

# Seasonal dynamics of water use efficiency of typical forest and grassland ecosystems in China

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**Abstract** We selected four sites of ChinaFLUX representing four major ecosystem types in China—Changbai-shan temperate broad-leaved Korean pine mixed forest (CBS), Dinghushan subtropical evergreen broadleaved forest (DHS), Inner Mongolia temperate steppe (NM), and Haibei alpine shrub-meadow (HBGC)—to study the seasonal dynamics of ecosystem water use efficiency ( $WUE = GPP/ET$ , where GPP is gross primary productivity and ET is evapotranspiration) and factors affecting it. Our seasonal dynamics results indicated single-peak variation of WUE in CBS, NM, and HBGC, which were affected by air temperature ( $T_a$ ) and leaf area index (LAI),

through their effects on the partitioning of evapotranspiration (ET) into transpiration (T) (i.e.,  $T/ET$ ). In DHS, WUE was higher at the beginning and the end of the year, and minimum in summer.  $T_a$  and soil water content affected the seasonal dynamics of WUE through their effects on GPP/T. Our results indicate that seasonal dynamics of WUE were different because factors affecting the seasonal dynamics and their mechanism were different among the key ecosystems.

**Keywords** Ecosystems in China · Eddy covariance · Seasonal dynamics · Water use efficiency

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## Introduction

Water use efficiency (WUE), an important index representing the relationship between carbon and water cycles (Reichstein et al. 2002; Ponton et al. 2006; Steduto et al. 2007), has obvious temporal variations. Understanding the seasonal dynamics of WUE may improve our knowledge of the relationship between carbon and water cycles during the growth of vegetation.

There are different types of seasonal dynamics in WUE. In the high-mid latitude ecosystems of the Northern Hemisphere, WUE rose to the peak value around June and remained constant for a long time (Ponton et al. 2006; Hu et al. 2008). This was caused by variation of the relative contributions of transpiration (T) and evaporation (E) to evapotranspiration (ET) (Hu et al. 2008; Huang et al. 2010). In the Mediterranean climatic region and the subtropical region in East Asia, WUE reached maxima both at the beginning and the end of a year, with lower WUE during the middle of the year (Reichstein et al. 2002; Song et al. 2006; Yu et al. 2008). Such seasonality may be

attributed to the decrease of soil water content (SWC) (Reichstein et al. 2002) or the increase of vapor pressure deficit (VPD) (Song et al. 2006). Two different patterns may result from the effects of abiotic or biotic factors on the different components of WUE.

Abiotic and biotic factors have very complicated effects on the seasonal dynamics of WUE, and the effects of single factors only have been investigated. For example, WUE decreased when VPD increased in ecosystems in northern America (Ponton et al. 2006), Spain (Testi et al. 2008), and China (Song et al. 2006). In European ecosystems, WUE increased as the SWC decreased (Reichstein et al. 2002). In grassland ecosystems of China, WUE increased with increasing leaf area index (LAI) (Hu et al. 2008; Huang et al. 2010). At the leaf scale, CO<sub>2</sub> concentration ([CO<sub>2</sub>]) robustly affected WUE (Steduto et al. 2007) but such a relationship between [CO<sub>2</sub>] and WUE was studied mainly in free air CO<sub>2</sub> enhancement (FACE) studies (Wullschlegel et al. 2002). At the ecosystem scale, the effect of [CO<sub>2</sub>] on the dynamics of WUE was still unclear.

Four types of ecosystem, i.e., temperate forest, subtropical forest, temperate grassland, and alpine meadow, are typical and important ecosystems in China. To represent these key ecosystems, we selected four sites of ChinaFLUX and analyzed the fluxes of CO<sub>2</sub> and H<sub>2</sub>O measured by use of the tower-based eddy covariance technique. Our objectives were:

1. to ascertain the seasonal dynamics of WUE in four different ecosystems; and
2. to identify the main factors controlling the seasonal dynamics of WUE and the underlying mechanisms.

