



Long-term variability and environmental control of the carbon cycle in an oak-dominated temperate forest



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ABSTRACT

Our understanding of the long-term carbon (C) cycle of temperate deciduous forests and its sensitivity to climate variability is limited due to the large temporal dynamics of C fluxes. The goal of the study was to quantify the effects of environmental variables on the C balance in a 70-year-old mixed-oak woodland forest over a 7-year period in northwest Ohio, USA. The net ecosystem exchanges (NEE) of C were measured using the eddy-covariance technique. Long-term mean NEE, ecosystem respiration (ER), and gross ecosystem productivity (GEP) were -339 ± 34 , 1213 ± 84 , and 1552 ± 82 g C m⁻² year⁻¹, respectively. Warming increased ER more than GEP when the available water was not limited, but decreased GEP more than ER when the available water was limited, resulting in decreasing net C fluxes under both conditions. The decreasing net C sink in summer was associated with increasing air temperature (T_a) in spring. The leaf area index (LAI), photosynthetically-active radiation (PAR), and T_a were the most important determinants of NEE for spring, summer, and winter, respectively; however, these variables failed to explain NEE for autumn. The most important determinants of ER and GEP were soil temperature (T_s) in spring, T_a and PAR in summer, and T_a in autumn. T_a was the only control of ER in winter. The annual variation in NEE was larger than that of GEP or ER. The controls of GEP on NEE were more pronounced seasonally and annually than those of ER. The annual GEP was consistently more variable than the annual ER. GEP was also seasonally and annually correlated with ER. Practical models derived from different combinations of independent variables effectively predicted 87%, 80%, and 93% of the monthly variability in NEE, ER, and GEP, respectively. We concluded that the variability in C fluxes was more responsive to increasing T_a and T_s than to variations in seasonal and annual precipitation. The study implies that a warmer climate is likely to reduce the forest productivity and C-sink capacity of oak ecosystems in the future, especially in instances when water inputs become limiting.

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1. Introduction

Global climate models predict an increase in air temperature (T_a) and spatiotemporal variation in local precipitation (P) and soil water dynamics in northern mid-latitudes (IPCC, 2007; Concilio et al., 2009; Yang et al., 2010). Such changes are anticipated to alter the carbon (C) cycles of forest ecosystems (Niu et al., 2008; Jassal et al., 2009). Temperature and water availability are two of the

most important determinants of interannual variability in the forest C balance (Ciais et al., 2005; Sun et al., 2011). Whether increases in T_a have positive effects or water stresses have negative effects on increases in net ecosystem exchanges (NEE, i.e., negative net ecosystem productivity, NEP) of C are still uncertain because of the complex interplay of T_a and water availability and forest productivity and ecosystem respiration (ER) (Sun et al., 2011). For example, a temperature rise may stimulate ER and possibly offset or negate increases in gross ecosystem productivity (GEP; Barr et al., 2002; Carrara et al., 2003; Chen et al., 2004a).

The NEE between the biosphere and atmosphere represents the difference of two large C fluxes between GEP and ER, both of which respond differently to T_a and water dynamics. NEE is difficult to

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quantify and costly to measure over long periods of time (Chen et al., 2008). We are currently unsure as to whether GEP and ER respond positively to a changing climate. Kirschbaum (2000) and Reichstein et al. (2002) postulated that both GEP and ER could increase with increases in T_a . However, Ciais et al. (2005) and Jassal et al. (2008) found that atmospheric warming and dry soils could lead to reductions in both GEP and ER. There is debate concerning interannual variability in GEP and ER and, thus, NEE and the C balance. Savage and Davidson (2001) showed that both GEP and ER had comparable ranges in interannual variation, both sources of variation were considerably larger than that of NEE. In contrast, Griffis et al. (2003), Allard et al. (2008), and Zha et al. (2009) concluded that there was more interannual variability in GEP than in ER and the variation in GEP contributed the most to NEE in deciduous boreal forests. Similarly, Arain et al. (2002) found that year-to-year variations in ER were small when compared to those in GEP of forests. Then again, Bubier et al. (2003) and Dunn et al. (2007) found that annual ER was more variable than annual GEP and ER was the main variable in the C balance of European forests.

Temperate deciduous forests in northern mid-latitudes sequester large amounts of atmospheric CO_2 and contribute significantly to the global C cycle (Barford et al., 2001; Pan et al., 2011). The high productivity and seasonal variability of these forests (Chen et al., 2002; Powell et al., 2006) provide a template for modeling multi-year controls of seasonal environmental variables on C fluxes (Curtis et al., 2005; Kljun et al., 2006; Stoy et al., 2006). A warmer climate may induce reductions in the leaf area index (LAI) and result in a decrease in the net C sink in temperate deciduous forests (Dantec et al., 2000; Law et al., 2002). However, long-term studies in these forests indicate that changes in C fluxes are highly variable across spatiotemporal scales (Xiao et al., 2008; 2010; Yuan et al., 2009) and more long-term datasets are required to better identify interannual variations in C fluxes and potential emergent-scale processes (Wilson and Baldocchi, 2001; Levin, 2002; Dunn et al., 2007; Allard et al., 2008).

Annual changes in NEE are usually attributed to climate variability (Barford et al., 2001; Ma et al., 2007), stand age (Chen et al., 2004b), and disturbance (Chen et al., 2004a,c), which impact ER and GEP directly (e.g., the responses of GEP to light, temperature, and soil water) and indirectly (e.g., the responses of GEP and ER to leaf phenology, canopy structure, and warm climate). Little is known about the multi-year effects of increasing temperatures, limiting water inputs and humidity, or dynamics of leaf area on seasonal GEP and ER or, thus, NEE in the widespread oak (*Quercus*) forests found in mid-latitude regions. We measured C and water fluxes continuously in a 70-year-old mixed-oak woodland forest over a 7-year period from 2004 through 2010. The eddy flux site is within a large remnant oak-woodland forest in Oak Openings Preserve Metropark of northwest Ohio, USA. The study region has a remarkable number of rare and endangered species including 145 plants that are potentially threatened or endangered in Ohio. The study site is one of the US–China Carbon Consortium (USCCC) sites (Sun et al., 2009), which has been incorporated into the Ameriflux network of sites.

The objectives of the study were to: (1) quantify variability in the C cycle; (2) understand how variability in the controlling variables influences the C balance in a temperate deciduous forest over multiple years; and (3) parameterize practical C models that can be readily used to estimate monthly NEE, ER, and GEP for similar forests.

2. Materials and methods

2.1. Study site

The eddy flux site is located in an oak-dominated forest near the city of Toledo (N 41.5545°, W 83.8438°), Ohio, USA. The long-term

means of annual mean air temperature (i.e., T_a) was 9.2 °C and annual total P was 840 mm (<http://www.ncdc.noaa.gov/oa/ncdc.html>). The research site, covering 107 km² (23%) of the Oak Openings region, is characterized by flat topography with elevations ranging from 200 m to 205 m. The study site sits on a band of sandy soil deposits along an ancient lakeshore that was created during the last glacial retreat, about 11,000 years ago. Sandy soil lies above a layer of clay that opposes the penetration of water and causes the perched groundwater table to be close to the surface. High exposed spots are xeric, providing conditions suitable for dry prairie communities, whereas low spots are moist to wet throughout the entire year, with standing water appearing in spring and winter.

Plant species composition and stand biometric properties were measured on 12 FIA-style plots within the 100 ha area using USDA Forest Service Forest Inventory and Analysis (FIA) plot design (<http://www.fia.fs.fed.us/library/>). All trees with diameter at breast height (dbh; 1.37 m above ground) >3 cm were tagged, identified to species, and measured annually. The mean of total biomass at the site was 20,345 ± 2180 g C m⁻², of which 9600 ± 650 g C m⁻² was in aboveground biomass, 1360 ± 1280 g C m⁻² in belowground biomass, 1140 ± 655 g C m⁻² in litter, and 8225 ± 2405 g C m⁻² in soil (Noormets et al., 2008). Phenological stages were defined by bud-break (start of pre-growth phase), 95% full leaf expansion (start of growth phase), start of leaf discoloration (start of pre-dormancy phase), and 95% leaf fall (start of dormancy phase), following DeForest et al. (2006). The landscape provides diverse habitats for plants. The heights of the dominant trees were ~24 m, with an average canopy height of ~20 m. As of 2012, the 70-year-old mixed-oak woodland forest is dominated by *Quercus rubra* (red oak; 31%), *Quercus alba* (white oak; 26%), *Quercus velutina* (black oak; 14%), *Quercus macrocarpa* (Bur Oak; 8%), and other species including *Acer rubrum* (red maple; 10%), *Prunus serotina* (black cherry; 5%), *Sassafras albidum* (sassafras; 2%), and *Carya* sp. (Hickory; <1%) (Brewer and Vankat, 2004; DeForest et al., 2006).

