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Effects of vegetation control on ecosystem water use efficiency within and among four grassland ecosystems in China

ZHONGMIN HU*†, GUIRUI YU*, YULING FU*, XIAOMIN SUN*, YINGNIAN LI‡, PEILI SHI*, YANFEN WANG† and ZEMEI ZHENG*†

**Key Laboratory of Ecosystem Network Observation and Modeling, Synthesis Research Center of Chinese Ecosystem Research Network, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China, †Graduate University of Chinese Academy of Sciences, Beijing 100039, China, ‡Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, China*

Abstract

Through 2–3-year (2003–2005) continuous eddy covariance measurements of carbon dioxide and water vapor fluxes, we examined the seasonal, inter-annual, and inter-ecosystem variations in the ecosystem-level water use efficiency (WUE, defined as the ratio of gross primary production, GPP, to evapotranspiration, ET) at four Chinese grassland ecosystems in the Qinghai-Tibet Plateau and North China. Representing the most prevalent grassland types in China, the four ecosystems are an alpine swamp meadow ecosystem, an alpine shrub-meadow ecosystem, an alpine meadow-steppe ecosystem, and a temperate steppe ecosystem, which illustrate a water availability gradient and thus provide us an opportunity to quantify environmental and biological controls on ecosystem WUE at different spatiotemporal scales. Seasonally, WUE tracked closely with GPP at the four ecosystems, being low at the beginning and the end of the growing seasons and high during the active periods of plant growth. Such consistent correspondence between WUE and GPP suggested that photosynthetic processes were the dominant regulator of the seasonal variations in WUE. Further investigation indicated that the regulations were mainly due to the effect of leaf area index (LAI) on carbon assimilation and on the ratio of transpiration to ET (*T*/ET). Besides, except for the swamp meadow, LAI also controlled the year-to-year and site-to-site variations in WUE in the same way, resulting in the years or sites with high productivity being accompanied by high WUE. The general good correlation between LAI and ecosystem WUE indicates that it may be possible to predict grassland ecosystem WUE simply with LAI. Our results also imply that climate change-induced shifts in vegetation structure, and consequently LAI may have a significant impact on the relationship between ecosystem carbon and water cycles in grasslands.

Keywords: alpine grassland, ChinaFLUX, eddy covariance, evapotranspiration, leaf area index, soil evaporation, temperate grassland, transpiration

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Introduction

Water use efficiency (WUE), the ratio of carbon assimilation to water loss, is a useful indicator of the relationship between terrestrial water and carbon cycles (Baldocchi, 1994; Yu *et al*., 2004; Ponton *et al*., 2006). Studies of the spatiotemporal dynamics in ecosystem WUE can enhance our ability to predict how climate change may affect the carbon and energy budgets. On the other hand, grasslands occupy nearly 40% of the world's ice-free territory and play an important role in regional carbon budget, hydrological regimes, and food security (Reynolds *et al*., 2005). During the past years, intensive work on carbon and water budget in grasslands has been conducted in Europe, North America, South Africa, Mediterranean, etc. (Law *et al*., 2002;

Correspondence: Guirui Yu, e-mail: yugr@igsnrr.ac.cn

Soussana *et al.*, 2007). But in China, where nearly 40% of its territory is occupied by grassland vegetation (Fan *et al.*, 2008), similar work is relatively deficient. Many studies have indicated that the Qinghai-Tibet Plateau and North China, where most of the Chinese grasslands are distributed, are very sensitive to global climate change (Ding *et al.*, 2006). To understand the relationship between carbon and water cycles and its climatic response in Chinese grassland ecosystems, studies on the variations in ecosystem WUE are needed.

At the ecosystem level, WUE can be calculated as the ratio of ecosystem gross carbon assimilation (i.e. GPP) to evapotranspiration (ET):

$$\mathrm{WUE} = \frac{\mathrm{GPP}}{\mathrm{ET}} = \frac{\mathrm{GPP}}{T} \times \frac{T}{\mathrm{ET}}, \qquad (1)$$

where T is the vegetation transpiration. In Eqn (1), GPP/T is the transpiration-based WUE, indicating the efficiency of plants in using water to produce dry matter, while T/ET, the ratio of transpiration to evapotranspiration, reflects how ecosystem water vapor flux is allocated between physical and biological processes. GPP/T and T/ET are affected by different processes. There have been many studies addressing ecosystem WUE variations by exploring mechanisms controlling GPP/T (e.g. Baldocchi, 1994; Verhoef *et al.*, 1996; Scanlon & Albertson, 2004; Ponton *et al.*, 2006), but few examined the importance of T/ET, even though variations in both GPP/T and T/ET affect the dynamics of ecosystem WUE.

In this study, we focused on how vegetation leaf area index (LAI) and environmental conditions affect T/ET, and hence ecosystem WUE. At the sites with sparse vegetation (e.g. most of the grasslands), evaporation from soil surface accounts for a high proportion of the whole ecosystem ET (Hillel & Tadmor, 1962; Paruelo & Sala, 1995; Ferretti *et al.*, 2003; Lauenroth & Bradford, 2006). It is suggested that the relative magnitude of plant transpiration and soil evaporation (i.e. T/ET) is mainly controlled by LAI (or aboveground biomass; Kato *et al.*, 2004; Lauenroth & Bradford, 2006). Thus, it is important to quantify the effect of LAI on ecosystem WUE in relatively long-term periods, when there are obvious changes in this vegetation parameter.