The results provide important insight into the relationship between carbon and water cycles in key ecosystems in East Asia.

## Materials and methods

### Site descriptions and field measurements

Experimental data including flux and meteorological data were collected at four sites of ChinaFLUX: Changbaishan temperate broad-leaved Korean pine mixed forest (CBS), Dinghushan subtropical evergreen broadleaved forest (DHS), Inner Mongolia temperate steppe (NM), and Haibei alpine shrub-meadow (HBGC) (Table 1).

At these four sites, CO<sub>2</sub> and H<sub>2</sub>O flux data were measured by use of the open path eddy covariance system, by use of an open-path infrared gas analyzer (model LI-7500; Licor, Lincoln, NB, USA), a 3-D sonic anemometer (model CSAT3; Campbell Scientific, Logan, UT, USA), and a datalogger (model CR5000; Campbell Scientific), recording

the EC signals at 10 Hz. All fluxes were computed by block averaging over 30 min. Simultaneously, the routine meteorological variables radiation, air temperature, relative humidity, soil temperature, and SWC were measured and recorded at 30-min intervals. Further details can be found in Yu et al. (2006).

### Data processing

#### Flux data

Data were processed as usual, including three-dimensional rotation (Aubinet et al. 1999), WPL correction (Webb et al. 1980), storage calculation (Hollinger et al. 1994), and spurious data removal. To exclude the low turbulence fluxes at night, the *u*\* threshold was calculated in accordance with Reichstein et al. (2005), and different *u*\* thresholds were used at each site and for each year. Negative CO<sub>2</sub> fluxes at nighttime and in the non-growing season were also removed. Whether the data can be classified as growing-season was judged by the air temperature (Mkhabela et al. 2009).

Nonlinear regression was used for data interpolation for nighttime CO<sub>2</sub> flux, in accordance with Falge et al. (2001) and Reichstein et al. (2005). During the growing season, daytime data gaps were filled by use of the Michaelis–Menten equation (Falge et al. 2001). For the non-growing season, respiration was deemed as the daytime flux.

Gross primary productivity (GPP) was calculated as the sum of net ecosystem productivity (NEP, i.e. negative of the measured net ecosystem exchange, NEE) and ecosystem respirations (RE, extrapolated from the nighttime equation and daytime meteorological variables).

$$GPP = NEP + RE \quad (1)$$

For H<sub>2</sub>O flux, data gaps were filled by use of the look-up table approach (Reichstein et al. 2005). To analyze the mechanisms of WUE dynamics, we separated ET into E and T by use of the Shuttleworth–Wallace model (Hu et al. 2009b).

#### Auxiliary data

Data gaps in the meteorological variables and [CO<sub>2</sub>] were filled by use of the mean diurnal variation method (Falge et al. 2001).

We estimated LAI with normalized difference vegetation index (NDVI) in grassland on an 8-day scale and linearly interpolated to a daily scale (Hu et al. 2008, 2009b). In forest ecosystems, we estimated the extinction coefficient (*k*) using the measured LAI and absorbed radiation, in accordance with the Lambert–Beer Law.

**Table 1** Site descriptions

Sites	CBS	DHS	NM	HBGC
Latitude (°)	42.40	23.17	43.53	37.66
Longitude (°)	128.09	112.57	116.67	101.32
Elevation (m)	738	300	1189	3293
MAT (°C) <sup>a</sup>	3.6	21	−1.1	−1.7
AP (mm) <sup>b</sup>	695	1956	350	570
Predominant species	<i>Pinus koraiensis</i> , <i>Tilia amurensis</i> , <i>Acer mono</i> , <i>Quercus mongolica</i> , <i>Fraxinus andshurica</i>	<i>Schima superba</i> , <i>Castanopsis chinensi</i> , <i>Pinus massoniana</i>	<i>Leymus chinensis</i> , <i>Stipa grandis</i> , <i>Koeleria cristata</i> , <i>Agropyron cristatum</i>	<i>Potentilla fruticosa</i> L., <i>Stipa aliena</i> , <i>Kobresia capillifolia</i> , <i>Kobresia humilis</i>
Soil type	Dark brown forest soil	Lateritic red soil, yellow soil	Dark chestnut (Mollic Gryic, Cambisols)	Dark chestnut (Mollic Gryic, Cambisols)
CH (m) <sup>c</sup>	26	20	0.5–0.6	0.6–0.7
HEC (m) <sup>d</sup>	40	27	2.5	2.5

