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Ten-year variability in ecosystem water use efficiency in an oak-dominated temperate forest under a warming climate

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ABSTRACT

The impacts of extreme weather events on water–carbon (C) coupling and ecosystem-scale water use efficiency (WUE) over a long term are poorly understood. We analyzed the changes in ecosystem water use efficiency (WUE) from 10 years of eddy-covariance measurements (2004–2013) over an oak-dominated temperate forest in Ohio, USA. The aim was to investigate the long-term response of ecosystem WUE to measured changes in site-biophysical conditions and ecosystem attributes. The oak forest produced new plant biomass of 2.5 ± 0.2 g C kg^{-1} of water loss annually. Monthly evapotranspiration (ET) and gross ecosystem production (GEP) were tightly coupled over the 10-year study period ($R^2 = 0.94$). Daily WUE had a linear relationship with air temperature (T_a) in low-temperature months and a unimodal relationship with T_a in high-temperature months during the growing season. On average, daily WUE ceased to increase when T_a exceeded 22 °C in warm months for both wet and dry years. Monthly WUE had a strong positive linear relationship with leaf area index (LAI), net radiation (R_n), and T_a and weak logarithmic relationship with water vapor pressure deficit (VPD) and precipitation (P) on a growing-season basis. When exploring the regulatory mechanisms on WUE within each season, spring LAI and P, summer R_n and T_a, and autumnal VPD and R_n were found to be the main explanatory variables for seasonal variation in WUE. The model developed in this study was able to capture 78% of growing-season variation in WUE on a monthly basis. The negative correlation between WUE and P in spring was mainly due to the high precipitation amounts in spring, decreasing GEP and WUE when LAI was still small, adding ET being observed to increase with high levels of evaporation as a result of high SWC in spring. Summer WUE had a significant decreasing trend across the 10 years mainly due to the combined effect of seasonal drought and increasing potential and available energy increasing ET, but decreasing GEP in summer. We concluded that seasonal dynamics of the interchange between precipitation and drought status of the system was an important variable in controlling seasonal WUE in wet years. In contrast, despite the negative impacts of unfavorable warming, available groundwater and an early start of the growing season were important contributing variables in high seasonal GEP, and thus, high seasonal WUE in dry years.

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1. Introduction

Ecosystem water use efficiency (WUE) is defined as a ratio of carbon (C) gain through photosynthesis to water loss through evapotranspiration (ET) at the ecosystem scale (Beer et al., 2009; Keenan

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et al., 2013). At the leaf-level, WUE is usually defined as the ratio of C assimilation to leaf transpiration. Yet, direct measurements of transpiration and C assimilation at the leaf level are generally unreliable (Beer et al., 2009; Jongen et al., 2011; Keenan et al., 2013). Moreover, the additional complications may affect the response of leaf-level WUE to environmental associations, when scaling from short to long-term intervals (Ponton et al., 2006; Chen et al., 2008; Linderson et al., 2012). Studying ecosystem-level WUE provides valuable information on the response of global water and C balances to climate change, including extreme environmental conditions (Kuglitsch et al., 2008; Niu et al., 2011). However, little is known about how ecosystem-level WUE of temperate forests responds to climate warming and drought over the long term, *e.g.*, ≥10 years.

Climate projections suggest that drought frequency and duration are likely to be enhanced, with extreme environmental conditions in northern mid-latitudes to be more frequent than in the past (IPCC, 2013). Drought have recently occurred in North America, even in temperate areas that are not typically known to be drought prone, resulting in substantial shifts in seasonal and interannual variations in GEP and ET in temperate forests (Noormets et al., 2008). For example, Law et al. (2002) and Jassal et al. (2008) found that atmospheric warming and dry soils could lead to reductions in gross ecosystem production (GEP) due to reductions in leaf area index (LAI). Zhao and Running (2010) have suggested that high air temperature (T_a) can lead to water stress and increases in ET. Moreover, climate change and extreme environmental conditions may counteract the positive fertilization effects of rising atmospheric CO_2 concentrations locally, causing GEP to decline and, thus, causing ecosystem WUE to decrease (Huang et al., 2015). Thus, a better understanding of seasonal-response mechanisms of water and C cycling in natural forests over a long-term basis is still needed.

There is a general lack of consensus as to the variability of water and C cycling to climate change over the long term due to complexity. For example, Zhao and Running (2010) reported a drought-induced reduction in global terrestrial net primary production from 2000 to 2009. Yet, Ballantyne et al. (2012) found a global increase in C uptake during the past 50 years. Bates et al. (2008) document an increasing evaporative demand in the atmosphere with rising T_a. Additionally, Keenan et al. (2013) record a decrease in long-term variability in ET. Given ongoing extreme changes in the climate system, a mechanistic understanding of long-term dynamics of ecosystem WUE and its key seasonal and interannual regulatory variables have become a critical research priority.

Ecosystem WUE is an important parameter to simulate ecosystem primary production in models (Roupsard et al., 2009; Zhou et al., 2015). The results from both modeling and experimental studies seem to support the view that ecosystem WUE should decrease with climate warming (De Boeck et al., 2006; Niu et al., 2011), especially in middle latitudes (Huang et al., 2015). Furthermore, a time series analysis of global annual mean WUE of forest ecosystems, spanning 2000–2013, indicates a distinctly decreasing trend in spite of rising atmospheric CO_2 concentrations (Tang et al., 2014). In contrast, Keenan et al. (2013) reports an increase in ecosystem WUE in northern temperate forests with rising atmospheric CO_2 concentrations over the past two decades. Thus, knowledge about the direction of ecosystem WUE of natural forests associated with atmospheric warming and episodic drying over the long term is particularly deficient.