The main objective of this study was to quantify the seasonal, inter-annual, and site-to-site variations in ecosystem WUE at four Chinese grassland ecosystems. In particular, we were interested in quantifying the effects of LAI on the variations in ecosystem WUE at various spatiotemporal scales. We hypothesized that (1) LAI determines the seasonal, inter-annual, and site-to-site variations in WUE of grassland ecosystems through its effects on T/ET, (2) ecosystem WUE varies consistently with GPP both temporally and spatially due to the greater effect of LAI on GPP than on ET. To test our hypotheses, we conducted our work with the eddy covariance (EC) technique, which monitors carbon and water fluxes of ecosystem continuously with high time resolution and over long period of time, and hence makes it feasible to directly analyze the relationship between ecosystem carbon and water exchange over multiple temporal scales (Baldocchi *et al.*, 2001).

Materials and methods

Study sites

Measurements were made over four grassland ecosystems located in the Qinghai-Tibet Plateau and North China. These communities represent the most prevalent grassland types in China and exhibit a water availability gradient (Yu *et al.*, 2006; Fan *et al.*, 2008), including Shidi (SD), an alpine swamp meadow ecosystem with free water under the canopy during the whole growing seasons; Gancaitan (GCT), an alpine shrub-meadow ecosystem with moderate soil moisture condition; Dangxiong (DX), an alpine meadow-steppe ecosystem with short sparse vegetation (about 10 cm) and sandy soil; and Neimeng (NM), a temperate steppe ecosystem under semi-arid climate. In order to discern GCT, DX, and NM from the swamp site SD, we call them 'dry' ecosystems in this paper. The four ecosystems are situated at three ChinaFLUX stations. Both GCT and SD are located at the Haibei station on the northeast edge of Qinghai-Tibet Plateau, with a distance of about 5 km from each other. DX is located at the Dangxiong station on the hinterland of Qinghai-Tibet Plateau. And NM is located at the Neimeng station in Inner Mongolia (Yu *et al.*, 2006). Brief summaries of the characteristics of these ecosystems are presented in Table 1. Detailed descriptions are available in Li *et al.* (2003) and Zhao *et al.* (2006) for GCT and SD, Shi *et al.* (2006) for DX, and Hao *et al.* (2006) and Fu *et al.* (2006b) for NM.

Measurements and data processing

Uniform measurement systems and sensor arrangements were used to monitor CO_2 and H_2O flux and micrometeorological conditions over the ecosystems. The EC system includes a three-dimensional sonic anemometer (Model CSAT3, Campbell Scientific Inc., Logan, UT, USA) and a CO_2/H_2O analyzer (Model LI-7500, Li-Cor Inc., NE, USA) sampling with a frequency of 10 Hz. Using the 10 Hz data, 30-min-mean fluxes were calculated online. Meteorological variables including solar radiation, net radiation (R_n), photosynthetic photon flux density (PPFD), air temperature (T_a), relative humidity (RH), rainfall, and soil volumetric water

Table 1 Site information of the four Chinese grasslands: Shidi (SD), Gancaitan (GCT), Dangxiong (DX), and Neimeng (NM)

Site	SD	GCT	DX	NM
Observation period	October 2002–December 2005	October 2002–December 2005	July 2003–December 2005	April 2003–December 2005
Location	37°37′N, 101°20′E	37°40′N, 101°20′E	30°51′N, 91°05′E	43°33′N, 116°40′E
Elevation (m)	3160	3293	4333	1252
Mean precipitation (mm)	580	580	480	350
Mean temperature (°C)	−2	−2	1.3	−0.4
Soil type	Silty clay loam	Silty clay loam	Sandy loam	Medium loam
Vegetation type	Alpine swamp meadow	Alpine shrub-grass meadow	Alpine meadow-steppe	Temperate steppe
Canopy height (cm)	40	55	10	45
Dominant species	*Kobresia tibetica*, *Carex moorcroftii*, *Carex atro-fusca*	*Potentilla fruticosa*, *Kobresia capillifolia*, *Kobresia humilis*	*Stipa capillacea*, *Carex montis*, *Kobresia pygmaea*	*Leymus chinesis*, *Stipa grandis*, *Agropyron cristatum*
Maximum LAI ($m^2 m^{-2}$)	3.9	2.8	1.0	1.5
Management	Grazed in winter	Grazed in winter	Grazed in winter	Fenced since 1979
Ground cover (%)*	75	75	40	~100

*At NM, most of the soil surface was covered with litter biomass due to more than 25 years fencing against grazing.

content at the depth of 5 cm (SW) were measured and calculated simultaneously at half-hourly intervals. Unfortunately, there was a dysfunction of rain gauge during July and August in 2003 at the NM site, and consequently the annual accumulation of precipitation was not available in this year. Detailed information about the monitoring systems is available in Yu *et al.* (2006).

When processing the raw 30-min flux data, we applied three-dimensional rotation to align the coordinate system with the mean wind (Wilczak *et al.*, 2001), and the WPL method to adjust density changes resulting from fluctuations in heat and water vapor (Webb *et al.*, 1980). Finally, several methods were adopted to fill missing and spurious data (see Fu *et al.*, 2006a). Gross photosynthesis (GPP) was derived as the sum of net ecosystem CO_2 exchange (NEE) and total ecosystem respiration (R_e), and R_e was estimated from the relationship between night-time NEE and soil temperature (or soil temperature and soil water content). At the daily scale, WUE was calculated as the ratio of daily GPP to daily ET. At the annual scale, WUE was calculated as the ratio of total GPP to total ET in each growing season (DOY 118-293).