CBS Changbaishan temperate broad-leaved Korean pine mixed forest, DHS Dinghushan subtropical evergreen broadleaved forest, NM Inner Mongolia temperate steppe, HBGC Haibei alpine shrub-meadow

<sup>a</sup> Mean annual air temperature, values are the average from 1985 to 2005

<sup>b</sup> Annual precipitation, values are also the average from 1985 to 2005

<sup>c</sup> Canopy height

<sup>d</sup> Height of EC equipment mounted

Then, using the absorbed radiation and  $k$ , we calculated the daily LAI (Gower et al. 1999).

#### Calculations of WUE

In this study, we defined the WUE at the ecosystem scale as:

$$\text{WUE} = \frac{\text{GPP}}{\text{ET}} \quad (2)$$

GPP and ET are the daily sums of half-hourly fluxes from the eddy covariance measurement. This definition of WUE denoted the relationship between carbon assimilation and water consumption on a daily basis (Yu et al. 2008).

We focused on different seasonal dynamics of WUE among ecosystems under long-term climate in this study. Thus WUE was calculated as follows: WUE in each Julian day from 2003 to 2008 was calculated first. WUE used in this study was then calculated as the average for the same Julian day from 2003 to 2008. By doing so, the seasonal dynamics of WUE was not affected by the inter-annual variation for two reasons:

first, the seasonal dynamics of WUE among years was similar, especially in the three northern ecosystems; and second, and the most important, a single year data added or removed from the data set did not affect the mean seasonal dynamics of WUE.

The difference between WUE obtained from data added and not added was not significant ( $P > 0.05$ ); the same was true for average values of biotic and abiotic factors.

#### Statistical analysis

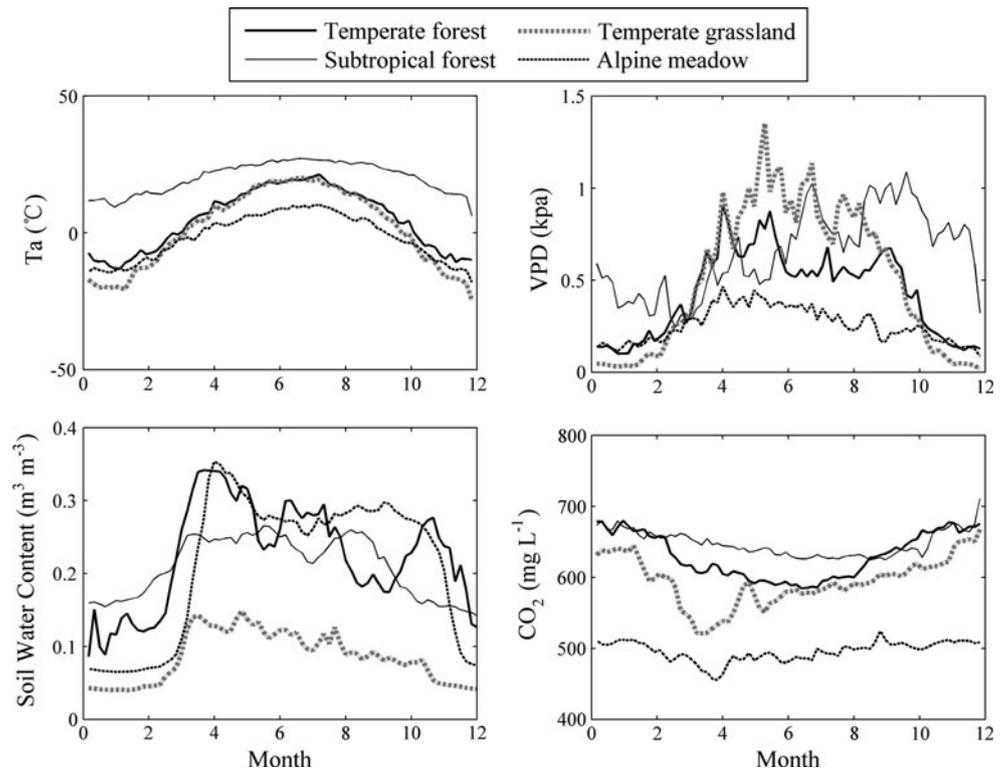
To determine which factor explained most of the variation of WUE, using bin separation, we compiled biotic (LAI) and abiotic (air temperature (Ta), VPD, SWC at 10 cm and [CO<sub>2</sub>]) factors as group variables. Then, multivariate analysis of variance (MANOVA) with daily data was used in accordance with Li et al. (2008). Relationships between WUE and biotic and abiotic factors were fitted with linear and polynomial equations. All analyses were conducted using Matlab 2008. Statistically significant differences were set as  $P < 0.05$  unless otherwise stated.

