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ORIGINAL ARTICLE

Water-use efficiency of a poplar plantation in Northern China

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Abstract The water-use efficiency (WUE) of an ecosystem—defined as the gross ecosystem production (GEP) divided by the evapotranspiration (ET)—is an important index for understanding the coupling of water and carbon and quantifying water–carbon trade-offs in forests. An open-path eddy covariance technique and a microclimate measurement system were deployed to investigate the WUE of a poplar plantation ecosystem in the Daxing District of Beijing, China, during the growing seasons in 2006, 2007, and 2008. We found that WUE values changed diurnally, peaking in early morning and showing a minimum between 2 pm and 3 pm. This pattern was regulated by photosynthetically active radiation, saturated vapor pressure deficit, and stomatal opening and closure. WUE had inter-daily variations but no substantial seasonal variation. The WUE decreased with increasing soil water content due to the higher sensitivity of ET than GEP to increased soil moisture. Under moist soil conditions (i.e., relative extractable water content >0.4), GEP was stable and WUE was generally low. These results suggest that the poplar plantation does not effectively use the available soil water for carbon uptake, and that soil moisture is lost to the atmosphere through ET.

Keywords Ecosystem water-use efficiency · Evapotranspiration · Gross ecosystem productivity · Poplar plantation

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Introduction

Forests cover about 31 % of the land surface, and represent a persistent carbon sink (Woodwell et al. 1978; Post et al. 1982; Vitousek 1991; Wright et al. 2000; Pan et al. 2011) that slows the increase in the concentration of carbon dioxide (CO_2) in the atmosphere and thus global warming (Dilling et al. 2003; IPCC 2007). China has the largest acreage of manmade forests in the world today, and poplar (i.e., *Populus* sp.) plantations account for about 14 % of the total acreage devoted to plantations in China (Chinese Forestry Society 2003), making it the most important tree species employed for afforestation in Northern China. As it is a fast-growing species, poplar exhibits high biomass accumulation but also high rates of water loss (Pearce and Rowe 1979; Gordon et al. 1998; Farley et al. 2005). However, water shortages in northern China are becoming increasingly serious, making them the limiting factor in forest production. Thus, recently, much research attention has focused on how best to use the limited water resources of Northern China and how to improve the efficiency of water use by manmade forests in this region.

Ecosystem water-use efficiency (WUE)—the ratio of CO_2 assimilation to water loss (Law et al. 2002; Yu et al. 2008)—is used to characterize and define the trade-off between the water loss and carbon gain of an ecosystem (Yu et al. 2004). Additionally, the WUE is as an effective way to assess ecosystem response to climate change (Baldocchi 1994; Bacon 2004; Hu et al. 2008; Beer et al. 2009). Therefore, studies on the ecosystem WUE of poplar plantations are helpful when attempting to understand and quantify how much water the plants need in order to assimilate a certain amount of carbon, and to determine how future climate-warming-induced hydrological changes will impact the carbon budgets of poplar plantation ecosystems. Eddy covariance (EC) systems measure both CO_2 and water vapor exchange between ecosystems and the atmosphere at a high temporal resolution (Wofsy et al. 1993). These measurements provide a unique approach to quantifying the characteristics of ecosystem gross ecosystem productivity (GEP), evapotranspiration (ET), and WUE, as well as their responses to global climate change (Law et al. 2002; Baldocchi 2003; Barr et al. 2007). Previous studies of variations in ecosystem WUE found that there were similar diurnal variations (Scanlon and Albertson 2004; Testi et al. 2008; Tong et al. 2009) but different seasonal variations of the ecosystem WUE in various forests (Reichstein et al. 2002; Ponton et al. 2006; Yu et al. 2008; Migliavacca et al. 2009). Some studies found that the ecosystem WUE was lower during severe droughts (Teskey et al. 1994; Reichstein et al. 2002; Migliavacca et al. 2009), while some other studies showed that the WUE increased during moderate drought (Linderson et al. 2007; Yu et al. 2008). The various results for the seasonal variation in the WUE stem in part from the different influences of environmental factors on carbon sequestration and water loss (Veron et al. 2002) and from the various responses of the WUE to environmental variables in different tree species.

Numerous studies have been conducted in China on poplar plantations over the last 20 years in terms of biomass measurement, biomass production and growth modeling, water use, and the relationships between stem density and physiological traits of poplar varieties (Cao et al. 2002; Peng et al. 2003; Xue and Yang 2004; Liang et al. 2006), but detailed studies on the relationship between carbon gain and water loss and their environmental controls at the ecosystem level are lacking. Therefore, an open-path eddy covariance system and an automatic micro-meteorology system were used to continually measure the carbon, water, and energy exchanges between the canopy of a 10-year-old poplar plantation and the atmosphere in the Daxing District of Beijing, China from 2006 to 2008. Our objectives were (1) to quantify the diurnal and seasonal variability of the ecosystem WUE of a poplar plantation, and (2) to determine the effects of environmental factors on the ecosystem WUE at different temporal scales.