2.2. Flux, meteorological, and vegetation measurements

The 34-m-tall scaffold tower was surrounded in all directions by a uniform canopy of similar tree species and ages, extending to approximately 600 m of unbroken fetch. Turbulent fluxes of CO_2 and H_2O between the forest canopy and atmosphere were measured using eddy-covariance (EC) instruments placed at the tower top. The open-path EC system consists of a LI-7500 infrared gas analyzer (IRGA; Li-COR Biosciences, Lincoln, NE, USA) and a 3-dimensional sonic anemometer (CSAT3; Campbell Scientific, Inc. (CSI), Logan, UT, USA). Instruments were mounted along the tower at 1.5, 5, 16, and 22 m above the ground. Each 30-min mean flux value was calculated as the covariance of vertical wind speed, air temperature, and $\text{CO}_2/\text{H}_2\text{O}$ densities using the Webb–Pearman–Leuning correction (Webb et al., 1980; Massman and Lee, 2002) using EC_processor software (<http://research.eee-science.utoledo.edu/lees/ECP/ECP.html>; Noormets et al., 2008). Wind coordinates to mean streamline plane were rotated (Wilczak et al., 2001), which were calculated from mean wind data over an entire year. Sonic temperature was corrected for changes in atmospheric humidity and pressure (Schotanus et al., 1983). Raw data spikes (>6 standard deviations) were removed and 30-min fluxes for the warming of the IRGA above air temperature were corrected (Burba et al., 2006; Grelle and Burba, 2007). The LI-7500 was calibrated every 4–6 months in the laboratory using zero-grade nitrogen, a dew-point generator (LI-610, Li-COR, Inc., Lincoln, NE, USA), and NOAA/CMDL-traceable primary CO_2 standards. NEEs ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ or $\text{g C m}^{-2} \text{ year}^{-1}$) were calculated as sums of corrected CO_2 fluxes and CO_2 storage changes in the canopy–air layer. We used the sign convention by which positive NEE indicated flux away from the surface (i.e., C release from the surface corresponds to $\text{NEE} > 0$). The CO_2 storage was estimated as the

mean rate of 30-min change in CO₂ concentrations, measured at four heights (i.e., 1.5, 5, 16, and 22 m) using a LI-800 analyzer (Li-COR) within the canopy (Noormets et al., 2007; Yang et al., 2007).

Latent heat (LE, W m⁻²) was calculated from the difference between measured water vapor flux and storage change in water vapor flux in the canopy–air space from EC measurements. ET (mm) was total ecosystem evapotranspiration, including plant transpiration (i.e., dry canopy transpiration) and evaporation from soil and plant surfaces (i.e., canopy interception or wet canopy evaporation). Daily, seasonal, and annual ET were calculated by summing the total corresponding 30-min values converted from LE. Sensible heat (H_s , W m⁻²) fluxes were measured by the EC system. A number of meteorological variables at multiple vertical levels were measured and reported as 30-min means. T_a (°C) and relative humidity (RH, %) were both measured by HMP45AC (Vaisala, Finland) above the canopy at the same height as the IRGA and below the canopy. Photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured by a LI-190SB (Li-COR) above and below the canopy. A CNR-1 sensor (Kipp and Zonen, Delft, The Netherlands) measured downward and upward shortwave and longwave radiation. Net radiation (R_n , W m⁻²) was derived by summing up net shortwave and longwave radiation using all four measured radiation components. Soil heat flux (G , W m⁻²) was measured at three locations using HFT3 flux plates (REBS, Seattle, WA, USA) buried 5 cm below the ground. The energy balance closure was evaluated, with the linear regression for each year, of the dependent flux variable (turbulent energy, $H_s + \text{LE}$) against the independently derived energy (available energy, $R_n - G$) on a 30-min basis. The mean R^2 and slopes of annual relationships of turbulent and available energy was 0.84 (± 0.02) and 0.57 (± 0.01) from 2004 through 2010. Annual R^2 varied from 0.75 in 2004 to 0.88 in 2008 and annual slopes varied from 0.55 in 2007 to 0.60 in 2008. Soil temperature (T_s , °C) was monitored using CS107 probes (CSI) at 5 cm depths, respectively. Soil volumetric water content (VWC, %) for the top 30 cm soil layer was measured using vertically inserted CS616 Time Domain Reflectometer probes (CSI). P (mm) was measured using tipping-bucket-type rain gauges (TE-525WS-L, Texas Electronics, Dallas, TX, USA). LAI (m² m⁻²) was obtained from 1-km resolution MODIS LAI/FPAR Collection 5 (<http://daac.ornl.gov/MODIS/modis.shtml>; Shabanov et al., 2005) with an online subset output of a 3 km \times 3 km pixel subset centered on the flux tower, which provided a time-series of LAI from 2004 through 2010.

2.3. Data quality control and gap-filling method

All 30-min flux data from the EC tower were quality checked, including stationarity, integral turbulence characteristics, and friction velocity (u_*) thresholds (Noormets et al., 2007, 2008). The threshold of u_* below which flux loss occurred was determined from the seasonal binned relationships between turbulent fluxes of CO₂ and u_* (Schmid et al., 2003). The threshold was consistent between different seasons, but differed slightly among years from 0.18 m s⁻¹ in 2004 and 0.21 m s⁻¹ in 2005. The periods with poor turbulent developments were filtered out and treated as gaps. Additionally, the gaps also occurred while the system or sensor malfunctioned or during periods of instrument calibration and site maintenance. Gaps were more frequent during the night than during the day. Data gaps were 38.1% of daytime and 44.1% of nighttime NEE in 2004, 39.5% and 44.1% in 2005, 37.2% and 41.7% in 2006, 53.6% and 58.9% in 2007, 43.7% and 54.3% in 2008, 43.7% and 54.3% in 2009, and 45.4% and 59.8% in 2010. The mean percentage of gaps in NEE was more than the network-wide average of 35% (Falge et al., 2001) and this is mainly typical of sites with open-path IRGAs that were sensitive to precipitation and condensation (Noormets et al., 2008). The

gap-filling models were chosen from among 32 evaluated model variants based on the magnitude and bias of residuals and the stability of model parameter estimates (Noormets et al., 2007). A comparison of our gap-filling algorithm against 16 other widely used approaches showed that the bias was about average for short-term gaps and among the lowest of all models for medium and long-term gaps (Moffat et al., 2007). The uncertainty in annual NEE, caused by gaps and gap-filling, was estimated according to Aurela et al. (2002) and Flanagan and Johnson (2005). The 30-min gap in NEE was filled using a dynamic parameter-process model as described by Noormets et al. (2007), which was based on a Lloyd and Taylor (1994) model. Firstly, the respiration model was parameterized using nighttime data:

$$\text{ER} = R_{10} \times e^{\{(E_a/R) \times [(1/T_{\text{ref}}) - 1/(T_a + 273.15)]\}} \quad (1)$$

where R_{10} is the reference respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), normalized to a base temperature ($T_{\text{ref}} = 283.15 \text{ K} = 10 \text{ }^\circ\text{C}$; $R_{10} = a_0 + a_1 \times \text{VWC}/100$; where a_0 and a_1 are equation parameters), E_a is the activation energy ($\text{kJ mol}^{-1} \text{ K}^{-1}$), R is the universal gas constant ($8.3134 \text{ J mol}^{-1} \text{ K}^{-1}$), and T_a is the air temperature above the canopy (°C).

Daytime ER was estimated from the nighttime NEE-based calibration of Eq.(1), assuming consistency of temperature sensitivity between the nighttime and daytime exchanges. Once daytime estimates of ER were available, gaps in daytime NEE were filled. The gap-filling of daytime NEE was achieved with:

$$\text{NEE} = \text{ER} + [(\alpha \times \text{PAR} \times P_{\text{max}})/(\alpha \times \text{PAR} + P_{\text{max}})] \quad (2)$$

where α is the apparent quantum yield ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$), PAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) is photosynthetically active radiation, and P_{max} is the maximum apparent photosynthetic capacity of the canopy ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). GEP was calculated as the difference between ER and NEE (i.e., $\text{GEP} = \text{ER} - \text{NEE}$).

Short gaps (<1.5 h) were filled by linear interpolation and longer gaps (≥ 1.5 h) were filled using the Mean Diurnal Variation method (Falge et al., 2001) for the 30-min missing meteorological variables. For the Mean Diurnal Variation method, missing values for any given 30-min gap were replaced with an average of values of the adjacent seven-day window, which was at exactly the same time of day. Missing P gaps were replaced by the P -values from the Toledo Express Airport weather station (N 41.5886°, W 83.8014°), which was ~ 3 km northeast of the flux site. Saturation vapor pressure (e_s , kPa), actual vapor pressure (e_a , kPa), and vapor pressure deficit (VPD, kPa) were calculated using filled T_a and RH above the canopy.

The growing season length was defined as the period between the first and last occurrences of three continuous days when daytime C uptake exceeded 5% of the summer maximum C uptake (Zha et al., 2009). The growing season started on April 15 in 2004 (DOY = 136), May 1 in 2005 (121), May 16 in 2006 (136), May 20 in 2007 (152), May 12 in 2008 (133), May 11 in 2009 (131), and May 14 in 2010 (134). We defined April through May as spring, June through September as summer, October through November as autumn, and the first 3 months and the last month of the year as winter. All data processing and statistical analyses were conducted using SAS 9.2 software (SAS, Institute, Inc., Cary, NC, USA). Variables T_s , T_a , P , VWC, PAR, VPD, and LAI were identified as potential drivers (i.e., independent variables). We determined the contribution of each variable on C fluxes on a monthly basis with the Pearson Correlation Coefficient (PCC).

