Seasonal variation in ecosystem water use efficiency in an urban-forest reserve affected by periodic drought

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\textbf{A B S T R A C T}

The impact of extreme weather events on water-carbon coupling and ecosystem water use efficiency (WUE) in arid to semi-arid conditions is poorly understood. Evapotranspiration (ET) and gross ecosystem production (GEP) were based on continuously eddy-covariance measurements taken over an urban-forest reserve in Beijing, in a 3-year period (2012–2014) to calculate WUE (GEP-ET). Our objective was to investigate the seasonal response of WUE to changing environmental and drought conditions at different timescales. Annually, the forest produced new plant biomass at 2.6 ± 0.2 g C per kg of water loss. Within each season, interactions of surface conductance (g\textsubscript{s}) and normalized difference vegetation index (NDVI; i.e., g\textsubscript{s} × NDVI) in spring, net radiation (R\textsubscript{n}) and air temperature (T\textsubscript{a}; i.e., R\textsubscript{n} × T\textsubscript{a}) in summer, and R\textsubscript{n} and vapor pressure deficit (D; i.e., R\textsubscript{n} × D) in autumn were found as the significant variables explaining seasonal variation in WUE. Daily WUE correlated positively with T\textsubscript{a} and NDVI during the growing season, but a negative relationship during excessively dry periods (i.e., 2014). Daily WUE decreased during warm and dry days or remained nearly constant at low levels due to proportional decreases in GEP and ET. An extreme drought during the leaf expansion led to a greater decline in GEP than in ET, causing WUE to be lower in 2012 and 2014 than that in 2013. In contrast, an extreme drought during the leaf coloration led to a greater decline in ET than in GEP, causing higher WUE in 2013 and 2014 than that in 2012. We concluded that: (i) high soil water content (SWC) during leaf expansion was more important than high SWC in mid-summer or autumn for maintaining a high seasonal WUE, and that (ii) seasonal water availability combined with variable drought severity and duration during periods of changing T\textsubscript{a} caused seasonal ET and GEP to respond differently, introducing significant variation in seasonal WUE.

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1. Introduction

Afforestation in China has been increasing since 1949, with levels of afforested areas expanding every year (Gao et al., 2014). As a consequence of global warming, local shortages of available water have been documented to occur more frequently, and its devastating impact is increasingly becoming apparent in Northeastern China (Zhai et al., 2010). Extreme warm and dry conditions of protected environments may locally counteract the positive effects of atmospheric CO\textsubscript{2} enrichment and plant fertilization, causing gross ecosystem production (GEP) and, thus, ecosystem water use efficiency (WUE) to decline (Huang et al., 2015). However, little is known about how ecosystem-level WUE of forest plantations respond to climate warming and extreme drought over extended...
periods (e.g., several years) due to the complexity of ecosystem response behaviors.

Ecosystem WUE is considerably important in the investigation of forest carbon (C) assimilation relative to water vapor loss by evapotranspiration (ET; Kuglitsch et al., 2008; Yang et al., 2010). Ecosystem-level assessment of WUE is effective at determining the adaptability of protected urban-forest plantations to variable climate (Beer et al., 2009; Xie et al., 2014). Current thinking about ecosystem-WUE responses to incidences of warming and drying conditions, or extreme climate events, is mixed throughout the scientific literatures. For example, modeling studies suggest that ecosystem WUE may decrease under conditions of climate warming (De Boeck et al., 2006; Bell et al., 2010; Niu et al., 2011). Consistent with this view, Reichstein et al. (2007) detected a slight decrease in WUE for European forests during a severe heatwave in the summer of 2003. Also, Ponton et al. (2006), Tang et al. (2006), and Kuglitsch et al. (2008) found WUE to be lower when precipitation was low. In contrast, Ponce-Campos et al. (2013) and Xiao et al. (2013) found that WUE tended to increase when air temperature ($T_a$) was high. Krishnan et al. (2006), Li et al. (2008), Yu et al. (2008), and Beer et al. (2009) reported similar increases in WUE during periods of excessive dryness.

Literature dissensus stems, in part, from: (i) the different ways in which data were acquired (e.g., stratified or non-stratified) and processed and/or the different timescales of integration (e.g., hourly, daily, or annual timescales; Yang et al., 2010); (ii) water losses from the canopy and soil surface (i.e., ET) are theorized to have different sensitivities to changes in $T_a$ and precipitation (Ponton et al. 2006; Hu et al., 2008; Niu et al., 2011); and (iii) lack of consensus as to atmosphere-plant exchanges of C and water vapor under different environmental conditions. For example, Law et al. (2002), Ponton et al. (2006), and Yu et al. (2008) found that increases in ET occurred faster than increases in GEP under increasing $T_a$. Zhang et al. (2014) reported an opposite trend, which is largely explained by the positive effects of optimum temperature on plant photosynthesis.