Ecosystem WUE can be expressed by the ratios of GEP to ET, net ecosystem production (NEP) to ET, or net ecosystem CO_2 exchange (NEE) to ET, with GEP/ET being the most commonly used for consistency and comparison among different ecosystems (Law et al., 2002; Ponton et al., 2006; Kuglitsch et al., 2008; Beer et al., 2009; Yang et al., 2010; Niu et al., 2011; Huang et al., 2015). The eddy covariance (EC) method, meanwhile, provides a means to acquire direct measurements of water and C fluxes and the accompanied environmental conditions on a nearly continuous basis at ecosystem level (Chen et al., 2004; Krishnan et al., 2006; Jongen et al., 2011; Sun et al., 2011a). We have operated an EC tower in a 75-year-old oak-dominated forest for a 10-year period from 2004 through 2013, providing continuous measurements of water and C fluxes. The 10-year measurement period covers episodes of extremely high to low annual precipitation (P) and higher air temperatures (T_a) relative to the past 30 years (1971–2000), under conditions of increasing potential and available energy. The 10-year dataset provides opportunity to investigate the response of site-specific ecosystem WUE to extreme weather events over time.

The study objectives were to: (a) determine seasonal and interannual regulatory variables of ecosystem WUE in an oak-dominated forest over a 10-year period, especially during dry and wet periods and extreme environmental conditions; (b) quantify the long-term variability in ecosystem-level WUE; and (c) develop empirical models that can be readily used to estimate growing-season WUE on a monthly basis for similar forests in middle latitudes. According to previous studies on long-term ecosystem WUE under climate change, we hypothesize that seasonal droughts, combined with the conditions of increasing T_a and net radiation (R_n), should produce a decrease in WUE over the 10-year period.

2. Material and methods

2.1. Study site

The flux tower was located in an oak-dominated forest near the city of Toledo (41.5545°N, 83.8438°W), Ohio, USA. Long-term annual means of T_a and total P were 9.2 °C and 840 mm, respectively (http://www.ncdc.noaa.gov/oa/ncdc.html). The experimental site, covering 107 km^2 (23%) of the Oak Openings Preserve Metropark in northwest Ohio, was characterized by flat topography at an elevation of 203 m above sea level. The site sat on a band of sandy soil deposits along an ancient lakeshore. The clay soil layer beneath the top sandy soil layer provided conditions for a perched groundwater table (WT), forming a surficial aquifer at a depth of about 1 m from ground surface.

The study region had a remarkable number of rare and endangered species, including 145 plants listed as potentially threatened or endangered in Ohio (Brewer and Vankat, 2004; Noormets et al., 2008). The average height of the dominant trees was ~25 m with an average canopy height of ~21 m. As of 2013, the 75-year-old oak-dominated forest included *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; Xie et al., 2014).

2.2. Flux, meteorological, and vegetation measurements

The flux tower was surrounded by relative homogenous forests. We performed a footprint analysis for each half-hourly data by using the model of Kormann and Meixner (2001). The major source areas (>80% contribution) were mostly located within the 0–600 m and 0–1500 m fetch in the daytime and nighttime, respectively. As our target variables, i.e., GEP, ET, and WUE, were largely derived from daytime measurements. The potential bias induced by a few small non-forested patches beyond the 600–1500 m fetch was assumed negligible.

Turbulent fluxes of CO_2 and H_2O between the forest canopy and atmosphere were measured using an open-path EC system placed at the top of the tower. This system consisted of an LI-7500 infrared gas analyzer (IRGA; Li-COR Biosciences, Lincoln, NE, USA) and a 3-D sonic anemometer (CSAT3; Campbell Scientific Inc., Logan, UT, USA). The LI-7500 IRGA was calibrated quarterly 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. Net ecosystem production (NEP, μmol CO_2 m^{-2} s^{-1}) was calculated as a sum of corrected CO_2-flux and CO_2-storage change in the canopy and air volume below the EC system.

The 30-min mean flux of CO_2 was computed as the covariance of vertical wind speed and CO_2 density, after removing spikes in the raw data (>6 standard deviation), 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://lees.geo.msu.edu/resources/ec_processor.html). The 30-min mean fluxes were corrected for fluctuations in air density using the Webb–Pearman–Leuning expression (Webb et al., 1980; Massman and Lee, 2002), including an additional adjustment to account for IRGA self-heating (Grelle and Burba, 2007).

Carbon-dioxide-storage change in the canopy air space was estimated from the change in the mean CO_2 density of sampled air from four different heights (1.5 m, 5 m, 16 m, and 22 m above the ground). Air samples from all four inlets were mixed in a 5-l PVC chamber before being measured by a temperature-controlled LI-800 CO_2 analyzer (Li-COR). Airflow rate (1 l min^{-1} total, 0.25 l min^{-1} per inlet) was regulated by a flowmeter (model 4112K35, McMaster-Carr Supply Company, Atlanta, GA, USA) and was driven by a continuously operating micro-diaphragm pump (model UNMP50KNDC-BLDC, KNF Neuberger, Trenton, NJ, USA).

Our sign convention followed that positive NEP indicates a downward CO_2 flux (*i.e.*, an uptake of CO_2 by plants corresponds to NEP > 0). Latent and sensible heat fluxes (W m^{-2}) were computed as the covariance of high-frequency vertical wind speed and H_2O-density and T_a fluctuations, respectively. ET was derived from estimates of latent heat flux, including plant transpiration (*i.e.*, dry canopy transpiration) and evaporation from soil and plant surfaces (*i.e.*, canopy interception or wet canopy evaporation).