3. Results

3.1. Microclimate and vegetation biomass

Mean annual T_a was 9.9 °C and T_s was 10.7 °C during 2004–2010 (Fig. 1a; Table 1). Annual T_a during the study period was always higher than the 1971 through 2000 mean of 9.2 °C. T_a was higher than the past 30-year mean across all study years, with the highest being 10.7 °C in 2006 and the lowest being 9.3 °C in 2008. The lowest T_a of daily minima varied from –28.2 °C in 2009 to –15.5 °C in 2006 and the highest T_a of daily maxima varied from 33.1 °C in 2009 to 40.5 °C in 2004 (Fig. 1a). Interannual differences in mean daily temperatures were larger in winter than in summer and winter T_s significantly increased annually (Fig. 1a). Year 2004 had the lowest mean daily PAR and year 2010 had the highest, with values being 186 and 211 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1b), respectively. The first and second highest LAI were 4.74 and 4.51 in July in 2006 and 2008 (Fig. 2). Mean seasonal LAI was 1.73 $\text{m}^2 \text{m}^{-2}$ in spring, 3.73 $\text{m}^2 \text{m}^{-2}$ in summer, and 0.79 $\text{m}^2 \text{m}^{-2}$ in autumn.

Soil volumetric water content (VWC) presented a maximum in spring and a minimum in summer (Figs. 1b and 3). Mean annual total P was 824 mm, varying substantially from 668 mm in 2004 to 1019 mm in 2006 (Fig. 1c; Table 1). Year 2010 had the lowest summer P of 265 mm (18% lower than the average summer P over the past 30 years) while 2008 had the highest summer P of 531 mm (65% higher than the average summer P over the past 30 years). The highest daily P varied from 29 mm in 2004 to 62 mm in 2006. The 7-year mean of daily maximum P varied from 14 mm to 48 mm in spring, from 27 mm to 62 mm in summer, from 16 mm to 34 mm in autumn, and from 17 mm to 47 mm in

winter. Mean monthly P was more than that of ET in winter, spring, and autumn but not in summer (Fig. 3). Seasonal ET was also correlated with seasonal P .

3.2. Seasonal and interannual changes in C fluxes

The C fluxes showed variability over the 7-year study period on a seasonal and interannual basis (Fig. 1d). Fig. 1e shows the beginning dates of the growing season. Cumulative GEP surpassed ER on DOY 190 in 2004, DOY 188 in 2005, DOY 189 in 2006, DOY 186 in 2007, DOY 188 in 2008, DOY 185 in 2009, and DOY 184 in 2010 (Fig. 1e). Mean summer ER and GEP accounted for 49% and 82% of their annual sums, respectively. The ER parameter of R_{10} was variable in summer and annual Q_{10} varied from 1.6 to 2.7. In each year, ER, GEP, and NEP were low in winter and early spring and rose sharply during leaf emergence and reached their respective maxima during early summer. ER, GEP, and NEP declined slowly during the fully leafed summer period and dropped sharply during leaf senescence in autumn. During late autumn, GEP < ER and the system was roughly C-neutral. The mean change in NEP ranged from 1.4 $\text{g C m}^{-2} \text{day}^{-1}$ to 3.9 $\text{g C m}^{-2} \text{day}^{-1}$ in winter.

Mean NEE, ER, and GEP were –339 (34), 1213 (84), and 1552 (82) $\text{g C m}^{-2} \text{year}^{-1}$ (Table 1), with coefficients of variance being –11, 7, and 5, respectively. NEE functioned as a C source in spring, autumn, and winter and a C sink in summer (i.e., seasonal GEP > ER only in summer; Fig. 1d and 4). Most C-source days occurred during rainy or cloudy days with low PAR (Fig. 1b–d). The highest daily C source varied from 4.6 g C m^{-2} in 2008 to 5.7 g C m^{-2} in 2009. The highest C sink varied from 10 $\text{g C m}^{-2} \text{day}^{-1}$ in 2010 to 13 $\text{g C m}^{-2} \text{day}^{-1}$ in 2007. Notably, there were C-source days in summer. Year 2006 had six C-source days with the highest daily NEE being 4 g C m^{-2} . Year 2007 had two C-source days with the highest daily NEE being 2 g C m^{-2} . Year 2009 had one C-source day with daily NEE being 3 g C m^{-2} . Year 2010 had two C-source days with the highest daily NEE being 1 g C m^{-2} . However, years 2004, 2005, and 2008 had no C-source days in summer. Mean spring NEE at 98 g C m^{-2} was lower than mean autumn NEE at 126 g C m^{-2} .

Correlative relationships between GEP and NEE were higher than those between ER and NEE on a seasonal basis. GEP explained 75%, 84%, and 43% of NEE ($p < 0.01$) in spring, summer, and autumn, respectively, while ER failed to explain NEE during those periods. ER was correlated with GEP in spring and summer with PCC being 0.80 and 0.79, respectively. Controls of GEP on NEE were more pronounced seasonally than annually. ER and GEP were correlated on an annual basis (Fig. 5). The mean of water use efficiency (WUE, g C kg^{-1}) as the ratio of GEP to ET was $3.4 \pm 0.09 \text{ g C kg}^{-1}$ in summers. Mean monthly WUE varied from 3.0 g C kg^{-1} in 2010 to 3.6 g C kg^{-1} in 2009 (Fig. 6).

3.3. Biophysical regulations

C fluxes were correlated with the following variables, in significance order from highest to lowest: estimated LAI > temperature (T_a and T_s) > energy input (PAR) and humidity (VPD) > water inputs (P and VWC) on an interannual basis. Annual GEP decreased more than annual ER and, thus, the net C sink decreased. High annual PAR was correlated with decreasing GEP (PCC = 0.80; $p < 0.04$). High annual T_a was correlated with the reduced net C sink (PCC = 0.96; $p < 0.001$). More importantly, there was a strong connection between high spring T_a and reduced summer C uptake (PCC = –0.78; $p < 0.04$). Table 2 shows the main controls on monthly NEE, ER, and GEP on a seasonal basis.

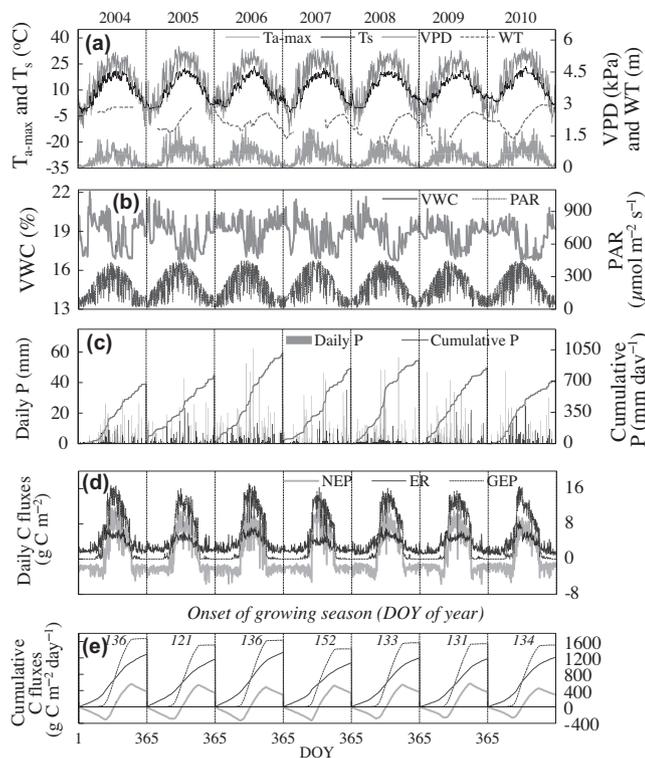


Fig. 1. Daily (a) maximal T_a ($T_{a-\text{max}}$, °C) and mean T_s (°C), VPD (kPa), and WT (m), (b) VWC (%) and PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$), (c) daily and cumulative P (mm day^{-1}), and (d) daily and (e) cumulative C fluxes (NEP, ER, and GEP, $\text{g C m}^{-2} \text{day}^{-1}$) from 2004 to 2010. WT was groundwater table depth. NEP was net ecosystem productivity and negative NEE. See Table 1 for other abbreviations. Measurement limit of the groundwater table was at approximately 3 m of soil depth.

Table 1

Annual totals of C fluxes [i.e., net ecosystem exchange of carbon (NEE), ecosystem respiration (ER), and gross ecosystem productivity (GEP); g C m^{-2}], P (mm), and ET (mm); annual means of T_a ($^{\circ}\text{C}$), T_s ($^{\circ}\text{C}$), VWC (%), PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$), and VPD (kPa); and the maxima of LAI ($\text{m}^2 \text{m}^{-2}$) during the growing season from 2004 to 2010. Values in parentheses indicate monthly standard errors (SE).

