leaved forest and a boreal pine forest. Tree Physiology, 16, 5-16.
- Barr, A.G., Griffis, T.J., Black T.A., Lee, X., Staebler, R.M., Fuentes, J.D., Chen, Z., and Morgenstern, K. 2002. Comparing the carbon budgets of boreal and temperate deciduous forest stands. Canadian Journal of Forest Research, 32, 813-822.
- Barr, A.G., Richardson, A.D., Hollinger, D.Y., Papale, D., Arain, M.A., Black, T.A.,
  Bohrer, G., Dragoni, D., Fischer, M.L., Gu, L., Law, B.E., Margolis, H.A.,
  McCaughey, J.H., Munger, J.W., Oechel, W., and Schaeffer, K. 2013. Use of
  change-point detection for friction-velocity threshold evaluation in eddycovariance studies. Journal of Agriculture and Forest Meteorology, 171-172, 3145.

- Black, T.A., Chen, W.J., Barr, A.G., Arain, M.A., Chen, Z., Nesic, Z., Hogg, E.H., Neumann, H.H., and Yang, P.C. 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. Geophysical Research Letters, 27, 1271-1274.
- Brodeur, J.J. 2013. Data methods and analyses for sustainable operation and defensible results of a long-term, multi-site ecosystem flux measurement program. McMaster University, School of Geography and Earth Sciences, Doctor of Philosophy dissertation.
- Blouin, Glen. 2001. An eclectic guide to trees east of the rockies. The Boston Mills Press. Erin, ON.
- Boutin, R. and Robitaille, G. 1995. Increased soil nitrate losses under mature sugar maple trees affected by experimentally induced deep frost. Canadian Journal of Forest Research, 25(4), 588-602.
- Brun, W.A. 1962. Rhythmic stomatal opening responses in banana leaves. Physiologia Plantarum, 15, 623- 630.
- Carolinian Canada. 2013. Available from http://www.carolinian.org/.
- Chen, W.J., Black, T.A., Yang, P.C., Barr, A.G., Neumann, H.H., Nesic, Z., Blanken,
  P.D., Novak, M.D., Eley, J., Ketler, R.J. and Cuenca, R. 1999. Effects of
  climatic variability on the annual carbon sequestration by a boreal aspen forest.
  Global Change Biology, 5, 41-53.
- Davidson, E.A., Belk, E., and Boone, R.D. 1998. Soil water content and temperature as independent or confounding factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology, 4 (2), 217-227.

- DeForest, J. L., Chen, J. and McNulty, S.G. 2009. Leaf liter is an important mediator of soil respiration in an oak-dominated forest. International Journal of Biometeorology, 53, 127-134.
- Dragoni, D., Schmid, H.P., Wayson, C.A., Potter, H., Grimmond, C.S.B. and Randolph, J.C. 2011. Evidence of increased net ecosystem productivity associated with a longer vegetated season in a deciduous forest in south-central Indiana, USA. Global Change Biology, 17, 886-897.
- Farnsworth, E.J., Nunez-Farfan, J., Careaga, S.A. and Bazzaz F.A. 1995. Phenology and growth of three temperate forest life forms in response to artificial soil warming. Journal of Ecology, 83, 967-977.
- Garrity, S.R., Bohrer, G., Maurer, K.D., Mueller, K.L., Vogel, C.S. and Curtis, P.S. 2011. A comparison of multiple phenology data sources for estimating seasonal transitions in deciduous forest carbon exchange. Journal of Agricultural and Forest Meteorology, 151, 1741-1752.
- Geider, R.J., Delucia, E.H., Falkowski, P.G., Finzi, A.C, Grime, J.P., Grace, J., Kana, T.M., Laroche, J., Long, S.P., Osborne, B.A., Platt, T., Prentice, I.C, Raven, J.A., Schlesinger, W.H., Smetacek, V., Stuart, V., Sathyendranath, S., Thomas, R.B., Volgemann, T.C., Williams, P. and Woodward, F.I. 2001. Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. Global Change Biology, 7(8), 849-882.
- Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C. and Wofsy, S.C. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science, 271, 1576-1578.
- Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.M., Sutton, D.J., Bazzaz, A. and Munger, J.W.