#### Results

##### Seasonal dynamics of abiotic and biotic factors

The main abiotic factors affecting ecosystem WUE were VPD, SWC, and [CO<sub>2</sub>] (Hu et al. 2009a); Ta, also, strongly affected plant growth and the carbon and water cycles (Yu et al. 2008). Therefore, we selected these four factors to find their effects on the seasonal dynamics of WUE. Single-peak variation was observed for Ta, with the peak occurring in approximately July in temperate forest, temperate grassland, and alpine meadow (Fig. 1). In subtropical forest, Ta was relatively high throughout the year with no obvious trend. The pattern of VPD was different from that of Ta with peaks from April to June except for the

**Fig. 1** Seasonal dynamics of biotic and abiotic factors in typical ecosystems



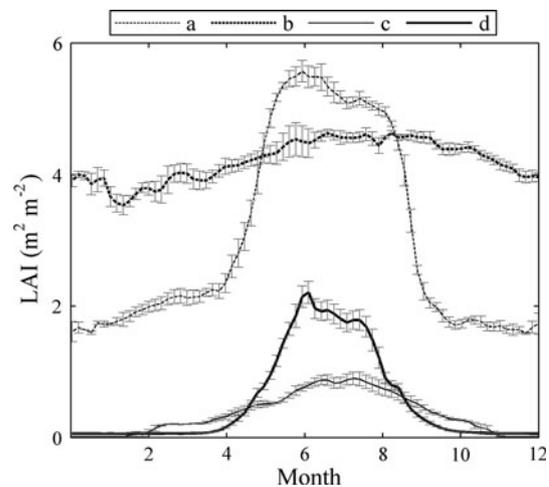
subtropical forest (Fig. 1). In these four ecosystems, SWC was lower during the beginning and end of the year (Fig. 1). In contrast, [CO<sub>2</sub>] was lower during the growing season. Alpine meadow had the lowest [CO<sub>2</sub>], mainly because of the high altitude.

The biotic factor was the synthetic response of vegetation to environmental factors, and may be represented by LAI; it has been suggested LAI also affected the seasonal dynamics of WUE (Hu et al. 2008). The LAI values of forest ecosystems were higher than those of grassland (Fig. 2).

Seasonal dynamics of WUE

Seasonal dynamics of WUE were clearly different among ecosystems (Fig. 3). In temperate forest, WUE reached its peak value in approximately July and was zero during the non-growing season because productivity was zero. This was also observed in temperate grassland and alpine meadow. In subtropical forest, WUE was lower in the middle of the year.