Year	NEE ($\text{g C m}^{-2} \text{ year}^{-1}$)	ER	GEP	P (mm year^{-1})	ET	T_a ($^{\circ}\text{C}$)	T_s	VWC (%)	PAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	VPD (kPa)	LAI ($\text{m}^2 \text{m}^{-2}$)
2004	-379 (39)	1292 (14)	1671 (50)	668 (12)	626 (12)	9.5 (2.7)	10.0 (2.1)	18.88 (0.25)	186 (26)	0.41 (0.07)	3.77
2005	-342 (38)	1173 (10)	1515 (47)	766 (10)	593 (12)	10.0 (3.0)	10.1 (2.2)	18.68 (0.26)	210 (30)	0.54 (0.10)	4.08
2006	-289 (38)	1342 (14)	1631 (52)	1019 (14)	611 (12)	10.7 (2.4)	10.5 (2.0)	19.14 (0.19)	197 (29)	0.50 (0.08)	4.74
2007	-338 (41)	1083 (10)	1421 (47)	840 (15)	603 (12)	10.0 (2.9)	10.2 (2.1)	18.80 (0.23)	207 (31)	0.54 (0.10)	4.46
2008	-367 (37)	1201 (14)	1568 (50)	930 (19)	594 (12)	9.3 (2.8)	10.6 (2.1)	18.82 (0.25)	208 (30)	0.49 (0.09)	4.51
2009	-362 (38)	1184 (13)	1546 (49)	847 (10)	578 (11.5)	9.4 (2.7)	11.1 (1.7)	18.76 (0.19)	204 (28)	0.48 (0.08)	3.82
2010	-298 (33)	1216 (16)	1514 (48)	700 (11)	670 (13.2)	10.5 (3.0)	12.1 (1.9)	18.51 (0.27)	211 (29)	0.55 (0.09)	4.37
Mean (\pm SE)	-339 (34)	1213 (84)	1552 (82)	824 (125)	611 (30)	9.9 (0.6)	10.7 (0.7)	18.80 (0.19)	203 (9)	0.50 (0.05)	4.25 (0.14)

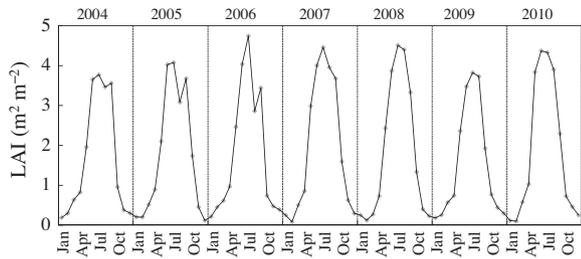


Fig. 2. Monthly leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$) from 2004 to 2010. LAI was obtained from 1-km resolution MODIS LAI/FPAR Collection 5 with an online subset output of a $3 \text{ km} \times 3 \text{ km}$ pixel subset centered on the flux tower, which provided a time series of LAI.

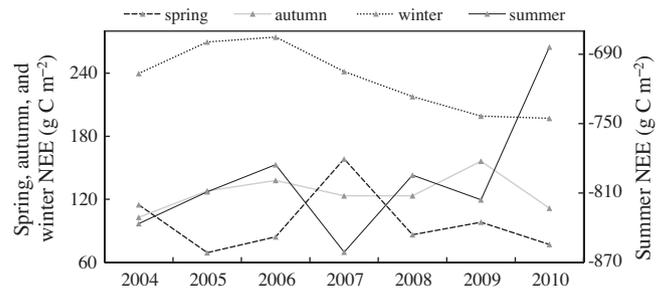


Fig. 4. Seasonal net ecosystem exchanges of C (NEE, g C m^{-2}) from 2004 to 2010. We defined April through May as spring, June through September as summer, October through November as autumn, and the first 3 months and the last month of the year as winter.

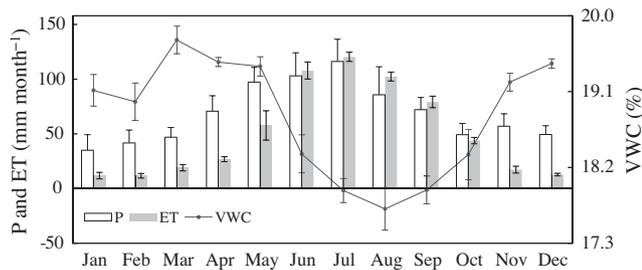


Fig. 3. Mean monthly precipitation (P , mm), actual evapotranspiration (ET, mm), and soil volumetric water content (VWC, %) with standard error values from 2004 to 2010.

3.4. Modeling monthly C fluxes

Different combinations of independent variables were tested to derive the best models to examine the influences on NEE, ER, and GEP on a monthly basis ($N = 7 \text{ years} \times 12 \text{ months} = 84$; $p < 0.0001$).

$$\text{NEE} = -576.56 + 34.01 \cdot \text{VWC} - 0.17 \cdot \text{LAI} \times \text{PAR} \quad (3)$$

$$\text{ER} = 57.76 + 19.48 \cdot \text{LAI} + 0.01 \cdot T_a \times P \quad (4)$$

$$\text{GEP} = 184.39 - 9.91 \cdot \text{VWC} + 4.27 \cdot \text{LAI} \times T_a \quad (5)$$

Table 3 shows F - and p -values, R^2 , and root mean square errors of the estimated models for NEE, ER, and GEP on the monthly basis, i.e., Eqs. (3)–(5). $\text{LAI} \times \text{PAR}$, $\text{LAI} \times P$, and $\text{LAI} \times T_a$ were the most

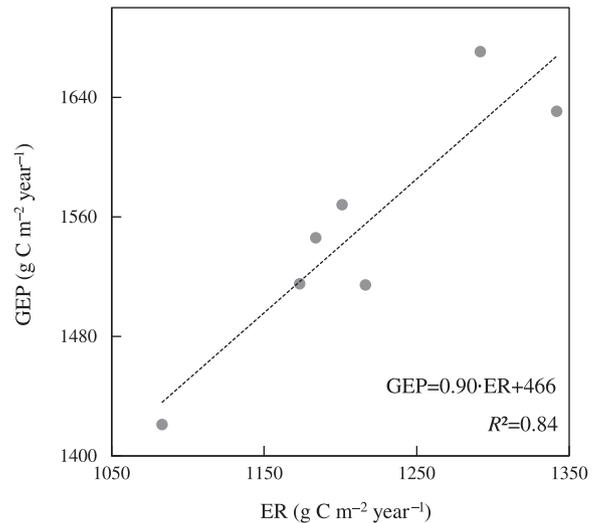


Fig. 5. Linear correlation between annual ecosystem respiration (ER, $\text{g C m}^{-2} \text{ year}^{-1}$) and gross ecosystem productivity (GEP, $\text{g C m}^{-2} \text{ year}^{-1}$) from 2004 to 2010 ($N = 7$).

important controls of NEE, ER, and GEP in a stepwise-selection-regression analysis. Scatter plots (Fig. 7) suggest that the three models can accurately predict monthly C fluxes.

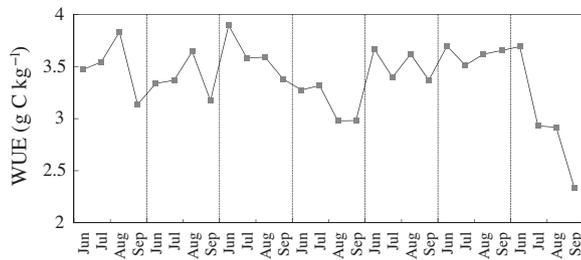


Fig. 6. Mean monthly water use efficiency (WUE, g C kg^{-1} ; the ratio of GEP to ET) in summers.

4. Discussion

4.1. Variability in C balance

The 70-year-old mixed-oak woodland forest was a C sink in all years from 2004 through 2010 (Fig. 1e; Table 1). The annual net C sinks, changing from 289 g C m^{-2} to 379 g C m^{-2} with a mean of $339 \pm 34 \text{ g C m}^{-2}$, were within the ranges of reported annual net C sinks ($70\text{--}739 \text{ g C m}^{-2}$) for temperate forests (Baldocchi et al., 2001). For example, the mean annual NEEs in two mixed oak forests were -224 g C m^{-2} (1991–1995) and -630 (1994–1990; Baldocchi et al., 2001). Annual NEEs varied among the 9 years from -55 g C m^{-2} to -367 g C m^{-2} (mean = -172 ± 94) in a temperate forests in Canada (Barr et al., 2007). Annual NEEs varied from -250 g C m^{-2} to -120 g C m^{-2} during 1993–2000 in a 60- to 80-year-old deciduous forest in northeastern USA (Barford et al., 2001). Daily NEEs (-10.0 to -2.7 g C m^{-2}) and seasonal sum NEEs (-853 to -676 g C m^{-2} ; ± 19) in summer at the site were also within the range of values reported for temperate forests. For example, summer NEEs in a northern temperate broadleaf forest were -6 to $-3 \text{ g C m}^{-2} \text{ day}^{-1}$ (Barr et al., 2002) and NEEs in a scrub oak forests were -2.4 to $-1 \text{ g C m}^{-2} \text{ day}^{-1}$ during the peak net-C-flux season (Powell et al., 2006). Mean summer NEE was -652 g C m^{-2} (± 17) in mature temperate forests in northern Wisconsin, USA (Noormets et al., 2007).

There was more interannual variability in GEP than that in ER, suggesting that the variations in GEP controlled NEE. Barr et al. (2002) and Griffis et al. (2003) yielded the same conclusions for deciduous boreal forests. We also found that annual variations in NEE were larger than those in GEP and ER. Keeling et al. (1996), Myneni et al. (1997), and Dunn et al. (2007) suggest that warming may lengthen the growing season and a net C sink may be increased for multiple years with P in excess of ET. Our study indicated that the length of the growing season had no obvious

Table 3

F - and p -values, R^2 , and root mean square errors ($\text{g C m}^{-2} \text{ month}^{-1}$) of the estimated models for NEE, ER, and GEP on a monthly basis, i.e., Eqs. (3)–(5).

