Drought during canopy development has lasting effect on annual carbon balance in a deciduous temperate forest

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Summary

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Received: *10 March 2008*
Accepted: *7 April 2008*

• Climate change projections predict an intensifying hydrologic cycle and an increasing frequency of droughts, yet quantitative understanding of the effects on ecosystem carbon exchange remains limited.
• Here, the effect of contrasting precipitation and soil moisture dynamics were evaluated on forest carbon exchange using 2 yr of eddy covariance and microclimate data from a 50-yr-old mixed oak woodland in northern Ohio, USA.
• The stand accumulated 40% less carbon in a year with drought between bud-break and full leaf expansion (354 ± 81 g C m^{-2} yr^{-1} in 2004 and 252 ± 45 g C m^{-2} yr^{-1} in 2005). This was caused by greater suppression of gross ecosystem productivity (GEP; 16% = 200 g) than of ecosystem respiration (ER; 11% = 100 g) by drought. Suppressed GEP was traced to lower leaf area, lower apparent quantum yield and lower canopy conductance. The moisture sensitivity of ER may have been mediated by GEP.
• The results highlight the vulnerability of the ecosystem to even a moderate drought, when it affects a critical aspect of development. Although the drought was preceded by rain, the storage capacity of the soil seemed limited to 1–2 wk, and therefore droughts longer than this are likely to impair productivity in the region.

Key words: canopy conductance, canopy development, drought, ecosystem respiration (ER), gross ecosystem productivity (GEP), leaf expansion, net ecosystem exchange of carbon (NEE), rainfall distribution.

Introduction

Climate change projections forecast greater variability of precipitation and higher frequency of drought events in the mid- and high latitudes (Houghton *et al.*, 2001; IPCC, 2007). The impact of a widespread drought on ecosystem carbon balance was seen in 2003 in Europe (Ciais *et al.*, 2005; Granier *et al.*, 2007; Reichstein *et al.*, 2007). While not all droughts are as severe and widespread, recent studies show that the variability in precipitation is already affecting ecosystem carbon exchange, even in temperate areas that are typically not considered drought-prone (Oren *et al.*, 1998; Ewers *et al.*, 2007; Noormets *et al.*, 2008). Soil moisture

availability is a key factor in regulating the onset of the growing season, and the drying of soil to different depths can affect gross ecosystem productivity (GEP) and ecosystem respiration (ER) to a different extent. Therefore, the dynamics of precipitation and water availability may be a key source of interannual variability in ecosystem carbon balance. However, the quantitative understanding of these effects remains limited because the lags and feedbacks between different processes depend on soil and other site-specific factors (Kljun *et al.*, 2006; Krishnan *et al.*, 2006; Barr *et al.*, 2007).

The mode of impact of moisture availability on C exchange may vary depending on the timing of the limitation. For example, dry soil conditions in spring may suppress canopy

development and peak leaf area. Drought in summer may affect plant C status by reducing carbon use efficiency (Ciais *et al.*, 2005). A drought during fall may accelerate leaf fall, shorten the growing season (Goulden *et al.*, 1996; Flanagan *et al.*, 2002), and thus decrease the seasonal cumulative GEP. In some ecosystems, it has been found that earlier leaf-out and rapid canopy development in spring significantly increase annual carbon uptake (Jackson *et al.*, 2001; Barr *et al.*, 2004), and that the lengthening of the growing season by a certain number of days in spring stimulates ecosystem C uptake more than a lengthening by the same number of days in the fall (Kramer *et al.*, 2000). This relationship has been attributed to greater radiative inputs and longer days (Barr *et al.*, 2004), as well as generally better moisture availability as the result of snowmelt and lower evaporative demand in spring than in fall. Soil moisture availability may also affect the decomposition of fresh litter, and drought may therefore affect the extent of litter decay before the dormant season (DeForest *et al.*, 2006). Krishnan *et al.* (2006) and Reichstein *et al.* (2002) hypothesized that short-term drought would suppress ER more than GEP because the litter and upper soil layers that dry first are the location of most heterotrophic respiration. Conversely, deeper soil layers that dry later could still sustain transpiration and assimilation.

In this study, we evaluated ecosystem carbon fluxes, and their sensitivities to environmental and physiological drivers during 2 yr with different precipitation and temperature dynamics. The year 2005 was warmer and dryer than 2004, with a pronounced drought during a critical period of canopy development. Even though our general understanding of the regulation of ecosystem C exchange has advanced greatly over the last decade (Friend *et al.*, 2007), quantitative forecasting of the effects of unusual and extreme weather patterns remains uncertain (Gu *et al.*, 2008). We hypothesized that the spring drought would suppress annual C uptake by decreasing GEP more than ER. We also expected ER to be more sensitive to temperature when moisture was not limiting (i.e. during the wetter year). Correspondingly, the sensitivity of C fluxes to soil moisture was expected to be greater during the drier year. The goal of the study was to quantify and partition the effect of a moderate drought on the carbon balance of a temperate forest.

Materials and Methods

Study site

The study site is located within the Oak Openings Region of northwest Ohio, USA (N41°33′16.98″, W83°50′36.76″) and comprises a mosaic of oak (*Quercus* spp.) forests, maple (*Acer* spp.) floodplains, and remnants of oak savanna, barrens and prairie (Brewer & Vankat, 2004). The region has a perched water table at the depth of 2 m, developed on a series of sandy glacial beach ridges and swales over fine textured till. The 30 yr mean annual temperature is 9.2°C and precipitation

is 840 mm. Our study area is a 100 ha woodland within the 1500 ha Metroparks of Toledo Area Oak Openings Preserve. The topography is flat with an elevation range of 200–205 m. Eighty per cent of the area is upland forest, dominated by oaks on a sandy mixed, mesic, Spodic Udipsamments. The remaining 20% of the forest is a lowland area near a stream where red maple (*Acer rubrum*) dominates on a sandy, mixed, mesic Typic Endoaquolls. Before European settlement, this area supported oak savanna in the uplands and wet prairie in the lowland areas. After settlement, portions of this area were grazed and farmed, but there is no evidence of widespread tree harvesting. At present, the main canopy consists primarily of 45-yr-old oaks, and the understory of 15-yr-old red maples.