1998. Sensitivity of boreal forest carbon balance to soil thaw. Science, 279 (5348), 214-217.

- Grace, J. Berninger, F. and Nagy, L. 2002. Impacts of climate change on the tree line. Annals of Botany, 90, 537-544.
- Greco, S. and Baldocchi, D.D. 1996. Seasonal variations of CO<sub>2</sub> and water vapour exchange rates over a temperate deciduous forest. Global Change Biology, 2, 183-197.
- Gregory, F.G. and Pearse, H.L. 1937. The effects on the behavior of stomata of alternating periods of light and darkness of duration. Annals of Botany, 1(1), 3-10.
- Holmgren, P., Jarvis, P.G., and Jarvis M.S. 1965. Resistances to carbon dioxide and water vapour transfer in leaves of different plant species. Physiologia Plantarum, 18, 557-573.
- Houghton, R.A., Boone, R.D., Fruci, R., Hobbie, J.E., Melillo, J.M., Palm, C.A.,
  Peterson, B.J., Shaver, G.R., Woodwell, G.M., Moore, B., Skole, D.L. and Myers,
  N. 1987. The flux of carbon from terrestrial ecosystems to the atmosohere in 1980 due to changes in land use: geographic distribution of the global flux. Tellus, 39B(1-2), 122-139.
- IPCC: Assessment Report of Working Group 1. 2012. Soloman, S.D., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L.
- Jarvis, P.G. 1995. The role of temperate trees and forests in CO<sub>2</sub> fixation. Vegetatio, 121, 157-174.
- Jarvis, P.G. and Leverenz, J.W. 1983. Productivity of temperature, deciduous and evergreen forests. Physiological Plant Ecology IV: Encyclopedia of Plant Physiology, 233-280.

- Jensen, T.S. and Nielson, O.F. 1986. Rodents as seed dispersers in a heath oak wood succession. Oecologia, 70, 214-221.
- Keeling, C.D., Chin, J.F.S., Whorf, T.P. 1996. Increased activity of northern vegetation inferred from atmospheric CO<sub>2</sub> measurements. Nature, 382, 146-149.
- Kramer, K., Leinonen, I. and Loustau, D. 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems. International Journal of Biometeorology, 44, 67-75.
- Kula, M. 2013. Determining the effects of climate variability and forest thinning on above ground carbon in temperate forests. McMaster University, School of Geography and Earth Sciences, Master of Science Thesis.
- Lauriault, J. 1989. Identification guide to the trees of Canada. National Museum of Natural Sciences. Fitzhenry & Whiteside. Markham, Ontario.
- Lee, X., Fuentes, J.D., Staebler, R.M. and Neumann, H.H. 1999. Long-term observation of the atmospheric exchange of CO<sub>2</sub> with a temperate deciduous forest in southern Ontario, Canada. Journal of Geophysical Research, 104, 15975-15984.
- Liao, C., Luo, Y., Fang, C. and Li, B. 2010. Ecosystem carbon stock influenced by plantation practice: implications for planting forests as a measure of climate change mitigation. PLoS ONE, 5(5), e10867.
- Linderholm, H.W. 2006. Growing season changes in the last century. Agricultural and Forest Meteorology, 137, 1-14.
- MacKay, S.L., Arain, M.A., Khomik, M., Brodeur, J.J., Schumacher, J., Hartmann, H. and Peichl, M. 2012. The impact of induced drought on transpiration and growth in a temperate pine plantation forest. Hydrological Processes, 26(12), 1779-1791.