Materials and methods

Study site

The study was conducted in a 10-year-old poplar plantation (*Populus euramericana* cv. "74/76") at the Daxing Forest Farm (116°15′07″E, 39°31′50″N, and elevation 30 m), located in a suburb of Beijing, China. The plantation covers an area of 0.8 km^2 and the density of planting was 3 m × 2 m. The average height and root depth of the trees were 14.8 ± 1.2 and 1.86 ± 1.02 m by the end of 2008, respectively, and the leaf area index (LAI) of the stand was 2.1 ± 0.6. The understory vegetation was sparse, containing perennial herbs such as *Chenopodium glaucum* Linn., *Medicago sativa* L., *Melilotus officinalis* (L.) Lam., *Salsola collina* Pall., and *Tribulus terrestris* L. The mean annual (i.e., 1952–2000) precipitation is 569 mm, of which ~65 % occurs between July and September. The mean annual (i.e., 1990–2009) temperature is 11.5 °C, as recorded at the Daxing Weather Station (116°19′56″E, 39°43′24″N). The top two meters of the soil profile were largely composed of well-drained fluvial sand with a pH of 8.3 and a bulk density of 1.45 g cm^{-3}. Further details are available in Zhou et al. (2013).

Field measurements

An open-path EC flux measurement system was deployed at the center of the study site for long-term measurements of CO_2, water vapor, and energy fluxes from 2006 to 2008. Footprint analysis using an analytical model (Hsieh et al. 2000) suggested that 80 % of the footprint contribution was in the range of the measurement region (Zhou et al. 2013). To obtain sufficient fetch, a CO_2/H_2O infrared gas analyzer (LI-7500, Li-Cor Inc., Lincoln, NE, USA) and a three-dimensional ultrasonic anemometer (CSAT3, Campbell Scientific, Inc., Logan, UT, USA) were mounted 16 m above ground level (AGL) in 2006 and lifted to 18 m AGL in 2007 and 2008. The raw 10-Hz data were logged into a CR5000 data logger (Campbell Scientific, Inc.).

Net radiation (R_n) and photosynthetically active radiation (PAR) were measured using a net radiometer (Q7.1, REBS, Seattle, WA, USA) and a quantum sensor (LI190 SB-L, Li-Cor Inc.) at 16 m AGL in 2006 and 18 m AGL in 2007 and 2008, respectively. Precipitation (P) and atmospheric pressure were measured at heights of 16 m AGL and 13 m AGL in 2006 and of 18 m AGL and 21 m AGL in 2007 and 2008 using a tipping-bucket rain gauge (TE525-L, Campbell Scientific, Inc.) and an air pressure gauge (CS105, Campbell Scientific, Inc.). Air temperature (T_a) and relative humidity were measured at four levels (2, 6, 10, and 14 m AGL in 2006 and 5, 10, 15, and 20 m AGL in 2007 and 2008) using relative humidity and air temperature sensors (HMP45C probe, Campbell Scientific, Inc.).

Soil temperature profiles and soil heat fluxes were measured by soil temperature sensors (TCAV107, Campbell Scientific, Inc.) and soil heat plates (HFT3, REBS) at depths of 5, 10, and 20. Volumetric soil water contents (VWC) were measured at depths of 20 and 50 cm by a time-domain reflectometry (TDR) soil moisture device (CS616, Campbell Scientific, Inc.). All micrometeorological data were stored at 30-min intervals on a data logger (CR5000, Campbell Scientific, Inc.).

Data processing

The turbulent fluxes were corrected for density fluctuations (Webb et al. 1980) and calculated in the planar fit coordinate system (Wilczak et al. 2001). All calculations were done with the EC_PROCESSOR 2.1 software package (http://www4.ncsu.edu/~anoorme/ECP/).

Quality screening included filters for periods of highly unstable and highly stable atmospheric conditions (Hollinger et al. 2004), nonstationarity in turbulent fluxes (Foken et al. 2004), and periods with rainfall. Data with friction velocities (u_*) lower than an appropriate threshold ($u_* = 0.18$ m s^{-1} in 2006; $u_* = 0.12$ m s^{-1} in 2007; $u_* = 0.14$ m s^{-1} in 2008) were eliminated to avoid the underestimation of fluxes in low-wind conditions.