Plant species composition and stand biometric properties were measured on 12 FIA-style plots within the 100 ha area using the USDA Forest Service Forest Inventory and Analysis (FIA) plot design (http://www.fia.fs.fed.us/library/). Each plot consisted of four circular subplots, 14 m in diameter and 36.5 m apart in a triangle formation. All trees with diameter at breast height (dbh; 1.5 m above ground) > 3 cm were tagged, identified to species and measured annually. The predominant species, by biomass, were *Quercus rubra* (32%), *Q. alba* (27%), *Q. velutina* (14%) and *Acer rubra* (20%). The remaining 7% were *Prunus serotina* (black cherry) and *Sassafras albidum* (sassafras). The woody ground cover was primarily *Vaccinium* spp. with very few tree seedlings. Standing biomass estimates were calculated from allometric relations established for the Great Lakes Region (Perala & Alban, 1994; Ter-Mikaelian & Korzukhin, 1997). Total biomass at the site was $20\,345 \pm 2180$ (mean $\pm$ SD) g C m^{-2}, of which 9600 ± 650 g C m^{-2} was in above-ground biomass, 1360 ± 1280 g C m^{-2} in below-ground biomass, 1140 ± 655 g C m^{-2} in litter, and 8225 ± 2405 g C m^{-2} in soil. Leaf area index (LAI) was estimated with LAI-2000 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA) in the vegetation plots. Measurements were made monthly in 2004, and once during peak canopy cover, in July, in 2005. In July, LAI was 4.6 ± 0.52 m^2 m^{-2} (mean $\pm$ SD) in 2004, and 4.0 ± 0.49 m^2 m^{-2} in 2005. In 2004, when additional measurements were available, peak LAI was observed in August, reaching 5.0 ± 0.39 m^2 m^{-2}. The cumulative leaf litterfall was 388 ± 19 g DW m^{-2} in 2004 and 333 ± 35 g DW m^{-2} in 2005, lending support to the observed difference in optical LAI estimates between the years. 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).

Micrometeorology and turbulent fluxes

The following micrometeorological parameters and turbulent exchange of carbon, water and energy were measured from a 32 m instrument tower, located in the center of the stand.

There was homogeneous fetch for a distance of at least 600 m in all directions. We measured 30-min means of air temperature (T_a (°C); HMP45AC, Vaisala, Finland) and relative humidity (RH (%); HMP45AC) above and below canopy, soil temperature at 5 cm (T_s (°C); CS107, Campbell Scientific Inc. (CSI), Logan, UT, USA), soil water content (SWC (%); CS616, CSI) in the top 20 cm, photosynthetically active radiation above and below canopy (PAR (μmol quanta m^{-2} s^{-1}); LI-190SB, Li-Cor), and precipitation (P (mm); TE525, Texas Electronics, Dallas, TX, USA).

Turbulent exchange of CO_2 (F_c) was measured using the eddy-covariance method (Lee *et al.*, 2004) 7 m above the forest canopy (canopy height 24 m) throughout 2004 and 2005. The eddy-covariance system consisted of a LI-7500 open-path infrared gas analyzer (IRGA, Li-Cor), a CSAT3 3-dimensional sonic anemometer (CSI), and a CR5000 data logger (CSI). The LI-7500 was calibrated every 3–4 months in the laboratory using chemically scrubbed nitrogen (in 2004) or zero-grade nitrogen (in 2005) for zeroing the CO_2 and H_2O, and a dew-point generator (LI-610, Li-Cor) and NOAA/CMDL-traceable primary CO_2 standards for setting the span. The 30-min mean flux of CO_2 was computed as the covariance of vertical wind speed and the concentration of CO_2, after removing spikes in raw data (> 6 STD), correcting sonic temperatures for humidity and pressure (Schotanus *et al.*, 1983), and rotating wind coordinates to the mean streamline plane (Wilczak *et al.*, 2001), using the EC_Processor software package (http://research.eeescience.utoledo.edu/lees/ECP/ECP.html). The 30-min mean fluxes were corrected for fluctuations in air density using the Webb–Pearman–Leuning expression (Webb *et al.*, 1980; Paw U *et al.*, 2000; Massman & Lee, 2002), including the term for the warming of IRGA above air temperature (Burba *et al.*, 2006; Grelle & Burba, 2007). This temperature difference leads to additional sensible heat flux that is proportional to ambient temperature and wind speed. The effect of Burba's correction on annual NEE, ER and GEP was +68, +61 and −7 g C m^{-2}, differing by 1–4 g between the two years. In both years, the correction affected ER more than GEP.

Change in the canopy air space CO_2 storage was estimated from the change in the mean CO_2 concentration by sampling air from four different heights (1.5, 5, 16 and 22 m above ground). Air from all four inlets was mixed in a 5 l PVC chamber before sampling with a temperature-controlled LI-800 CO_2 analyzer (Li-Cor). The flow of air (1 l min^{-1} total, 0.25 l min^{-1} per inlet) was regulated with a flowmeter (model 4112K35, McMaster-Carr Supply Company, Atlanta, GA, USA) and driven by a continuously operating microdiaphragm pump (model UNMP50KNDC BLDC, KNF Neuberger, Trenton, NJ, USA). The IRGA was connected after the flowmeter and before the pump to avoid excess pressure in the IRGA. The NEE is the sum of the corrected turbulent flux and the storage flux. We use the sign convention by which positive NEE indicates flux away from the surface. Daytime ER was estimated from night-time measurements,

assuming consistency of temperature sensitivity between night- and daytime exchange. GEP was calculated as the difference between NEE and ER (GEP = ER − NEE).

