Water-use efficiency of forest ecosystems in eastern China and its relations to climatic variables

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Summary

- Carbon (C) and water cycles of terrestrial ecosystems are two coupled ecological processes controlled partly by stomatal behavior. Water-use efficiency (WUE) reflects the coupling relationship to some extent. At stand and ecosystem levels, the variability of WUE results from the trade-off between water loss and C gain in the process of plant photosynthetic C assimilation.
- Continuous observations of C, water, and energy fluxes were made at three selected forest sites of ChinaFLUX with eddy covariance systems from 2003 to 2005. WUE at different temporal scales were defined and calculated with different C and water flux components.
- Variations in WUE were found among three sites. Average annual WUE was 9.43 mg CO_2 g^{-1} H_2O at Changbaishan temperate broad-leaved Korean pine mixed forest, 9.27 mg CO_2 g^{-1} H_2O at Qianyanzhou subtropical coniferous plantation, and 6.90 mg CO_2 g^{-1} H_2O at Dinghushan subtropical evergreen broad-leaved forest. It was also found that temperate and subtropical forest ecosystems had different relationships between gross primary productivity (GPP) and evapotranspiration (ET).
- Variations in WUE indicated the difference in the coupling between C and water cycles. The asynchronous response of GPP and ET to climatic variables determined the coupling and decoupling between C and water cycles for the two regional forest ecosystems.

Key words: ChinaFLUX, evapotranspiration (ET), forest ecosystem, gross primary productivity (GPP), North–South Transect of Eastern China (NSTEC), water-use efficiency (WUE).

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Introduction

In the terrestrial ecosystem, carbon (C) and water cycles closely couple because they both exchange between biosphere and atmosphere via the same pathway, namely the stomata. At the stand and ecosystem scales, the variability of water-use efficiency (WUE) reflects trade-off between water loss and C gain in the process of plant photosynthetic C assimilation. The WUE indicates water-use strategy among different species or at different life stages of plants (Donovan & Ehleringer, 1991). At the ecosystem level, WUE can be used to quantify the coupling between C and water cycles (Yu *et al.*, 2004). To predict the associated changes in productivity and distribution of plant species, it is essential to understand how WUE of different species change with climate (Xu & Hsiao, 2004). However, the processes of water loss and C gain are very complicated at the ecosystem level. It is difficult to accurately measure and evaluate ecosystem WUE because current observation methods are limited to obtaining only a certain component of water and C fluxes. Eddy covariance techniques, which can measure CO_2 and water vapor exchange between ecosystems and atmosphere with a high time-resolution (Wofsy *et al.*, 1993), provide powerful tools to evaluate ecosystem gross primary productivity (GPP), evapotranspiration (ET) and WUE, and to measure their responses to environmental change (Law *et al.*, 2002; Huxman *et al.*, 2004).

The observations of FLUXNET can provide plenty of information for studying the characteristics of ecosystem GPP, ET and WUE, and their responses and adaptations to global climate change (Baldocchi *et al.*, 2003; Barr *et al.*, 2006). Law *et al.* (2002) showed that C assimilation increased linearly with water loss under conditions without environmental stresses, suggesting that ecosystem WUE was conservative if gas exchange was controlled by stomata only. Huxman *et al.* (2004) reported that at the sites with low mean annual precipitation (MAP), efficient water use associated with growth rates of individual plants was translated to high GPP and high WUE at the ecosystem level. In comparison, at the sites with high MAP, plants with high growth rates and strong competition for other resources were favorably selected. Bert *et al.* (1997) investigated the variations of intrinsic WUE during last century based on the analysis of $\delta^{13}C$ in tree rings of a western forest ecosystem. They found that the WUE increased by 30% between the 1930s and the 1980s mainly because of long-term environmental changes, such as the continuous rise in atmospheric CO_2 concentration and in nitrogen deposition. Saurer *et al.* (2004) obtained similar conclusion for the forest in north Eurasia. They pointed out that the tendency to maintain a constant ratio of intercellular to ambient CO_2 concentration was the main reason for the increase in WUE under enhanced CO_2 concentration. Results by Beer *et al.* (2007) provided additional relationships between WUE and two ecosystem state properties: available soil water holding capacity and leaf area index.

The climate in Asia differs from that in Europe and North America because of the influence of eastern Asia monsoons (Yu *et al.*, 2006). As a result, some distinct regional characteristics might be associated with the relationship between C assimilation and water loss in eastern Asia forest ecosystems. Unfortunately, to date, there has been little study of WUE variations, seasonal patterns and their responses to the climate change of forest ecosystems in eastern Asia. Zonal forest ecosystems, from tropical to cold temperate, are distributed along the north–south transect of Eastern China (NSTEC). Comparing the WUE of these forest ecosystems will help elucidate the ecosystem response and adaptation to the climate change. In this study, three different forest sites of ChinaFLUX located along the NSTEC were selected. The objectives of the research were to analyse the WUE variability, compare the seasonal variations of WUE among ecosystems, explore the responses of GPP, ET and WUE to the seasonal and interannual climate change, and examine the climate gradient impacts on the spatial pattern of WUE of the forest ecosystems in eastern China. Achieving these objectives should improve our understanding of the mechanism underlying the coupling of C and water cycles, which is of great importance in predicting the effects of climate change on ecosystem C budget and water resources.

Materials and Methods

Site descriptions

Experimental data were observed at three ChinaFLUX sites, Changbaishan temperate broad-leaved Korean pine mixed forest (CBS), Qianyanzhou subtropical coniferous plantation (QYZ) and Dinghushan subtropical evergreen broadleaved forest (DHS). The stand ages of these three sites were *c.* 200 yr, 21 yr and 100 yr, respectively. The sites are distributed from north to south in eastern China, spanning wide ranges of precipitation and temperature. The mean annual temperatures are 3.6°C, 17.9°C and 21.0°C, and the average annual precipitation are 695 mm, 1485 mm and 1956 mm for CBS, QYZ and DHS, respectively. Table 1 provides extensive descriptions of the sites.