Previous studies have shown that WUE is controlled by the interactions between the number of sites and biophysical variables (Kuglitsch et al., 2008). However, information about these controls, especially for protected urban forests during extreme environmental conditions, is lacking. Although the role of environmental variables in regulating ecosystem WUE in urban forests is complicated and challenging to investigate, improved understanding of ecosystem WUE is clearly central to assessing acclimatization of urban forests to extreme dry conditions, as reductions in regional precipitation intensify with climate change. Given the ongoing, extreme changes in the climate system, attaining a mechanistic understanding of the long-term dynamics of ecosystem WUE, including identification of its key controlling variables, is an important research objective.

In this study, we measured water vapor and C fluxes over a manmade nature reserve in Beijing, China (i.e., Beijing Olympic Forest Park) during a three-year period (2012–2014). Flux measurements were acquired with the eddy covariance (EC) technique. This technique provides direct measurements of water vapor and C exchanges between forests and the atmosphere, providing a basis in examining forest WUE at the ecosystem level (Falge et al., 2001; Zha et al., 2013). The measurement period covers events with extreme annual total precipitation levels (from extremely low to very high) and annual mean $T_a$ (high), compared to the past 50 years. The particular objectives of this study were to: (i) determine the environmental variables affecting ecosystem WUE in an urban forest over several timescales, and (ii) examine the seasonal response of WUE to climate extremes, particularly drought, common to the northeastern China.

### 2. Materials and methods

#### 2.1. Study site

The study site is located in Beijing Olympic Forest Park (40.02° N, 116.38° E), Beijing, China. It is the largest manmade urban-forest park in Asia, with an area of 680 ha and vegetation coverage of about 90%. The forest reserve is located in the middle of the northeastern section of the park, an area committed to ecological conservation and recovery. Tourists are restricted from entering the study area and recreational facilities are minimized in order to reduce human disturbance.

The area is classified as having a continental, semi-humid monsoon climate, with a mean annual $T_a$ of 12.5°C and frost-free period of about 190 days. Mean annual total precipitation is 592 mm, of which 80% falls between June and August. The soil is mainly of the fluvo-aquic type, with soil porosity of 40.3%, pH of 7.8, and an estimated field capacity and permanent wilting point of 26% and 10%, respectively. Historical climate data are from the Chaoyang District meteorological station nearby, and are summarized as averages over a 50-year period (1961–2010).

The flux site is characterized by flat topography with slopes <5° and elevations of 51 m above sea level (a.s.l.). Plant species composition and stand biometric properties were measured in a 1-ha permanent sampling plot. The young urban-plantation forest consisted of several tree species, with a shallow rooting depth of 0.08–0.40 m and mean age of 20 years, based on the age of overstory trees. The site is dominated by Pinus tabuliformis; other species include Plantycocladus orientalis, Sophora japonica L., Fraxinus chinensis, and Ginkgo biloba; with an understory of Iris tectorum and Dianthus chinensis. All trees were tagged and identified by species, with diameter at breast height (DBH) >3 cm being assessed annually. Stand density in 2013 was 210 trees ha$^{-1}$, with a mean tree height of 7.7 m and a mean DBH of 0.2 m. Cover ratio of trees to shrubs was about 7:3. The shrubs included Prunus davidiana, Amygdalus triloba, Swida alba, and Syzygium aromaticum, with a mean height of 2.8 m. The growing season is defined as the period between the first and last occurrence of three consecutive days, when GEP is <5% of the summer maximum C uptake. We defined March through May as spring, June through August as summer, and September through November as autumn. Normally, tree leaf expansion and coloration stages begin in April and October, respectively. We defined duration and severity of “drought” according to mean SWE <12.5% from spring to autumn; dry-soil periods during each year, are identified in Fig. 1a.