- Mariko, S., Nishimura, N., Mo, W., Matsui, Y., Kibe, T., and Koizumi, H. 2000. Winter CO<sub>2</sub> flux from soil and snow surfaces in a cool-temperate deciduous forest, Japan. Ecological Research, 15(4), 363-372.
- Martin, P.H., Nabuurs, G.J., Aubinet, A., Karjalainen, T., Vine, E.L., Kinsmen, J. and Heath, L.S. 2001. Carbon sinks in temperate forests. Annual Review of Energy and Environment, 260, 435-465.
- McBean, E.and H. Motiee. 2008. Assessment of impact of climate change on water resources: A long term analysis of the Great Lakes of North America. Hydrology and Earth System Sciences, 12 (1), 239-255.
- Morgenstern, K., Black, T.A., Humphreys, E.R., Griffis, T.J., Drewitt, G.B., Cai, T., Nesic, Z., Spittlehouse, D.L., and Livingston, N.J. 2004. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas fir forest during an El Niño/La Niña cycle. Journal of Agriculture and Forest Meteorology, 123, 201-219.
- Musselman, R.C. and Fox, D.G. 1991. A review of the role of temperate forests in the global CO<sub>2</sub> balance. Journal of the Air and Waste Management Association, 41, 798–807.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., and Nemani, R.R. 1997 Increased plant growth in the northern high latitudes from 1981-1991. Nature, 386, 698-702.
- Nicholls, N., Gruza, G.V., Jouzel, J., Karl, T.R., Ogallo L.A., and Parker, D.E. Observed climate variability and change. Climate Change 1995: The Science of Climate Change. Edited by Houghton, J.T. et al. pp. 133-192, Cambridge University Press, Cambridge, 1996.
- Niu, S., Luo, Y. Fei, S., Yuan, W., Schimel, D., Law, B.E., et al. 2012. Thermal optimality of net ecosystem exchange of carbon dioxide and underlying mechanisms. New Phytologist, 194, 775-783.

- Olsen, J.S., Pfuderer, H.A., and Chan Y.H. 1978. Changes in the global carbon cycle in the biosphere. ORNL/EIS-109. Oak Ridge Laboratroy, Oak Ridge, TN. 169 pp.
- Pan, Y.D., Birdsey, R.A., Fang, J.Y., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips,
  O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala,
  S.W., McGuire, D.A., Piao, S., Rautiainen, A., Sitch, S. Hayes, D. (2011) A large and persistent carbon sink in the world's forests. Science, 333, 988-993.
- Piao, S., Ciais, P., Friedlingstein, P., Peylin, P. Reichstin, M., Luyssaert, S. Margolis, H., Fang, J., Barr, A., Chen, A., Grelle, A., Hollinger, D.Y., Laurila, T., Lindroth, A., Richardson, A.D. and Vesala, T. 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature, 451(3), 49-53.
- Peichl, M., Brodeur, J.J., Khomik, M. and Arain, M.A. 2010. Biometric and eddy covariance based estimates of carbon fluxes in an age-sequence of temperate pine forests. Agricultural and Forest Meteorology, 150, 952-965.
- Present, E.W. and Acton, C.J. 1984. Soils of the regional municipality of Haldimand-Norfolk. Ontario Institute Pedology, Ontario Ministry of Agriculture and Food. Report No. 57, vol 1.
- Randerson, J.T., Field, C.B., Fund, I.Y., and Tans, P.P. 1999. Increases in early season ecosystem uptake explain recent changes in the seasonal cycle of atmospheric CO<sub>2</sub> at high northern latitudes. Journal of Geophysical Research, 26, 2765-2768.
- Richardson, A.R., Black, T.A., Ciais, P., Delbart, N., Friedl, M.A., et al. 2010. Influence of spring and autumn phenological transitions of forest ecosystem productivity.
  Philosophical Transactions of the Royal Society: Biological Sciences, 365, 3227-3246.
- Richardson, A.D., Keenan T.F., Migliavacca, M. Ryu, Y., Sonnentag, O. and Toomey,M. 2013. Climate change, phenology, and phenological control of vegetation

feedbacks to the climate system. Agricultural and Forest Meteorology, 169, 156-173.

- Richart, M. and Hewitt, N. 2008. Forest remnants in the Long Point region, Southern Ontario: Tree species diversity and size structure. Landscape and Urban Planning, 86, 25-37.
- Schmid, H.P., Grimmond, C.S.B., Cropley, F., Offerle, B. and Su, H.B. 2000.
   Measurements of CO<sub>2</sub> and energy fluxes over a mixed hardwood forest in the mid-western United States. Forest and Agriculture Meteorology, 103, 357-374.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Gudmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S. and Jarvis, P.G. 2000. Respiration as the main determinant of carbon balance in European forests. Nature, 404, 861-865.
- Van Dijk, A.I.J.M and Dolman A.J. 2004. Estimates of CO<sub>2</sub> uptake and release among European forests based on eddy covariance data. Global Change Biology, 10, 1445-1459.
- Vitasse, Y., Porte, A.J., Kremer, A., Michalet, R., and Delzon, S. 2009. Response of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. Oecologia, 161, 187-198.
- Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L. and Bazzaz, F.A. 1993. Net exchange of CO<sub>2</sub> in a mid-latitude forest. Science, 260, 1314 – 1317.
- Woods, D.B. and Turner, N.C. 1971. Stomatal response to changing light by four tree species of varying shade tolerance. New Phytologist. 70, 77-84.