Data quality control resulted in the elimination of 37–45 % of the original EC data. Gaps in the 30-min NEE were filled by dynamic parameter mechanistic models (Lloyd and Taylor 1994; Law et al. 2002; Noormets et al. 2007), where the respiration (R_e) was obtained using a simple modification of the Lloyd–Taylor equation (Lloyd and Taylor 1994; Noormets et al. 2007, 2008):

$$R_e = R_{10} e^{\frac{E_a}{R} \cdot \left(\frac{1}{T_{ref}} - \frac{1}{T_a}\right)} \tag{1}$$

$$R_{10} = a_0 + a_1 \cdot \mathrm{VWC}, \tag{2}$$

where R_{10} is the reference respiration at a common temperature ($T_{ref} = 283.15$ K = 10 °C), 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 a_0 is considered to be the same as R_{10} under moisture-saturated conditions. a_1 is the unit change in R_{10} per unit change in VWC. The nighttime data were used to fit the Lloyd–Taylor equation and the daytime respiration was estimated using T_a and VWC data fitted monthly. Missing latent heat (LE) values were filled by applying a mean diurnal variation (MDV) method (Falge et al. 2001) using mean values for the monthly or weekly fixed MDV. Further details about the methods used to fill the gaps in the NEE data can be found in Zhou et al. (2013).

Calculation of the WUE and relative extractable water content

Energy balance closure was evaluated by performing a statistical regression of the non-gap-filled, half-hourly turbulent energy flux (i.e., sensible and latent heat) against 3 years of the available quality-controlled energy data. The energy balance during 2006–2008 at this site was studied by Liu et al. (2009) and Zhang et al. (2014), and had slopes of 0.86 ($R^2 = 0.87$, $N = 12{,}716$, $P < 0.0001$), 0.78 ($R^2 = 0.84$, $N = 11{,}625$, $P < 0.0001$), and 0.75 ($R^2 = 0.85$, $N = 13{,}950$, $P < 0.0001$) in 2006, 2007, and 2008, respectively. The ecosystem WUE can be calculated by various methods depending on the scientific discipline and the spatial and temporal scales of interest (Huxman et al. 2004; Yu et al. 2008). In this study, the ecosystem WUE was calculated as the ratio of the GEP (the sum of the turbulent flux, the canopy storage term, and the estimated ecosystem respiration, R_e; Zhou et al. 2013) to the corresponding ET. The canopy storage of CO_2 was estimated from the half-hourly changes in the mean CO_2 concentration, using the approach of Hollinger et al. (1994). The ET was derived by dividing the LE by the heat of vaporization (Sun et al. 2008).

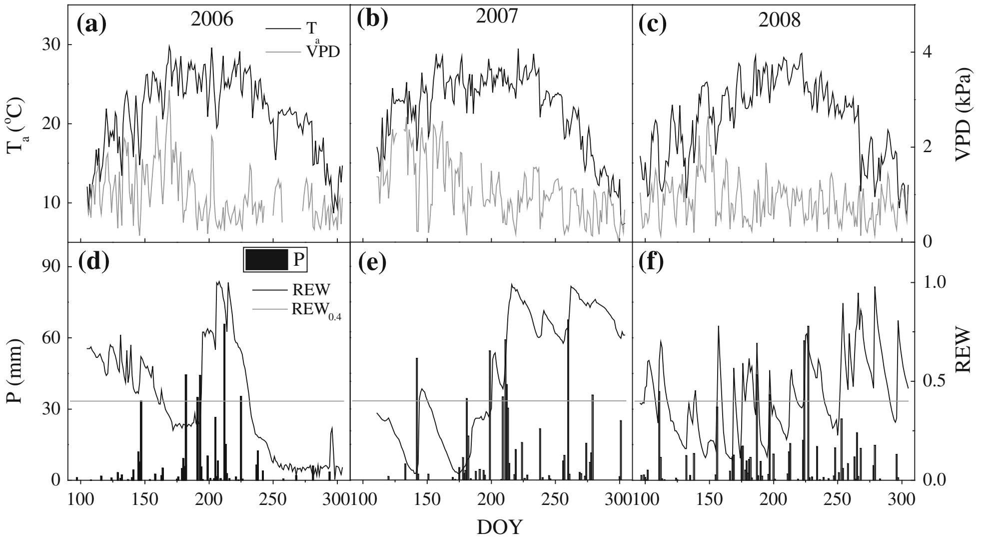
Key processes that control carbon transfer and storage vary over multiple temporal scales. Therefore, the ecosystem WUE varies with the temporal scale (Stoy et al. 2006). In this study, we considered the WUE in various guises: as the half-hourly WUE, the daily WUE, and the annual ecosystem WUE (the growing season). Each of these WUE terms was calculated using a dataset with the corresponding temporal resolution.

The relative extractable water content (REW) is an index that is used to quantify the ecosystem drought intensity. A soil drought occurs when the REW drops below 0.4 (Granier et al. 1999, 2007; Bernier et al. 2002), and the daily REW is calculated from the soil water content as follows:

$$\mathrm{REW} = \frac{\mathrm{VWC} - \mathrm{VWC_{min}}}{\mathrm{VWC_{max}} - \mathrm{VWC_{min}}}, \tag{3}$$

where VWC is the actual soil volumetric water content at a depth of 50 cm, and $\mathrm{VWC_{min}}$ and $\mathrm{VWC_{max}}$ are the minimum and maximum soil volumetric water contents at a depth of 50 cm, respectively.