#### 2.2. Flux, meteorological, and vegetation measurements

A 12-m-tall tower is surrounded by uniform forest cover with a homogeneous fetch of about 680 m in all directions. Carbon dioxide (CO$_2$) and water vapor (H$_2$O) exchanges are based on high-frequency measurements (at 10 Hz) obtained with EC equipment placed at the top of the tower (11.5-m height from ground). The EC system consists of a closed-path infrared gas analyzer (IRGA; model EC-155, Campbell Scientific, Inc. (CSI), Logan, UT, USA) and a sonic anemometer (CSAT3; CSI). The IRGA is calibrated quarterly using 99.99% nitrogen gas (zero offset calibration) and a standard CO$_2$ concentration of 650 ppm and a dew point generator (LI-610, LI-COR Inc., USA). Continuous data were collected and processed to calculate the corresponding fluxes at 30-min. intervals following the method described in Massman and Lee (2002). Sonic temperature was corrected for changes in atmospheric humidity and pressure (Schotanus et al., 1983). Net ecosystem CO$_2$ exchange (or negative net ecosystem production, NEP, $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$) was calculated as the sum of the corrected CO$_2$ flux and the CO$_2$-storage change in the canopy-air layer. We adopted the sign convention
that positive NEP denotes CO₂ fluxes moving toward the surface, associated with CO₂ uptake by plants.

Latent heat and sensible heat fluxes (W m⁻²) are also derived from EC data. Above-canopy meteorological variables were measured at the top of the tower and also reported as 30-min means, including relative humidity (RH, %) and T_air (°C) with HMP-45C sensors (Vaisala, Helsinki, Finland), photosynthetically active radiation (PAR, μmol m⁻² s⁻¹) with PAR-LITE sensors (Kipp and Zonen, Delft, the Netherlands), and net radiation (R_n, W m⁻²) with a CNR-4 sensor (Kipp and Zonen, Delft, the Netherlands). Normalized difference vegetation index (NDVI) was calculated after Hinnima et al. (2013). Precipitation (mm) was recorded with a tipping bucket rain gauge (TE-525 MM, CSI) set at 0.7-m above the ground surface. Soil heat fluxes (G, W m⁻²) were measured at four locations with HFP-01 flux plates (CSI) buried in the ground. Soil temperatures (T_s, °C) were monitored at four locations with CS-109 probes (CSI) placed at a 10-cm depth below ground. Volumetric soil water content (SWC, %) within the top 10-cm of the soil was measured at four locations using horizontally inserted CS-616 time domain reflectometers (CSI).

2.3. Data quality control and gap-filling

Eddy covariance 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 (Acevedo et al., 2009). All 30-min fluxes were checked for quality and consistency (Noormets et al., 2007), including stationarity, integral turbulence characteristics, and friction velocity (u*) thresholds. The threshold of u* below which flux loss occurred was determined from the seasonal binned relationships between nighttime turbulent fluxes of CO₂ and u* (Schmid et al., 2000). Nighttime NEP-data were excluded, whenever corresponding u*’s were <0.15 in 2012, 0.20 in 2013, and 0.18 m s⁻¹ in 2014. Data gaps accounted for 4%, 6%, and 5% of daytime and 28%, 31%, and 27% of nighttime NEP in 2012, 2013, and 2014, respectively. Mean percentage of gaps in NEP formed <35% of the total data reported in other studies (Xie et al., 2015; Falge et al., 2001).

A gap-filling model was chosen among evaluated model variants, based on magnitude and bias of residuals and stability of model-parameter estimates (Noormets et al., 2007). Uncertainty in annual NEP, which were caused by gaps in the data and the gap-filling model, were estimated according to the method described in Flanagan and Johnson (2005). Uncertainty in annual estimates of NEP (237 ± 26, g C m⁻²), GEP (1 195 ± 58, g C m⁻²), and ecosystem respiration (ER; 958 ± 70, g C m⁻²) were all within reported ranges (Baldocchi and Meyers, 1998; Falge et al., 2001; Xiao et al., 2013).

Different treatments were applied to daytime and nighttime gaps in CO₂ datasets. Specifically, gaps during the nighttime (PAR <3 μmol m⁻² s⁻¹) were filled according to the relationship between ER and T_air [i.e., Eq. (1); Zha et al., 2007], whereas those during the daytime (PAR ≥3 μmol m⁻² s⁻¹) were filled on the basis of the relationship between daytime NEP, PAR, and ER [i.e., Eqs. (1)
After 30-min estimates of ER were calculated with Eq. (1), gross ecosystem production (GEP) was calculated as the sum of NEP and ER (i.e., GEP = NEP + ER). Each 30-min gap in NEP was filled using a dynamic parameter-setting procedure described by Noormets et al. (2007). The approach is based on a Lloyd–Taylor type equation (Lloyd & Taylor, 1994). The ER model was parameterized using nighttime data:

\[ ER = R_0 \times Q_{10}^{(T_s/10)} \]  