Carbon and water fluxes in the three forest ecosystems were measured from 2003 to 2005 with eddy covariance (EC) systems consisting of open-path infrared gas analysers (model LI-7500; Licor Inc., Lincoln, NB, USA) and a 3-D sonic anemometer (model CSAT3; Campbell Scientific Inc., Logan, UT, USA). A datalogger (model CR5000; Campbell Scientific Inc.) recorded the EC signals at 10 Hz for archiving and on-line computation of the turbulence statistics. All fluxes were computed by block averaging over 30 min. Routine meteorological variables, such as radiation, air temperature and relative humidity, were measured simultaneously and continuously. Soil temperature and soil moisture were also measured with a thermocouple probe (105T; Campbell Scientific Inc.) and a water content reflectometer (CS616; Campbell Scientific Inc.), respectively. All the micrometeorological measurements were recorded at 30-min intervals with dataloggers (CR10X and CR23X; Campbell Scientific Inc.). More information on the routine meteorological system are given in the Supplementary Material, Table S1. Table 1 presents the observation heights of different sensors. Detailed descriptions on observation of the sites can also be found in Yu *et al.* (2006), Wen *et al.* (2006) and Zhang *et al.* (2006).

Data processing and WUE calculations

Flux data processing Three-dimensional rotation of the coordinate was applied to the wind components for avoiding the effect of instrument tilt or irregularity on the airflow (Aubinet *et al.*, 2000). Correction was made for the effect of fluctuations of air density on the fluxes of CO_2 and water vapor (Webb *et al.*, 1980). Storage below the EC height was also corrected (Hollinger *et al.*, 1994).

Table 1 Description of site characteristics

Sites	CBS	QYZ	DHS
Location	42°24′N, 128°05′E	26°44′N, 115°03′E	23°10′N, 112°34′E
Elevation (m)	738	102	300
Mean annual temperature (°C)[a]	3.6	17.9	21.0
Annual precipitation (mm)[a]	695	1485	1956
Predominant species	*Pinus koriaensis, Tilia amurensis, Acer mono, Quercus mongolica, Fraxinus mandshurica*	*Pinus massoniana* Lamb, *Pinus elliottii* Engelm, *Cunninghamia lanceolata* Hook	*Schima superba, Castanopsis chinensi, Pinus massoniana*
Stand age (yr)	*c.* 200	21	*c.* 100
Canopy height (m)	26	12	20
Leaf area index (LAI)	6.1	3.5	4.0
Leaf N content (%)[b]	1.91 ± 0.34	0.78 ± 0.45	1.72 ± 0.29
Atmospheric nitrogen deposition (kg N ha^{-1} yr^{-1})	17.63	20.72	38.4
Ozone concentration (×10^{-9}, v : v)[d]	29 ± 0.25	21 ± 0.16	5 ± 0.14
Soil type	Dark brown forest soil	Red soil	Lateritic red soil, yellow soil
Height of eddy covariance (EC) (m)[c]	40	39.6	27
Profiles of air temperature and humidity (m)[c]	2.5, 8.0, 22.0, 26.0, 32.0, 50.0, 61.8	1.6, 7.6, 11.6, 15.6, 23.6, 31.6, 39.6	4, 9, 15, 21, 27, 31, 36
Depth of soil temperature (m)[c]	0, 0.05, 0.1, 0.2, 0.5, 1	0.02, 0.05, 0.2, 0.5, 1	0.05, 0.1, 0.2, 0.5, 1
Depth of soil moisture (m)[c]	0.05, 0.2, 0.5	0.05, 0.2, 0.5	0.05, 0.2, 0.5

CBS, Changbaishan temperate broad-leaved Korean pine mixed forest; QYZ, Qianyanzhou subtropical coniferous plantation: DHS, Dinghushan subtropical evergreen broad-leaved forest.
[a]Values are the averages from 1985–2005.
[b]Leaf N content was measured by element analyzer (ThermoFinnigen).
[c]Height and depth indicate the location of the sensors mounted.
[d]Data source: database of Chinese Ecosystem Research Network (CERN).

Spurious data were removed from the dataset if the instrument performance and experimental condition were abnormal. The problems were largely caused by rainfall, water condensation or system failure (*c.* 20.1% of the half-hourly data). Night-time fluxes with friction velocity u_* less than 0.2 m s^{-1} were not used. Negative fluxes at night (i.e. apparent photosynthesis) were also taken out of the database. Gaps in the EC dataset were filled using a look-up table method (Falge *et al.*, 2001a,b). Flux data processing is further described in the Supplementary Material, Text S1.

Calculations of ecosystem GPP and WUE

Estimations of ecosystem GPP Net ecosystem CO_2 exchange (NEE), the balance between photosynthetic C assimilation and C-releasing respiration, can be measured directly by EC techniques. Negative NEE is called as net ecosystem productivity (NEP). Gross ecosystem primary productivity (GPP) can be estimated by

$$\mathrm{GPP} = \mathrm{NEP} + R_e = -\mathrm{NEE} + R_e \qquad \text{Eqn 1}$$

(R_e is total ecosystem respiration). The Lloyd & Taylor (1994) equation for the temperature-dependency of respiration is usually adopted to estimate R_e. However, according to the results of Yu *et al.* (2005) and Wen *et al.* (2006), soil moisture might also affect R_e, especially for ecosystems suffering from seasonal drought. Therefore, temperature and soil water content were taken into account in determining R_e in this study,

$$R_e = R_{e,ref}\, e^{\ln(Q_{10})(T_a - T_{ref})/10} \qquad \text{Eqn 2}$$

$$Q_{10} = a - bT_a + cS_w + dS_w^2 \qquad \text{Eqn 3}$$

($R_{e,ref}$ is the ecosystem respiration rate at reference temperature (T_{ref}); Q_{10} is temperature sensitivity of respiration; T_a is air temperature (°C); S_w is soil water content; *a*, *b*, *c* and *d* are fitted site-specific parameters in which $b > 0$ and $d \leq 0$).