At each site, although LAI was measured by harvesting the aboveground biomass at 2-week intervals or longer, such data was only available in active growing seasons, and there were even no records of LAI in some years (e.g. DX and NM in 2003). To configure integrated LAI dataset with relatively fine time resolution, the NDVI data (8 days averaged with 1 km resolution, http://remotesensing.unh.edu) was adopted for the estimation of LAI. We fit the relationship between NDVI and measured LAI with exponential functions ($R^2 > 0.94$), and used these functions and NDVI data to estimate LAI for the whole growing seasons in 2003–2005.

Model

In order to quantify the effect of LAI on T/ET, the estimate of T is necessary. We used the Shuttleworth–Wallace (S–W) model (Shuttleworth & Wallace, 1985) to partition ET into its two components T and soil evaporation with half-hourly resolution. The S–W model, characterized by its strength in partitioning ecosystem ET, has been widely used since its publication (Wessel & Rouse, 1994; Tourula & Heikinheimo, 1998; Kato *et al.*, 2004). In this model, approaches for estimating soil surface resistance (R_{ss}) and canopy resistance (R_c) are usually study specific. In this paper, R_{ss} was calculated with an empirical function of surface soil water content (Mahfouf & Noihan, 1991):

$$R_{ss} = b_1 \left(\frac{\theta_s}{\theta}\right)^{b_2} + b_3, \qquad (2)$$

where θ is the average soil water content between 0 and 10 cm (SW at 5 cm in this study), θ_s is the saturated water content of surface soil, and b_1, b_2, b_3 are the empirical constants. R_c was calculated with the modified Ball–Berry model (Ball *et al.*, 1987; Wang & Leuning, 1998):

$$R_c = \frac{1}{g_0 + a_1\left(\frac{\theta-\theta_w}{\theta_f-\theta_w}\right)P_n h_S/C_S}, \tag{3}$$

where g_0 and a_1 are the empirical parameters, θ_f and θ_w are the surface soil contents at field capacity and wilting point, P_n is the photosynthetic rate (GPP in this study), h_s is the leaf surface relative humidity, and C_s is the leaf surface CO_2 concentration.

The five parameters b_1, b_2, b_3, g_0, and a_1 in Eqns (2) and (3) were estimated with a parameter optimizer PEST using the Gauss–Marquardt–Levenberg method (Doherty, 2004). Estimations of other resistances (i.e. the aerodynamic resistance from leaf surface to canopy source height, from soil surface to canopy source height and from canopy source height to reference height) of the S–W model were consistent with Shuttleworth & Wallace (1985). As shown in Fig. 1, the model could successfully estimate ET for each ecosystem.

Results

Seasonal and inter-annual dynamics of environmental conditions and LAI

The seasonal and inter-annual variations in T_a, vapor pressure deficit (VPD), SW, and rainfall are shown in Figs 2 and 3. Seasonal T_a at the four ecosystems showed similar one-peak pattern, with the peak values achieved in the most active period in July. The maximum T_a at NM, which is located at a lower altitude, was much higher than that at the other three alpine ecosystems. Similarly, the VPD at the NM site was the highest among the four ecosystems as well, owing to its high air temperature and low rainfall. The soil water condition was distinct at each site (Fig. 3). SW at GCT, with the continual rainfall events, remained relatively high throughout the growing seasons. At DX, however, SW was more variable than that at GCT, both seasonally and inter-annually, despite the comparable precipita-

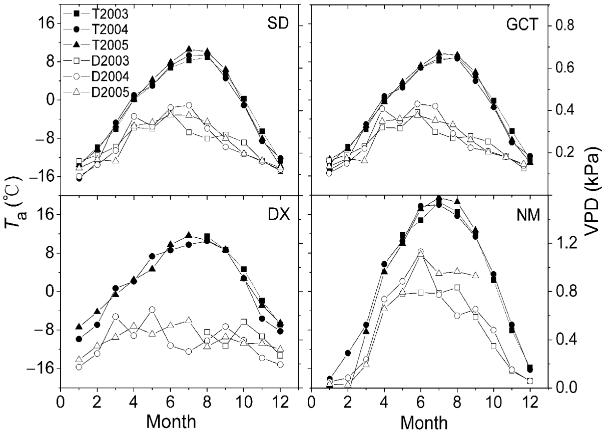

Fig. 2 Seasonal and inter-annual variations in monthly mean air temperature (T2003, T2004, T2005) and vapor pressure deficit (D2003, D2004, D2005).