(1)

where \( R_0 \) is the nighttime ER-rate when \( T_s \) is at 0 °C, \( Q_{10} \) is a temperature coefficient of respiration (i.e., the factor by which respiration increases with a 10 °C rise in \( T_s \)), and \( T_s \) is the soil temperature at a 10-cm depth (°C). Eq. (1) was established on a monthly scale before it was applied to estimate daytime ER, assuming there was consistent temperature sensitivity between nighttime and daytime exchanges. After daytime estimates of ER were generated, daytime NEP were filled with:

\[ NEP = \frac{\alpha \times PAR \times P_{\text{max}}}{\alpha \times PAR + P_{\text{max}}} - ER \]  

(2)

where PAR is photosynthetically active radiation (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)), \( P_{\text{max}} \) is the maximum apparent photosynthetic capacity of the canopy (\( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} \)), and \( \alpha \) is the apparent quantum yield (\( \mu \text{mol CO}_2 \mu \text{mol}^{-1} \text{PAR} \)). The first term to the right-hand-side of Eq. (2) provides a calculation of GEP.

Gaps in precipitation were replaced by precipitation records from the Chaoyang District meteorological station. Vapor pressure deficit (D, kPa) was calculated from the gap-filled \( T_s \) and RH records above the canopy. Other 30-min gaps of <1.5 h in meteorological variables with underlying diurnal cycles, were filled by linear interpolation, and longer gaps (i.e., gaps ≥ 1.5 h) were filled with the Mean Diurnal Variation method of Falge et al. (2001).

2.4. Ecosystem WUE

Ecosystem WUE is defined here according to the definition used by ecologists—ratio of GEP to ET. Although ecosystem WUE can be expressed in other ways (e.g., NEP:ET), GEP:ET is most commonly used (Law et al., 2002; Ponson et al., 2006; Kuglitsch et al., 2008; Yu et al., 2008; Niu et al., 2011; Huang et al., 2015). Extent of ET was estimated from measurements of latent heat flux, accounting for water vapor losses by plant transpiration (i.e., dry-canopy transpiration) and evaporation from soil and plant surfaces (i.e., canopy interception or wet-canopy evaporation). Park management activities, such as irrigation and other practices, which were not permitted within the fenced-area of the study site, should not hinder our interpretation of ET and WUE. Water use efficiency was calculated on various timescales. Daily GEP and ET were derived by summing their respective daytime daily values (PAR ≥ 3 \( \mu \text{mol m}^{-2} \text{s}^{-1} \); Zha et al., 2007). Daily, seasonal, and annual WUE were quantified by daily, seasonal, and annual ratios of GEP:ET.
2.5. Surface conductance

Instantaneous surface conductance \( (g_c, \text{ mm s}^{-1}; \text{ Yoshida et al., 2010; Zha et al., 2013}) \) was calculated by inverting the Penman–Monteith equation, giving

\[
g_c = \frac{\lambda E g_a}{\Delta R_a + \rho_v C_p R_a D - \lambda E (\Delta + \gamma)} \tag{3}
\]

where \( \lambda \) is the latent heat of vaporization \( (\text{J kg}^{-1}) \), \( E \) is measured \( \text{ET in kg m}^{-2} \text{s}^{-1} \), \( \gamma \) (kPa·C\(^{-1}\)) is the psychrometric constant modified to account for variation in canopy and atmospheric resistances, \( \Delta \) (kPa·C\(^{-1}\)) is the slope of the saturation water vapor pressure vs. temperature curve, \( \rho_v \) is the density of dry air \( (\text{kg m}^{-3}) \), and \( C_p \) is the specific heat of air at constant pressure \( (\text{J kg}^{-1} \text{K}^{-1}) \). Aerodynamic conductance, \( g_a \) (m\(^{-1}\)), was calculated from \( u^* \) and wind speed above the canopy, which was measured with the sonic anemometer. Available energy, \( R_a \) (W m\(^{-2}\)), was calculated as the difference of net radiation \( (R_n) \), total energy storage in the forest-air column \( (S_t) \), and the soil heat flux \( (G) \), i.e., \( R_a = R_n - S_t - G \).