	F values	$Pr > F$	R^2	Root mean square errors
NEE	262.2	<0.0001	0.87	46.59
ER	163.0	<0.0001	0.80	20.23
GEP	541.9	<0.0001	0.93	43.60

change and the net C sink decreased when the annual P exceeded ET across all study years; i.e., ET/P ranged from 68.3% to 95.8% (Table 1; Xie et al., 2013). Additionally, positive controls of high P on C fluxes were lost due to the low water-holding capacity of sandy soils at the site. Kljun et al. (2006) suggested that the relative extent of drought effects on the C balance depended on the characteristics of soils. Where minor amounts of water were stored in the soil because of its coarse texture, benefits of added P were small. Moreover, mean P was lower than ET by 8.7% during summer periods (Fig. 3), likely inducing severe soil water deficit under warming conditions (Fig. 1a); thus, decreasing the annual net C sink. Schwalm et al. (2010) reported that drought-induced decreases in GEP were $\approx 50\%$ more than decreases in ER and, thus, resulted in a decrease in the net C sinks in deciduous forests across the FLUXNET sites. The C-source days during the summer were due to combined controls of climate variability (i.e., cloudy and rainy days with low PAR; Fig. 1b–d).

4.2. Biophysical controls on seasonal C balance

High T_s and T_a enhanced both ER and GEP; LAI was correlated with ER, GEP, and NEE and PAR was correlated with GEP in spring (Table 2). Kirschbaum (2000) and Reichstein et al. (2002) found that both GEP and ER increased with temperature. Griffis et al. (2004) found that GEP increased as a result of a phenological response to warm springs in a southern boreal aspen forest. Moreover, the spring warming with elevated P and high soil water content (i.e., VWC; $p < 0.01$; Fig. 3) increased ER more than GEP and hence NEE increased (Fig. 4). Anthoni et al. (1999) suggested that large P had significant impacts on increasing respiration and respiration was higher in wet seasons than in dry seasons.

Increases in T_a generally meant increases in water loss (Sun et al., 2010). Although the mean annual P exceeded ET by 30%, summer warming induced drought from insufficient water conditions (e.g., P was $< ET$; P and VWC decreased, as indicated by a decreasing groundwater table; Figs. 1 and 3), which suppressed GEP more than ER and, thus, reduced the C-sink capacity of the site (Fig. 4). High PAR was correlated with reduced GEP and net C sink, high T_a and T_s were correlated with reduced ER and GEP, and

Table 2
Pearson correlation coefficient (PCC) between the significant variables (SV) and NEE, ER, and GEP on a monthly basis in spring, summer, autumn, and winter over the 7-year study. See Table 1 for abbreviations.

		NEE	ER	GEP
Spring	SV	LAI ^{***} , PAR ^{**} , T_s , T_a *	T_s ^{****} , T_a ^{****} , LAI ^{***}	T_s ^{****} , LAI ^{***} , T_a ^{**} , PAR ^{**}
	PCC	-0.68, -0.68, -0.60, -0.55	0.90, 0.86, 0.74	0.88, 0.84, 0.82, 0.71
Summer	SV	PAR ^{****} , LAI ^{***} , T_a ^{**} , VPD ^{**}	T_a ^{**} , T_s ^{**}	PAR ^{****} , T_a ^{****} , LAI ^{***} , T_s [*] , VPD ^{**}
	PCC	-0.84, -0.65, -0.62, -0.53,	0.49, 0.47	0.78, 0.66, 0.61, 0.43, 0.40
Autumn	SV	NA	T_a ^{**} , T_s [*]	T_a ^{**} , PAR ^{**} , VWC [*] , T_s [*]
	PCC		0.68, 0.62	0.67, 0.64, -0.62, 0.58
Winter	SV	T_a [*]	T_a [*]	NA
	PCC	0.41	0.41	

**** The significance of p values < 0.0001 .

*** The significance of p values < 0.001 .

** The significance of p values < 0.01 .

* The significance of p values < 0.05 .

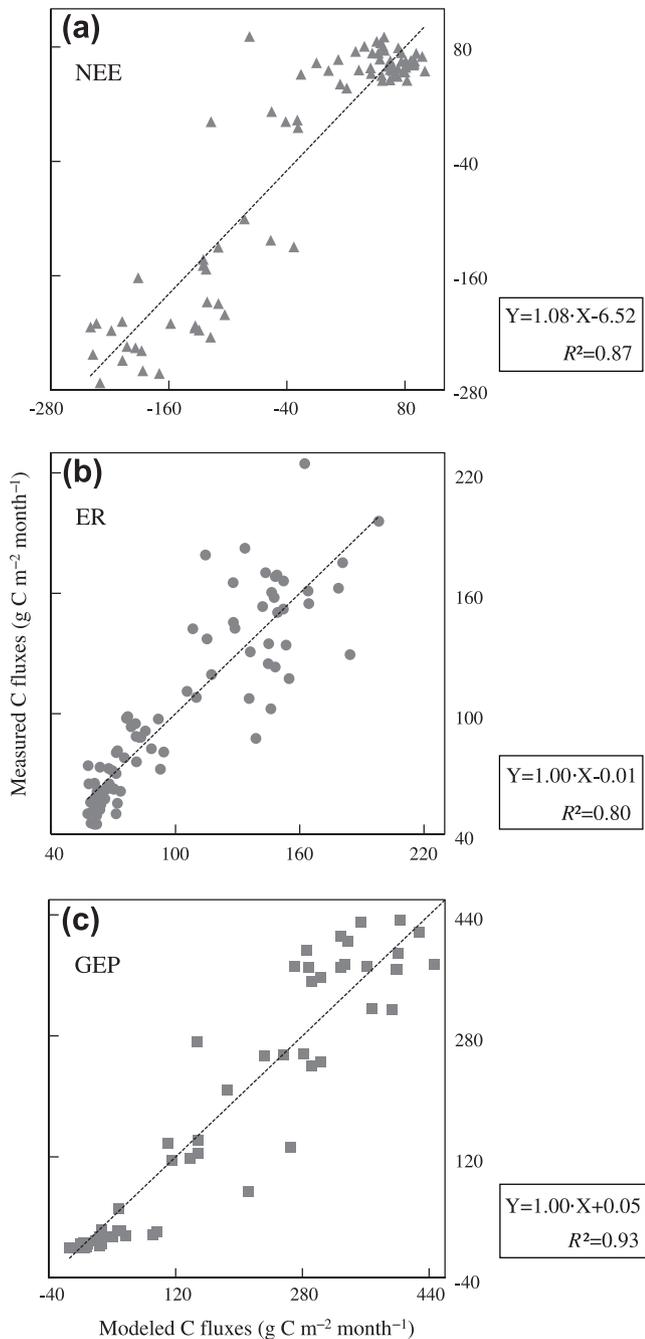


Fig. 7. Linear relationships between modeled carbon fluxes; i.e., (a) NEE, (b) ER, and (c) GEP and measured values using Eqs. (3)–(5) on a monthly basis ($N = 7 \text{ years} \times 12 \text{ months} = 84$).

decreasing GEP was related to decreasing ER leading to lower net C sinks during the summer (Table 2). Similar findings by Ciais et al. (2005) and Granier et al. (2007) show that ER decreases in unison with decreases in GEP, rather than accelerating with increases in T_a when soil water is limited and NEE is reduced with soil water depletion. Barr et al. (2007) reported that drought suppressed both ER and GEP during the growing season, while Griffis et al. (2004) found that decreases in ER resulted from drought in boreal forests.

In autumn, high T_s and T_a led to increases in both ER and GEP (Table 2). However, warm and dry conditions (e.g., decreasing P and VWC; Figs. 1 and 3) depressed GEP more than ER and, thus, NEE increased (Fig. 4). Decreasing VWC was correlated with decreasing GEP, which was correlated with a lower net C sink. Piao

et al. (2008) suggested that the net C sinks of a northern ecosystem were reduced in response to autumnal warming. In winter, GEP = - zero and ER was in balance with NEE; T_s increased ($p < 0.001$) while P and ER decreased ($p < 0.03$ and $p < 0.0002$, respectively; Fig. 4). High infiltration rates and low water-holding capacity of sandy soils and flat topography contributed to the ***diseasing VWC during the first half of the growing season (Fig. 3). Soil water storage and shallow groundwater recharge were essential in supplying the increasing VWC during the second half of the growing season when ET exceeded P (Xie et al., 2013).

Monthly C fluxes were related to the seasonal controls. T_a and T_s controlled C fluxes across all four seasons. PAR and VPD had no obvious effect on C fluxes during the autumn or winter. Spring LAI, summer PAR (Fig. 8b), and winter T_a (Fig. 8d) were the most important determinants of NEE, while no variables were correlated with NEE in autumn. Summer, autumn, and winter T_a (Fig. 8c) and spring T_s were the most important determinants of ER. Spring T_s , summer PAR, and autumn T_a were the most important determinants of GEP. The second most important determinants of ER in spring, summer, and autumn were T_a , T_s , and T_s ; those of GEP were LAI (Fig. 8a), T_a , and PAR. T_a was the most important determinant of ER, while that of GEP was PAR in summer. Ciais et al. (2005) and Schwalm et al. (2010) suggested that environmental controls influenced GEP and ER in different ways in forests. Law et al. (2002) found that ER and GEP responded to temperature differently in temperate deciduous forests. LAI was a key determinant and T_s was the second determinant of NEE on an interannual basis.