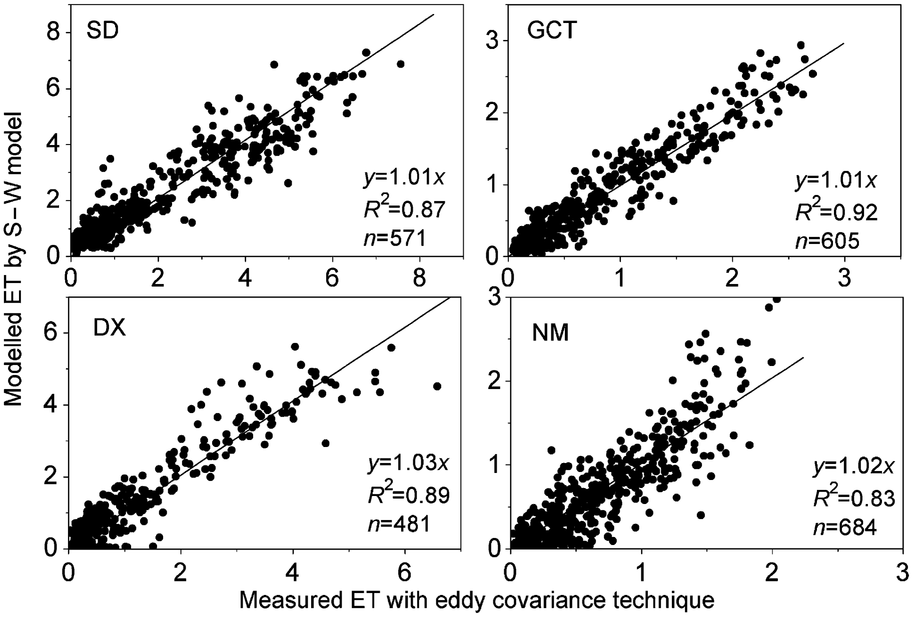

Fig. 1 Measured vs. modeled evapotranspiration (ET) at the daily scale. Data selected for this comparison were those without rainfall events on each day.

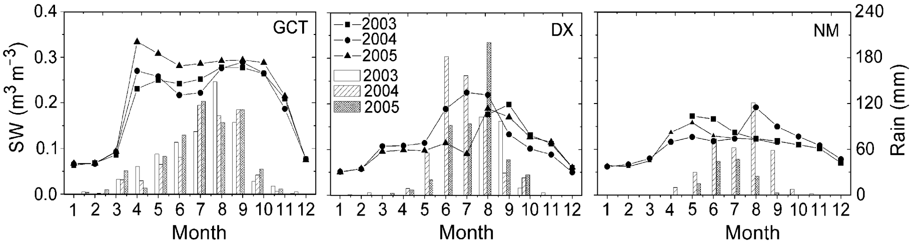

Fig. 3 Seasonal and inter-annual variations in monthly mean soil volumetric water content (SW) and monthly rainfall. The symbolic lines represent soil moisture at 5 cm and the histograms represent monthly rainfall. Shidi (SD) was not included, because soil water was over-saturated throughout the growing seasons.

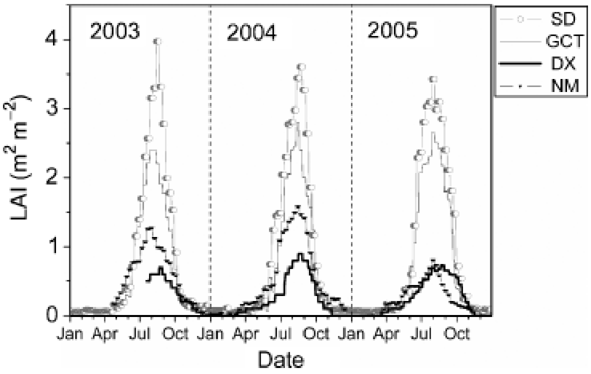

Fig. 4 Seasonal and inter-annual variations of leaf area index (LAI) at Shidi (SD), Gancaitan (GCT), Dangxiong (DX), and Neimeng (NM).

tion. This was mainly because the soil at DX was arenaceous with about 30% little gravels, resulting in low water holding capacity and being prone to water stress. Precipitation and SW at the semi-arid site NM were much lower than that at the other ecosystems. Especially in 2005 when it experienced unordinary low precipitation, SW remained at a very low level during most of the time of the growing season.

The seasonal dynamics of LAI also showed one-peak patterns, with the maximum occurring in the late July or early August. The general LAI order for the four ecosystems was SD > GCT > NM > DX (Fig. 4). Specially at the NM site, LAI in 2005 was much lower than that in the other years and even lower than that at DX due to the severe drought. Likewise, there was also a decline in LAI at DX in 2005 resulted from the low precipitation.

Seasonal variations in GPP, ET, and WUE

Seasonal dynamics of GPP, ET, and WUE during 2003–2005 is shown in Fig. 5. GPP showed apparent seasonal pattern with one peak in late July and early August at the three alpine ecosystems (i.e. SD, GCT, and DX). However, it varied greatly with two or three peaks during each growing season at NM, which was mainly the result of the variable soil moisture and air temperature (Fu *et al.*, 2006b; Hao *et al.*, 2006). For example, as Fig. 5 demonstrates, there was an obvious trough in GPP during the period of 15–28 July in 2004, which was mainly caused by the poor soil moisture and high air temperature during this period. The seasonality of ET at GCT and NM showed similar patterns as GPP, suggesting the coupling between carbon and vapor flux. However, when suffering severe drought in 2005, such close relationship at NM was greatly decoupled (Fig. 5). With the sufficient water supply or the large portion of bare ground, the seasonal ET at SD and DX were different from that at GCT and NM, varying independently from GPP.

For all ecosystems, WUE showed similar seasonal dynamics as that of GPP. It was high in the active periods and low in the early and the late of growing seasons (Fig. 5). Statistical analysis indicated that WUE was highly correlated with GPP ($P<0.001$). Such consistency between WUE and GPP suggests that, controlled by some processes, the variations in GPP were greater than those in ET. During the study period, maximum daily WUE at each ecosystem was as follows: 2.84 g C kg^{-1} H_2O at SD, 2.60 g C kg^{-1} H_2O at GCT, 0.95 g C kg^{-1} H_2O at DX, and 2.85 g C kg^{-1} H_2O at NM, respectively.