Definition and calculation of ecosystem WUE

In this study, WUE was defined as the ratio of GPP to evapotranspiration (ET), in which GPP was estimated from Eqn 1, and ET was measured directly by EC technique,

$$\mathrm{WUE} = \mathrm{GPP}/\mathrm{ET} \qquad \text{Eqn 4}$$

Key processes that determine C transfer and storage in forested ecosystems can vary over multiple temporal scales for the changing canopy structure (Siqueira *et al.*, 2006) in different seasons. Thus, the ecophysiological implications of

WUE estimated from Eqn 4 at different temporal and spatial scales also vary. In this study, different concepts of WUE were defined according to temporal scale.

Annual ecosystem WUE (WUE_{yr}) is

$$WUE_{yr} = GPP_{yr}/ET_{yr} \quad \text{Eqn 5}$$

(GPP_{yr} and ET_{yr} are the accumulations of GPP and ET in a whole year, respectively). WUE_{yr} denotes the relationship between ecosystem C assimilation and water consumption in a given year. The reciprocal of WUE_{yr}, namely the water requirement coefficient, reflects the water cost of per unit C assimilation at annual scale.

Vegetative season ecosystem WUE (WUE_{gs}) is

$$WUE_{gs} = GPP_{gs}/ET_{gs} \quad \text{Eqn 6}$$

(GPP_{gs} and ET_{gs} are the accumulations of GPP and ET in vegetative season, respectively). WUE_{gs} expresses the relationship between C fixation and water consumption during vegetative season. The CBS forest ecosystem is a northern temperate forest with obvious growing and nongrowing seasons, while QYZ and DHS are two evergreen forests, where there are no rigid division between growing season and non-growing season. Therefore, we consider the growing period of CBS (i.e. from May 1 to August 31) as vegetative season for WUE comparison among the three forest ecosystems.

Daily ecosystem WUE (WUE_{dd}) is

$$WUE_{dd} = GPP_{dd}/ET_{dd} \quad \text{Eqn 7}$$

(GPP_{dd} and ET_{dd} are the sum of GPP and ET for a whole day, respectively). WUE_{dd} expresses the relationship between C fixation and water consumption during a day. The reciprocal of WUE_{dd} reflects the water cost per unit C assimilation during a day.

Daytime ecosystem WUE (WUE_{dt}) is

$$WUE_{dt} = GPP_{dt}/ET_{dt} \quad \text{Eqn 8}$$

(GPP_{dt} and ET_{dt} are the sum of GPP and ET in the daytime, respectively). To get rid of the data measured under stable and neutral conditions, the data collected from 10:00 h to 16:00 h were used to calculate WUE_{dt}. The statistical value of WUE_{dt} excludes the contribution of night-time ecosystem respiration to WUE, and can thus be considered as the ecosystem WUE determined mainly by plant transpiration and photosynthesis. WUE_{dt} expresses the control of plant physiological processes on the coupling between C fixation and water consumption in ecosystem.

The maximum ecosystem WUE in daytime (WUE_{dmax}) is

$$WUE_{dmax} = GPP_{dmax}/ET_{dmax} \quad \text{Eqn 9}$$

(GPP_{dmax} and ET_{dmax} are the maximum GPP and the concurrent ET during daytime). WUE_{dmax} should be considered as the potential WUE for an ecosystem, which could be used to show the control of plant stomatal behavior and physiological activity to water use.

Statistical analysis

One-way ANOVA with Fisher's LSD test was performed to test the difference in WUE of different forest types and timescales. The relationship between GPP, ET and climatic variables were fitted with linear, polynomial and exponential growth equations. All analyses were conducted using SAS package. Statistical significant differences were set with $P < 0.05$ unless otherwise stated.

Results

Seasonal variations of environmental conditions

From the north to the south, the latitudinal span is *c.* 19°. Large temperature and precipitation gradients exist among CBS, QYZ and DHS sites (Fig. 1 and Table 1). The monthly precipitation, mean air temperature and saturated vapor pressure deficit (VPD) at QYZ and DHS sites were much higher than those at CBS. The difference between the maximum and minimum monthly mean temperature were much less at QYZ and DHS sites than at CBS (Fig. 1).

The seasonal pattern of temperature was in good agreement with that of precipitation at CBS (Fig. 1), that is, when the maximum precipitation occurred in June and July air temperature was also highest. Such coincident variations favored high efficiency of ecosystem water use. By contrast, seasonal distributions of precipitation and temperature were asynchronous at QYZ and DHS sites. These two subtropical forest ecosystems suffered from frequent seasonal drought (Fig. 1), resulting in low efficiency of water use. At both sites, the precipitation decreased, to some degree, in July, whereas the air temperature reached the maximum as VPD increased significantly. As a result, the water consumption was much larger than that of water supply, resulting marked decrease in soil water content. Carbon assimilation and plant growth were suppressed under this environmental stress.

Seasonal variations of ecosystem GPP, ET and WUE_{dd}

The seasonal variations of GPP, ET and WUE_{dd} for the three forest ecosystems from 2003 to 2005 are shown in Fig. 2. The GPP and ET data were 5-d averages. Among the three sites, the peak value of ecosystem GPP was largest at CBS and smallest at DHS. Evapotranspiration was greatest at QYZ.