Quality checking and gap-filling

Eddy-covariance data were screened for quality, by flagging periods of highly stable and highly unstable atmosphere (Hollinger *et al.*, 2004), nonstationary turbulent fluxes (Foken *et al.*, 2004; Göckede *et al.*, 2004), rain, dew or ice on sensors, low turbulence, out-of-range fluxes and power failures. The threshold of friction velocity (u^*) below which flux loss occurred was determined from the seasonal binned relationship between turbulent flux of CO_2 and friction velocity (u^*) (Schmid *et al.*, 2003). The threshold was consistent between different seasons, but differed slightly between years: 0.18 m s^{-1} in 2004 and 0.21 m s^{-1} in 2005. No directional effects were observed on fluxes during the growing season, but in winter the sectors with conifers closer than 1 km (at directions 150–160°, 180–190° and 210–270°) exhibited different exchange rates than other wind sectors and were excluded from developing temporal integrals (treated as gaps).

The data gaps were more frequent during the night than during the day. Overall, 54% of daytime and 76% of night-time fluxes had to be gap-filled in 2004, and 43 and 58% in 2005, which is higher than the network-wide average of 35% (Falge *et al.*, 2001), but typical of sites with open-path IRGAs that are sensitive to precipitation and condensation. The gaps were filled with dynamic parameter mechanistic models as described by Noormets *et al.* (2007), simultaneously fitting both day- and nighttime data. 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. While the complete details of the model selection process go beyond the intended scope of this paper, the residuals of ER were smaller with dynamic temperature-sensitivity models than with Q_{10} models, and smaller with T_a than with T_s. Residuals of annual (fixed-parameter) models showed temporal bias, which was eliminated with a seasonally fit (i.e. dynamic) parameters. 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 & Johnson (2005). The structure of the gap-filling model was:

$$\text{NEE} = \text{ER} + \frac{\alpha \phi P_{max}}{\alpha \phi + P_{max}} \qquad \text{Eqn 1}$$

where α is apparent quantum yield (μmol CO_2 μmol^{-1} PAR), ϕ is PAR (μmol quanta m^{-2} s^{-1}), P_{max} (μmol CO_2 m^{-2} s^{-1}) is the maximum apparent photosynthetic capacity of the canopy (μmol CO_2 m^{-2} s^{-1}), and ER is the eddy covariance-based

ecosystem respiration which, in turn, was expressed as a function of air temperature (T_a, K) using a version of the Lloyd & Taylor (1994) model:

$$ER = R_{10} e^{\frac{E_a}{R}\left(\frac{1}{T_{ref}} - \frac{1}{T_a}\right)}$$ Eqn 2

where E_a is the activation energy (kJ mol^{-1} K^{-1}), R is the universal gas constant (8.3134 J mol^{-1} K^{-1}), and R_{10} is the reference respiration, normalized to a common temperature (T_{ref} = 283.15 K = 10°C). R_{10} was estimated as a constant in spring, fall and winter, when respiration was insensitive to variations in soil moisture content (data not shown), or as a function of soil volumetric water content (SWC, %) during summer months when significant ($P < 0.1$) residual trends in ER were observed after accounting for temperature dependence. Thus, the model became:

$$ER = \left(a_0 + a_1 * SWC\right) e^{\frac{E_a}{R}\left(\frac{1}{T_{ref}} - \frac{1}{T_a}\right)}$$ Eqn 3

where a_0 is equal to R_{10} at moisture saturation, or in the absence of moisture sensitivity ($a_1 = 0$). Parameter a_1 indicates unit change in R_{10} per unit change in SWC. Including moisture sensitivity terms in the gap-filling model improved the fit only during the growing season, whereas during pre-growth, pre-dormancy and dormancy only the temperature-based model was used.

Canopy conductance

Canopy conductance (g_e; m s^{-1}) to water vapor was estimated as (Morris *et al.*, 1998; Anthoni *et al.*, 2002):

$$g_e = \frac{P * E}{\rho * VPD} : \frac{R_d}{R_w}$$ Eqn 4

where P is atmospheric pressure (kPa), E is evapotranspiration (kg m^{-2} s^{-1}), ρ is air density (kg m^{-3}), VPD is vapor pressure deficit (kPa) and R_d and R_w are universal gas constants for dry air and water vapor, respectively.

Statistics

The comparison of carbon fluxes and SWC between the years was done using repeated-measures analysis of variance (PROC MIXED, SAS 9.1.3), and the comparison of classes with different SWC and time-integrated P was done using direct analysis of variance (PROC MIXED). All analyses were carried out at $\alpha = 0.05$, and significant differences between years or groups are indicated with different subscripted capitals.

Results

Weather

The monthly mean T_a was consistently 1–2°C above long-term mean (1971–2000; http://www.ncdc.noaa.gov/oa/ncdc.html)
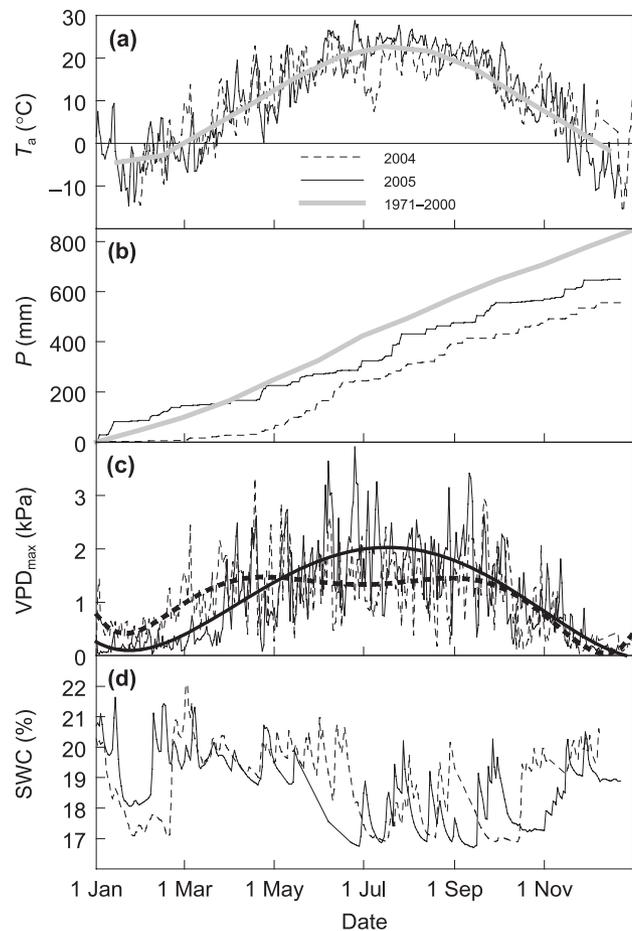
Fig. 1 Temporal dynamics of daily mean and monthly normal air temperatures (T_a) (a), daily cumulative measured and monthly cumulative normal precipitation (*P*) (b), daily maximum vapor pressure deficit (VPD$_{max}$) (c) and daily mean soil water content (SWC) (d) in an oak woodland in Ohio, USA, during 2004 and 2005. The curves fitted to VPD$_{max}$ are best-fit sixth-degree polynomials to highlight seasonal trends. The 30-yr mean indicators are from National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html).