Effects of LAI on the seasonal variations in WUE

During the period investigated, LAI significantly correlated with daily WUE at all ecosystems, indicating its considerable effect on WUE (Fig. 6). Notably, the correlation was weaker for ecosystems with lower LAI. For example, LAI explained 81% of the variance in daily WUE at SD, but only 30% at DX. In comparison with LAI, the correlation between VPD and WUE was rather weak for each ecosystem ($R^2<0.07$). To elucidate the mechanism that LAI affected WUE, the relationship between LAI and T/ET was analyzed. Results indicated that LAI was significantly correlated with T/ET at each site (Fig. 7). For instance, the daily T/ET at DX and NM never exceeded 80% over whole seasons due to the low

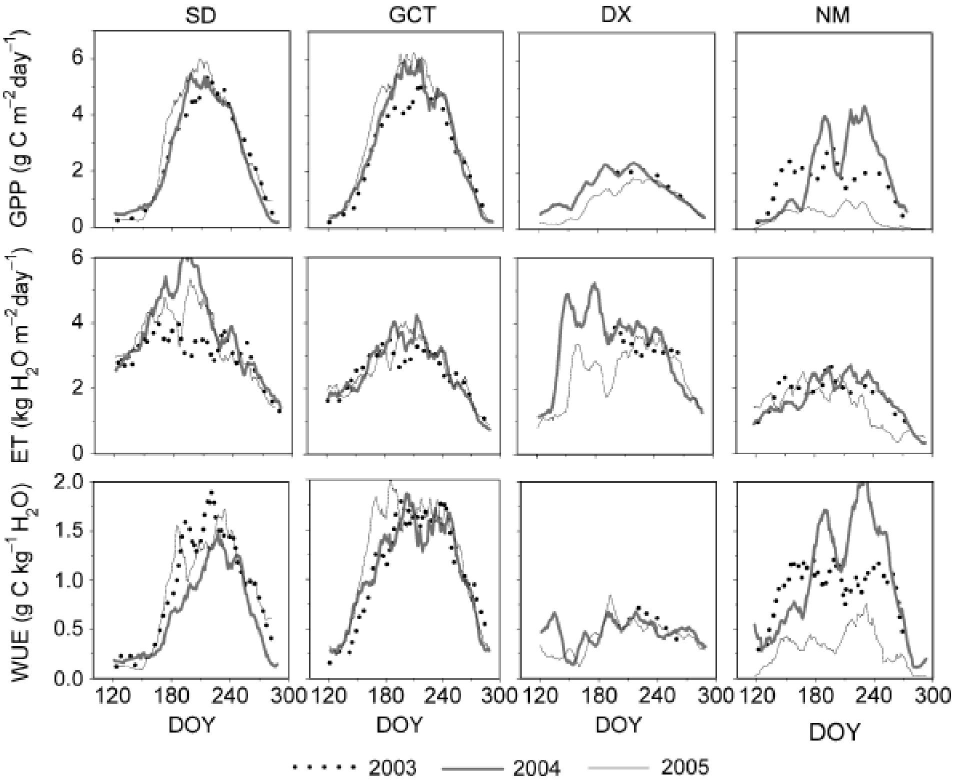

Fig. 5 Seasonal dynamics of CO_2 assimilation (GPP), evapotranspiration (ET), and ecosystem water use efficiency (WUE) at each ecosystem during 2003–2005 (10-day moving averaged).

LAI magnitudes. At SD, when LAI was less than about $3\,m^2\,m^{-2}$, T/ET increased linearly with the increase of LAI, but it remained relatively constant when LAI exceeded this threshold (Fig. 7).

Inter-annual and inter-ecosystem variations in GPP, ET, and WUE

The inter-annual variations in WUE also exhibited consistently with GPP at the three 'dry' ecosystems (i.e. GCT, DX, and NM), indicating that the inter-annual variations in GPP were greater than the corresponding ET (Table 2). For example, although the ET in 2004 was 20 mm more than that in 2003 at GCT, WUE in 2004 was still higher as a result of the higher productivity. However, the result at the swamp site SD was the opposite, with the inter-annual variations in WUE being ascribed to ET rather than GPP. For instance, WUE at 2004 was the lowest among the 3 years, owing to the high value of ET in this year. In contrary, the highest WUE took place in 2003 with the lowest ET (Table 2). WUE at the alpine ecosystems (i.e. SD, GCT, and DX) remained relatively conservative among the years. Mean (±SD) value in each ecosystem was $0.71 \pm 0.04\,g\,C\,kg^{-1}\,H_2O$ at SD, $1.26 \pm 0.13\,g\,C\,kg^{-1}\,H_2O$ at GCT, and $0.41 \pm 0.01\,g\,C\,kg^{-1}\,H_2O$ at DX, respectively. For the temperate site NM, however, variations in WUE were large due to the high inter-annual variation in precipitation. In years with normal precipitation (i.e. 2003, 2004), the WUE was comparable to that at GCT, but it sharply decreased to a level even lower than that at DX when suffered severe drought in 2005. The mean WUE at NM during the three growing seasons was $0.80 \pm 0.44\,g\,C\,kg^{-1}\,H_2O$.

The correlations between GPP and WUE, ET and WUE at annual time scale and across sites are shown in Fig. 8. Overall, GPP and ET were both positively correlated with WUE at GCT and NM, but they were negatively correlated with WUE at SD, and the correlations seemed to be neutral at DX (Fig. 8). Considering the four ecosystems together, a spatial pattern emerged that ecosystems with high productivity also had high WUE. Notably, WUE at SD was lower than the expected from its GPP magnitude according to the spatial fit line (Fig. 8a).