Fig. 1 Seasonal variations in: daily mean air temperature (T_a) and daily mean saturated vapor pressure deficit (VPD) in **a** 2006, **b** 2007, **c** 2008; daily precipitation (P) and relative extractable water content (REW; 50 cm) in **d** 2006, **e** 2007, **f** 2008



Results

Meteorology

Figure 1 illustrates the seasonal variations in air temperature (T_a), vapor pressure deficit (VPD), precipitation, and soil water content in 2006, 2007, and 2008, respectively. The daily mean T_a during the 2008 growing season was 20.5 ± 0.5 °C, which was a little lower than those in 2006 (21.3 ± 0.6 °C) and 2007 (21.9 ± 0.6 °C) (Fig. 1a–c).

Precipitation differed among the 3 years, in terms of both amount and seasonal distribution (Fig. 1d–f). The year 2006 was dry with a total precipitation of 433 mm during the growing season (April–October). Although irrigation (35 mm in April and 21 mm in May) was applied during growing season, the total water supply in 2006 was also less than the multi-year (1990–2009) mean rainfall of 527 mm (Zhang et al. 2014). The precipitation was 631 and 632 mm during the growing seasons of 2007 and 2008, respectively. However, there was a drought period in 2007 during April to June, and a much lower VPD was observed in 2008 (especially in the spring) compared with those of 2006 and 2007 (Fig. 1a–c).

Seasonal changes in REW closely followed the variations in precipitation (Fig. 1d–f). A long dry period in 2006 and 2007 resulted in severe water deficits in the autumn of 2006 and spring of 2007 when the REW dropped below 0.4. However, no lasting drought was observed in 2008.

Diurnal and seasonal variations in WUE

The instantaneous WUE showed a diurnal trend, with a primary maximum WUE ranging from 3 to 5 g C kg^{-1} H_2O in the early morning and a secondary maximum ranging from 2 to 4 g C kg^{-1} H_2O in the evening (Fig. 2). Ecosystem WUE decreased by about 30–60 % during the daytime compared with the early morning and reached its minimum between 14:00 and 15:00. Besides, the morning WUE was higher than that in the afternoon.

Seasonal patterns of the ecosystem GEP, ET, and WUE from 2006 to 2008 are shown in Fig. 3. The mean daily WUE during the growing season was 2.3 ± 0.9, 2.4 ± 0.9, and 2.3 ± 1.1 g C kg^{-1} H_2O in 2006, 2007, and 2008, respectively. The mean daily GEP was 6.4 ± 2.9, 6.4 ± 2.4, and 7.5 ± 3.8 g C m^{-2} d^{-1} in 2006, 2007, and 2008, respectively (Zhou et al. 2013). The mean daily growing season ET was 2.7 ± 1.3, 2.7 ± 1.2, and 3.3 ± 1.6 kg H_2O m^{-2} d^{-1} in 2006, 2007, and 2008, respectively. During the 3-year study, daily GEP and ET peaked in July or August with rates of 12–15 g C m^{-2} d^{-1} and 3.6–4.7 kg H_2O m^{-2} d^{-1}, respectively. However, ecosystem WUE fluctuated and did not show a seasonal cycle during the growing seasons.

Responses of GEP, ET, and WUE to climate factors

Instantaneous WUE was negatively related to PAR and VPD (Fig. 4). Therefore, WUE declined with increasing PAR and VPD until 2 pm or 3 pm, and increased with decreasing PAR and VPD during the rest of the afternoon (Fig. 5). However, beginning at sunrise, WUE increased with increasing PAR and VPD.

GEP and ET (both measured per day) showed positive correlations with PAR ($P < 0.05$), while the sensitivity of GEP to PAR was different to the sensitivity of ET to PAR, regardless of the soil moisture conditions present (Fig. 6a–c). The relatively large increase in ET at low PAR compared to that of GEP led to a tendency of WUE to decrease

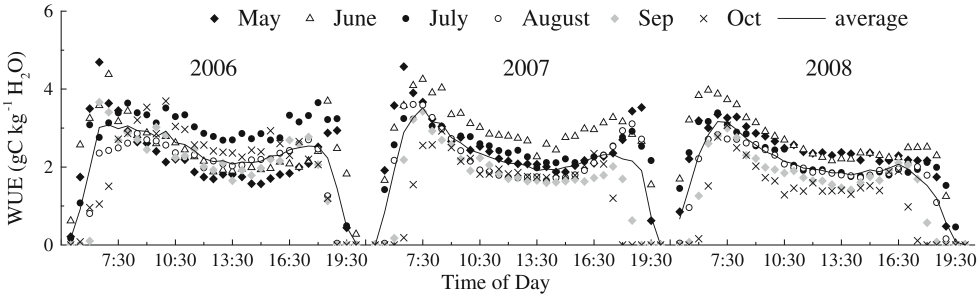


Fig. 2 Diurnal patterns of instantaneous ecosystem water-use efficiency (WUE) during the growing seasons in 2006, 2007, and 2008. *Black lines* show the average instantaneous WUE during the growing season

