



Ecosystem water use efficiency in an irrigated cropland in the North China Plain

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SUMMARY

The eddy covariance technique and the cuvette method were used to investigate water use efficiency in an irrigated winter wheat (*Triticum aestivum* L.)/summer maize (*Zea mays* L.) rotation system in the North China Plain. The results show that ecosystem water use efficiency (WUE_e) changed diurnally and seasonally. Daily maximal WUE_e appeared in the morning. WUE_e generally peaked in late April in wheat field and in late July/early August in maize field. From 2003 to 2006, seasonal mean WUE_e was 6.7–7.4 mg CO_2 g^{-1} H_2O for wheat and 8.4–12.1 mg CO_2 g^{-1} H_2O for maize. WUE_e was much lower than canopy water use efficiency (WUE_c) under small leaf area index (LAI) but very close to WUE_c under large LAI. With the increase in LAI, WUE_e enlarged rapidly under low LAI but slowly when LAI was higher than one. WUE_e was greater on the cloudy days than on the sunny days. Under the same solar radiation, WUE_e was higher in the morning than in the afternoon. The ratio of internal to ambient CO_2 partial pressure (C_i/C_a) decreased significantly with the increase in photosynthetically active radiation (PAR) when PAR was lower than the critical values (around 500 and 1000 $\mu mol\ m^{-2}\ s^{-1}$ for wheat and maize, respectively). Beyond critical PAR, C_i/C_a was approximately constant at 0.69 for wheat and 0.42 for maize. Therefore, when LAI and solar radiation was large enough, WUE_e has negative correlation with vapor pressure deficit in both of irrigated wheat and maize fields.

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Introduction

The North China Plain (NCP) is one of the main regions of food production in China. Since the 1990's, water shortage in the NCP is more and more serious and becomes the most important limiting factor for local agricultural production. Much attention has been received on how to use the limited water resource and improve the efficiency of water use by crops. Water use efficiency is one of the important index to evaluate agricultural production and the reasonable utilization of water resource. Understanding water use efficiency of vegetation and their biotic and abiotic controls is prerequisite in addressing carbon and water cycles in arid and semi-arid environments (Fowler, 1986).

Water use efficiency is generally given by the ratio of net assimilation to water loss. Net assimilation may be expressed as net CO_2 exchange, dry matter or economic yield, and water loss may be described as transpiration or evapotranspiration (Jones, 1992). Water use efficiency can be determined under biomass, leaf or ecosystem levels. Since leaf water use efficiency (WUE_l) cannot be used to

interpret the contribution of non-leaf components at the ecosystem scale and it is difficult to measure leaf photosynthesis and transpiration over long periods, the ratio of canopy net CO_2 flux to water vapor flux is used as a useful index of water use efficiency (Baldocchi, 1994). Among micrometeorological techniques, the eddy covariance (EC) method has been one of the powerful tools to study WUE_e due to its high observation precision, no need diffusion coefficient and atmosphere stability correction, and measuring water vapor and CO_2 fluxes directly. Ecosystem water use efficiency (WUE_e) measured by micrometeorological techniques involves stomatal (photosynthesis and transpiration) and non-stomatal components (soil respiration and evaporation). At seedling stage, plants are so small that WUE_e is mainly controlled by nonstomatal factors and cannot reflect actual crop water use. Thereby, other methods are necessary to be the references to exactly evaluate WUE_e . Using Bowen ratio/energy balance (BREB) method and the cuvette technique, Steduto et al. (1997) found diurnal WUE_e was very close to WUE_l in a well watering sorghum field when leaf area index (LAI) was about three. However, there was no report on the comparison between WUE_e and WUE_l under low LAI. For biomass water use efficiency (WUE_b), it is unsuitable to compare it with WUE_e because many published estimation of

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WUE_b, neglected root dry matter (e.g. Feddes, 1985; Rouphael and Colla, 2005) and the dry weight proportion of root to the whole plant changed largely with soil moisture conditions.