Effects of LAI on the inter-annual and inter-ecosystem variations in WUE

In order to examine the effects of LAI at annual scale, we calculated the sum of daily LAI over the whole

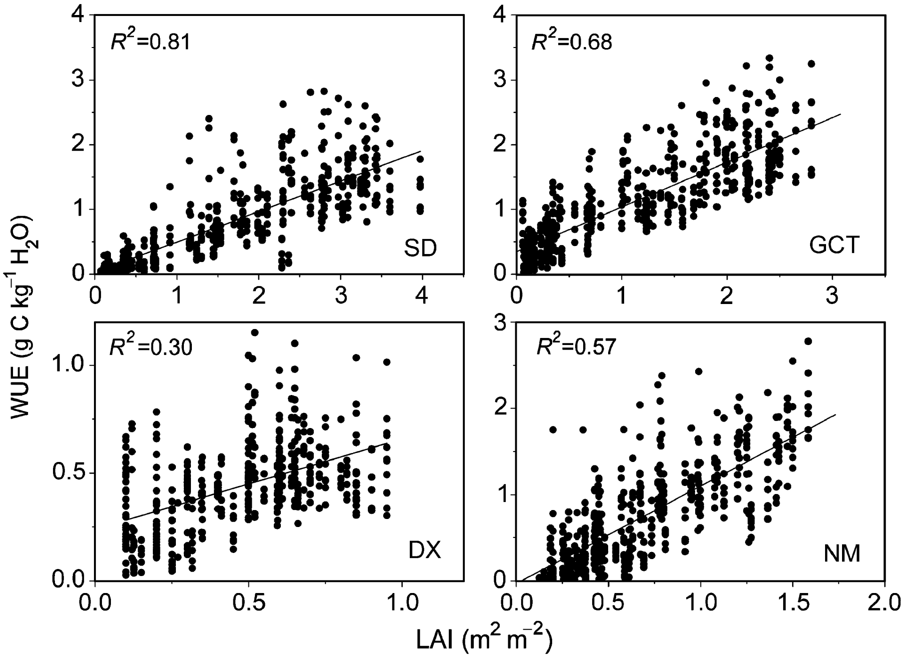

Fig. 6 Correlations between LAI and daily WUE during the growing seasons of 2003–2005.

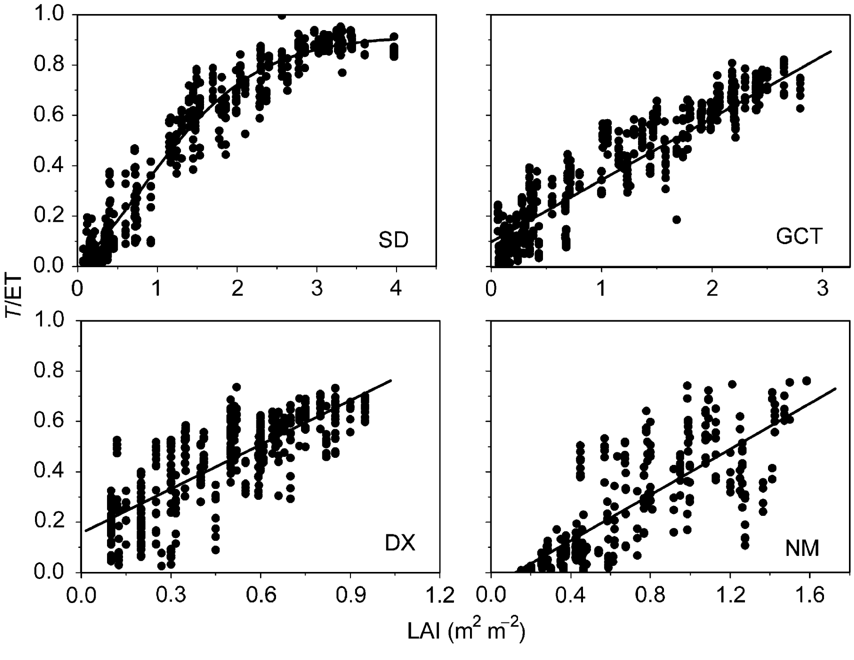

Fig. 7 Effect of LAI on T/ET (the ratio of transpiration to evapotranspiration) during the growing seasons in 2003–2005 (daily scale). The correlation between LAI and T/ET was significant at all sites ($P < 0.001$).

growing season (LAI$_{\mathrm{sum}}$), and related it with annual T/ET. Results showed that annual T/ET was closely correlated with LAI$_{\mathrm{sum}}$, both inter-annually and across sites (Fig. 9). At each ecosystem, the increased LAI$_{\mathrm{sum}}$ obviously enhanced the annual T/ET. Among ecosystems, the T/ET also followed the order of LAI$_{\mathrm{sum}}$: SD>GCT>NM>DX (Fig. 9a). For further investigation, we quantified the relationship between LAI$_{\mathrm{sum}}$ and WUE. Results indicated that WUE increased with LAI$_{\mathrm{sum}}$, both inter-annually and spatially for the 'dry'

Table 2 Sum of daily GPP, ET, precipitation, LAI during each growing season (DOY 118-293) and annual WUE at Shidi (SD), Gancaitan (GCT), Dangxiong (DX), and Neimeng (NM)