4.3. Variability in annual NEE

Our study suggested that a moderate warming with sufficient soil water enhanced GEP more than ER and, thus, the net C sink increased. Soil water storage and shallow groundwater at the study site played important roles in supporting ecosystem-water demands during the growing season. Year 2004 had the second-highest dryness index ($I_a = \text{potential ET}/P$; Xie et al., in press) of 1.3 and had the highest GEP and net C sink, which resulted from mid-range temperature, soil water storage, and shallow groundwater conditions. For example, year 2004 had the highest spring VWC (19.7%) and the second-highest autumn P (126 mm). Although, this year had the lowest P (668 mm) but not the lowest ET (i.e., the second-highest annual value of 626 mm), as indicated by a decreased groundwater table (Fig. 1a), which dropped to its lowest recorded level (>2.5 m) from 2004 through 2010. Therefore, year 2004 had the highest of both GEP and net C sink (379 and 1671 g C m⁻², respectively; Table 1).

A wet and warm climate enhanced ER more than GEP and thus, decreased the net C sink. Year 2006 had the highest annual ER and the lowest net C sink (1342 and 289 g C m⁻² year⁻¹, respectively). Year 2006 also had the highest winter and summer ER (274 and 675 g C m⁻², respectively). These were because year 2006 had the highest annual and seasonal temperatures and water input, likely because year 2006 had the highest annual and winter T_a (10.7 and 1.7 °C, respectively), the highest annual, autumn, and winter P (1019, 143, and 239 mm, respectively), and the highest annual, summer, and autumn VWC (19.1%, 18.3%, and 19.6%, respectively). Additionally, year 2006 had the highest summer P , with the highest daily P reaching up to 62.1 mm day⁻¹. Similar conclusions for deciduous forests indicated that a warmer climate had influence on decreasing a net C sink (Hogg et al., 2002; Barr et al., 2007; Schwalm et al., 2010). Moreover, according to I_a , year 2006 was the only humid year with the lowest I_a being 0.9. The I_a varied from 0.9 in 2006 to 1.5 in 2010. Years 2005 and 2009 were under moderate warming with low ET. Year 2005 had the second-lowest annual ET of 593 mm and 2009 had the lowest annual ET of 578 mm. Thus, the net C sink capacities increased in both years.

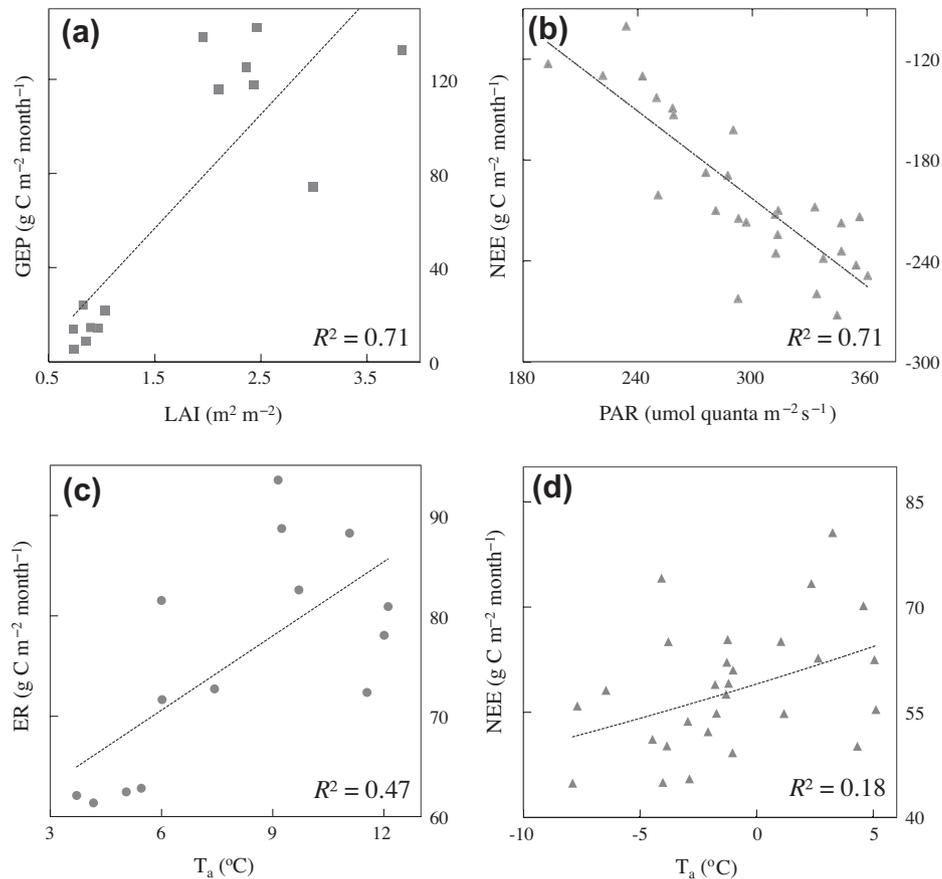


Fig. 8. Representative scatter plots showing the linear relationships between the main determinants and C fluxes ($\text{g C m}^{-2} \text{ month}^{-1}$) on a monthly basis over the 7-year study. (a) LAI and GEP in spring, (b) PAR and NEE in summer, (c) T_a and ER in autumn, and (d) T_a and NEE in winter. See Table 1 for abbreviations.

A warm climate with soil water stress suppressed GEP more than ER and, thus, decreased the net C sink. Year 2010 was the only dry year with the highest I_a being 1.5. Year 2010 had the second-lowest annual net C sink and annual and summer GEP (298, 1514, and 1331 g C m^{-2} , respectively). These were because year 2010 had the highest annual, spring, summer, and autumn T_s (12.1, 13.3, 19.5, and $10.5 \text{ }^\circ\text{C}$, respectively) and the highest spring T_a ($14.6 \text{ }^\circ\text{C}$). Year 2010 also had the lowest annual, spring, and summer VWC (18.5%, 19.2%, and 17.5%, respectively) and the lowest summer P (265 mm). Several deciduous forest sites worldwide have demonstrated that atmospheric warming with a soil water deficit can lead to lower net C sink (Ciais et al., 2005; Allard et al., 2008; Jassal et al., 2009). Zhao and Running (2010) found that drought induced a reduction in terrestrial net primary productivity globally.

4.4. Monthly models of C fluxes

Practical models have been widely used to estimate NEE, ER, and GEP due to the high cost of measuring C fluxes on large spatio-temporal bases (Falge et al., 2001; Xing et al., 2007, 2008a,b; Sun et al., 2011). Long-term monitoring of ecosystems allows for the quantification of temporal relationships between the controls and C fluxes. The developed monthly models (Fig. 7) can be used to estimate C fluxes in oak forests if meteorological and basic parameters are available. This modeling exercise also suggests that C fluxes are mainly controlled by interactions of estimated LAI, energy inputs (T_a and PAR), and water inputs (P and VWC). These models offer new insights into basic external and internal controls on C fluxes and can assist in quantifying C fluxes under normal climatic conditions and in gap-filling mean monthly C fluxes of similar temperate forests.

5. Conclusions

The 70-year-old mixed-oak woodland forest of northwest Ohio, USA, acted as a C sink, sequestering $289\text{--}379$ (339 ± 34.4) $\text{g C m}^{-2} \text{ year}^{-1}$ from 2004 through 2010. The study provided evidence that the interannual C fluxes of temperate deciduous forests are conditional upon the combined environmental controls and on the inter-relationships between ER and GEP. The results indicate that the variability in the net C balance depends more on LAI, T_s , T_a , PAR, and VPD than on P and VWC in the forest ecosystem of the study. Soil water storage and shallow groundwater at the study site played an important role in supporting ecosystem water demands for sustaining forest productivity during the growing season. Warming increased ER more than GEP when water was not limiting, but warming decreased GEP more than ER when water was limiting. Three models parameterized from this study offer new insights on the basic external and internal environmental controls on C fluxes. The study implies that a warmer climate is likely to reduce the C-sink capacity of oak ecosystems in the future, especially during drought episodes. Forest management practices such as prescribed burning and thinning that reduce plant competition for water may be useful to minimize the potential water stress, maximize the carbon sequestration potential, and maintain ecosystem health.