At CBS, GPP and ET varied with temperature, showing obvious seasonal variations. The values of GPP and ET attained the maximum in July and August, respectively. During the

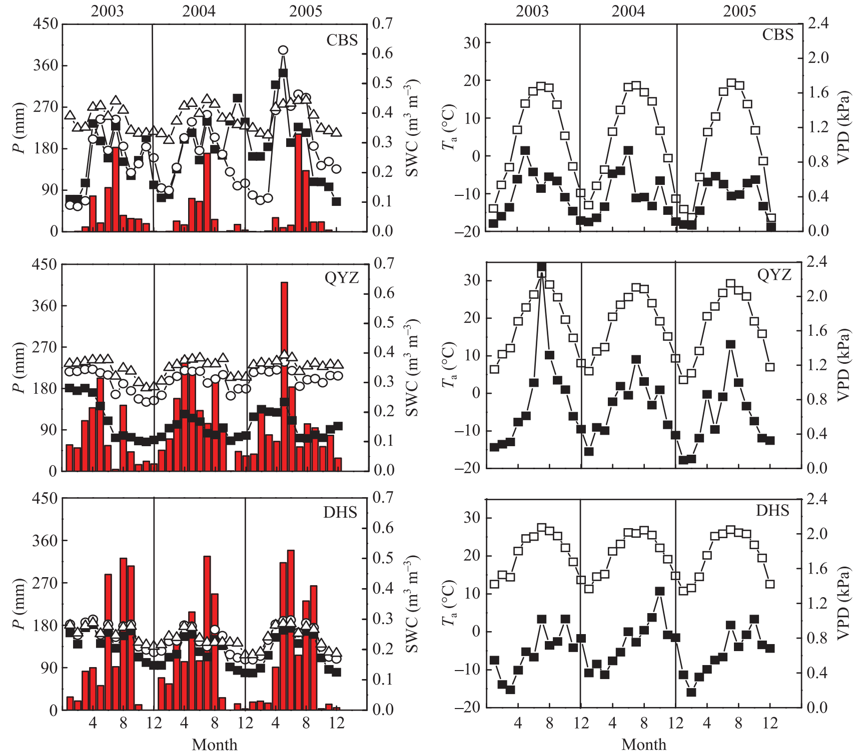

Fig. 1 The seasonal variation of precipitation (*P*, columns), soil water content (SWC; closed squares, open circles and triangles are SWC at depths of 5 cm, 20 cm and 50 cm, respectively), air temperature (T_a, open squares) and saturated vapor pressure deficit (VPD, closed squares) at CBS (Changbaishan temperate broad-leaved Korean pine mixed forest), QYZ (Qianyanzhou subtropical coniferous plantation) and DHS (Dinghushan subtropical evergreen broad-leaved forest) sites from 2003 to 2005.

dormancy period (from November 15th to March 15th, deduced from temperature variation), GPP was close to zero.

Plant photosynthesis and respiration continued at QYZ and DHS even in the coldest month (still > 0°C) of the sites. Ecosystem GPP and ET at these two sites reached the maximum in vegetative season, but amplitudes of the variations were not as large as those at CBS. The seasonal drought, especially in the summer of 2003, had significant effect on the GPP and the ET (Fig. 2). The minimum GPP and ET occurred in January and February at QYZ, but occurred in March at DHS.

The WUE_{dd} at CBS had a distinct seasonal variation pattern: it was nearly constant during the vegetative season and almost zero beyond the vegetative season (Fig. 2). This pattern suggests that GPP and ET were affected by meteorological conditions in similar ways. However, at QYZ and DHS, WUE_{dd} was more than zero in winter, and fluctuated greatly during the vegetative season. Seasonal variations of WUE_{dd} differed from those of GPP and ET, with the maximum in winter and the minimum in the peak vegetative season. Reichstein *et al.* (2002) found a similar seasonal variation of WUE in three Mediterranean evergreen forest ecosystems, and they attributed it to the drought effects.

At QYZ, ET in 2005 was much less than that in 2003 and 2004, but GPP did not differ much among the three years. Precipitation mainly occurred in May and June in 2005 at QYZ. Although there was little rain in July and August, solar radiation in 2005 was much less than that in 2003 and 2004. Cloudy and overcast weather conditions might have reduced the incident radiation in 2005 and have decreased the latent heat flux. Consequently, ecosystem WUE_{dd} at QYZ was larger in 2005 than in 2003 and 2004.

Comparisons of WUE among the three sites

The GPP_{yr} averaged from 2003 to 2005 was 5.70 ± 0.41 kg CO_2 m^{-2} yr^{-1} at QYZ, 4.72 ± 0.40 kg CO_2 m^{-2} yr^{-1} at DHS and 4.52 ± 0.51 kg CO_2 m^{-2} yr^{-1} at CBS. It is obvious that the GPP_{yr} at QYZ was significantly higher than at the other two sites. The 3-yr average of ET_{yr} was 685.10 ± 29.28 kg H_2O m^{-2} yr^{-1} at DHS, 632.70±144.45 kg H_2O m^{-2} yr^{-1} at QYZ, and 480.54 ± 22.95 kg H_2O m^{-2} yr^{-1} at CBS. The ET_{yr} at CBS was significantly smaller than at DHS (Fig. 3a,b). During the vegetative season, GPP_{gs} significantly differed among the three sites, while no obvious difference in ET_{gs} among the three sites (Fig 3a,b).

For the same site, percentage of the GPP in the vegetative season to the GPP in the whole year (GPP_{gs}/GPP_{yr}) was close to that of ET (ET_{gs}/ET_{yr}). However, there were significant differences among the three ecosystems. The values were *c.* 70% in CBS, *c.* 50% in QYZ and *c.* 40% in DHS (Fig. 3a,b).