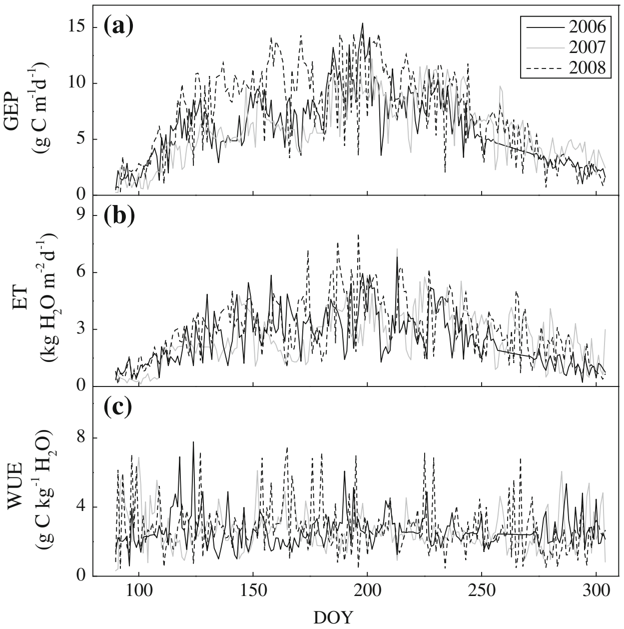


Fig. 3 Seasonal variations in **a** gross ecosystem productivity (GEP), **b** evapotranspiration (ET), and **c** ecosystem water-use efficiency (WUE) from 2006 to 2008

with increasing PAR under low-PAR conditions (Fig. 6a–c, f). Neither GEP, ET, nor WUE were significantly correlated with VPD on a daily basis ($P > 0.5$).

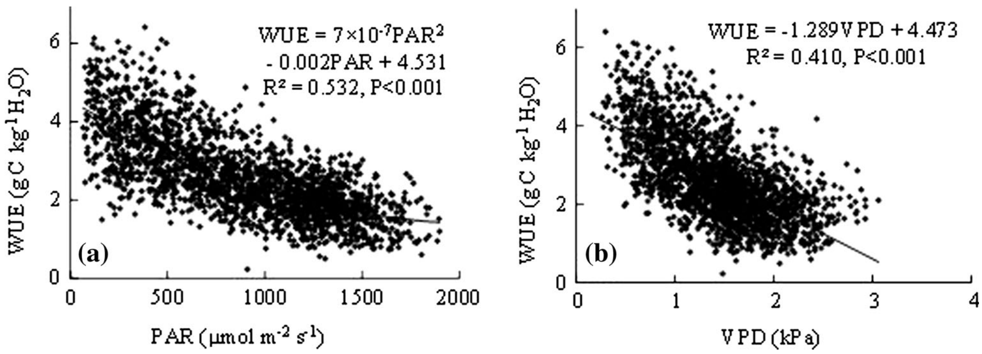
Although the impact of soil water on the daily GEP and ET was not statistically significant ($P > 0.5$, Fig. 7), the sensitivities of GEP and ET to PAR varied with the REW (Fig. 6d, e). A power equation was found to give a good fit to a plot of daily GEP against daily PAR for different REWs, while a good linear fit was obtained for a plot of daily ET against PAR when REW >0.4. A low REW significantly limited ET, and this effect became more pronounced as PAR increased (Fig. 6e). The slope of the daily GEP–PAR relationship was smallest when REW <0.1, but there was no significant effect of soil water on the relationship between GEP and PAR when $0.1 < \mathrm{REW} < 0.4$ and for $\mathrm{REW} > 0.4$ (Fig. 6d). Ecosystem GEP and ET were significantly correlated during the growing seasons of 2006–2008 under various soil water conditions (i.e., $\mathrm{REW} < 0.1$: $R^2 = 0.78$, $P < 0.001$; $0.1 < \mathrm{REW} < 0.4$: $R^2 = 0.56$, $P < 0.001$; $\mathrm{REW} > 0.4$: $R^2 = 0.44$, $P < 0.001$), but the slope of the GEP–ET relationship, which is a measure of WUE, declined with increasing soil moisture (i.e., $\mathrm{REW} < 0.1$: slope = 2.1, $R^2 = 0.78$; $0.1 < \mathrm{REW} < 0.4$: slope = 1.6, $R^2 = 0.56$; $\mathrm{REW} > 0.4$: slope = 1.4, $R^2 = 0.44$) (Fig. 4).