Meteorological variables at multiple vertical levels along the tower were measured and reported as 30-min means. Relative humidity (RH, %) and T_a (°C) were measured by HMP45AC probes (Vaisala, Finland) installed above the canopy at the same height as the IRGA. Photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) was measured by a LI-190SB (Li-COR) set above the canopy. A CNR-1 sensor (Kipp and Zonen, Delft, The Netherlands) placed above the canopy measured both shortwave and longwave radiation, downward and upward. R_n (W m^{-2}) was then derived by summing up net shortwave and longwave radiation using all four radiation components. Soil heat flux (G, W m^{-2}) was measured at three locations using HFT3-flux plates (REBS, Seattle, WA, USA) buried 0.02–0.03 m below the ground. Soil water content (SWC, %) within the top 0.30 m of the soil layer was measured with vertically inserted CS616 time domain reflectometers (Campbell Scientific, Inc.). The WT position was estimated with a pressure transducer that measures water pressure above a sensor head (Infinities USA, Port Orange, Florida, USA). Precipitation (mm) was measured with a tipping-bucket rain gage (TE-525WS-L, Texas Electronics, Dallas, TX, USA). Leaf area index (m^2 m^{-2}) was based on 1 km resolution MODIS LAI/FPAR Collection 5 products (http://daac.ornl.gov/MODIS/modis.shtml; Shabanov et al., 2005) with an online subset output of a 3 × 3 km^2 pixel subset centered at the flux tower, which provides a time series of LAI from 2004 through to 2013.

2.3. Data quality control and gap-filling

The EC data were screened for quality by flagging periods of highly stable or unstable atmospheric conditions, non-stationary turbulent fluxes, weather influence (*e.g.*, rain, dew, or ice on sensors), low turbulence, out-of-range fluxes, and power failures (Gockede et al., 2004; Acevedo et al., 2009; van Gorsel et al., 2011). The threshold of friction velocity below which fluxes were underestimated was determined from the seasonal binned relationship between turbulent flux of CO_2 and friction velocity (Noormets et al., 2008). The threshold of friction velocity was consistent between different seasons, but differed between years: 0.17 m s^{-1} in 2012 and 0.22 m s^{-1} in 2007.

The gap-filling model was chosen from 32 model variants evaluated based on the magnitude and bias of residuals and stability of model-parameter estimates (Noormets et al., 2007). Each 30-min gap in NEP was filled using a dynamic parameter-setting approach described in Noormets et al. (2007), centered on an application of a Lloyd and Taylor (1994) model.

The respiration model was parameterized using the nighttime data:

$$\mathrm{ER} = R_{10} \times e^{(E_a/R)\times((1/T_{\mathrm{ref}})-(1/T_a))} \quad (1)$$

where R_{10} was the reference respiration (μmol CO_2 m^{-2} s^{-1}), normalized to a base temperature (*i.e.*, T_{ref} = 283.15 K or 10 °C; $R_{10} = a_0 + a_1 \times \mathrm{SWC}/100$; where a_0 and a_1 were equation parameters), E_a was the activation energy (kJ mol^{-1} K^{-1}), R was the universal gas constant (8.3134 J mol^{-1} K^{-1}), and T_a was the air temperature above the canopy (°C).

By assuming a consistent temperature sensitivity between nighttime and daytime respiratory fluxes, daytime ER was estimated from a nighttime ER-based calibration of Eq. (1). Following 30-min calculations of ER, GEP was calculated as the sum of NEP and ER (*i.e.*, GEP = NEP + ER). The gap-filling of NEP was achieved with:

$$\mathrm{NEP} = \frac{\alpha \times \mathrm{PAR} \times P_{\max}}{\alpha \times \mathrm{PAR} + P_{\max}} - \mathrm{ER} \quad (2)$$

where α (μmol CO_2 μmol^{-1} PAR) was the apparent quantum yield, PAR (μmol m^{-2} s^{-1}) was photosynthetically active radiation, and $P_{\max}$ (μmol CO_2 m^{-2} s^{-1}) was the maximum apparent photosynthetic capacity of the canopy. The first term on the right-hand side of Eq. (2) provided an estimate of GEP.

Gaps in P were replaced by P records from the Toledo Express Airport weather station (41.5886°N, 83.8014°W), which was ~3 km northeast of the flux tower. Water vapor pressure deficit (VPD, kPa) was calculated from the gap-filled T_a and RH records above the canopy. Gaps <1.5 h in other meteorological variables with inherent diurnal cycles were filled by linear interpolation, while longer gaps (*i.e.*, gaps ≥ 1.5 h) were filled with the Mean Diurnal Variation method after Falge et al. (2001).

2.4. Ecosystem water use efficiency (WUE)

Ecosystem WUE was defined similarly to the definition commonly used by ecologists for entire ecosystems, *i.e.*, the ratio of GEP to ET (Niu et al., 2011; Huang et al., 2015). The coupling of ET and GEP was generally stronger than those of ET and NEP or ET and NEE since NEP and NEE depended on ER. Monthly GEP and ET were derived by summing their respective daily daytime values in each month. Information on the times of sunrise and sunset of each day for Toledo City was downloaded from the Naval Oceanography Portal website. Key processes controlling GEP and ET varied over multiple time scales. Each term in the definition of WUE was calculated from datasets with corresponding temporal resolutions. We did not include data from the winter, when trees were dormant.

Growing season was defined as the period between the first and last occurrence of three consecutive days, when GEP exceeded 5% of the summer maximum C uptake (Zha et al., 2009). The growing season typically lasted for six months (May–October). We defined March through May as the spring, June through August as the summer, and September through November as the fall (*i.e.*, each season involved three months).

2.5. Dryness index (I_{dry})

Dryness index (I_{dry}) was adopted to characterize seasonal and annual dryness. The I_{dry} was calculated as a ratio of potential ET (PET) to P (Sun et al., 2011a; Xie et al., 2013), where PET was calculated following the algorithms of the United Nations' Food and Agriculture Organization (FAO; Allen et al., 1994). This model was a simplified version of the Penman–Monteith equation and widely used in agriculture as a standard method to represent potential water use by reference crops (*i.e.*, grass). Daytime PET and P were summarized to obtain the monthly totals for PET and P, respectively. Monthly, seasonal, and annual I_{dry} were quantified by daily, seasonal, and annual ratios of PET to P. Daily PET was estimated as a function of:

$$\mathrm{PET} = \frac{0.408\Delta(R_n - G) + \gamma\left(900/T_a + 273\right)u_2(e_s - e_a)}{\Delta + \gamma(1 + 0.34u_2)}, \quad (3)$$

where Δ (kPa °C^{-1}) was the slope of saturation water vapor pressure *vs.* temperature curve, γ (kPa °C^{-1}) was the psychrometric constant that was modified to account for the ratio of canopy resistance to atmospheric resistance, e_s and e_a (kPa) were the saturation and actual partial vapor pressure, u_2 (m s^{-1}) was the mean wind speed at a 2 m height, and 900 was a unit conversion factor.

