



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

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