in the summer of 2005, whereas 2004 was at, or slightly below, the long-term mean (Fig. 1a). However, in late April and early May 2005, there was a distinct cold spell, with implications for canopy development and carbon exchange. The deviations in 2004 (e.g. the cold spell in July) suppressed ER but were generally less important in terms of implications for the carbon fluxes.

Both years had less rain than the long-term average (Fig. 1b), and while the cumulative annual *P* was higher in 2005 (765 mm) than in 2004 (668 mm), there was a prolonged dry period through May and June of 2005. The timing of rainfall events differed significantly between the two years. Over 42% of total annual *P* fell in January, February, November and December in 2005, but only 24% fell during the same period in 2004. During the months of May and
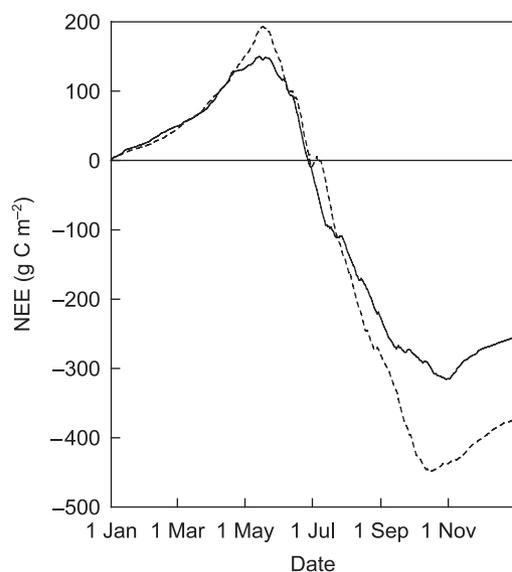
Fig. 2 Yearly cumulative net ecosystem exchange (NEE) of carbon in an oak woodland in Ohio, USA, in 2004 (dashed line) and 2005 (solid line).

Table 1 Absolute and standardized annual carbon fluxes, and the normalizing parameters in an oak woodland in Ohio, USA, during the two years of measurement

Parameter	2004	2005	2004 : 2005 ratio
NEE (g C m^{-2} yr^{-1})	-354 ± 81	-252 ± 45	1.40
ER (g C m^{-2} yr^{-1})	894	795	1.12
GEP (g C m^{-2} yr^{-1})	1248	1047	1.19
LAI (m^2 m^{-2})	4.6	4.0	1.15
α (peak)	-0.06	-0.044	1.36
(mol CO$_2$ mol^{-1} PAR)			
CUP	152	169	0.90
CRP	213	196	1.09
CAP	208	203	1.02
ER : GEP	0.72	0.76	0.95
GEP : LAI	271	262	1.03
α : LAI	-0.013	-0.011	1.18
NEE : CUP	-2.33	-1.49	1.56
NEE$_{CUP}$: CUP	-4.1	-2.8	1.46
NEE$_{CRP}$: CRP	1.3	1.1	1.18
GEP : CAP	6.00	5.16	1.16
P_{annual} (mm)	667	765	0.87
$P_{Mar-Apr}$ (mm)	85	91	0.93
$P_{May-Jun}$ (mm)	195	98	1.99
$P_{Jul-Aug}$ (mm)	146	152	0.96
$P_{Sep-Oct}$ (mm)	84	88	0.95

The error estimate for NEE is uncertainty because of gap-filling (Aurela *et al.*, 2002; Flanagan & Johnson, 2005).
NEE, net ecosystem exchange; ER, ecosystem respiration; GEP, gross ecosystem productivity; LAI, leaf area index; α, apparent quantum yield; CUP, carbon uptake period (NEE < 0 g d^{-1}); CRP, carbon release period (NEE > 0 g d^{-1}); CAP, carbon assimilation period (GEP > 0 g d^{-1}); P, precipitation.

June, a period critical for plant development and growth, 2005 had nearly 100 mm less rainfall compared with the same period in 2004, and 80 mm less than the long-term average. The rainfall was more similar between the years during the second half of the growing season, but it was more uniformly distributed in 2004, whereas in 2005 most of it fell in a few large events.

Soil water content followed the dynamics of rain events (Fig. 1d), with a peak SWC approx. 1.5–2 d after the rain. The growing season mean SWC differed only by 0.46% between the two years, but this difference was statistically significant ($P < 0.001$). The higher T_a and lower P in 2005 than in 2004 led to consistently higher daily maximum VPD (VPD$_{max}$; the years differed by 0.55–0.63 kPa during the growing season, $P < 0.001$; Fig. 1c). The differences were smaller in daily mean VPD, but they remained significant from May through August (not shown).