2.6. Statistical analysis

Linear and logarithmic regressions were used to examine the relationships between WUE and selected biophysical and environmental variables (i.e., NDVI, \( g_c \), \( T_a \), \( R_n \), D, SWC, and precipitation) at various timescales. We used Pearson’s correlation coefficient \( (\text{PCC}) \) to describe associated linear relationships. All data processing and statistical analyses were conducted using the Statistical Analysis System v. 9.2 for Windows software (SAS, Institute, Inc., Cary, NC, USA).

3. Results

3.1. Microclimate

Annual mean \( T_a \) above the canopy increased over the three years, with the lowest annual value appearing in 2012 and the highest in 2014 (Table 1). All three years were warmer than the 50-year (1961–2010) average of 12.5°C. Daily and monthly \( T_a \) and NDVI were highest in July or August (Figs. 1a, b, 2a, b). Over the three years, the highest daily mean \( R_n \) and D occurred in May, June, or July (Fig. 1b).

Although annual total precipitation in 2012 was 146 mm higher than the 50-year average, 2012 was noted for its many irregular and intensive precipitation events, compared to 2013 or 2014. For example, 24% of the annual total precipitation in 2012 fell during a single summer rain event (i.e., 176 mm on DOY 203, dashed vertical line in Fig. 1c), yielding the greatest daily total precipitation in the last 50 years. In contrast, annual total precipitation in 2013 and 2014 were well below the 50-year average, especially with 2014 being short of about 321 mm from the long-term average. Daily precipitation events in 2013 were generally moderate in nature, whereas 2014 had few rainfall events (Fig. 1c). Annualized ratios of ET-to-precipitation (i.e., evaporation effectiveness) increased during the three years, with ratios of 0.8 in 2012, 0.9 in 2013, and 1.6 in 2014.

Summer SWC in 2012 and 2013 were about the same, with seasonal means of 20.4% and 19.9%, respectively (Fig. 1a). Although annual precipitation was highest in 2012, soils in spring were generally drier in 2012 than in 2013, with seasonal SWC of 13.6% in 2012 and 16.9% in 2013 (Fig. 1a). Moderately high spring SWC in 2013 was mainly a result of high autumnal precipitation (168 mm) during the preceding year (i.e., 2012; Fig. 1a, c).

Years 2012 and 2013 were both dry years, but not as dry as 2014. According to the number of consecutive low SWC days during the growing season, 2012 had one extreme dry-soil period (DOY 140–155) in spring, with a mean SWC of 11.2% (Fig. 1a). Year 2013 had one extreme dry-soil period (DOY 303–334) during the leaf-coloration period, with mean SWC of 10.9% (Fig. 1a). Year 2014 had the lowest annual and seasonal SWC (Table 1), with three extreme dry-soil periods (DOY 67–117, 191–228, and 289–334) during leaf-expansion, summer, and leaf-coloration periods, with mean SWC of 10.6%, 12.3%, and 10.8%, respectively (Fig. 1a).

3.2. Variation in water, carbon fluxes, and WUE

Highest annual ET and GEP both occurred in 2012, coinciding with the highest growing-season NDVI and longest growing-season.
3.3. Seasonal regulation of WUE

Within each season, interaction of daily NDVI and \( g_c \) (i.e., \( g_c \times NDVI \)) explained 38% of spring variation in WUE over the three years (\( n = 277; \ p < 0.05; \) Table 2). Daily interactions of \( R_h \times T_a \) and \( R_h \times D \) were more important in summer (\( n = 277; \ p < 0.05) \) and autumn (\( n = 273; \ p < 0.05) \), explaining 44% and 32% of seasonal variation in WUE, respectively (Table 2).

Daily WUE had a negative relationship with \( T_a \) across all years, particularly in July of 2012 and 2013, and May, August, and September of 2014. On average, daily WUE had negative relationships with \( D, R_h \) and \( g_c \) during the May-to-October period for all years (Fig. 4). A negative logarithmic function was able to describe the relationship between daily values of WUE and corresponding \( D, R_h \) and \( g_c \) fairly well. In general, daily WUE decreased radically as these factors increased, when \( D < 1.1 \) kPa, \( R_h < 70 \) W m\(^{-2}\), or \( g_c < 0.6 \) mm s\(^{-1}\) (Fig. 4).