In early studies, water use efficiency was regarded as a conservative index and determined by the genotype of plant species (Farquhar and Richards, 1984). It was demonstrated that water use efficiency was positive proportional to specific leaf weight (Malse and Farquhar, 1988; Nageswara Rao and Wright, 1994; Johnson and Li, 1999). However, water use efficiency was found inconstant and varied diurnally and seasonally with environmental factors. Under biomass level, water use efficiency was related to solar radiation and temperature by negative relationships (Kumar et al., 1996; Rouphael and Colla, 2005). Biomass water use efficiency declined with increasing soil water content and could be enhanced by moderate water stress (Turk and Hall, 1980; Green and Read, 1983; Rosenthal et al., 1987; Dean-Knox et al., 1998; Liu et al., 2005). Under ecosystem or leaf levels, there was negative relationship between water use efficiency and vapor pressure deficit (VPD) (Baldocchi et al., 1985; Baldocchi, 1994; Steduto et al., 1997; Li et al., 1997; Berbigier et al., 2001; Scanlon and Albertson, 2004; Ponton et al., 2006). Nevertheless, no report shows the relationship of WUE_e with the environmental factors other than humidity.

The objectives of this study are: (1) to compare water use efficiency obtained by the EC technique and the cuvette method and estimate how much the ecosystem water use efficiency represents actual crop water use under different LAI; (2) to investigate diurnal, seasonal and annual patterns of WUE_e; and (3) to reveal the effects of humidity, solar radiation and LAI on WUE_e.

Materials and methods

Site description

CO₂ and water vapor fluxes were continuously measured from 2003 to 2006 in a cropland of Yucheng Comprehensive Experimental Station (36°57'N, 116°36'E, 22 m elev.), Chinese Academy of Sciences. The station is located in the North China Plain, with a warm temperate continental monsoon climate. In recent 40 years, annual average air temperature is 13.2 °C. The warmest and coldest months appear in July (26.9 °C) and January (−2.4 °C), respectively. Annual precipitation is 585 mm and the seasonal distribution is uneven. The amount of rainfall from June to August accounts for 70% of the whole year. Soil type is alluvium deposited by the water of the Yellow River and soil texture of the root zone is sandy loam. Soil organic content and total nitrogen in the tillage layer are 1.2% and 0.14%, respectively. Soil pH is 7.1–8.5. Winter wheat (*Triticum aestivum* L.)/summer maize (*Zea mays* L.) double cropping system dominates in this region. Winter wheat is usually planted in early October and harvested in early June. The growing season of summer maize is from mid-June to late September/early October. Detailed descriptions of field managements can be found in Tong et al. (2007).

Field measurements

The eddy covariance system was composed of a three-dimensional sonic anemometer (model CSAT3, Campbell Sci. Inc., USA) and an open-path and fast response infrared gas analyzer (model LI-7500, Li-Cor Inc., USA) that can measure wind speed, air temperature, air humidity and CO₂ concentration. The height of sensors was 3.10 m for maize from the elongation stage to harvest and 2.10 m for wheat growing season and seedling stage of maize. Raw data were continuously collected at 10 Hz with a data logger (model CR5000, Campbell Sci. Inc., USA) and output was the 30-min mean data.

Micrometeorological gradient observation system included two anemometers (model AR-100, Vector Instruments, UK) and two psychrometers (model HMP-45C, Vaisala, Finland). The heights of sensors were 4.25 m and 3.05 m for maize from the elongation stage to harvest and 3.25 m and 2.05 m for wheat growing season and seedling stage of maize. The fetch from the tower was greater than 200 m in all directions and satisfied the demand of micrometeorological gradient measurements. Soil temperature transducers were placed at the depths of 0, 5, 10, 15, 20 and 30 cm. Soil moisture was monitored by time domain reflectometers (TDR) at depths of 10 cm and 30 cm. In addition, solar radiation (*Q*), photosynthetically active radiation (PAR), soil heat flux, air pressure and precipitation were measured. Two soil heat flux plates were buried in the depth of 2 cm, one in the interrow, and another in the interplant. Average soil heat flux was obtained and corrected to its value at ground surface using the method described by Fuchs and Tanner (1968). All apparatuses were controlled with a data logger (model CR23x, Campbell Sci., USA) and the data were stored at 30-min intervals.

Leaf areas of winter wheat and summer maize were determined weekly by the leaf area instrumentation (Li-3100, Li-Cor Inc., USA) during the growing seasons. Leaf photosynthesis and transpiration were measured at different crop layers using a portable photosynthesis system (Li-6400, Li-Cor Inc., USA), all with three replications. For one replication, six leaves were randomly selected for gas-exchange measurements in each layer. The number of observation layers was one at seedling stage and two or three after elongation stage.