Discussion

Influence of climate on WUE

The primary environmental driver for changes in the 30-min WUE was the VPD, and thus the cyclical nature of the VPD resulted in a consistent diurnal cycle for WUE. The negative linear relationship between WUE and VPD was due to the limitations of a high VPD on the stomatal conductance of the plantation, as known from a previous study performed at this site (Zhou et al. 2013) and other

Fig. 4 Relationships between **a** water-use efficiency (WUE) and photosynthetically active radiation (PAR) and between **b** WUE and saturated vapor pressure deficit (VPD)



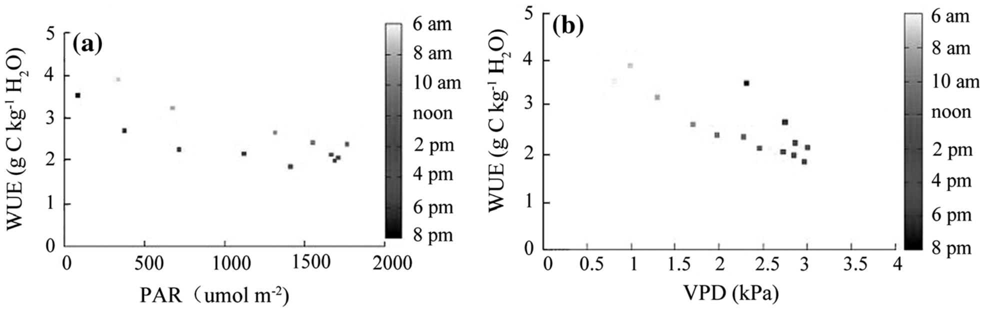


Fig. 5 Relationships between **a** half-hourly WUE and photosynthetically active radiation (PAR) and **b** half-hourly WUE and saturated vapor pressure deficit (VPD) between 6 am and 8 pm during the growing seasons in 2006–2008. (Available in color online)

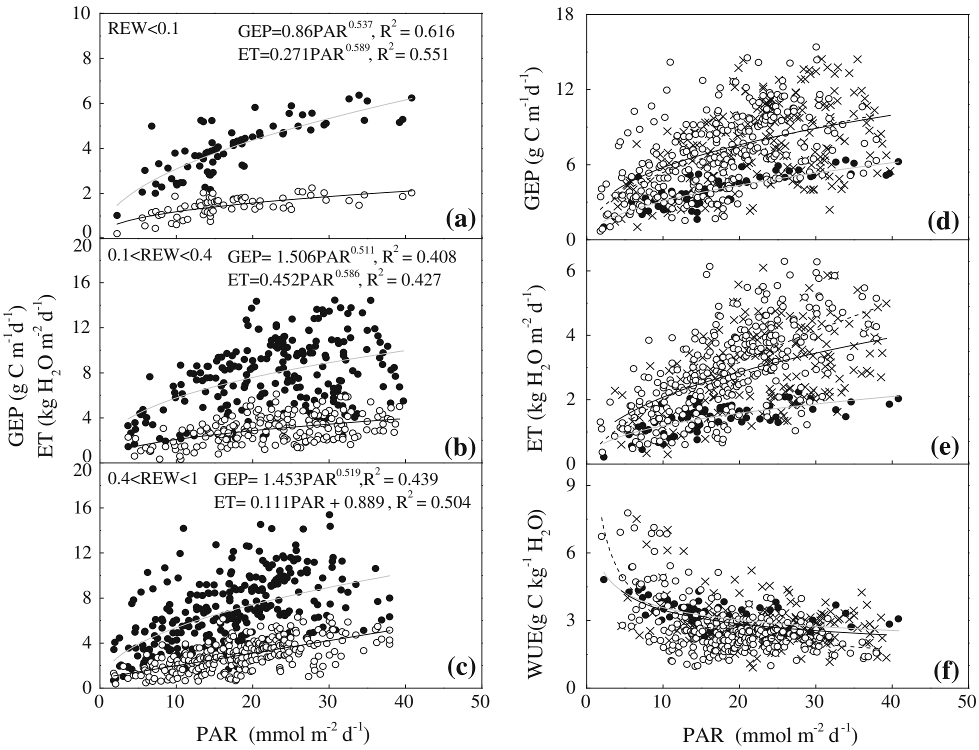


Fig. 6 Responses of gross ecosystem productivity (GEP), evapotranspiration (ET), and water-use efficiency (WUE) to photosynthetically active radiation (PAR) at different relative extractable water content (REW) levels during the growing seasons in 2006–2008. **a–c** GEP (*filled circles*) and ET (*unfilled circles*), **d–f** WUE (*filled circles* REW < 0.1; *crosses* $0.1 <$ REW < 0.4; *unfilled circles* REW > 0.4:)

studies performed at both the leaf level (Schulze and Hall 1982) and the ecosystem level (Baldocchi 1994; Law et al. 2002; Scanlon and Albertson 2004; Ponton et al. 2006). Although stomatal conductance influences both carbon gain and water loss, more water was lost by transpiration during the photosynthetic uptake of CO_2 under high VPD. This led to a tendency of WUE to decrease with increasing VPD at the leaf and ecosystem levels (Baldocchi 1994; Dewar 1997; Berbigier et al. 2001; Law et al. 2002; Mahrt and Vickers 2002; Scanlon and Albertson 2004; Ponton et al. 2006; Tang et al. 2006).