In contrast, daily WUE had a positive relationship with SWC and NDVI in June and/or July in 2012 and 2013 (Fig. 4). In contrast, daily WUE formed a negative relationship with SWC and NDVI in an excessively dry year (i.e., 2014; Fig. 4), particularly in May, June, and August. On average, daily WUE decreased radically when SWC < 16% in 2014, with a measured peak value of 14.1 g C kg\(^{-1}\) H\(_2\)O in 2014 (Fig. 4). On a monthly basis, WUE also had a negative relationship with \( T_a \), NDVI, precipitation, and SWC across all years (Fig. 2), i.e., WUE was lowest in summer, when values of the explanatory variables were high.

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**Table 1**

<table>
<thead>
<tr>
<th>Year</th>
<th>WUE</th>
<th>( T_a )</th>
<th>( R_h )</th>
<th>D</th>
<th>SWC</th>
<th>P</th>
<th>ET</th>
<th>GEP</th>
<th>NDVI</th>
<th>GSL</th>
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<td>2012</td>
<td>2.2</td>
<td>12.9</td>
<td>80</td>
<td>0.9</td>
<td>15.5</td>
<td>738</td>
<td>577</td>
<td>1295</td>
<td>0.64</td>
<td>197</td>
</tr>
<tr>
<td>2013</td>
<td>2.9</td>
<td>13.4</td>
<td>80</td>
<td>0.8</td>
<td>15.0</td>
<td>476</td>
<td>414</td>
<td>1196</td>
<td>0.55</td>
<td>183</td>
</tr>
<tr>
<td>2014</td>
<td>2.6</td>
<td>15.0</td>
<td>84</td>
<td>1.0</td>
<td>12.4</td>
<td>271</td>
<td>429</td>
<td>1094</td>
<td>0.60</td>
<td>192</td>
</tr>
<tr>
<td>Mean</td>
<td>2.6</td>
<td>13.8</td>
<td>81</td>
<td>0.9</td>
<td>14.3</td>
<td>495</td>
<td>473</td>
<td>1195</td>
<td>0.60</td>
<td>192</td>
</tr>
<tr>
<td>SD</td>
<td>0.2</td>
<td>0.6</td>
<td>1.3</td>
<td>0.1</td>
<td>0.9</td>
<td>135</td>
<td>52</td>
<td>58</td>
<td>0.08</td>
<td>4</td>
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**Table 2**

Pearson’s correlation coefficient (PCC) between daily water use efficiency (WUE, g C kg\(^{-1}\) H\(_2\)O) and the most important regulatory variables (RV) during spring (March–May), summer (June–August), and autumn (September–November) of years 2011, 2012, and 2013; where \( n = 92 \) for each season. Tested variables included biophysical and environmental variables, i.e., daily mean stomatal conductance (\( g_c \), mm s\(^{-1}\)), air temperature (\( T_a \), °C), net radiation (\( R_h \), W m\(^{-2}\)), vapor pressure deficit (D, kPa), normalized difference vegetation index (NDVI) and soil water content (SWC, %), and total precipitation (P, mm).

<table>
<thead>
<tr>
<th>Season</th>
<th>RV</th>
<th>PCC</th>
<th>D</th>
<th>NDVI</th>
<th>( g_c )</th>
</tr>
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<tr>
<td>Spring</td>
<td>RV</td>
<td>0.38</td>
<td>0.44</td>
<td>0.42</td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>( g_c )</td>
<td>-0.43</td>
<td>-0.47</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn</td>
<td>NDVI</td>
<td>D</td>
<td>( R_h )</td>
<td>( g_c )</td>
<td>-0.38</td>
</tr>
</tbody>
</table>
3.4. Seasonal water availability in regulating WUE

Daily WUE decreased during dry days or remained nearly constant at low levels during extremely dry days over the growing season (Figs. 1 f, 5 f). An extreme dry-soil period in 2014 (DOY 191–210) caused GEP and WUE to remain low under high Ta and hyper-arid conditions, with a low mean SWC of 11% (Fig. 5). In addition, daily WUE decreased from 10.1 g C kg$^{-1}$ H$_2$O on DOY 192–3.4 g C kg$^{-1}$ H$_2$O on DOY 196 in 2013, with no precipitation and a decreasing SWC of 27.3–22.0% during this period. Similarly, on a monthly basis, WUE remained relatively constant from May to August of 2014, with high monthly Ta, low monthly SWC, and extremely low monthly precipitation (Fig. 2). Although July received the greatest quantity of precipitation, it was generally a dry month for both 2012 and 2013 and an extremely dry month for 2014, with 10 consecutive non-rainy days in July in 2012 (DOY 193–202), 10 days in 2013 (DOY 198–207), and 15 days in 2014 (DOY 183–197; Fig. 5c).