Site	Year	Precipitation* (mm)	LAI_{sum} ($m^2 m^{-2}$)	GPP ($g C m^{-2}$)	ET ($kg H_2O m^{-2}$)	WUE ($g C kg^{-1} H_2O$)
SD	2003	460.17	275.04	406.51	541.80	0.75
	2004	438.00	289.10	429.23	643.70	0.67
	2005	393.00	306.56	435.31	601.93	0.72
GCT	2003	465.37	201.34	457.27	409.23	1.12
	2004	430.96	211.69	555.31	431.20	1.29
	2005	471.90	232.76	580.37	420.18	1.38
DX	2004	535.40	85.20	230.62	567.94	0.41
	2005	444.00	79.20	167.65	423.15	0.40
NM	2003	–	134.08	287.59	301.83	0.95
	2004	344.90	152.15	344.14	298.64	1.15
	2005	152.80	71.60	78.67	252.09	0.31

*Precipitation data at NM in 2003 was not available because of the dysfunction of rain gauge.
The sum of LAI is indicated as LAI_{sum}.

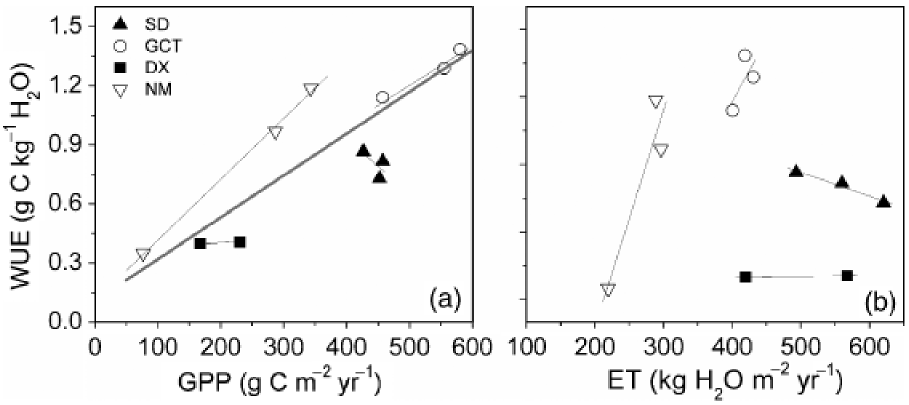

Fig. 8 Inter-annual and inter-ecosystem correlations between (a) GPP and WUE, and (b) ET and WUE (annual scale).

ecosystems (i.e. GCT, DX, and NM; Fig. 9b). But the swamp ecosystem SD was unique. No positive correlation between T/ET and WUE was found at this site. Besides, SD also deviated from the LAI_{sum}–WUE relationship exhibited by the other three sites. Such particularities illustrated that LAI at SD was not the factor determining the inter-annual variation in WUE, and was not the main factor determining its disparate WUE magnitude from other ecosystems either.

Discussion

Comparisons of WUE with other grassland ecosystems

Although there have been many studies concerning ecosystem-level WUE based on the EC measurements, the definition in each study was somewhat different (some calculated WUE as GPP/ET, and some as NEE/ET). Here, we selected very limited work with the same definition as ours for comparison. Law *et al.* (2002) summarized mean monthly WUE in the growing seasons for the main ecosystems of FLUXNET sites. They found that WUE at the grassland sites ranged from 0.1 to 6 $g CO_2 kg^{-1} H_2O$ (i.e. 0.03–1.64 $g C kg^{-1} H_2O$). According to the values in this study (with the range of 0.31–1.38 $g C kg^{-1} H_2O$), WUEs at the Chinese alpine and temperate grasslands are similar to that at grasslands in other regions of the world. During the peak growing seasons, daily WUE reached the maximum. Comparing with the results of Ponton *et al.* (2006), the maximum WUE at the Chinese temperate steppe site NM (2.85 $g C kg^{-1} H_2O$) is a little lower than that in North American temperate grassland (ca. 4 $g C kg^{-1} H_2O$). In the drought years, the maximum daily WUEs at DX and NM were less than 1 $g C kg^{-1} H_2O$, which is similar

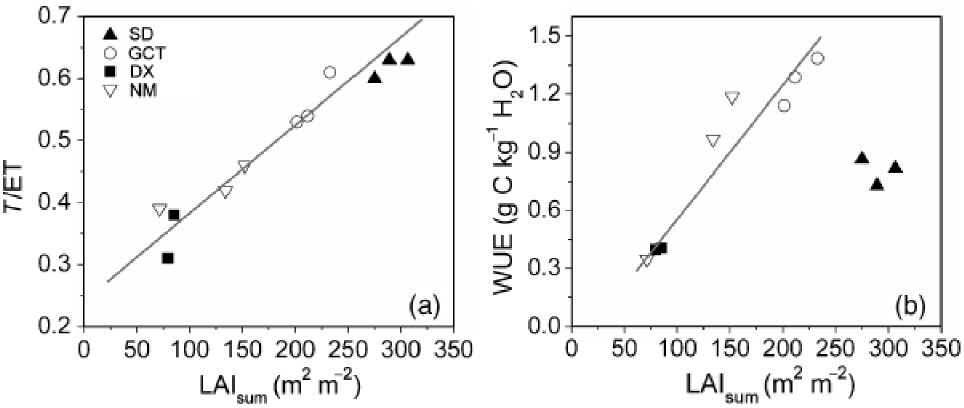

Fig. 9 (a) Effect of the sum of daily leaf area index within growing season (LAI_{sum}) on the ratio of transpiration to evapotranspiration (T/ET), and (b) relationship between LAI_{sum} and ecosystem WUE both inter-annually and across ecosystems.

to the New Zealand tussock grassland in the year with drought climate and poor vegetation condition (Hunt *et al.*, 2002).