Phenology and carbon fluxes

The higher T_a in the spring and an earlier snowmelt led to an earlier bud-break in 2004 (DOY 98) than in 2005 (DOY 103). A 2-wk cold spell in late April 2005 (DOY 112–125) delayed full leaf expansion and the onset of ecosystem carbon uptake even further (Fig. 2). The end of the growing season was triggered by first night frost and the daily mean T_a falling below 10°C, which occurred at a similar time in both years (DOY 316 in 2004 and DOY 315 in 2005).

The mean daily NEE during the growth phenophase was $-4.0 \pm 3.8_B$ g C m^{-2} d^{-1} in 2004 (mean ± SD, statistically significant differences between years are indicated with

subscript capitals, $P < 0.05$) and $-3.0 \pm 2.6_A$ g C m^{-2} d^{-1} in 2005, and peak uptake was -10.9 (2004) and -9.0 g C m^{-2} d^{-1} (2005). The daily ER averaged $3.4 \pm 0.2_A$ and $3.6 \pm 0.2_A$ g C m^{-2} d^{-1}, and GEP averaged $7.5 \pm 3.4_A$ and $6.6 \pm 2.6_B$ g C m^{-2} d^{-1} during the growing seasons of 2004 and 2005, respectively. The mean ER during winter dormancy was $+1.2 \pm 0.5_A$ g C m^{-2} d^{-1} in 2004 and $+1.0 \pm 0.6_A$ g C m^{-2} d^{-1} in 2005. The annual sums of NEE, ER and GEP, as well as fluxes normalized by the length of carbon uptake and release periods (CUP and CRP), are given in Table 1.

The differences in the magnitude of C fluxes between the years were reflected in standardized flux capacities. The maximum photosynthetic capacity (P_{max}) was *c.* 10 µmol CO$_2$ m^{-2} s^{-1} greater in May and June of 2004 than in 2005 (Fig. 3a). The apparent quantum yield (α) exhibited greater and longer-lasting difference, with consistently 35% lower values in 2005 than in 2004 (Fig. 3c). The temperature-normalized respiratory capacity, R_{10}, followed the seasonal dynamics of T_a, and was generally higher in 2005 than in 2004 (Fig. 3b). The temporal dynamics of the $P_{max} : R_{10}$ ratio (Fig. 3d) depicted the effects of moisture stress on the rate of development of the assimilatory
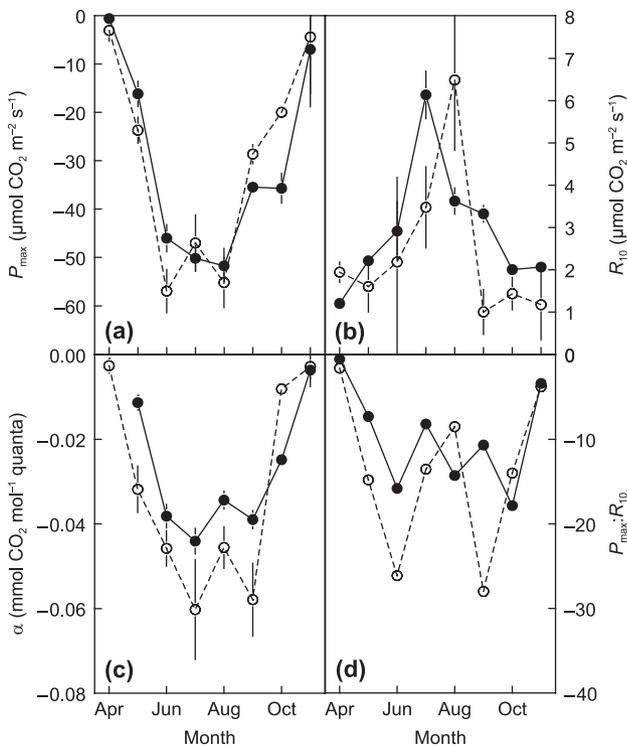
Fig. 3 Monthly canopy maximum photosynthetic capacity (P_{max}) (a), reference respiration (R_{10}) (b), apparent quantum yield (α) (c), and the ratio of P_{max} and R_{10} during the two years of study (2004, open circles; 2005, closed circles). Error bars represent 1 SE of the parameter estimate.

Fig. 4 Daily gross ecosystem productivity (GEP), ecosystem respiration and daily total precipitation (P) in a nondrought year, 2004 (a), and a drought year, 2005 (b). Larger rain events suppress GEP and stimulate ecosystem respiration (ER).

capacity in spring 2005, as well as the effect of the summer drought in 2004.

Sensitivity of GEP and ER to micrometeorological drivers

Moisture stress on GEP was mediated by both SWC and VPD. GEP decreased with increasing VPD on diurnal and synoptic timescales, whereas a distinct moisture optimum was observed with SWC. In 2005, days with the highest SWC ($18.3 \pm 0.15\%_A$) were always associated with the lowest GEP, whereas the highest GEP occurred with intermediate SWC ($17.7 \pm 0.09\%_B$). Days with the lowest SWC ($17.0 \pm 0.21\%_C$) had intermediate GEP. These periods also differed in time-integrated precipitation, with GEP decreasing in the order of 14 > 6 > 18 mm of precipitation over six preceding days. This pattern suggests a tradeoff between SWC limitation and light limitation on GEP.

The SWC sensitivity of ER (a_1 in Eqn 3) was well defined during the growing season, and did not differ between the years (0.18 ± 0.008 µmol CO_2 $\%^{-1}$ SWC in 2004, 0.16 ± 0.014 µmol CO_2 $\%^{-1}$ SWC in 2005; mean $\pm$ SE). However, within individual months, a_1 was poorly defined, so there are no corresponding a_1 values for the R_{10} on Fig. 3. In

2004, when T_a was lower and uniform throughout the summer (Fig. 1a), E_a was poorly defined and the seasonal changes in ER correlated better with SWC than with T_a. Conversely, the broader variability of T_a during the 2005 growing season allowed the temperature-based model to describe the changes in ER more accurately, and the gain in model fit upon adding SWC was smaller than in 2004. Furthermore, the year-to-year differences in T_a dynamics and E_a correlated with the differences in gap-filling uncertainty.