In contrast, daily WUE was higher on rainy days than on rain-free days ($p<0.05$, based on a t-test; Figs. 1 f, 2). In general, a small increase in WUE was observed on rainy days, due to a larger decrease in ET than in GEP, with both GEP and ET increasing on the second day (Fig. 5). A slight increase in WUE occurred in both 2012 and 2013 during consecutive rainy days (DOY 183–197), with both ET and GEP increasing during this period (Fig. 5). Daily WUE increased during this period from 0.9 to 4.9 g C kg$^{-1}$ H$_2$O in 2012 and 2.0–27.1 g C kg$^{-1}$ H$_2$O in 2013, with total precipitation of 56 mm in 2012 and 89 mm in 2013 (Fig. 5). In addition, an extremely intense precipitation event on DOY 203, 2012, caused ET to decrease more than GEP on that day, resulting in an increase in WUE compared to its level during the preceding day ($+1.2$ g C kg$^{-1}$ H$_2$O; Fig. 5). This extremely intense precipitation had a one-day lag effect, increasing ET more than GEP, resulting in a low daily WUE of 1.4 C kg$^{-1}$ H$_2$O with a high SWC of 35.7% on DOY 204, 2012 (Fig. 5).

4. Discussion

4.1. Comparison of annual WUE with other sites

Mean ecosystem WUE (GEP:ET; 2.2–2.9 g C kg$^{-1}$ H$_2$O) for this protected urban forest fell within the reported annual ranges of 2.1–3.8 g C kg$^{-1}$ H$_2$O for naturally-growing temperate conifer forests (Kuglitsch et al., 2008; Beer et al., 2009). Our mean annual WUE was also very close to the annual value reported for another forest plantation in the suburbs of Beijing (i.e., 2.5 g C kg$^{-1}$ H$_2$O; Xiao et al., 2013); while notwithstanding mean annual GEP, ET, and precipitation at our site were significantly lower than those reported at the other site, giving a mean difference of 239 g C m$^{-2}$, 113 mm, and 74 mm between sites. These differences suggest that relatively dry conditions at our site likely decreased both GEP...
and ET proportionally; causing annual WUE to fall within those reported ranges.

Our study site is located in an urbanized area (i.e., Beijing city) and the urban heat-island effect should have intensified as a result of contrasting responses of urban- and rural-surface energy budgets to intense heating (Li et al., 2015). Yet, impacts of urbanization at our site, including high CO₂ concentrations, were not significant on account of (a) Beijing’s policy, which restricts human disturbance on protected parkland ecosystems in the middle of the northeastern section of the park; and (b) the large physical dimensions of the forest reserve, which potentially helped to offset a significant level of urban warming by stimulating greater ET and cooling of the area.

4.2. WUE response to seasonal drought and for different phenophases

The three-year study (2012–2014) provided a unique opportunity to study the seasonal and interannual responses of ecosystem WUE to extreme drought. Seasonal water availability combined with variable drought severity and duration during periods of changing Ta caused seasonal ET and GEP to respond differently, introducing significant departures in WUE to localized drought. Dry soils during leaf expansion and increasing Ta led to a lower annual WUE in 2012 and 2014, compared to 2013 (Fig. 1a, f; Table 1), which was likely due to a larger reduction in GEP than in ET during leaf expansion (Fig. 1d, e). Additionally, extreme drought during leaf coloration (i.e., in October), caused WUE to increase in 2013 and 2014, mainly as a result of drought and low Ta, SWC, and NDVI. This caused ET to decrease significantly more than GEP (Figs. 1, 2). In contrast, high monthly SWC during early spring to early summer (i.e., from March to June; Figs. 1 a, 2 d) of 2013 likely caused the high growing-season WUE, compared to the WUE of the same time period in 2012 and 2014 (Fig. 1a, f; Table 1). We concluded that high SWC during the leaf-expansion period was more important than SWC in mid-summer or autumn for maintaining a high seasonal WUE (Figs. 1 a, f, 2 d, e), and thus, regulating interannual variation in WUE.

 Extremely dry conditions, coupled with the highest annual Ta, caused annual WUE to be of moderate value due to proportional reductions in seasonal GEP and ET in 2014 (Table 1; Figs. 1, 2). In the extremely dry July of 2014, when Ta and Rs reached their individual maxima, water availability to the urban forest was substantially limited, resulting in extremely low SWC (Fig. 5a, b, f). Such summer warming and extreme drought potentially reduced both transpiration and photosynthetic capacity, resulting in inhibited plant growth as a result of self-protection by stomatal regulation against water losses (Fig. 3); in other words the stomata minimized the possibility of xylem cavitation and adjusted to maintain a sustainable flow of water (Kuglitsch et al., 2008; Niu et al., 2011). Consequently, monthly GEP and ET in July of 2014 were both lowest among the three years. Yet, GEP decreased more than ET, causing WUE to be low (Fig. 5d–f).