The WUE at different temporal scales represents the integrated effects of various ecophysiological processes on ecosystem water use. The average WUE_{yr} for CBS, QYZ and DHS were 9.43 ± 1.28 mg CO_2 g^{-1} H_2O, 9.27±1.77 mg CO_2 g^{-1} H_2O and 6.90 ± 0.69 mg CO_2 g^{-1} H_2O, respectively. The average WUE_{gs} of these sites were 10.47 ± 1.53 mg CO_2 g^{-1} H_2O, 8.48 ± 2.39 mg CO_2 g^{-1} H_2O and 6.06 ± 0.62 mg CO_2 g^{-1}

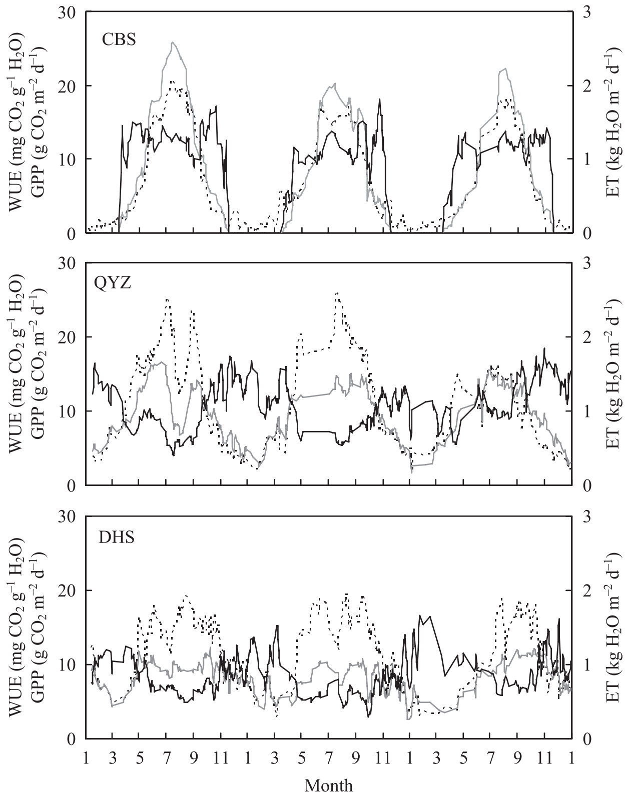

Fig. 2 The seasonal variation of gross primary productivity (GPP, grey line), evapotranspiration (ET, dashed line) and daily water-use efficiency (WUE_{dd}, black line) at CBS (Changbaishan temperate broad-leaved Korean pine mixed forest), QYZ (Qianyanzhou subtropical coniferous plantation) and DHS (Dinghushan subtropical evergreen broad-leaved forest) sites from 2003 to 2005. Lines are 5-d running average.

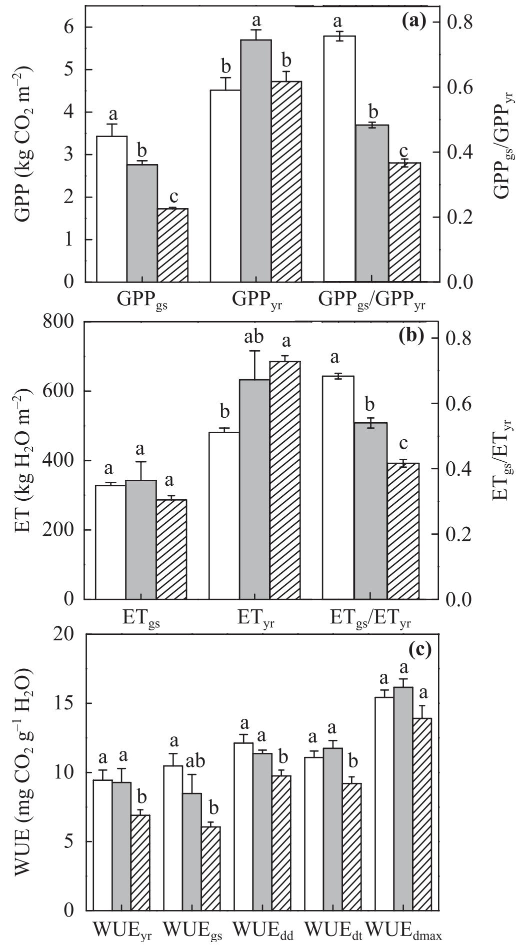

Fig. 3 Comparison of mean values of gross primary productivity (GPP), evapotranspiration (ET) and water use efficiency (WUE) for different timescales at CBS (Changbaishan temperate broad-leaved Korean pine mixed forest, open columns), QYZ (Qianyanzhou subtropical coniferous plantation, grey columns) and DHS (Dinghushan subtropical evergreen broad-leaved forest, hatched columns) sites from 2003 to 2005. Different letters among three sites mean significant differences or the other way round (LSD comparison).

H_2O, respectively (Fig. 3c). Except for WUE_{dmax}, WUE at other temporal scales in the deciduous forest ecosystem (e.g. CBS), in agreement with the results of Law *et al.* (2000), were significantly higher than those in the subtropical evergreen forest ecosystems (e.g. DHS) ($P < 0.05$) (Fig. 3c). In addition, there was significant difference in WUE_{yr}, WUE_{dd} and WUE_{dt} between the two subtropical sites (QYZ and DHS), partly owing to the differences in stand age (Freyer, 1979; Francey & Farquhar, 1982; Bert *et al.*, 1997) and dominant species (broadleaved vs coniferous).

Discussion

Implications of different WUE definitions

The different WUE terms defined in this study deal with different characteristics of the effects of ecosystem respiration on ecosystem WUE and provide important information for evaluating the effects of water resources on the function of ecosystem C sink/source and for predicting ecosystem productivity under changing climate. WUE_{dmax} refers to the ecosystem WUE under optimum conditions, which is mainly controlled by plant stomata, and could be considered as the potential WUE of an ecosystem. The difference between WUE_{yr} and WUE_{gs} or between WUE_{dd} and WUE_{dt} resulted from ecosystem respiration in nonvegetative season or at night, because assimilated C was partly consumed in respiration.

The reciprocal of WUE (i.e. ecosystem water requirement coefficient) represents water consumption per unit C assimilation. At CBS, fixation of 1 g of CO_2 needs 106 ± 15 g H_2O based on the whole-year average, and 100 ± 15 g H_2O based on the vegetative season average. At QYZ, the values were 108 ± 19 g H_2O and 111 ± 30 g H_2O, respectively, and they were 150 ± 15 g H_2O and 158 ± 18 g H_2O at DHS, respectively. Variations that existed among different forest ecosystems and among different years provided useful information for evaluating ecosystem water consumption during the process of C assimilation.