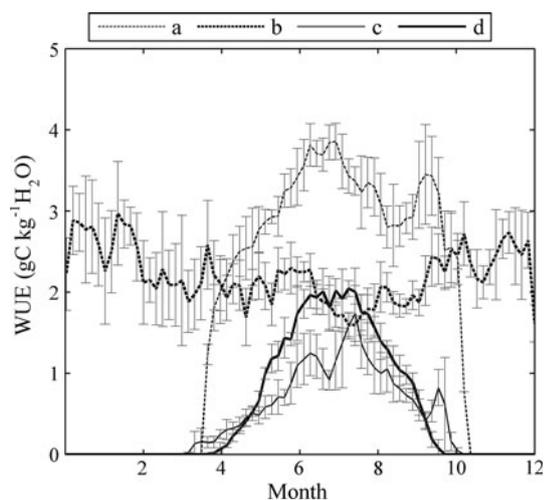
The peak value of WUE varied among ecosystems. Temperate forest had the highest WUE (3.45 gC kg<sup>-1</sup>H<sub>2</sub>O) whereas that of subtropical forest was 2.97 gC kg<sup>-1</sup>H<sub>2</sub>O. The peak values of WUE for forest ecosystems were higher than those for temperate grassland (1.74 gC kg<sup>-1</sup>H<sub>2</sub>O) and alpine meadow (2.04 gC kg<sup>-1</sup>H<sub>2</sub>O).



**Fig. 2** Seasonal dynamics of LAI in typical ecosystems, data used here are average values for each Julian day from 2003 to 2008; error bars indicate the variations among years. For clarity the five-day average is shown here (the same is true for Fig. 3 also). a Temperate forest; b Subtropical forest; c Temperate grassland; d Alpine meadow

Abiotic and biotic factors affecting the seasonal dynamics of WUE

In this study, MANOVA was used to distinguish the main factors affecting the seasonal dynamics of WUE; data for the non-growing season were excluded.



**Fig. 3** Seasonal dynamics of water use efficiency in typical ecosystems. *a* Temperate forest; *b* Subtropical forest; *c* Temperate grassland; *d* Alpine meadow

Ta significantly affected the seasonal dynamics of WUE in all ecosystems (Supplement Table 1). In addition to Ta, WUE was also affected by SWC in forest ecosystems and by LAI in grassland. WUE increased linearly with the increasing Ta in all ecosystems except subtropical forest (Fig. 4), whereas a linear decrease or a convex parabolic curve was observed with increasing SWC (Supplement Fig. 1).

LAI affected the seasonal dynamics of WUE in most ecosystems (Supplement Table 1). On the basis of the combined datasets from four ecosystems, WUE increased almost linearly with LAI until it reached approximately 3,

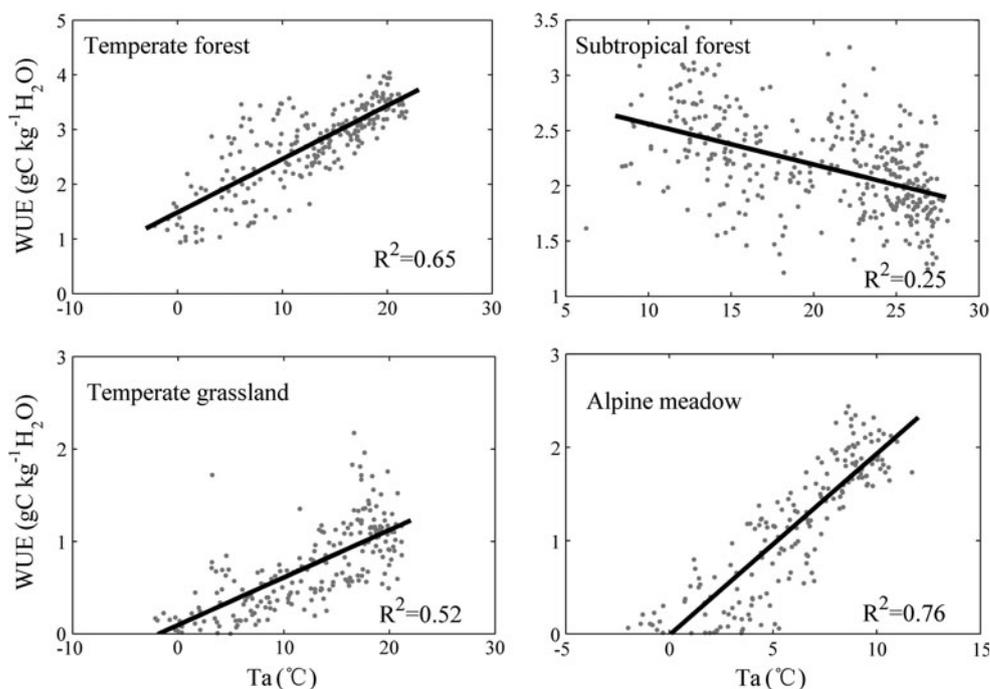
but remained relatively constant beyond that threshold (Supplement Fig. 2).