4.3. Biophysical controls on WUE evolution at multiple timescales

An advantage of WUE, which is estimated at the ecosystem-level, is that it essentially reflects a compromise between water loss and biomass gain. Ecosystem water and C fluxes were intimately linked (Fig. 6), since transpiration and photosynthesis C fixation are both affected by stomatal opening. The slope of the coupled ET and GEP was higher in 2013 and lower in 2012 and 2014 (Fig. 6), of which the annual trends observed were consistent with those of WUE appearing in Table 1. Additionally, we found that coupled daily ET and GEP was stronger than coupled daily ET and NEP on an annual basis. Since determination of NEP depends on ER, and ER is not strongly coupled to water fluxes, this may obscure the coupling of canopy water and C fluxes.

It has been found that biophysical controls of ET and GEP in a forest ecosystem were reflected in the form of gₑ, change, which controlled the response of WUE to seasonal drought (Zha et al., 2013). Hourly WUE was simultaneously regulated by gₑ during the growing season (Fig. 3). Lower hourly gₑ and WUE in the summer months of 2013 and 2014 are likely because of the partial closing of the stomata, which was in response to high summer Ta, Rs, and D and low precipitation and SWC, jointly causing GEP to decrease more than ET partly due to metabolic limitations. There was a clear decrease in hourly WUE from 10:00 to 14:00 LST under conditions of increased Ta and Rs for both 2013 and 2014 (Fig. 3), which increased ET relatively more than GEP because of higher diffusivity of water vapor than CO₂ in air. Although gₑ calculated from Eq. (4) does not explicitly represent the biophysical parameter of stomatal conductance, theoretical and experimental investigations have shown that gₑ is often related to the weighted integration of individual leaves (Baldocchi and Meyers, 1998). Thus, gₑ can be considered as a biological control on ecosystem WUE.

Ecosystem responses to environmental change are usually driven by the response of a dominant species at the site. Seasonal and interannual variation in WUE suggest that afforestation of urban-forest parks mainly mixed with P. tabuliformis, provides a means of increasing C uptake with an acceptable investment in external water resources. We concluded that a short-term, off-season acute drought (e.g., during the leaf-coloration period of 2013) failed to lead to a low autumn or annual WUE, likely as a result of not only abundant spring soil water but also drought-resistance characteristics of P. tabuliformis. Yet, the negative impact of long-lasting droughts may cause water stress in urban forests to develop and further impede plant growth, resulting in a GEP decrease and
an associated decline in WUE. Negative relationships between daily WUE and $T_a$, $R_n$, and $g_r$ during the growing season (Fig. 4) reflected that urban forests consisting of *P. tabuliformis* generally consume water more effectively at moderate levels of $T_a$, $R_n$, and $g_r$. Thus, moderate levels of available energy (through $T_a$ and $R_n$) and $D$ and $g_r$ were sufficient to maintain a relatively high-growing-season WUE. Since current measurements span over three years, a long-term study is needed to (i) assess the effects of extreme droughts at different phenophases on interannual variability in WUE; and to (ii) investigate the role that the urban heat-island effect may have on the interannual variability in an urban forest's WUE.

5. Conclusions

Patterns in ecosystem WUE of a protected urban forest were examined in light of combined influences of biological and extreme environmental variables. Moderate levels of available energy (through $T_a$ and $R_n$), $D$ and $g_r$ were sufficient to maintain a relatively high-growing-season WUE for this forest plantation. Seasonal and interannual variation in WUE suggests that afforestation of urban-forest park mainly mixed with *P. tabuliformis* provides a means to increase C uptake with an acceptable investment in external water resources. Daily WUE was decreased by seasonal warming and drying. Seasonal WUE remained unaffected during an extreme drought in the summer due to proportional decreases in GEP and ET. We concluded that the magnitude of an urban forest's WUE was modified by differential responses in GEP and ET to seasonal water stress for different phenophases. A long-term study is needed to evaluate the impact of extreme drought and the "urban heat-island effect" on interannual variability in an urban forest's WUE.

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References