2.6. Statistical analysis

We used Pearson's correlation coefficient to describe the relationships between WUE and other variables (*i.e.*, LAI, T_a, R_n, VPD, SWC, P, and I_{dry}) at different temporal scales. Different combinations of variables were tested to derive the best-fit monthly WUE model during the growing season representative of the 10 years. Model significance was evaluated based on the F-statistic and a significance level of 0.05. All data processing and statistical analyses were conducted using the Statistical Analysis System v. 9.2 (SAS, Institute, Inc Cary, NC, USA).

3. Results

3.1. Microclimate

Annual mean T_a over the 10 years were all higher than the mean of 1971–2000. Annual mean T_a varied from 9.3 °C in 2008 to 12.5 °C in 2012, with an annual average of 10.3 ± 0.9 °C. In particular, 2012 was the warmest year within the 10-year period, as well as the second warmest over the past century. The lowest monthly mean T_a was −7.9 °C in January of 2009 and the highest was 25.7 °C in July of 2012 (Fig. 1a). The highest monthly mean of R_n was 182 W m^{-2} in July of 2012 (Fig. 1c) and VPD was 1.1 kPa in June of 2007 (Fig. 1a). Annual mean T_a and R_n exhibited increasing trends (with R_n being significant at $p < 0.01$) during the 10-year period (Fig. 1). The highest monthly mean LAI was 5.1 m^2 m^{-2} in July of 2006 (Fig. 1a).

3.2. Water and carbon fluxes and WUE

Mean annual ET was 628 ± 41 mm, with a coefficient of variation (CV) of 6.5%. Mean annual total P was 843 ± 152 mm, with a CV of 18%. Mean annual P during the study period was close to the 30-year mean of the normal period in 1971–2000. The largest difference in annual total ET was 132 mm, while that of P was 457 mm. Relative to sizable year-to-year variation in monthly total P (Fig. 1d), monthly change in ET was minor from one year to another (Fig. 1e).

Years 2010 and 2012 were the two dry years, with annual total P as low as 700 mm and 635 mm and annual I_{dry}'s of 1.5 and 1.6, respectively (Fig. 2). Annual ratios of ET:P (*i.e.*, evaporation efficiency) was highest in 2012, with annual ET exceeding total P by 76 mm. In contrast, 2011 was an extremely wet year, with a record-breaking precipitation amount of 1092 mm (Fig. 2), which was the highest annual P over the past century according to the long-term climate records of Ohio. Annual total P was greater than PET in 2006, 2011, and 2013 (*i.e.*, the wet years), with annual P exceeding PET by 66 mm (annual I_{dry} = 0.9), 214 mm (0.8), and 74 mm (0.9; Fig. 2).

The average of annual mean SWC was 18.8 ± 0.2%, with the highest annual value in 2011 and the lowest in 2010. Monthly mean SWC was usually at a maximal level in spring and a minimal level in summer (Fig. 1b). By the end of the summer, monthly SWC increased until the next spring, partly due to the supply from groundwater, direct-P fall, and low water demand by the trees (Fig. 1b).

The annual GEP was the lowest in 2007 (1421 g C m^{-2}) and the highest in 2012 (1738 g C m^{-2}) (Fig. 1f). Mean annual GEP was 1574 ± 89 g C m^{-2}, with a CV of 5.7%. Monthly ET and GEP were tightly coupled over the 10 years, giving an R^2-value of 0.94. The slope of this relationship was 2.8, which was close to mean annual WUE. Annual mean WUE ranged between 2.3 g C kg^{-1} H_2O in 2010 and 2.7 g C kg^{-1} H_2O in 2009 (Fig. 2), with a CV of 6.0%. A decreasing trend was observed in spring and summer, with a significant decrease in summer across the 10 years ($p < 0.01$; $n = 10$ years; Table 1 and Fig. 3a). In contrast, an increasing trend was observed in autumnal records of WUE across the 10 years (Table 1). The highest monthly mean WUE usually occurred sometime between June and September, varying from 3.0 g C kg^{-1} H_2O in June of 2013 to 3.9 g C kg^{-1} H_2O in June of 2006 (Fig. 1g).

3.3. Biophysical and environmental regulations on WUE

Multiple combinations of variables were tested to derive a best-fit monthly WUE model during the growing season. The final model was evaluated to ensure independence among all variables (*i.e.*, absence of multi-collinearity), which was derived as:

$$\mathrm{WUE} = -0.92 + 0.19 \times T_a + 0.0004 \times \mathrm{LAI} \times P. \quad (4)$$

The monthly model produced an R^2 of 0.78, RMSE of 0.647, and dependent mean of 2.11 g C kg^{-1} H_2O (Fig. 5). Test of significance for the model, intercept, and parameter estimates all generated p-values <0.01.

Negative relationships between monthly GEP and biophysical explanatory variables (*i.e.*, LAI, T_a, R_n, VPD, and P) determined negative relationships between monthly WUE and the variables during the growing season over the ten years (Fig. 4). For example, GEP

Table 1
Interannual tendency of water use efficiency (WUE; g C kg^{-1} H_2O) over a 10-year period and its most important explanatory variables over a 10-year period (2004–2013) on an annual basis ($n = 10$ in each season; $p < 0.05$). P (mm) is precipitation; T_a (°C) is air temperature; and R_n (W m^{-2}) is net radiation. We defined March through May as the spring, June through August as the summer, and September through November as the fall (*i.e.*, each season involved three months).