Data processing and the calculation of water use efficiency

The three-dimensional coordination rotation (Wilczak et al., 2001) and WPL correction (Webb et al., 1980) were applied to obtain half-hourly mean heat, water vapor and CO₂ fluxes. The abnormal data were deleted due to the malfunction of instruments and weather effects such as rain, dew. If flux data deviated from mean monthly values were larger than three times variance, the data were rejected. The missing data less than 2 h were filled using the linear interpolation, and large gaps (more than 2 h) were filled using the mean diurnal variation method (Falge et al., 2001).

Based on gas-exchange approaches, water use efficiency can be studied at ecosystem, canopy and leaf levels. Ecosystem water use efficiency (WUE_e) can be calculated by the ratio of daytime net ecosystem productivity (NEP) to the corresponding evapotranspiration (ET):

$$WUE_e = \frac{NEP}{ET} = -\frac{NEE}{ET} \quad (1)$$

where NEE is net ecosystem exchange of CO₂. Both NEE and ET were obtained using the eddy covariance technique. Leaf water use efficiency (WUE_l) may be derived from the ratio of net photosynthesis (*P_n*) to transpiration (*T*):

$$WUE_l = \frac{P_n}{T} \quad (2)$$

Both *P_n* and *T* were measured by the cuvette technique. After the weighting averages of *P_n* and *T* at different layers were calculated, canopy water use efficiency (WUE_c) was given as follow:

$$WUE_c = \frac{\sum_{i=1}^n P_{n,i}(LAD_i)/LAI}{\sum_{i=1}^n T_i(LAD_i)/LAI} \quad (3)$$

where LAD_{*i*} is the leaf area density at layer *i*.

Results and discussion

Conditions of climate, soil and vegetation

To investigate crop water use in a farmland, it is necessary to understand the seasonal variations of key environmental factors. In the main growing seasons for wheat and maize, Q was lowest in 2003 among four years. Air temperature (T_a) and vapor pressure deficit (VPD) in February and March 2004 were higher than in the same periods of 2003, 2005 and 2006. Seasonal average T_a in maize growing season was almost same from 2003 to 2006. Seasonal mean VPD in maize growing season was higher in 2006 than in 2003–2005. Though precipitation varied much between years, seasonal average SWC differed little between years owing to sufficient

irrigation (Fig. 1). Due to the early warming in spring 2004, the maximal LAI appeared in early April. In the other years, LAI peaked in early/mid-May. The maximal LAI was 4.2, 6.9, 5.7 and 6.7 in the years 2003–2006, respectively. For maize, the peak of LAI appeared in mid-August/early September and maximal LAI was 5.3, 4.1, 4.3, 4.6 in the years 2003–2006, respectively (Table 1 and Fig. 1d).

Diurnal variations of ecosystem water use efficiency

The diurnal variations of WUE_e were remarkable in the main growing seasons of winter wheat and summer maize (Fig. 2). In the morning, photosynthesis enhanced more rapidly than evapotranspiration under increasing solar radiation and led to a high WUE_e . The peaks of WUE_e occurred from 8:00 to 9:00 for wheat