## TABLES

 Table 1. Site Characteristics

Stand Parameter	Condition
Location	42° 38' 7.124'' N 80° 33' 27.222'' W
Elevation	210.6 m
Tower Height	35 m
<b>Dominant Overstory Species</b>	white oak (Quercus alba)
Secondary Overstory Species	red oak ( <i>Quercus rubra</i> ) sugar maple ( <i>Acer saccharum</i> ) white pine ( <i>Pinus strobus</i> ) red maple ( <i>Acer rubrum</i> ) American beech ( <i>Fagus grandifolia</i> ) yellow birch ( <i>Betula alleghaniensis</i> )
Understory Species	<pre>putty root (Aplectrum hyemale) yellow mandarin (Disporum     lanuginosum) Canada mayflower (Maianthemum     canadense) red trillium (Trillium erectum) black cherry (Prunus serotina) horsetail (Equistum) prostrate tick-trefoil (Desmodium     rotundifolium) wood violet (Viola palmata)</pre>
Maximum Leaf Area Index (LAI) (m <sup>2</sup> m <sup>-2</sup> )	8.0
Average Diameter at Breast Height (DBH) (cm) <sup>a</sup>	$22.29 \pm 14.02$ cm
Average Tree Height (m) <sup>a</sup>	$25.7 \pm 4.77 \text{ m}$
Stem Density (ha <sup>-1</sup> ) <sup>a</sup>	$504 \pm 18$
Mean Tree Basal Area (m <sup>2</sup> ) <sup>a</sup>	$0.0578 \pm 0.0133$

<sup>a</sup> Kula (2013)

i dole 2. Soli characteristics

	Ap horizon	Upper Bm horizon	Lower Bm horizon
<b>Texture Classification</b>	loamy sand	sand	sand
% sand	84.3	92.7	92.2
% silt	9.1	4.0	4.5
% clay	6.6	3.3	3.3
Organic Matter (%)	18.0	1.7	1.4
Bulk Density (g cm <sup>-3</sup> )	0.89	1.17	1.13
Water Content (cm <sup>3</sup> cm <sup>-3</sup> )	0.14	0.10	0.08
Phosphorus (ppm)	21	38	53
Potassium (ppm)	32.4	9.6	20.0
Magnesium (ppm)	139	30	27
Calcium (ppm)	1468	276	260
Sodium (ppm)	7.2	11	10
рН	5.3	5.0	5.3
K/Mg ratio	0.074	0.09	0.25

Season	PAR	Ta	θ	VPD	Precipitation	GEP	R	NEP
	$(\mu \text{ mol } m^{-2} \text{ s}^{-1})$	(°C)	$(m^3 m^{-3})$	(kPa kPa <sup>-1</sup> )	(mm)	$(g C m^{-2})$	$(g C m^{-2})$	$(g C m^{-2})$
Winter	147.3	1.68	0.13	0.214	252.3	0	78.5	-78.5
Spring	409.6	14.42	0.12	0.74	193.6	332.2	262.3	67.6
Summer	439.1	22.9	0.05	0.99	296.9	767.9	417.0	346.4
Autumn	142.0	7.83	0.11	0.30	258.6	92.2	164.4	-72.4
Annual Totals					1001.4	1192.3	922.2	263.1

Table 3. Seasonal daily average or total meteorological variables and carbon fluxes measured at TPD in 2012.

PAR is incoming photosynthetic active radiation,  $T_a$  is ambient air temperature,  $\theta$  is average soil moisture in uppermost 30cm layer of soil, VPD is vapour pressure deficit.

Precipitation, GEP, R and NEP are seasonal totals.