Interannual tendency of seasonal WUE over a 10-year period	Most important seasonal explanatory variable	Relationship between WUE and variable
Decreasing in spring	P	Negative
Decreasing in summer	T_a	Negative
Increasing in autumn	R_n	Negative

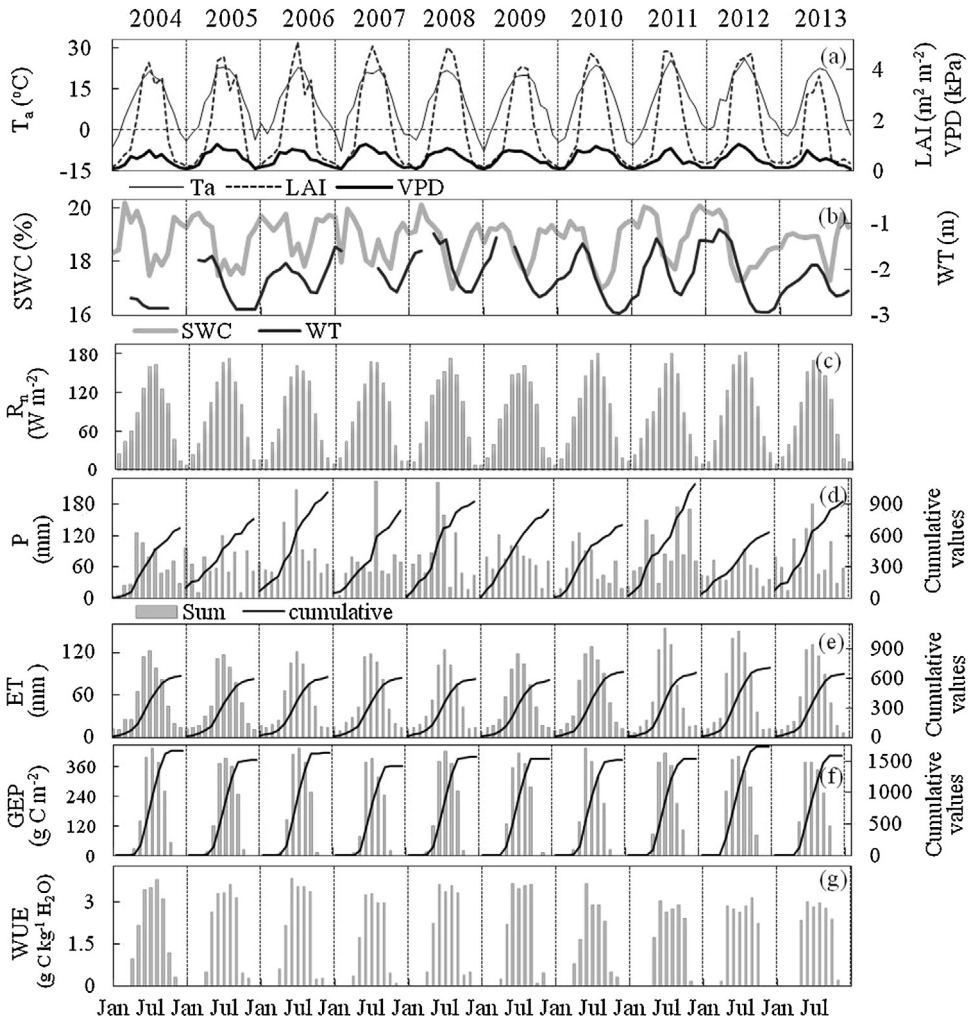

Fig. 1. Monthly (a) mean T_a (°C), LAI ($m^2\,m^{-2}$), and VPD (kPa), (b) SWC (%) and WT (m), (c) R_n ($W\,m^{-2}$) and total and cumulative (d) P (mm), (e) ET (mm), and (f) GEP ($g\,C\,m^{-2}$), and (g) mean WUE ($g\,C\,kg^{-1}$ H_2O) from 2004 to 2013.

and WUE both formed negative linear relationships with P in May, both R_n and T_a in summer months, VPD in autumn months, and LAI in October (Fig. 4). Monthly GEP, ET, and WUE had strong positive linear relationships with LAI, T_a, and R_n and weak logarithmic relationships with VPD and P on a growing-season basis (Fig. 4). Monthly LAI, T_a, and R_n explained growing-season variations in GEP and ET better than in WUE, with the three variables on average explaining 71% in growing-season variation in GEP, 72% in ET, and 47% in WUE.

When exploring the regulatory mechanisms on WUE within each season (*i.e.*, each season involved three months), (a) spring LAI, summer R_n, and autumn VPD were the most important explanatory variables of the monthly variation in WUE ($n = 30$, in each season); and (b) spring P, summer T_a, and autumn R_n were

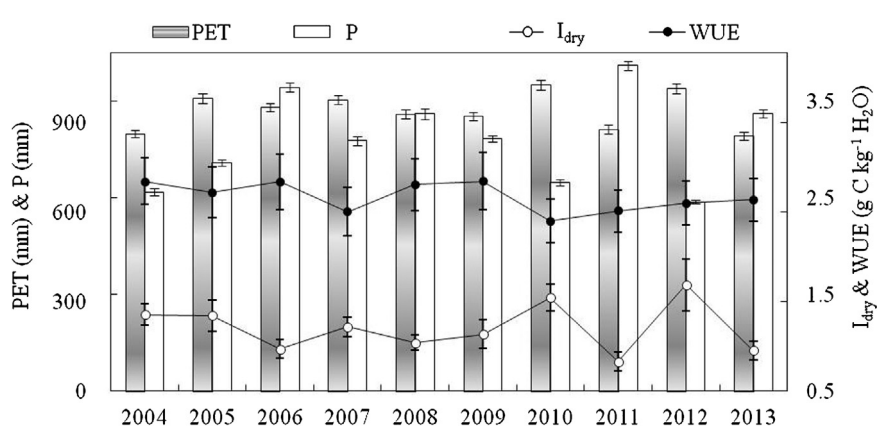

Fig. 2. Annual total potential ET (PET, mm) and P (mm) and mean dryness index (I_{dry}) and WUE ($g\,C\,kg^{-1}$ H_2O) from 2004 through to 2013. The bars indicate monthly standard errors.