Although the stimulation of ER by increased moisture availability after rain events was much smaller in absolute as well as relative terms than the PAR-driven decrease in GEP (Fig. 4), these changes had a discernible effect on stand carbon balance because the rain-induced stimulation of ER lasted for up to several weeks. These individual responses resulted in spikes in the ER : GEP ratio (Fig. 5a) that were larger and longer-lived in 2005 than in 2004. Furthermore, the sustained stimulation of ER by SWC following the rain events led to a positive relationship between ER : GEP and SWC in 2005 but not in 2004 (Fig. 5b). While the ER : GEP ratio generally returned to pre-rain values after each spike, there was a trend for increase throughout the growing season (0.0012 and 0.0019 d^{-1} in 2004 and 2005, respectively), leading to an overall higher growing season mean in 2005 (0.53) than in
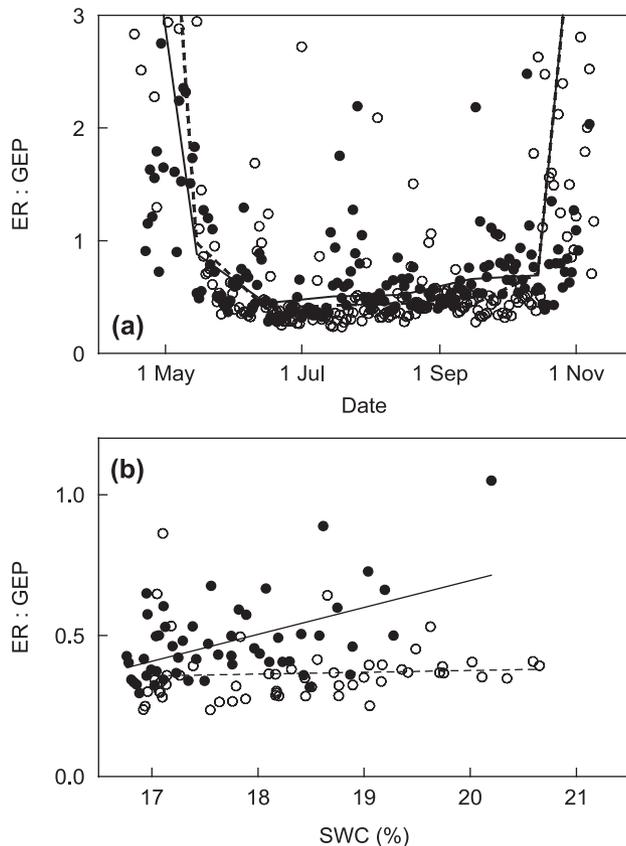
Fig. 5 The seasonal dynamics of the daily cumulative ecosystem respiration (ER) : gross ecosystem productivity (GEP) ratio and the ratios of monthly totals (a), and the dependence of the daily ratio on daily mean soil water content (SWC) during nonrainy days during the growing season (b). 2004, open circles; 2005, closed circles.

Fig. 6 Comparison of the dependence of canopy conductance (g_e) on vapor pressure deficit (VPD) at midday (12:00–13:00 central daylight time (CDT); mean ± SE, each group during the same month in the same year has the same number of observations) between the two years (2004, open circles; 2005, closed circles) in an oak woodland in Ohio, USA.

2004 (0.43). This trend was a combined result of the extended stimulation of ER by rain events, and more rapid decline in GEP throughout the growing season (Fig. 4) in 2005 compared with 2004. The rain-related suppression of GEP was often big enough to turn the ecosystem from a strong C sink to a source, which occurred on 22 d in 2004 and 17 d in 2005.

Canopy conductance

Canopy conductance to water vapor (g_e) ranged from 5 to over 30 mm s^{-1}. It varied seasonally and diurnally with VPD, and was higher in 2004 than in 2005 (Fig. 6). The diurnal change in g_e decreased from c. 20 mm s^{-1} under unstressed conditions at the beginning of the growing season to as low as 7 mm s^{-1} during summer drought. The water stress was greater in 2005 than in 2004, as indicated by suppressed g_e at VPD < 1 kPa (Fig. 6). At VPD > 1, the g_e differences between years were small, as stomata closed to limit water loss during both years. The differences between years decreased at all VPD values in August and September, as moisture stress increased in 2004. The reduction in the PAR-normalized midday NEE (ΔNEE) paralleled the decrease in g_e (Fig. 7). In 2005, NEE remained sensitive to VPD even in August and September when the suppression of g_e had weakened. In 2004, by contrast, NEE was suppressed by VPD only in September, although g_e had already responded in August.