## Discussion

A single peak was observed in variation of the WUE for temperate forest, whereas WUE was nearly a constant for mid-high latitude mature forest of Canada (Jassal et al. 2009). This may be attributed to the different climate. In the work by Jassal et al. (2009), for example, the annual mean air temperature was  $>8^{\circ}\text{C}$  and annual precipitation was  $>1400\text{ mm}$ . In subtropical forest, the seasonal dynamics of WUE were similar to those of the grassland in southern Portugal (Reichstein et al. 2002). The single peak patterns for temperate grassland and alpine meadow were in accordance with those for the grassland of Canada (Jassal et al. 2009), Mongolia (Li et al. 2008), Inner Mongolia (Hu et al. 2008; Huang et al. 2010), and Northeast China (Dong et al. 2011).

The effect of Ta on WUE observed in our study has not been reported in the literature. In most cases, WUE decreased when SWC increased (Reichstein et al. 2002), as found in this study. If SWC was too low to support vegetation, WUE would decrease. LAI was the main factor affecting the variation of WUE in grassland, which was consistent with other studies (Hu et al. 2008; Huang et al. 2010). WUE did not change significantly with the variation of VPD, contradicting the findings of other studies (Testi et al. 2008). This indicates that the effect of VPD on WUE should be reconsidered. Furthermore,  $[\text{CO}_2]$  did not affect the seasonal variation of WUE in this study.

**Fig. 4** The relationship between WUE and air temperature (Ta) in typical ecosystems



WUE as given by Eq. (2) can be separated into two parts (Hu et al. 2008). One was the transpiration efficiency as the ratio of GPP to T, representing water use efficiency during photosynthesis. The other was the ratio of T to ET, indicating the relationship between water loss through physiological processes and total water loss.

$$WUE = \frac{GPP}{ET} = \frac{GPP}{T} \times \frac{T}{ET} \quad (3)$$

It is important to understand the relative roles of these two terms to gain insight into the mechanisms underlying the seasonal dynamics of WUE. The relationships between WUE and its two components were different among ecosystems (Fig. 5). For temperate forest and grassland ecosystems, WUE strongly linearly correlated with T/ET. In contrast, for subtropical forest, WUE correlated with GPP/T, because relatively constant LAI-canopy structure would not change significantly throughout the year. Although T/ET for subtropical forest had a single-peak pattern, the range of variation in T/ET was narrow (Supplement Fig. 3). For alpine meadow, WUE was sensitive to changes in both GPP/T and T/ET, because of a wide range of variation in the partitioning of ET to T throughout the year.