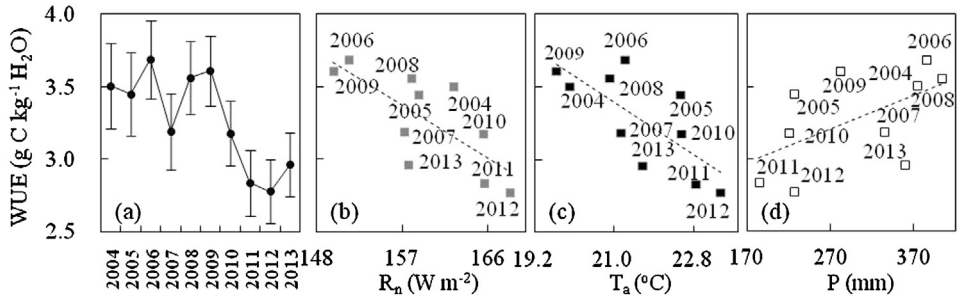

Fig. 3. (a) A significant decrease in summer WUE (g C kg^{-1} H_2O) across the 10 years and linear relationships between WUE and (b) R_n (W m^{-2}), (c) T_a (°C), and (d) P (mm) in summer from 2004 to 2013 (n = 10, p < 0.05). Dashed lines are fitted linear relationships.

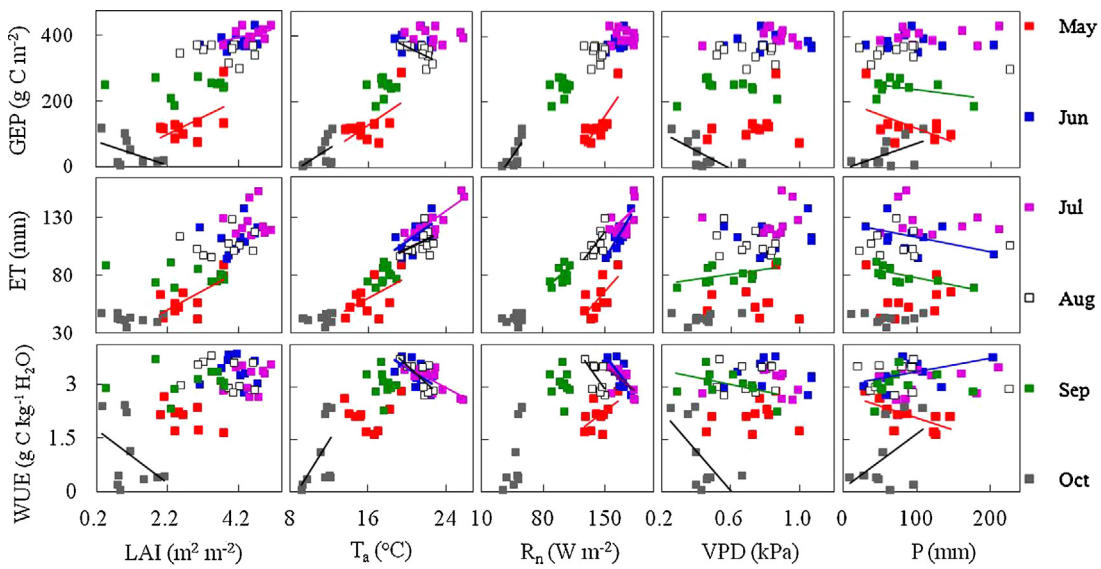

Fig. 4. Linear relationships between monthly mean GEP (g C m^{-2}), ET (mm), and WUE (g C kg^{-1} H_2O) and main explanatory variables LAI (m^2 m^{-2}), T_a (°C), R_n (W m^{-2}), VPD (kPa), and P (mm) from May to October over the 10-year period (2004–2013; n = 10 for each month and n = 60 for each plot). Dashed lines are fitted linear relationships (p < 0.05).

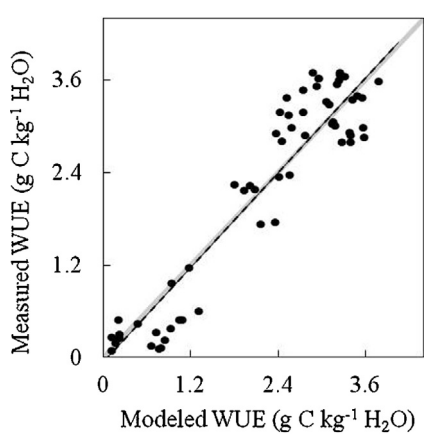

Fig. 5. Linear relationship between modeled WUE (g C kg^{-1} H_2O; Eq. (4)) and measured values during the growing season, on a monthly basis (R^2 = 0.78, slope = 1.02, and intercept = 0.06). The black dashed line represents the fitted tendency between modeled and field-based records; the grey solid line indicates 1:1 correspondence.

the most important explanatory variables of annual variation in WUE (n = 10, in each season; Table 1).

Air temperature was the most important explanatory variable of WUE on a growing-season basis. Daily WUE had a weak linear relationship with T_a in low-temperature months (*i.e.*, May and October) and a unimodal relationship with T_a in high-temperature months (*i.e.*, from June to September) during the growing season for both wet and dry years (Fig. 6). On average, daily WUE in 2010 was 0.5 g C kg^{-1} H_2O lower than that in 2006 (Fig. 6). Daily WUE ceased to increase where daily mean T_a was >21 °C in June, 24 °C in July, 25 °C in August, and 19 °C in September (Fig. 6).