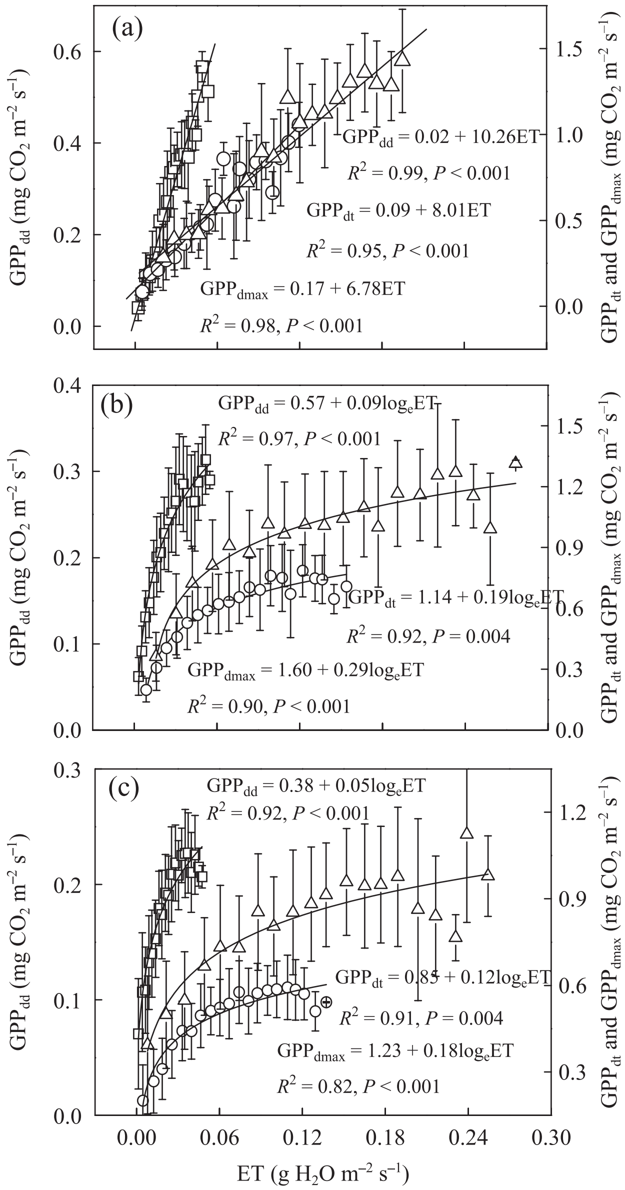

Fig. 4 The relationships between gross primary productivity (GPP) and evapotranspiration (ET) for different timescales at CBS (Changbaishan temperate broad-leaved Korean pine mixed forest), QYZ (Qianyanzhou subtropical coniferous plantation) and DHS (Dinghushan subtropical evergreen broadleaved forest) sites from 2003 to 2005. GPP_{dd} (squares) and GPP_{dt} (circles) are the averages of whole-day and daytime, respectively. GPP_{dmax} (triangles) is the maximum GPP during daytime. Evapotranspiration includes ET_{dd}, ET_{dt}, and ET_{dmax}. Here the value of GPP was aggregated in classes of increasing ET.

Compared with the results reported in the literature, WUE values in this research were in the normal range (i.e. 2.4–19.8 mg CO_2 g^{-1} H_2O) (Law *et al.*, 2000, 2002; Zeller & Nikolov, 2000; Berbigier *et al.*, 2001; Mahrt & Vickers, 2002; Winner *et al.*, 2004; Ponton *et al.*, 2006). The Supplementary Material (Table S2) briefly summarizes the results of different studies. When compared with forests of the same latitudinal range, the WUE of CBS forest was similar to that of Central Oregon forest, USA (Law *et al.*, 2000), but much higher than those of Bordeaux, France (Berbigier *et al.*, 2001), and Glacier Lakes Ecosystem Experiments Site (GLEES, WY, USA) Zeller & Nikolov, 2000). The large variations of WUE among different types of forest ecosystems as reported in the literature are mainly attributable to the differences in climate conditions and dominant species.

Effects of climatic variables on the coupling between GPP and ET

There was a strong correlation between GPP and ET, and the slope of the relationship could be considered as an indicator of ecosystem WUE (Law *et al.*, 2002). The relationship between GPP and ET for temperate forest ecosystem (e.g. CBS) was obviously different from those of subtropical forest ecosystems (e.g. QYZ and DHS) at different temporal scales (daily, daytime and the moment of GPP maximum at daytime) (Fig. 4). At CBS, GPP was significantly correlated to ET at different temporal scales (Fig. 4a), showing a strong linear relationship between C gain and water loss. The similar patterns of ET and GPP variations led to relatively constant WUE throughout the vegetative season. However, the relation was nonlinear for the subtropical forests (Fig. 4b,c), suggesting that the coupling between GPP and ET was weak under the changing environmental conditions as analysed later.

Understanding the effects of climate change on forest ecosystem productivity, C sink/source functions and water balance is useful to analysis of the responses of GPP and ET to climatic variables in various forest ecosystems. Figure 5 compares the responsive characteristics of GPP and ET to air temperature (T_a), VPD and net radiation (R_n) at the three sites. It is shown that the responses of GPP and ET to three meteorological factors were very different between the two zonal forest ecosystems. The different responses presumably led to the coupling and decoupling between GPP and ET.