There was no doubt that Ta and LAI affected the seasonal dynamics of WUE in northern ecosystems. As Ta and LAI increased, the increase of vegetation cover led to the increase of T/ET (Hu et al. 2008; Huang et al. 2010), and, thus, WUE increased. In the subtropical forest, affected by the Asian monsoon, SWC and Ta increased simultaneously. The increase of Ta and SWC enriched the available water, leading to the increase of T and, thus, the decrease of GPP/T. The correlation coefficient between Ta

and GPP/T was  $-0.82$  whereas that between GPP/T and SWC was  $-0.72$ , which were both significant ( $P < 0.05$ ). Thus, GPP/T decreased with increasing SWC and Ta. T/ET was in a narrow range (Supplement Fig. 3) and, therefore, the pattern of WUE was similar to that of GPP/T.

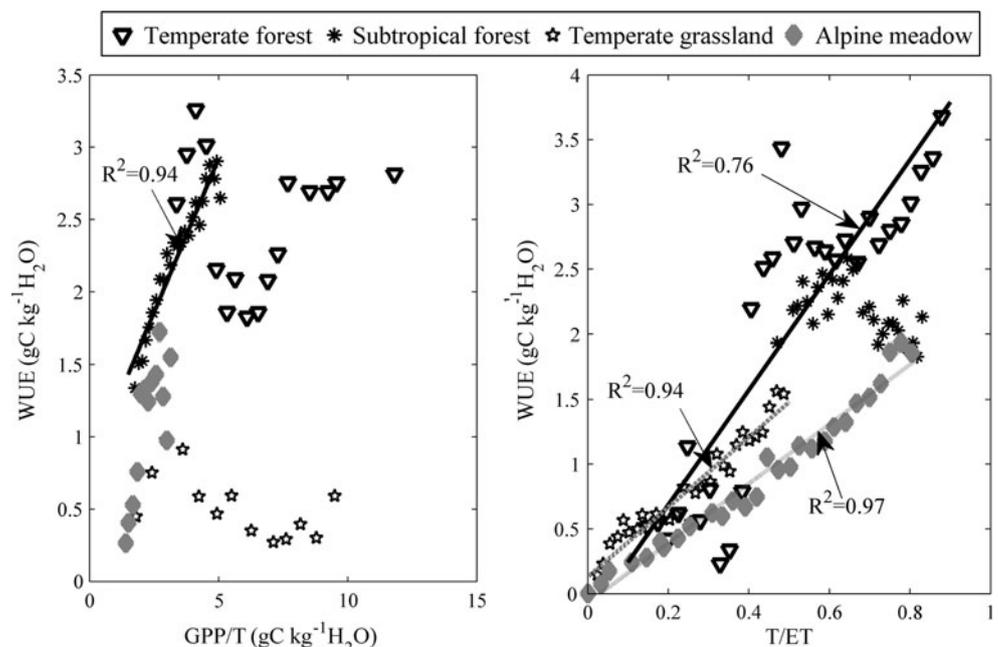
### Conclusions

In this study we reported the seasonal dynamics of WUE in typical ecosystems in China based on data obtained by use of the eddy covariance technique. Sites were selected on the basis of vegetation type, and represented temperate forest, subtropical forest, temperate grassland, and alpine meadow. The seasonal dynamics of WUE and the response to abiotic and biotic factors were investigated. Major findings were:

1. the dynamics of WUE had a single-peak in approximately July in temperate forest, temperate grassland, and alpine meadow whereas those of subtropical forest were higher at the beginning and the end of the year;
2. in forest ecosystems, Ta and SWC were the main factors affecting the seasonal dynamics of WUE whereas Ta and LAI were the main factors for grassland and alpine meadow systems; and
3. in temperate forest, temperate grassland, and alpine meadow, the dynamics of WUE were mainly determined by variation of T/ET whereas those in subtropical forest resulted from the change of GPP/T.

Thus, ecosystem structure affecting the partition of ET into T determined the seasonal dynamics of WUE in

**Fig. 5** Relationship between WUE and GPP/T and T/ET for typical ecosystems; data in this figure were binned as GPP/T or T/ET



temperate ecosystems, whereas those of the subtropical ecosystem were mostly affected by the inherent coupling between carbon and water cycles in plants, indicated by GPP/T.

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