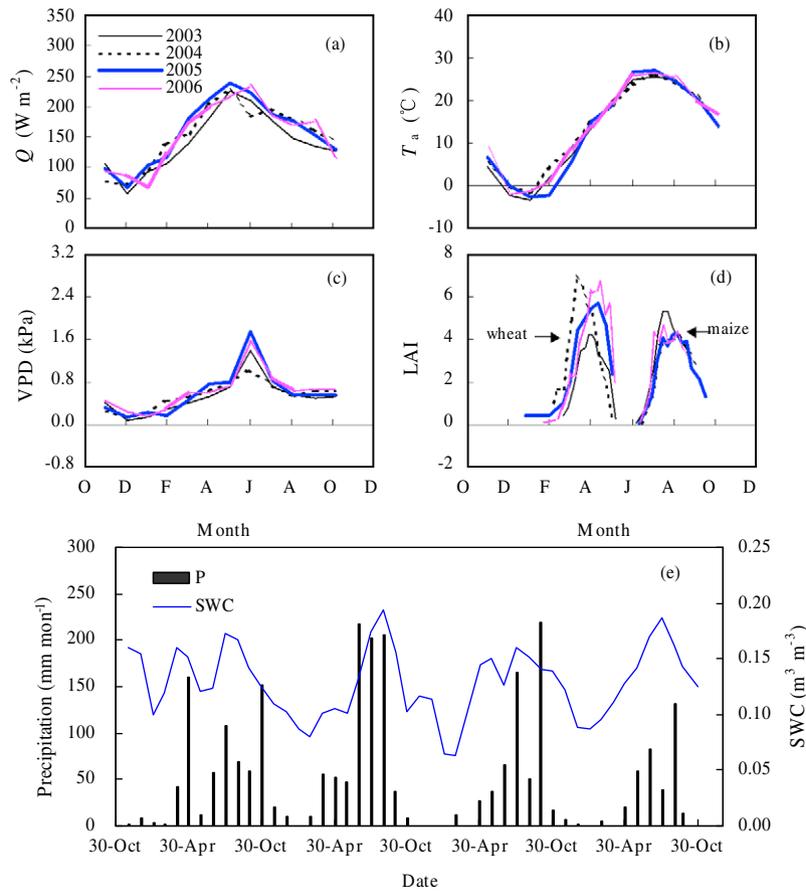


Fig. 1. Seasonal variations of solar radiation (Q), air temperature (T_a), vapor pressure deficit (VPD), soil water content at the depth of 10 cm (SWC), precipitation (P) and leaf area index (LAI) in the years 2003–2006.

Table 1

Seasonal average net ecosystem productivity (NEP), evapotranspiration (ET), ecosystem water use efficiency (WUE_e), air temperature (T_a), solar radiation (Q), soil water content (SWC), precipitation (P) and leaf area index (LAI) in wheat and maize fields.

Crop	Year	NEP ($g\ CO_2\ m^{-2}\ d^{-1}$)	ET ($kg\ H_2O\ m^{-2}\ d^{-1}$)	WUE_e ($mg\ CO_2\ g^{-1}\ H_2O$)	T_a ($^{\circ}C$)	Q ($W\ m^{-2}$)	VPD (kPa)	SWC ($m^3\ m^{-3}$)	P (mm)	Maximal LAI
Wheat	2003	31.4	3.9	7.4	15.4	334	0.75	0.14	215	4.2
	2004	34.4	4.7	7.2	15.8	359	0.89	0.10	155	6.9
	2005	39.5	5.1	7.0	15.4	388	0.93	0.12	65	5.7
	2006	40.1	5.5	6.7	17.0	375	0.93	0.13	78	6.7
Maize	2003	38.9	4.5	8.4	25.5	280	0.86	0.16	237	5.3
	2004	51.6	4.5	11.8	25.5	318	0.92	0.17	445	4.1
	2005	42.4	3.8	11.1	24.8	313	0.96	0.14	435	4.3
	2006	58.2	4.4	12.8	26.4	317	1.04	0.16	184	4.6

Remark: Precipitation is the seasonal total amount and T_a , Q , VPD and SWC were seasonal mean values.

and from 9:00 to 10:00 for maize. Thereafter, WUE_e decreased gradually and reached its minimum before sunset. WUE_e was usually lower in the afternoon than in the morning (Fig. 2). The reason

was that declining photosynthesis and increasing respiration led to a decrease of net carbon exchange in the afternoon with higher temperature and VPD (Weis and Berr, 1988; Baldocchi, 1994; Crau-

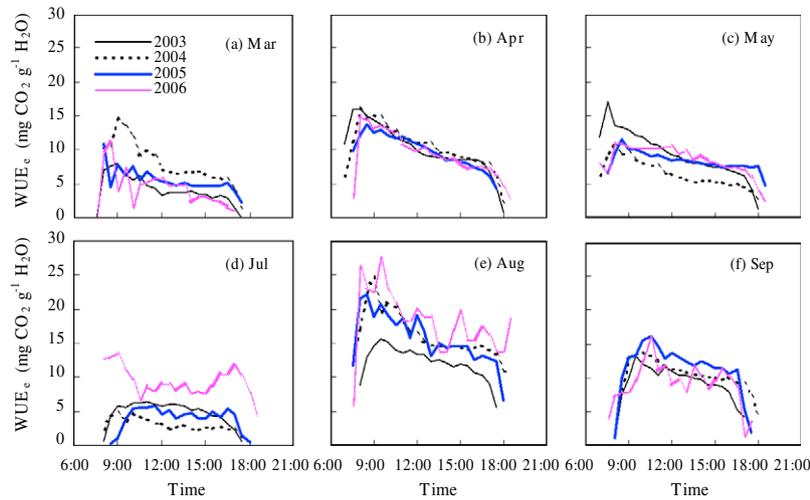


Fig. 2. Monthly mean diurnal variations of ecosystem water use efficiency (WUE_e) in wheat (a–c) and maize (d–f) fields.