As it is a driving factor in both photosynthesis and evapotranspiration, solar radiation is one of the most important factors influencing WUE. Instantaneous and daily WUE showed negative correlations with PAR (Figs. 4a, 5a, 6f), possibly due to the high evapotranspiration rate induced by strong radiation (Monteith 1989). Similar results were also seen in both forests and cropland ecosystems (Rouphael and Colla 2005; Tong et al. 2009). The fact that the minimum WUE was observed between 2 and 3 pm also supports the results indicating that there was a greater increase in ET than in GEP under strong radiation (Fig. 2). The higher WUE seen in the morning than in the afternoon for the same PAR was mainly due to low feedback inhibition of photosynthesis in the morning (Tong et al. 2009). In the morning, the photosynthetic rate was strong even when the light intensity was low, due to low carbohydrate levels in leaves. Strong photosynthesis and a weak ET led to a maximum WUE in the morning. In the afternoon, feedback inhibition of photosynthesis led to a lower carbon uptake, while ET increased due to the higher temperature and VPD in the afternoon (Baldocchi 1994; Tong et al. 2009).

Soil water content was another environmental controller of WUE (Fig. 6f). Low soil moisture suppressed stomatal conductance (Law et al. 2000; Ponton et al. 2006) and therefore limited carbon and water exchange (Fig. 6d, e). Daily GEP and ET showed significant relationships during the growing seasons with different soil moisture conditions (i.e., REW < 0.1: $R^2 = 0.78$, $P < 0.001$; $0.1 <$ REW < 0.4: $R^2 = 0.56$, $P < 0.001$; REW > 0.4: $R^2 = 0.44$, $P < 0.001$) (Fig. 7). Similar relationships were found between GEP and ET across various biome types, and the slope of this relationship can be used to characterize the ecosystem WUE (Law et al. 2002). Our results suggested that the slope increased with decreasing soil moisture. Even though stomatal conductance decreases during a drought, WUE can increase so long as the internal resistance to CO_2 diffusion is kept constant (Yu et al. 2004). Some studies obtained similar results during moderate droughts at both the leaf (Huber et al. 1984; Nijs et al. 1989; Liang and Maruyama 1995) and ecosystem (Linderson et al. 2007; Yu et al. 2008) scales. However, during severe drought, WUE decreased or remained constant (Teskey et al. 1994; Reichstein et al. 2002; Granier et al. 2007; Migliavacca et al. 2009) due to increased internal resistance to CO_2 diffusion caused by decreased photosynthetic capacity (Baldocchi et al. 1983). Carbon and water showed more feedbacks at the ecosystem scale than at the leaf level, so photosynthetic capacity was not the only reason for the changes in WUE under water-limited conditions. The fraction of the evaporation that occurs from the forest floor is significant in forest ecosystems (Baldocchi and Ryu 2011). The low LAI observed at this site probably supports the notion that the forest floor makes a significant contribution. When the shallow layer is dry, the contribution of the forest floor to evapotranspiration becomes small, but poplars can maintain transpiration by taking up water through their deep root systems. Therefore, in our study, WUE was higher under low soil water conditions, even when the soil water content was lower than the wilting point (i.e., WP, VWC = 6 %, REW = 0.2) (Tan et al. 2009) (Fig. 6d–f).

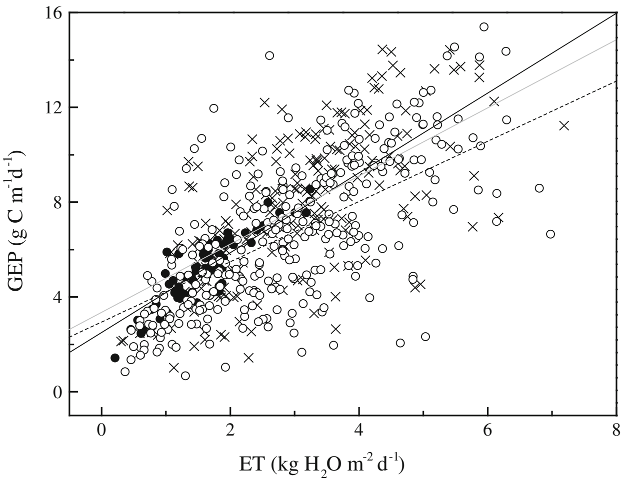


Fig. 7 Relationship between gross ecosystem productivity (GEP) and evapotranspiration (ET) for different relative extractable water contents (REWs) (*filled circles* $0 <$ REW < 0.1; *crosses* $0.1 <$ REW < 0.4; *unfilled circles* REW > 0.4:) during the growing seasons in 2006–2008. Regression lines: REW < 0.1: GEP = 2.11ET + 1.889, $R^2 = 0.779$; $0.1 <$ REW < 0.4: GEP = 1.63ET + 2.845, $R^2 = 0.562$; REW > 0.4: GEP = 1.41ET + 2.497, $R^2 = 0.437$