At CBS, both GPP and ET increased with T_a, VPD and R_n (Fig. 5a–c). These relationships suggest that the seasonal variations in climatic variables drove photosynthesis and evapotranspiration with approximately equal strength and, consequently, the coupling between GPP and ET was maintained at a high level all the time. At QYZ and DHS, GPP and ET responded to climatic variables differently. The relations between GPP and meteorological factors (T_a, VPD and R_n) were fitted with quadratic function (Fig. 5d–i), whereas those between ET and meteorological factors were fitted with linear or exponential growth equation. At QYZ, GPP was obviously depressed when $T_a > 25$°C, VPD > 1.75 kPa and $R_n > 580$ W m^{-2}. At DHS, the temperature value for GPP depression was 21°C.

Asynchronous responses of GPP and ET to changing environmental variables determined the relationship between

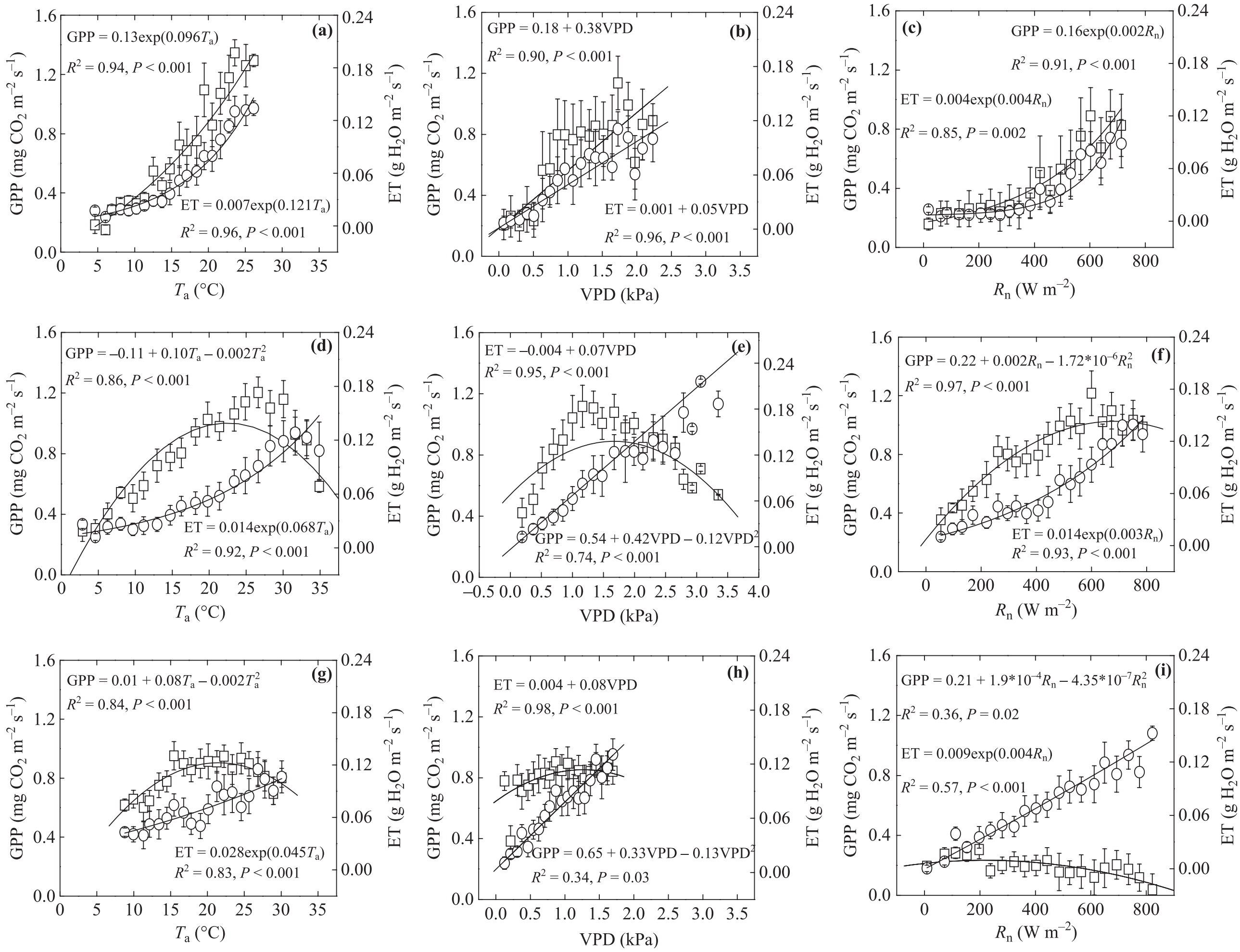

Fig. 5 The relationship between gross primary productivity (GPP, squares), evapotranspiration (ET, circles) and climatic variables (air temperature (T_a), saturated vapor pressure deficit (VPD) and net radiation (R_n)) at CBS (Changbaishan temperate broad-leaved Korean pine mixed forest, a–c), QYZ (Qianyanzhou subtropical coniferous plantation, d–f) and DHS (Dinghushan subtropical evergreen broad-leaved forest, g–i) sites from 2003 to 2005. Half-hourly data of GPP and ET were aggregated in classes of increasing T_a, VPD and R_n.

GPP and ET, as well as the reduced WUE in the vegetative season. For the two subtropical forests, the increasing rate of ET was much larger than that of GPP under high temperature, strong radiation and low humidity conditions in summer. Although the responsive characteristics of GPP and ET to environmental factors were very similar between the two subtropical forests, the extent of their responses to extreme climatic events was different.

Seasonal drought, usually occurring during the vegetative season, is a typical climate characteristic in subtropical regions of China (Fig. 1 and the Supplementary Material Fig. S1). During the drought period transpiration is reduced by stomatal control and affects leaf energy balance. Consequently, there is a rise in leaf temperature, promoting photorespiration, affecting electron transport and carboxylation capacity, and thereby potentially reducing C gain and WUE (Harley & Tenhunen, 1991; Baldocchi, 1997).