Discussion

Source of NEE difference

The 100 g C m^{-2} (40%) difference in NEE between the two years was caused by greater suppression of GEP than ER during the dry year. The difference in the annual GEP derived from the combined effects of the declining GEP through the growing season (Fig. 4), lower g_e (Fig. 6), and later start of the growing season. The steeper decline of GEP in 2005 (-0.058_B g C d^{-1}) than in 2004 (-0.038_A g C d^{-1}) correlated with declining SWC, and could be related to accelerated leaf aging (Hanan *et al.*, 2002). Similar trends of seasonally declining
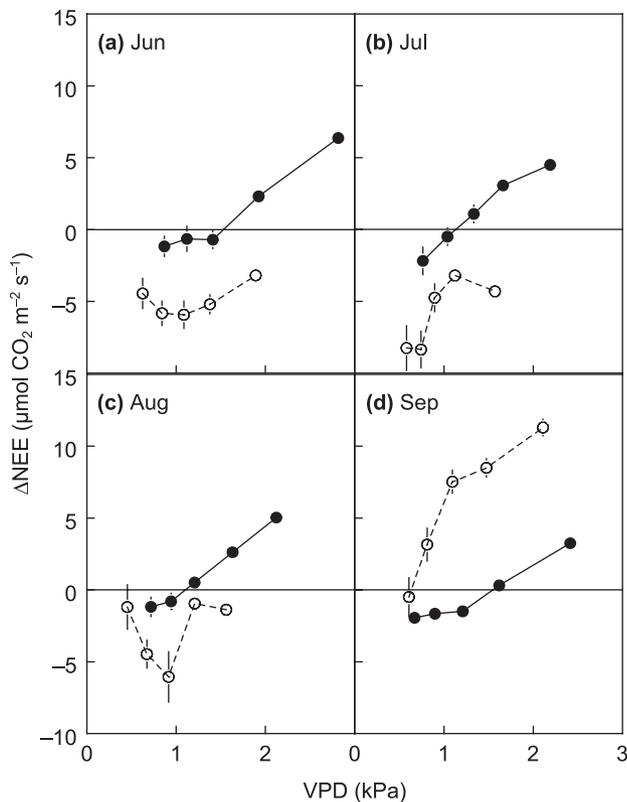
Fig. 7 Response of photosynthetically active radiation (PAR)-normalized net ecosystem exchange (NEE) of carbon to vapor pressure deficit (VPD) at midday (12:00–13:00 CDT; mean ± SE, each group during the same month in the same year has the same number of observations). 2004, open circles; 2005, closed circles. The dependence of NEE on PAR in low-VPD conditions was calculated from data with VPD below the median using Eqn 1. The figure shows the difference between observed and modeled values for the upper 50% of the data. Positive values indicate VPD-induced suppression of the magnitude of NEE.

affecting GEP because the drying of litter and surface soil would affect the primary domain of heterotrophic respiration, whereas GEP could be supported by moisture accessible to roots in deeper soil layers. We hypothesize that the limited effect of drought on ER is related to a small heterotrophic contribution to ER (J. L. DeForest, unpublished), attributable to low litter moisture suppressing heterotrophic activity on recalcitrant oak leaf litter. Given the limited SWC response of ER, and that low SWC and high VPD often coincided with high T_a, we conclude that the stimulation of ER in 2005 by T_a must have exceeded the inhibition by SWC.

Both GEP and ER exhibited symptoms of SWC limitation (Figs 3, 4) when rain-free periods exceeded 1–2 wk. Although the spring drought in 2005 and the summer drought in 2004 were both preceded by big rain events, the sandy soils at the site have limited water-holding capacity. Likewise, the higher than average P from January through April of 2005 did little to sustain SWC through May when P was low. The dependence on regular rain events suggests that the area may be vulnerable to irregular precipitation dynamics.

Environmental regulation of GEP and ER

While the seasonal dynamics of GEP followed the dynamics of T_a, P, SWC and VPD, much of the year-to-year difference was explained by differences in LAI. Normalizing GEP by LAI (Table 1) shows that this alone accounted for much of the observed difference between the years. In 2005, peak LAI was *c.* 13% lower than in 2004, suppressed by drought and a cold spell between bud-break and full leaf expansion (Fig. 1a,d). As the amount of photosynthetic structures in the leaf is determined by conditions at the time of leaf development (Kull & Tulva, 2002; Niinemets *et al.*, 2004), the lack of precipitation in May and June of 2005 had a detrimental effect on α for the entire growing season, lasting past the duration of the dry period. Similar to our observations, Flanagan *et al.* (2002) reported suppressed P_{max} and α during dry years in a semi-arid grassland. Unlike in the current study, they observed greater changes in P_{max} than in α, but this could well be the result of higher light intensities in a grassland, whereas in a forest ecosystem most of the canopy operates below light saturation (Kull, 2002). In the current study, P_{max} recovered towards the end of the growing season, whereas α remained *c.* 35% lower throughout the growing season in 2005 than in 2004 (Fig. 3).

The observation that the T_a and SWC sensitivity of ER correlated with the variability in each factor falsified our initial hypothesis that SWC would constrain ER more during a dry than during a wet year. It also contrasts with the findings of Lavigne *et al.* (2004), who observed that the relationship between soil respiration (SR) and SWC changed more between wet and dry years than did the relationship between SR and T_s. Yet, our findings are similar to those of Lavigne *et al.* (2003), in that respiration varied less in cooler than in

assimilatory capacity have been reported in other temperate forests (Schmid *et al.*, 2003; Noormets *et al.*, 2007), but we are not aware of an earlier documentation of a relationship with moisture availability. In the current study, the seasonal changes in the $P_{max} : R_{10}$ ratio (Fig. 3d) suggest acclimation at the biochemical level. Often, interannual variation in NEE is a direct function of growing season length (Goulden *et al.*, 1996; Barr *et al.*, 2002; Griffis *et al.*, 2003). Yet, as the differences in CAP-normalized GEP were similar to those in absolute GEP (Table 1), the differences in phenology were probably inconsequential.

The observation that the year-to-year difference in GEP exceeded that in ER contrasts with earlier reports of interannual variability in NEE being driven more by ER than GEP (Goulden *et al.*, 1996; Lee *et al.*, 1999; Pilegaard *et al.*, 2001; Ehman *et al.*, 2002; Flanagan & Johnson, 2005). It also goes against the hypothesis (Reichstein *et al.*, 2002; Krishnan *et al.*, 2006) that drought conditions would suppress ER before

Table 2 The parameters of linear regression between the residuals of ecosystem respiration (ER) temperature response (Eqn 2) and cumulative gross ecosystem productivity (GEP) over preceding days during the growing season