Independent Variable	Parameter Estimate	<b>Standard Error</b>	t Score	p Value
(a) NEP				
VPD	-1.34352	0.04937	-15.50	<.0001
Downwards PAR	7.49965	0.08670	117.03	< . 0001
Soil Temperature (T <sub>s</sub> )	-0.03219	0.06408	-0.26	0.7973
Soil Moisture $(\theta)$	-0.76199	0.07900	-9.65	<.0001
Air Temperature (T <sub>a</sub> )	0.47031	0.13316	3.53	0.0004
(b) GEP				
VPD	-2.26168	0.13666	-16.55	<.0001
Downwards PAR	5.56753	0.10283	54.14	<.0001
Soil Temperature (T <sub>s</sub> )	3.44405	0.21673	15.89	<.0001
Soil Moisture $(\theta)$	0.34863	0.12869	2.71	0.0068
Air Temperature (T <sub>a</sub> )	0.60583	0.24495	2.47	0.0134
(c) R				
VPD	0.03245	0.01469	2.21	0.0272
Downwards PAR	-0.05733	0.01086	-5.28	<.0001
Soil Temperature (T <sub>s</sub> )	1.43084	0.02123	67.38	<.0001
Soil Moisture $(\theta)$	0.09824	0.01338	67.87	<.0001
Air Temperature (T <sub>a</sub> )	0.05268	0.02256	2.34	0.0195

**Table 4.** Results of multivariate linear analysis for carbon fluxes.



**Figure 1.** The annual course of meteorological variables for January 1 to December 30 2012. (a) daily mean incident photosynthetic active radiation (PAR<sub>down</sub>) in  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>, (b) daily mean air temperature (T<sub>a</sub>) measured above canopy (solid line), and daily mean soil temperature (T<sub>s</sub>) for 30cm soil layer (dashed line) in °C, (c) daily mean specific humidity (Q<sub>s</sub>) in g kg<sup>-1</sup>, (d) daily mean soil volumetric water content ( $\theta$ ) for 30cm soil layer in m<sup>3</sup> m<sup>-3</sup> and (e) daily total precipitation (P) in mm day<sup>-1</sup>.



**Figure 2**. Annual net ecosystem productivity, NEP (a); gross ecosystem productivity (GEP) (solid line) and ecosystem respiration (R) (dashed line) (b). NEP, GEP and R for 2012 are estimated at  $263 \pm 30$ , 1192 and 922 g C m<sup>-2</sup>, respectively.



**Figure 3.** Daily NEP in g C m<sup>-2</sup> day<sup>-1</sup> (a); daily mean ambient air temperature above forest canopy ( $T_a$ ) in °C (b); daily mean soil moisture content for uppermost 30cm soil layer ( $\theta$ ) in m<sup>3</sup> m<sup>-3</sup> (c).



**Figure 4.** Relationship between half-hourly gross ecosystem productivity (GEP) in  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> and incoming photosynthetically active radiation (PAR) in  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> for the 2012 growing season. Symbols represent bin-averaged GEP values using a PAR bin size of 25  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. The curve of best fit is a rectangular hyperbola with an r<sup>2</sup> goodness of fit of 0.96.



**Figure 5.** Gross ecosystem productivity (GEP) in g C m<sup>-2</sup>day<sup>-1</sup> response to daily mean vapor pressure deficit (VPD) in kPa. The non-linear curve is fit with the equation  $GEP = -6.5983 \text{ VPD}^2 + 16.7795 \text{ VPD} - 1.9379$ .



**Figure 6.** Gross ecosystem productivity (GEP) in g C m<sup>-2</sup>day<sup>-1</sup> response to daily mean soil moisture ( $\theta$ ) for top 30 cm soil layer in m<sup>3</sup> m<sup>-3</sup> day<sup>-1</sup>. The non-linear curve is fit by the equation GEP = -79.1489  $\theta^2$  - 42.1981  $\theta$  + 10.8659.



**Figure 7**. Water use efficiency (WUE) curve for 2012 growing season: daily mean gross ecosystem productivity (GEP) in g C  $m^{-2} day^{-1} vs$  daily total evapotranspiration (E) in mm day<sup>-1</sup> (or kg  $m^{-2} day^{-1}$ ) for spring, summer and autumn months of the growing season. The non-linear curve is fit by the equation: GEP = -0.5704 E<sup>2</sup> + 4.5977 E + 0.6219.