4. Discussion

4.1. Comparison of annual WUE with other sites

The oak-forest ecosystem in this study produced new plant biomass of 2.5 ± 0.2 g C kg^{-1} of water loss (*i.e.*, ET). Annual ranges of mean ecosystem WUE (2.3–2.7 g C kg^{-1} H_2O) fell within annual ranges of 1.2–5.0 g C kg^{-1} H_2O reported for other temperate forests (Kuglitsch et al., 2008; Beer et al., 2009). Tang et al. (2014) reported a mean annual WUE of 2.8 g C kg^{-1} H_2O for broad-leaved deciduous forests and 2.2 g C kg^{-1} H_2O for mixed-species forests. In general, forest-ecosystem WUE exhibited relatively small interannual variability due to stomatal constraints, affecting ET and GEP in a similar way (Law et al., 2002; Reichstein et al., 2007; Brummer et al., 2012).

Although there is no obvious annual trend in WUE, summer WUE had a significant decreasing trend across the 10 years (Fig. 3a) mainly due to annual increases in potential and available energy, which supports our initial hypothesis. Keenan et al. (2013) reported some increase in WUE in temperate forests over the past two decades; however, this increase was not statistically significant.

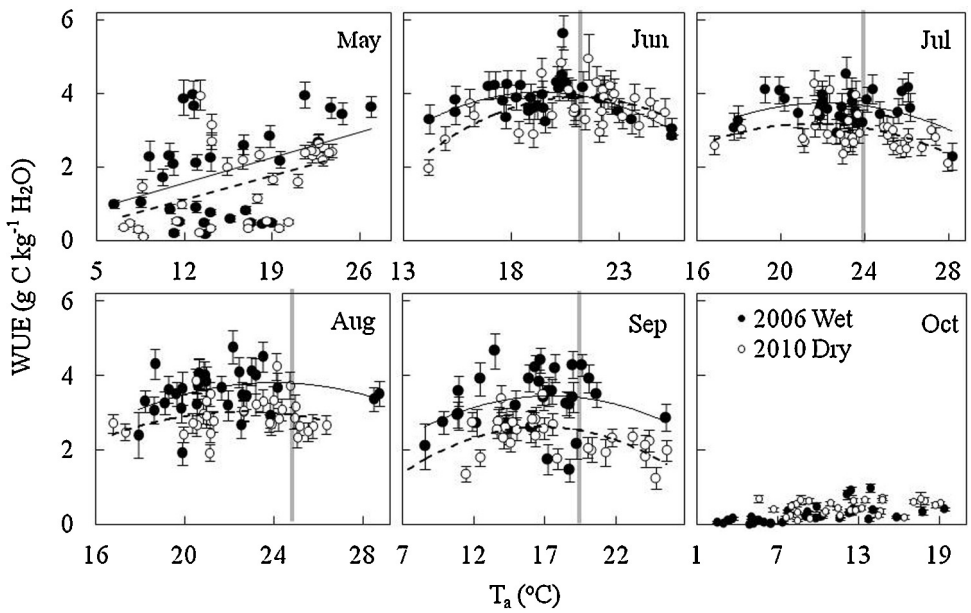

Fig. 6. Comparison of relationships between mean daily WUE (g C kg^{-1} H_2O) and T_a (°C) between wet (2006) and dry (2010) years from May to October; $n = 30$ during each month. Dashed lines are fitted lines.

Additionally, some studies adjusted WUE for VPD as inherent WUE (IWUE), *i.e.*, IWUE = (GEP × VPD)/ET (Beer et al., 2009; Eamus et al., 2013) because they found that ET had a stronger relation with GEP × VPD than with GEP. Here, we found the opposite to be the case, which was most likely attributable to VPD being a poor determinant of WUE at large temporal scales, *i.e.*, at the growing-season and annual time scales. Consequently, we did not adjust our calculations of WUE. Kuglitsch et al. (2008) and Zhou et al. (2015) also reported that ecosystem WUE tended to have a better correlation with environmental variables on a daily or even smaller time scales than on larger time scales.

4.2. Variables controlling seasonal and interannual variations in WUE

The responses in GEP and ET to biophysical variables over a long-term period determined seasonal and interannual variations in WUE. This is because ecosystem water loss is coupled with potential photosynthetic C uptake and the slope of this relationship could be considered as an indicator of WUE (Law et al., 2002). The negative correlation between WUE and *P* in spring (*i.e.*, May) was mainly due to the high precipitation amounts in spring, decreasing GEP when LAI was still small (Table 1; Fig. 4). Additionally, ET was observed to increase with high levels of evaporation as a result of high SWC in spring, causing WUE to decrease during this period. This reflected the contribution of soil–water evaporation in the determination of WUE, which was measured as part of ET through EC measurements.

In contrast, summer drought and warming with strong radiation decreased GEP, causing ET to increase and WUE to decrease in summer (Table 1; Figs. 3 and 4). Stomatal control in general reduces photosynthetic capacity under drought, especially in water-wasting tree species with broad leaves due to their ineffective structural protection from water loss, resulting in a reduction in C assimilation (Niu et al., 2011). In autumn, low seasonal VPD increased GEP, but decreased ET, causing WUE to increase (Table 1; Fig. 4). Although elevated atmospheric CO_2 concentrations are suggested to enhance photosynthetic productivity globally (IPCC, 2013), summer drought may locally offset the positive effects of CO_2 fertilization on increasing GEP. Additionally, the resultant warming by elevated atmospheric CO_2 concentrations may cause GEP to decrease more than ET.