Effects of LAI on variations in ecosystem WUE at seasonal timescale

Our study demonstrated that WUE at all the grasslands varied consistently with GPP due to the dominance of seasonal variations in GPP over ET (Fig. 5), which is in accordance with several other studies (Hunt *et al.*, 2002; Grunzweig *et al.*, 2003; Hastings *et al.*, 2005). For instance, Hunt *et al.* (2002) measured net carbon and water vapor exchange at a tussock grassland ecosystem over a growing season, finding that NEE varied in the same way as WUE did. Besides, our results also confirmed the important role of LAI in controlling the seasonal variations of WUE through its regulation on T/ET (Fig. 7), which is the primary reason for the consistent variations between GPP and WUE.

Different from our results, however, many studies indicated that the variation in WUE was mainly controlled by VPD rather than LAI (e.g. Baldocchi, 1994; Verhoef *et al.*, 1996; Scanlon & Albertson, 2004; Ponton *et al.*, 2006). Such discrepancy may be mainly caused by the differences in the timescales investigated. Most of the previous measurements concerning the variations in ecosystem WUE were conducted at relatively short term (from hours to several weeks), and few were conducted over whole growing seasons. We assume that there is very narrow range of the change in LAI within a short period, which makes T/ET remain relatively constant. Under such circumstance, it is predictable that VPD controls the variation in WUE for its high variability and dissimilar effects on photosynthesis and transpiration (de Wit, 1958; Xu & Hsiao, 2004). This assumption could be supported by the different explanatory abilities of LAI on the variations in WUE among the ecosystems in this study. As Fig. 6 demonstrates, the values of R^2 for the relationship between LAI and WUE decreased with the decrease in the maximum LAI, implying that the impact of LAI was less prominent when its variation range was reduced. In addition, many of the studies showing the good relationship between WUE and VPD were conducted at the ecosystems with well-developed canopy (e.g. forest). Under such canopy condition, the soil evaporation is negligible, which makes it applicable to consider the canopy as a 'big leaf', when WUE is mainly controlled by air evaporative demand and leaf stomatal behavior with little effect of LAI (Herbst *et al.*, 2002).

Effects of LAI on the inter-annual and inter-ecosystem variations in ecosystem WUE

The results at the three 'dry' ecosystems (i.e. GCT, DX, and NM) are consistent with our hypothesis that variations in annual GPP would be positively correlated with that of WUE. As Fig. 9 confirms, LAI played a key role in bringing on such correlation through its regulation on annual T/ET. Such role of LAI, in addition, could also be supported by the positive correlation between the annual ET and WUE (Fig. 8b). Statistically, ET might be negatively correlated with WUE, but such statistical negative effects were suppressed as the overwhelming impact of LAI, causing the positive correlation between ET and WUE, as we see in Fig. 8b. Combining the three ecosystems together, it was also found that ecosystems with higher productivity also had higher WUE due to the differences in LAI at each site (Fig. 9). Similarly, Paruelo *et al.* (1999) investigated grassland precipitation use efficiency (PUE) along a precipitation gradient. They found that the ecosystems with moderate precipitation had higher PUE than that under dry climate condition. Webb *et al*. (1978) also found that, across the diverse American ecosystems, forests had the highest PUE, followed by grassland, and then hot desert. Differently, Ponton *et al*. (2006) compared ecosystem WUE among Douglas-fir forest, aspen forest, and grassland, finding that the site-to-site variation in WUE was primarily controlled by the differences in VPD magnitude. The main reason probably is that they 'screened ET data measured by EC, so that ET overwhelmingly represented transpiration'.

At the swamp site SD, however, both GPP and ET were negatively correlated with WUE, indicating that the inter-annual variation in WUE was mainly ascribed to the changes in ET and not determined by LAI (Figs 8 and 9b). It is likely that VPD and solar radiation at this site determine the inter-annual variation in ET, and hence WUE. For example, VPD and solar radiation in 2004 were the highest among the 3 years (Fig. 2), and correspondingly, ET was the highest and WUE was the lowest in this year (Table 2). In comparison with the other ecosystems, despite its high values in T/ET, WUE at SD is much lower than expected (Fig. 9). According to Eqn (1), low transpiration use efficiency (i.e. GPP/T), which is affected by the stomatal conductance and VPD, should cause such low WUE values at this site. Measurements at the leaf level also indicated that the photosynthetic capacities of the main plant species at SD were much lower than those at its nearby site GCT (data not published). The deviation of SD from the other ecosystems indicates that plants in environments with and without sufficient water supply may have distinct water use strategies.

Conclusion

Our study indicates that LAI is the primary factor controlling the seasonal variations in ecosystem WUE at all four grassland ecosystems in China, resulting in similar dynamics between GPP and WUE within growing seasons. Except for the swamp site SD, LAI also shows influences on year-to-year and site-to-site variations in WUE, such that the years or ecosystems with high productivity also have high WUE. In many practical applications, there is a critical lack of data in productivity and ET to estimate ecosystem WUE at various temporal and spatial scales. This study provides the feasibility to predict this valuable index simply with the community LAI values in grassland ecosystems. Our results also imply that, as a consequence of global climate change, changes in vegetation structure and consequently LAI may have a significant impact on the relationship between ecosystem carbon and water cycles in grasslands.

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