Comparison with other ecosystems

Reported ecosystem-level WUE values of different forests are briefly summarized in Table 1. Compared to another poplar plantation forest of a similar age and soil type, the GEP was similar during the growing season but WUE was

Table 1 Average annual ecosystem water-use efficiency (WUE) of different ecosystems

Ecosystem type	Latitude, longitude	WUE (g C kg^{-1} H_2O)	Reference
Ponderosa pine	44°30′N, 121°37′W	3.0	Law et al. (2000)
Maritime pine	44°42′N, 0°46′W	0.9	Berbigier et al. (2001)
Young Jack pine	53°52′N, 104°38′ W	1.0	Mahrt and Vickers (2002)
Aspen	55°53′N, 98°40′W	2.3	Mahrt and Vickers, (2002)
Deciduous broadleaf forest	2°–65°N, 20°W–25°E	0.9	Law et al. (2002)
Evergreen conifer forest	2°–65°N, 20°W–25°E	0.8	Law et al. (2002)
Aspen	53°38′N, 106°12′W	3.6[a]	Ponton et al. (2006)
Douglas fir	49°54′N, 125°22′W	5.4[a]	Ponton et al. (2006)
Deciduous forest	42°24′N, 128°05′E	2.6	Yu et al. (2008)
Conifer plantation forest	26°44′ N, 115°03′E	2.5	Yu et al. (2008)
Evergreen broadleaf forest	23°10′N, 112°32′E	1.9	Yu et al. (2008)
Poplar plantation	45°12′N, 9°03′E	3.6[b]	Migliavacca et al. (2009)
Hybrid poplar plantation	54°18′N, 111°30′W	1.7	Cai et al. (2011)
Poplar plantation	39°31′N, 116°15′E	2.3[b]	This research

[a] Daily average

[b] Growing season

56 % lower at our site, which was largely because the ET was 25 % higher in our study (Migliavacca et al. 2009). Cai et al. (2011) reported the carbon and water fluxes of a 5-year-old hybrid poplar plantation, which indicated a 52 % lower annual ET, a 65 % lower annual GEP, and a 26 % lower WUE than at our study site. The WUE of a boreal aspen forest was 56 % higher (Ponton et al. 2006) due to a 28 % lower annual ET and a 7 % lower annual GEP than in the current study (Barr et al. 2007). Besides, Mahrt and Vickers (2002) reported a similar WUE for aspen from the southern study area of the Boreal Ecosystem and Atmospheric Study. In addition, WUE was 13 % lower in our study due to a 9 % higher GEP and a 17 % higher ET compared with those of another deciduous forest at a higher latitude in eastern China (Yu et al. 2008).

We found diurnal WUE patterns at our study site that were similar to those previously reported (Baldocchi 1994; Lindroth and Cienciala 1996; Moren et al. 2001; Scanlon and Albertson 2004; Testi et al. 2008; Tong et al. 2009), while the seasonal variation in WUE was different (Reichstein et al. 2002; Ponton et al. 2006; Yu et al. 2008; Migliavacca et al. 2009). Reichstein et al. (2002) and Yu et al. (2008) found that the maximum WUE occurred in wet ecosystems in winter, whereas the minimum occurred during the peak vegetation season. However, other studies found no apparent seasonal trend in WUE during the growing season (Ponton et al. 2006; Yu et al. 2008). In our study, although there was substantial inter-daily variation in the WUE, no seasonal variation was observed during the growing season. This may suggest that the seasonal changes in WUE were due to factors such as site conditions, climate, and vegetation type, including the understory and growing season length (Veron et al. 2002).

Conclusions

The WUE of the poplar plantation forest examined in this study presented no apparent seasonal variations, but did show a significant diurnal trend during the growing season. Maximum WUE was observed in the morning, and minimum WUE was seen between 2 and 3 pm. This was regulated by stomatal closure and VPD. Seasonally, there was substantial inter-daily variation in WUE due to the influences of both the PAR and the soil water conditions. A higher sensitivity of ET than GEP to soil moisture led to a decreasing ecosystem WUE with increasing soil moisture. Therefore, soil moisture was not effectively used by carbon uptake. Instead, soil water was returned to the atmosphere through evapotranspiration.

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