Several types of WUE models have been developed to estimate water and C fluxes due to the high cost of measuring them on a large spatiotemporal basis (Falge et al., 2001; Sun et al., 2011b; Xie et al., 2014; Zhou et al., 2015). Long-term monitoring of ecosystem WUE allows for the quantification of temporal relationships between WUE and various controls in the ecosystems. Our model (Eq. (4)) explained 78% of the growing-season variation in WUE on a monthly basis under a warming climate (Fig. 5). We were unable to achieve a high R^2 value with this model mainly because dominant controlling mechanisms were likely different at the beginning and end of the growing season from those at the peak of the growing season. Additionally, when LAI was outside of the peak of the growing season, evaporation from soils could potentially become a noticeable component of ET. We suggest that ecosystem-level WUE models include the effects of *P* due to the importance of monthly *P* on interannual variation in WUE over the growing season. Eq. (4) can be useful in quantifying growing-season WUE on a monthly basis at other similar mid-latitude temperate deciduous forests, in the cases where direct and simultaneous measurements of ET and GEP are absent.

4.3. Comparison of seasonal variation in WUE between dry and wet years

The 10-year study period, which covered a record-breaking high *P* year and warm year under conditions of increasing potential and available energy, provided an exceptional opportunity to study field-level response of forest WUE and predict variation in WUE under conditions similar to what have been projected for scenarios of future climate change. Daily WUE was generally lower in dry years than that in wet years (Fig. 6). Daily WUE ceased to increase when T_a reached a threshold in warm months during the growing season for both wet and dry years (Fig. 6). This was probably due to light inhibition and stomatal closure during the day (*i.e.*, photoinhibition of CO_2 assimilation and decreasing WUE; Fu et al., 2006). A low WUE was observed in relatively warm and dry years (*e.g.*, 2010 and 2012), largely due to higher T_a, R_n, VPD, LAI, and I_{dry} and lower *P* and SWC than those of other years (Fig. 1). In contrast, high

WUE in relatively cold and wet years (*e.g.*, 2006 and 2008) was mainly due to lower T_a, R_n, VPD, LAI, and I_{dry} as well as higher P and SWC than those of other years (Fig. 1).

Seasonal dynamics of the interchange between P and drought status of the system appeared as a primary variable in controlling seasonal WUE in a wet year. For example, the combined conditions of spring and autumn wetness and summer dry soil conditions accompanied by high T_a and R_n increased annual ET more than annual GEP, resulting in a moderate annual WUE for 2011. In summer, soil water availability to the whole plant system was limited by high T_a, R_n, and VPD, or low P and high I_{dry}, leading to slow plant growth as a result of stomatal regulation against water loss and the possibility of xylem cavitation (Brummer et al., 2012; Xiao et al., 2013). Additionally, seasonal GEP was observed to decrease because of the "Birch effect" (Birch, 1964), culminating from the excessive spring and autumn P. High rates of CO_2 were released from the organic surface layers following P events, which was attributed to rapidly increasing mineralization rates by soil microorganisms in response to changing moisture conditions. Unger et al. (2012) reported unfavorable effects of excessive autumn P following a severe summer drought in a Mediterranean oak forest, where these effects accounted for 195 g C m^{-2} loss in the month of October out of an annual GEP of 756 g C m^{-2}.

Despite the negative impacts of unfavorable warming and drought conditions, annual WUE was supported by several positive environmental conditions, which partially offset the expected decline in WUE during a dry year. For example, the warmest and driest year on record (2012), yielded a moderate annual WUE (Fig. 2). The first of the positive environmental conditions was associated with the favorable supply of soil water provided by: (a) high available soil water in spring from the preceding year (*i.e.*, 2011, with the highest annual P), and (b) groundwater as indicated by the declining WT-level during the growing season (>2.9 m, Fig. 1b). The second of these conditions seemed associated with canopy photosynthesis being able to withstand the deleterious effects of warm and dry conditions, due to the positive effects of optimal temperatures in this area. The third of these conditions related to an early start of the growing season as a result of spring warming and sufficient soil water in 2012, which increased GEP more than ET. The fourth of the positive environmental conditions was likely associated with the insensitivity of slow-growing old forests to warming and drought on an annual basis (Law et al., 2002). Accordingly, the hot and dry conditions failed to cause a significant drop in the year's annual WUE. Moreover, both annual ET and GEP were the highest in 2012, representing 13.2% and 10.5% exceedances from their 10-year averages, respectively. The data suggested that: (a) the oak forest of this study was not overly water-stressed during the driest year because of groundwater sources and the supply of P-water from preceding years, and (b) a short-term acute drought lasting 1–2 years may not necessarily lead to a reduction in WUE. Temperate deciduous forests with a moderate WUE can serve as a high annual C sink, when soil water is not limiting. It is unclear how long-lasting droughts may affect GEP, ET, and WUE in water-stressed forests following depletion of shallow groundwater reserves.

5. Conclusions

We demonstrated the importance of a long-term EC study over a 10-year period and its ability to reveal complex effects of climatic and biophysical conditions on WUE for an oak-dominated forest ecosystem. Daily WUE showed a thresholded-response to air temperature, especially during the warmer months of the growing season. Dry years generally had lower WUE than wet years. We concluded that monthly ecosystem models of WUE should take P into consideration when estimating WUE. A short-term, but acute, drought lasting 1–2 years may not necessarily lead to a low WUE, mainly as a result of an early start of the growing season and abundant available soil water accessible from adequately-charged groundwater following a P-rich year. We conclude that temperate deciduous forests have the potential to maintain their C-sink strength if groundwater is accessible during short periods of excessive dryness in the soil surface. The negative impacts of long lasting droughts (>2 years) may potentially deplete shallow groundwater and cause water stress in forests to develop, resulting in an overall decrease in GEP and a decline in WUE in the future. Future studies should examine how long lasting droughts may potentially deplete shallow groundwater, cause water stress, and affect C balances.

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