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References

- Allard, V., Ourcival, J.M., Rambal, S., Joffre, R., Rocheteau, A., 2008. Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France. *Global Change Biol.* 14, 714–725.
- Anthoni, P.M., Law, B.E., Unsworth, M.H., 1999. Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. *Agric. For. Meteorol.* 95, 151–168.
- Arain, M.A., Black, T.A., Barr, A.G., Jarvis, P.G., Massheder, J., Verseghy, D.L., Nescic, Z., 2002. Effects of seasonal and interannual climate variability on net ecosystem productivity of boreal deciduous and conifer forests. *Can. J. For. Res.* 32, 878–891.
- Aurela, M., Laurila, T., Tuovinen, J.P., 2002. Annual CO₂ balance of a subarctic fen in northern Europe: importance of the wintertime efflux. *J. Geophys. Res.* 107, 4607.
- Baldocchi, D.D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Fuentes, J., Goldstein, A., Katul, G., Law, B.E., Lee, X., Mahli, Y., Meyers, T., Munger, W., Oechel, W., Paw, U.K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S.W., 2001. FLUXNET, a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. *Bull. Am. Meteorol. Soc.* 82, 2415–2434.
- Barford, C.C., Wofsy, S.C., Goulden, M.L., Munger, J.W., Pyle, E.H., Urbanski, S.P., Hutrya, L., Saleska, S.R., Fitzjarrald, D., Moore, K., 2001. Factors controlling long- and short-term sequestration of atmospheric CO₂ in a mid-latitude forest. *Science* 294, 1688–1691.
- Barr, A.G., Black, T.A., Hogg, E.H., Griffis, T.J., Morgenstern, K., Kljun, N., Theede, A., Nescic, Z., 2007. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. *Global Change Biol.* 13, 561–576.
- Barr, A.G., Griffis, T.J., Black, T.A., Lee, X., Staebler, R.M., Fuentes, J.D., Chen, Z., Morgenstern, K., 2002. Comparing the carbon budgets of boreal and temperate deciduous forest stands. *Can. J. For. Res.* 32, 813–822.
- Brewer, L.G., Vankat, J.L., 2004. Description of vegetation of the Oak Openings of northwestern Ohio at the time of Euro-American settlement. *Ohio J. Sci.* 104, 76–85.
- Bubier, J.L., Bhatia, G., Moore, T.R., Roulet, N.T., Lafleur, P.M., 2003. Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems* 6, 353–367.
- Burba, G.G., Anderson, D.J., Xu, L., McDermitt, D.K., 2006. Correcting apparent off-season CO₂ uptake due to surface heating of an open path gas analyzer, progress report of an ongoing study. In: *Proceedings of 27th Annual Conference of Agricultural and Forest Meteorology, San Diego, California*, 13pp.
- Carrara, A., Kowalski, A.S., Neiryneck, J., Janssens, I.A., Yuste, J.C., Ceulemans, R., 2003. Net ecosystem CO₂ exchange of mixed forest in Belgium over 5 years. *Agric. For. Meteorol.* 119, 209–227.
- Chen, J., Brosfokske, K.D., Noormets, A., Crow, T.R., Bresee, M.K., Le Moine, J.M., Euskirchen, E.S., Mather, S.V., Zheng, D., 2004a. A working framework for quantifying carbon sequestration in disturbed land mosaics. *Environ. Manage.* 33, S210–S221.
- Chen, J., Davis, K.J., Meyers, T.P., 2008. Ecosystem-atmosphere carbon and water cycling in the temperate northern forests of the Great Lakes region. *Agric. For. Meteorol.* 148, 155–157.
- Chen, J., Falk, M., Euskirchen, E., Paw, U.K.T., Suchanek, T.H., Ustin, S.L., Bond, B.J., Brosfokske, K.D., Phillips, N., Bi, R., 2002. Biophysical controls of carbon flows in three successional Douglas-fir stands based on eddy-covariance measurements. *Tree Physiol.* 22, 169–177.
- Chen, J., Paw, U.K.T., Ustin, S., Suchanek, T., Bond, B.J., Brosfokske, K.D., Falk, M., 2004b. Net ecosystem exchanges of carbon, water, and energy in young and old-growth Douglas-fir forests. *Ecosystems* 7, 534–544.
- Chen, J., Song, B., Moeur, M., Rudnicki, M., Bible, K., Shaw, D.C., Braun, D.M., Franklin, J.F., 2004c. Spatial relationships of production and species distribution in an old-growth *pseudotsuga* forest. *Forest Science* 50, 364–375.
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437, 529–533.
- Concilio, A., Chen, J., Ma, S., North, M., 2009. Precipitation drives interannual variation in soil respiration in an experimental forest. *Clim. Change* 92, 109–122.
- Curtis, P.S., Vogel, C.S., Gough, C.M., Schmid, H.P., Su, H.-B., Bovard, B.D., 2005. Respiratory carbon losses and the carbon use efficiency of a northern hardwood forest, 1999–2003. *New Phytol.* 167, 437–456.
- Dantec, V.L., Dufrene, E., Saugier, B., 2000. Interannual and spatial variation in maximum leaf area index of temperate deciduous stands. *Forest Ecol. Manage.* 134, 71–81.
- DeForest, J.L., Noormets, A., McNulty, S.G., Sun, G., Tenney, G., Chen, J., 2006. Phenophases alter the soil respiration–temperature relationship in an oak-dominated forest. *Int. J. Biometeorol.* 51, 135–144.
- Dunn, A.L., Barford, C.C., Wofsy, S.C., Goulden, M.L., Daube, B.C., 2007. A long-term record of carbon exchange in a boreal black spruce forest, means, responses to interannual variability, and decadal trends. *Global Change Biol.* 13, 577–590.
- Falge, E., Baldocchi, D.D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jensen, N.O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B.E., Meyers, T., Moncrieff, J., Moors, E., Munger, J.W., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. For. Meteorol.* 107, 43–69.
- Flanagan, L.B., Johnson, B.G., 2005. Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agric. For. Meteorol.* 130, 237–253.
- Granier, A., Reichstein, M., Breda, N., Janssens, I.A., Falge, E., Ciais, P., Grünwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Facini, O., Grassi, G., Heinesch, B., Ilvesniemi, H., Keronen, P., Knohl, A., Kostner, B., Lagergren, F., Lindroth, A., Longdoz, B., Loustau, D., Mateus, J., Montagnani, L., Nys, C., Moors, E., Papale, D., Peiffer, M., Pilegaard, K., Pita, G., Pumpanen, J., Rambal, S., Rebmann, C., Rodrigues, A., Seufert, G., Tenhunen, J., Vesala, T., Wang, Q., 2007. Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year, 2003. *Agric. For. Meteorol.* 143, 123–145.
- Grelle, A., Burba, G., 2007. Fine-wire thermometer to correct CO₂ fluxes by open-path analyzers for artificial density fluctuations. *Agric. For. Meteorol.* 147, 48–57.
- Griffis, T.J., Black, T.A., Gaumont-Guay, D., Drewitt, G.B., Nescic, Z., Barr, A.G., Morgenstern, K., Kljun, N., 2004. Seasonal variation and partitioning of ecosystem respiration in a southern boreal aspen forest. *Agric. For. Meteorol.* 125, 207–223.
- Griffis, T.J., Black, T.A., Morgenstern, K., Barr, A.G., Nescic, Z., Drewitt, G., Gaumont-Guay, D., McCaughey, H., 2003. Ecophysiological controls on the carbon balances of three southern boreal forests. *Agric. For. Meteorol.* 117, 53–71.
- Hogg, E.H., Brandt, J.P., Kochtubajda, B., 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Can. J. For. Res.* 32, 823–832.
- IPCC, 2007. *Climate Change 2007, Synthesis Report, Contribution of Working Groups I, II and III to the fourth assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland.
- Jassal, R.S., Black, T.A., Novak, M.D., Gaumont-Guay, D., Nescic, Z., 2008. Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand. *Global Change Biol.* 14, 1305–1318.
- Jassal, R.S., Black, T.A., Spittlehouse, D.L., Brmer, C., Nescic, Z., 2009. Evapotranspiration and water use efficiency in different-aged Pacific Northwest Douglas-fir stands. *Agric. For. Meteorol.* 149, 1168–1178.
- Keeling, C.D., Chin, J.F.S., Whorf, T.P., 1996. Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature* 382, 146–149.
- Kirschbaum, M.U.F., 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* 48, 21–51.
- Kljun, N., Black, T.A., Griffis, T.J., Barr, A.G., Gaumont-Guay, D., Morgenstern, K., McCaughey, J.H., Nescic, Z., 2006. Response of net ecosystem productivity of three boreal forest stands to drought. *Ecosystems* 9, 1128–1144.
- Law, B.E., Falge, E., Gu, L., Baldocchi, D.D., Bakwin, P.S., Berbigier, P., Davis, K.J., Dolman, A.J., Falk, M., Fuentes, J.D., Goldstein, A.H., Granier, A., Grelle, A., Hollinger, D., Janssens, I.A., Jarvis, P.G., Jensen, N.O., Katul, G., Malhi, Y., Matteucci, G., Meyers, T., Monson, R.K., Munger, J.W., Oechel, W., Olson, R., Pilegaard, K., Paw, U.K.T., Thorgeirsson, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agric. For. Meteorol.* 113, 97–120.
- Levin, S.A., 2002. Complex adaptive systems, exploring the known, unknown and unknowable. *Bull. Am. Meteorol. Soc.* 40, 3–19.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315–323.
- Ma, S., Baldocchi, D.D., Xu, L., Hehn, T., 2007. Inter-annual variability in carbon dioxide exchange of an oak/grass savanna and open grassland in California. *Agric. For. Meteorol.* 147, 157–171.
- Massman, W.J., Lee, X., 2002. Eddy covariance flux corrections and uncertainties in long-term studies of carbon and energy exchanges. *Agric. For. Meteorol.* 113, 121–144.
- Moffat, A.M., Papale, D., Reichstein, M., Hollinger, D.Y., Richardson, A.D., Barr, A.G., Beckstein, C., Braswell, B.H., Churkina, G., Desai, A.R., 2007. Comprehensive comparison of gap filling techniques for eddy covariance net carbon fluxes. *Agric. For. Meteorol.* 147, 209–232.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., Nemani, R.R., 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386, 698–702.
- Niu, S., Wu, M., Han, Y., Xia, J., Li, L., Wan, S., 2008. Water-mediated responses of ecosystem C fluxes to climatic change in a temperate steppe. *New Phytol.* 177, 209–219.
- Noormets, A., Chen, J., Crow, T.R., 2007. Age-dependent changes in ecosystem carbon fluxes in managed forests in northern Wisconsin, USA. *Ecosystems* 10, 187–203.