Effects of climate gradients on the spatial pattern of ecosystem WUE along NSTEC

Understanding the spatial pattern of WUE and its environmental control mechanisms is of great significance for estimating the effect of water condition change on ecosystem C budget and for evaluating the spatial pattern of water carrying capacity of ecosystems and its variation under changing climate. A comparison of different ecosystems along a terrestrial transect driven by certain environmental gradients can provide a useful approach to spatial analyses of ecosystem functioning (Han *et al.*, 2006). The three forest ecosystems located along the NSTEC spanned a wide range of environmental conditions. Although they may not represent all types of ecosystems in eastern China, this study provides valuable information for investigating the effects of climate change on the spatial pattern of ecosystem WUE.

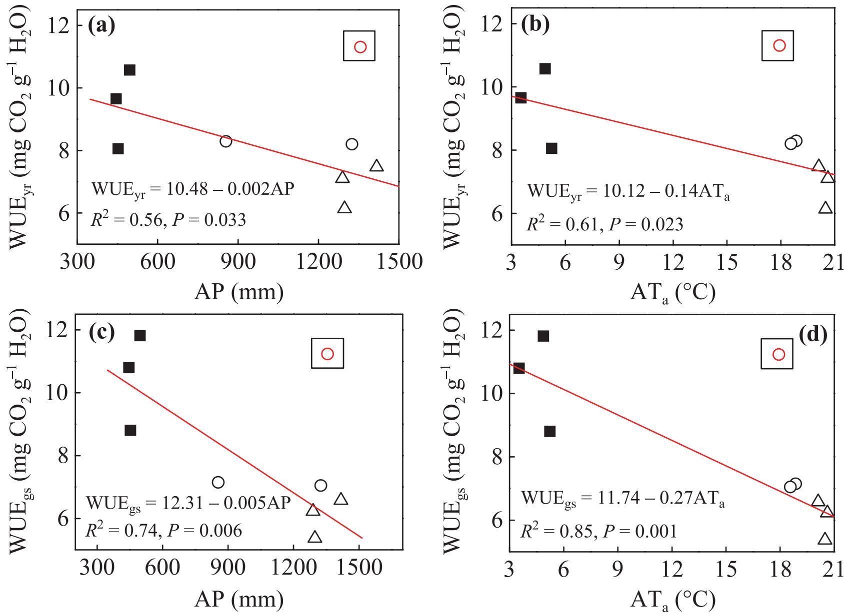

Fig. 6 The variations of vegetative season ecosystem water-use efficiency (WUE_{gs}) and annual ecosystem WUE (WUE_{yr}) with increasing annual precipitation (AP) and mean annual temperature (AT_a). Sites were: CBS (Changbaishan temperate broad-leaved Korean pine mixed forest, squares), QYZ (Qianyanzhou subtropical coniferous plantation, circles) and DHS (Dinghushan subtropical evergreen broad-leaved forest, triangles). The inset circle is the WUE of QYZ in 2005.

Air temperature and precipitation increased but ecosystem WUE decreased from north to south along NSTEC (Table 1 and Fig. 3). Figure 6 showed the relationship between WUE_{yr}, WUE_{gs}, annual precipitation (AP) and mean annual temperature (AT_a). Both WUE_{yr} and WUE_{gs} decreased linearly with increasing AP and AT_a, but the relations were not significant at the level of $P < 0.05$ (Fig. 6). If the WUE of QYZ in 2005 was excluded, the relations became significant at $P < 0.05$ (Fig. 6). However, further exploration is needed to clarify the difference in the relationships between 2005 and other years. In addition, compared with WUE_{yr}, the correlation between WUE_{gs} and climatic variables was more significant, likely owing to the weaker correlation between respiration and evaporation than between C assimilation and transpiration.

Based on the observed results, WUE can be described as a function of AP and AT_a,

$$WUE_{yr} = 10.249 + 0.001AP - 0.109AT_a,\quad R^2 = 0.61,\ P = 0.097$$

$$WUE_{gs} = 11.742 + 0.00003AP - 0.266AT_a,\quad R^2 = 0.85,\ P = 0.008$$

It is obvious that AT_a and AP were the main factors controlling the spatial pattern of WUE for the forest ecosystems in eastern China, especially in vegetative season. The relationships turned out to respond for over 85% of the variations of ecosystem WUE. Therefore, it might be an effective way to predict and evaluate WUE and water consumption per C fixation of ecosystems by AT_a and AP. This result needs verification by long-term observation across geographical sites.

In addition to meteorological variables, a potentially significant component of climate, such as air quality in terms of ozone and deposition of SO_2 and nitrogen, can significantly affect GPP and WUE. McLaughlin *et al.* (2007a,b) reported that exposure to ozone and ozone interactions with climate were main contributors to the observed decrease in plant growth and increase in water use of mature forest trees. We presume that ozone might also be a factor that influenced the spatial pattern of WUE, based on the data collected for the study sites. Mean ozone concentration at DHS ranged from $29 \pm 0.25 \times 10^{-9}$ v : v, significantly higher than that the value ($5 \pm 0.14 \times 10^{-9}$ v : v) at CBS. A relatively high ozone concentration can also have a contribution to the lower WUE at DHS. Furthermore, the atmospheric nitrogen deposition increased from 17.63 to 38.4 kg N ha^{-1} yr^{-1} from north to south along the NSTEC (Table 1). Our results showed that air nitrogen deposition can increase nitrogen content and WUE of leaf to certain extend, for instance, at CBS. However, it noteworthy that an excessive input of reactive nitrogen (> 25 kg N ha^{-1} yr^{-1}) could destroy plant organs and decrease WUE (e.g. at DHS) (Li *et al.*, 2004).

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Supplementary Material

The following supplementary material is available for this article online:

Fig. S1 Figure verifying the severe seasonal drought in QYZ in 2003

Table S1 Table with information of routine meteorological system

Table S2 List of WUE reported in the literature

Text S1 Methods for flux data processing

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-8137.2007.02316.x (This link will take you to the article abstract).

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