Preceding period (d)	Slope	Intercept	P-value	R^2
2004				
Current	0.077 ± 0.034	7.5 ± 0.4	0.02	0.04
−1	0.033 ± 0.019	7.7 ± 0.5	0.09	0.02
−2	0.012 ± 0.013	8.1 ± 0.5	0.37	0.01
−3	0.004 ± 0.010	8.3 ± 0.5	0.71	0.00
−4	0.000 ± 0.008	8.5 ± 0.5	0.96	0.00
−5	-0.002 ± 0.007	8.6 ± 0.5	0.81	0.00
−6	-0.003 ± 0.006	8.8 ± 0.5	0.57	0.00
−7	-0.005 ± 0.005	9.0 ± 0.5	0.37	0.01
−8	-0.006 ± 0.005	9.1 ± 0.5	0.24	0.01
−9	-0.006 ± 0.004	9.2 ± 0.5	0.15	0.01
2005				
Current	0.440 ± 0.051	4.2 ± 0.7	< 0.001	0.35
−1	0.232 ± 0.028	3.9 ± 0.7	< 0.001	0.33
−2	0.147 ± 0.020	4.2 ± 0.8	< 0.001	0.28
−3	0.107 ± 0.016	4.3 ± 0.8	< 0.001	0.25
−4	0.084 ± 0.013	4.5 ± 0.9	< 0.001	0.23
−5	0.068 ± 0.011	4.6 ± 0.9	< 0.001	0.21
−6	0.057 ± 0.010	4.7 ± 0.9	< 0.001	0.20
−7	0.049 ± 0.009	4.8 ± 0.9	< 0.001	0.18
−8	0.041 ± 0.008	5.1 ± 1.0	< 0.001	0.16
−9	0.035 ± 0.007	5.4 ± 1.0	< 0.001	0.14

warmer conditions. However, it is unclear if the spatial gradients of their study reflect similar functional bases of the temporal differences observed in current study.

In addition to the potentially confounding direct effects of T_a and SWC (Hanson *et al.*, 2000; Davidson *et al.*, 2006), our data suggested that the SWC effect on ER may have been mediated by GEP. The dependence of ER on plant carbohydrate status was detected by evaluating the relationship between the residuals of the temperature response function of ER (Eqn 2) and the daily GEP during the preceding days. This relationship was stronger by an order of magnitude in the dry year (2005) than in the wet year (2004). The ER to GEP relationship was strongest with the GEP of the same day, and weakened, but remained statistically significant through at least 10 d cumulative GEP in 2005 (Table 2). In 2004, only the current-day GEP had a distinct stimulating effect on ER. The positive slope of the relationship indicates that the ER was increasingly underestimated, the greater the daily cumulative GEP, with a maximum bias of 0.44 µmol CO_2 m^{-2} s^{-1} per g C GEP per day. Extrapolated to 24 h, this amounts to 0.45 g ER g^{-1} GEP.

In a separate study, we report that GEP-mediated effects on ER were detectable in nearly 50% of 19 site-years of eddy-covariance data (A. Noormets *et al.*, unpublished), but the connection between this link and SWC is not apparent. In the current study, the dependence of ER on GEP was observed with the residuals of the temperature-based model (Eqn 2), but not when accounting for both temperature and moisture

effects (Eqns 2 and 3 combined). This suggests that GEP and SWC co-varied, and accounting for the effect of one on ER effectively accounted for both. Given that SWC did not peak until 24–48 h after each rain event (data not shown), we hypothesize that carbohydrate status must have had a comparable lag before affecting rhizosphere respiration. This is in agreement with the time it takes for recent assimilates to move from leaves to the base of stem and roots (Carbone *et al.*, 2007; Högberg *et al.*, 2008). Given that the model parameters describing the ER–SWC and ER–GEP relationships are not independent (Davidson *et al.*, 2006; Noormets *et al.*, 2008), it is difficult to say if the positive correlation between the observed GEP sensitivity of ER with T_a sensitivity and the negative correlation with SWC sensitivity have a physiological basis or are merely the artifacts of different seasonal variabilities in these factors. However, the timing of the increase of ER in the spring of 2005 suggests that it was affected by the late onset of GEP (Fig. 4).

Indicators of moisture stress

Although the year-to-year differences in GEP and ER were modest, they combined so as to provide various indications of moisture stress on ecosystem C exchange from daily to seasonal timescales. Indications of instantaneous moisture limitation manifested as suppressed g_e (Figs 6, 7) and increased daily ER : GEP ratio (Fig. 5), periods of sustained moisture stress led to acclimation of α, P_{max} and R_{10} (Fig. 3), and the severest effects affected canopy structural properties (LAI; Table 1). We also observed consistent changes in the balance of annual ER : GEP, as well as the ratio of mean NEE during carbon-uptake period to mean NEE during carbon-release period (|NEE$_{CUP}$: NEE$_{CRP}$|; Churkina *et al.*, 2005). The annual ER : GEP increased from 0.72 in 2004 to 0.76 in 2005, while the |NEE$_{CUP}$: NEE$_{CRP}$| decreased from 3.15 in 2004 to 2.55 in 2005, as the result of greater suppression of GEP than ER by the spring drought in 2005 (Table 1). Our findings, along with other recent studies (Malhi *et al.*, 1999; Gifford, 2003), show that while conservative, the ER : GEP and other related ratios (e.g. carbon use efficiency, CUE = 1 − ER/GEP) are not constant. They respond to environmental conditions and provide a synthetic indicator of the state of ecosystem carbon balance. This observation has implications for large-scale C exchange modeling, because ecosystem models utilizing the concept of CUE (Running & Coughlan, 1988; Potter *et al.*, 1993) currently do not view it as a dynamic parameter.

Conclusions

The difference in annual NEE between the two years was traced to differences in LAI, apparent quantum yield (α), and canopy conductance (g_e) that were lower and suppressed GEP during the drought year. Differences in ER were explained with those in T_a, whereas the temperature and moisture

sensitivities of ER did not significantly differ between the years, but were correlated with the magnitude of variability in these environmental conditions. Thus, it revoked our initial hypotheses that T_a and SWC would assume greater significance during periods when they are more limiting (i.e. SWC sensitivity being greater during the drought year and vice-versa). Furthermore, the SWC effect on ER during the drought year may have been mediated through GEP. Overall, the drought and preceding cold spell during canopy development in spring had long-lasting effects on ecosystem C balance that went beyond the immediate moisture stress, and remained even when moisture availability improved.

Acknowledgements

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