- Noormets, A., McNulty, S.G., DeForest, J.L., Sun, G., Li, Q., Chen, J., 2008. Drought during canopy development has lasting effect on annual carbon balance in a deciduous temperate forest. *New Phytol.* 179, 818–828.
- Pan, Y., Birdsey, R.A., Fang, J., 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, A.D., 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., Reichstein, M., Luysaert, S., Margolis, H., Fang, J., Barr, A., Chen, A., Grelle, A., Hollinger, D.Y., Laurila, T., Lindroth, A., Richardson, A.D., Vesala, T., 2008. Carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* 451, 49, U43.
- Powell, T.L., Bracho, R., Li, J., Dore, S., Hinkle, C.R., Drake, B.G., 2006. Environmental controls over net ecosystem carbon exchange of scrub oak in central Florida. *Agric. For. Meteorol.* 141, 19–34.
- Reichstein, M., Tenhunen, J.D., Ourcival, J.M., 2002. Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean sites, revision of current hypothesis? *Global Change Biol.* 8, 999–1017.
- Savage, K.E., Davidson, E.A., 2001. Interannual variation of soil respiration in two New England forests. *Global Biogeochem. Cycl.* 15, 337–350.
- Schmid, H.P., Su, H.-B., Vogel, C.S., Curtis, P.S., 2003. Ecosystem-atmosphere exchange of carbon dioxide over a mixed hardwood forest in northern lower Michigan. *J. Geophys. Res.* 108, D14, 4417.
- Schotanus, P., Nieuwstadt, F.T.M., De Bruin, H.A.R., 1983. Temperature measurement with a sonic anemometer and its application to heat and moisture fluxes. *Boundary-Layer Meteorol.* 26, 81–93.
- Schwalm, C.R., Williams, C.A., Schaefer, K., Arneth, A., Bonal, D., Buchmann, N., Chen, J., Law, B., Lindroth, A., Luysaert, S., Reichstein, M., Richardson, A., 2010. Assimilation exceeds respiration sensitivity to drought, a FLUXNET synthesis. *Global Change Biol.* 2, 657–670.
- Shabanov, N.V., Huang, D., Yang, W., Tan, B., Knyazikhin, Y., Myneni, R.B., Ahl, D.E., Gower, S.T., Huete, A.R., Member, I.E.E.E., Aragão, L.E.O.C., Shimabukuro, Y.E., 2005. Analysis and optimization of the MODIS leaf area index algorithm retrievals over broadleaf forests. *IEEE Trans. Geosci. Remote Sens.* 43, 1855–1865.
- Stoy, P.C., Katul, G.G., Siqueira, M.B.S., Juang, J.-Y., Novick, K.A., Uebelherr, J.M., Oren, R., 2006. An evaluation of models for partitioning eddy covariance-measured net ecosystem exchange into photosynthesis and respiration. *Agric. For. Meteorol.* 141, 2–18.
- Sun, G., Caldwell, P., Noormets, A., McNulty, S.G., Cohen, E., Myers, J.M., Domec, J.-C., Treasure, E., Mu, Q., Xiao, J., John, R., Chen, J., 2011. Upscaling key ecosystem functions across the conterminous United States by a water-centric ecosystem model. *J. Geophys. Res.* 116, G00J05.
- Sun, G., Noormets, A., Gavazzi, M.J., McNulty, S.G., Chen, J., Domec, J.C., King, J.S., Amatya, D.M., Skaggs, R.W., 2010. Energy and water balance of two contrasting Loblolly pine plantations on the lower coastal plain of North Carolina USA. *Forest Ecol. Manage.* 259, 1299–1310.
- Sun, G., Sun, O.J., Zhou, G., 2009. Water and carbon dynamics in selected ecosystems in China. *Agric. For. Meteorol.* 149, 1789–1790.
- Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapor transfer. *Quart. J. Roy. Meteorol. Soc.* 106, 85–106.
- Wilczak, J.M., Oncley, S.P., Stage, S.A., 2001. Sonic anemometer tilt correction algorithms. *Boundary-Layer Meteorol.* 99, 127–150.
- Wilson, K.B., Baldocchi, D.D., 2001. Comparing independent estimates of carbon dioxide exchange over 5 years at a deciduous forest in the southeastern United States. *J. Geophys. Res.* 106, 167–178.
- Xiao, J., Zhuang, Q., Baldocchi, D.D., Law, B.E., Richardson, A.D., Chen, J., Oren, R., Starr, G., Noormets, A., Ma, S., Verma, S.B., Wharton, S., Wofsy, S.C., Bolstad, P.V., Burns, S.P., Cook, D.R., Curtis, P.S., Drake, B.G., Falk, M., Fischer, M.L., Foster, D.R., Gu, L., Hadley, J.L., Hollinger, D.Y., Katul, G.G., Litvak, M., Martin, T.A., Matamala, R., McNulty, S.G., Meyers, T.P., Monson, R.K., Munger, J.W., Oechel, W.C., Paw, U.K.T., Schmid, H.P., Scott, R.L., Sun, G., Suker, A.E., Torn, M.S., 2008. Estimation of net ecosystem carbon exchange for the conterminous United States by combining MODIS and AmeriFlux data. *Agr. Forest Meteorol.* 148, 1827–1847.
- Xiao, J., Zhuang, Q., Law, B.E., Chen, J., Baldocchi, D.D., Cook, D.R., Oren, R., Richardson, A.D., Wharton, S., Ma, S., Martin, T.A., Verma, S.B., Suyker, A.E., Scott, R.L., Monson, R.K., Litvak, M., Hollinger, D.Y., Sun, G., Bolstad, P.V., Burns, S.P., Curtis, P.S., Drake, B.G., Falk, M., Fischer, M.L., Foster, D.R., Gu, L., Hadley, J.L., Katul, G.G., Matamala, R., McNulty, S.G., Meyers, T.P., Munger, J.W., Noormets, A., Oechel, W.C., Paw, U.K.T., Schmid, H.P., Starr, G., Torn, M.S., Wofsy, S.C., 2010. A continuous measure of gross primary production for the conterminous U. S. derived from MODIS and AmeriFlux data. *Remote Sens. Environ.* 114, 576–591.
- Xie, J., Sun, G., Chu, H.-S., Liu, J., McNulty, S.G., Noormets, A., John, R., Ouyang, Z., Zha, T., Li, H., Guan, W., Chen, J., 2013. Long-term variability in water budget and its controls in an oak-dominated temperate forest. *Hydro. Process.* 14 p. <http://dx.doi.org/10.1002/hyp.10079>.
- Xing, Z., Bourque, C.P.A., Meng, F.R., Cox, R., Swift, E., Zha, T.S., Chow, T., 2008a. Modification of an ecosystem model for the filling of medium-sized gaps in tower-based estimates of net ecosystem productivity. *Ecol. Model.* 213, 86–97.
- Xing, Z., Bourque, C.P.A., Meng, F.R., Cox, R.M., Swift, D.E., Zha, T.S., Chow, L., 2008b. A process-based model designed for filling of large data gaps in tower-based measurements of net ecosystem productivity. *Ecol. Model.* 213, 165–179.
- Xing, Z., Bourque, C.P.A., Meng, F.R., Zha, T.S., Cox, R.M., Swift, D.E., 2007. A simple net ecosystem productivity model for gap filling of tower-based fluxes: an extension of Landsberg's equation with modifications to the light interception term. *Ecol. Model.* 206 (3–4), 250–262.
- Yang, B., Hanson, P.J., Riggs, J.S., Pallardy, S.G., Heuer, M., Hosman, K.P., Meyers, T.P., Wullschlegel, S.D., Gu, L.H., 2007. Biases of CO₂ storage in eddy flux measurements in a forest pertinent to vertical configurations of a profile system and CO₂ density averaging. *J. Geophys. Res.* 112, D20123.
- Yang, B., Pallardy, S.G., Meyers, T.P., Gu, L.H., Hanson, P.J., Wullschlegel, S.D., Heuer, M., Hosman, K.P., Riggs, J.S., Sluss, D.W., 2010. Environmental controls on water use efficiency during severe drought in an Ozark Forest in Missouri, USA. *Global Change Biol.* 16, 2252–2271.
- Yuan, W., Luo, Y., Richardson, A.D., Oren, R., Luysaert, S., Janssens, I.A., Ceulemans, R., Grünwald, T., Aubinet, M., Bernhofer, C., Baldocchi, D.D., Chen, J., Dunn, A.L., DeForest, J.L., Goldstein, A.H., Moors, E., Munger, J.W., Monson, R.K., Suyker, A.E., Starr, G., Scott, R.L., Tenhunen, J., Verma, S.B., Vesala, T., Wofsy, S.C., 2009. Latitudinal patterns of interannual variability in net ecosystem exchange. *Global Change Biol.* 15, 2905–2920.
- Zha, T.S., Barr, A.G., Black, T.A., McCaughey, J.H., Bhatti, J., Hawthorne, I., Krishnan, P., Kidston, J., Saigusa, N., Shashkov, A., Nesic, Z., 2009. Carbon sequestration in boreal jack pine stands following harvesting. *Global Change Biol.* 15, 1475–1487.
- Zhao, M.S., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329, 940–943.