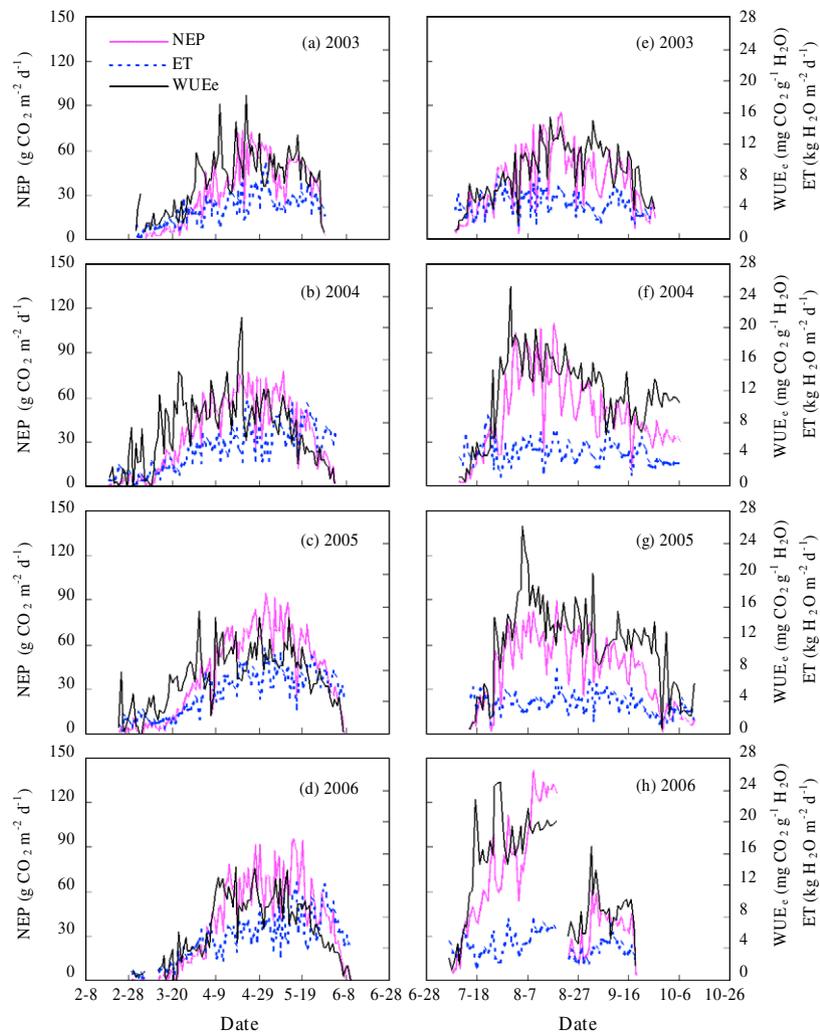


Fig. 3. Seasonal variations of daytime average ecosystem water use efficiency (WUE_e), net ecosystem productivity (NEP) and evapotranspiration (ET) in winter wheat (a–d) and summer maize (e–h) fields.

furd et al., 1999). The diurnal pattern of WUE_e was similar to other reports for cropland (Baldocchi, 1994; Li et al., 1997) and forest (Scanlon and Albertson, 2004; Testi et al., 2008).

Both diurnal maximum and diurnal amplitude (maximum minus minimum) of WUE_e were higher in maize field than in wheat field (Fig. 2). Evapotranspiration in the main growing season was higher in the wheat field than in the maize field. As a C_4 plant, maize has higher ability to assimilate CO_2 and hence higher WUE_e than wheat, a C_3 plant. The orders of both diurnal maximum and diurnal amplitude were April > May > March for wheat field and August > September > July for maize field. Compared to other months, the diurnal maximum and amplitude of WUE_e were low in July corresponding to seedling and elongation stages when LAI was low and net CO_2 uptake was weak in the maize field.

Seasonal variations of ecosystem water use efficiency

Seasonal patterns of WUE_e were similar to NEP and ET in the main growing season of winter wheat (Fig. 3a–d). NEP, ET and WUE_e were low at the reviving stage due to low temperature and small LAI. At the elongation stage (early-mid April), net photosynthesis rate and evapotranspiration enhanced with the increases in temperature, solar radiation and LAI. The increasing amplitude of photosynthetic rate was higher than that of evapotranspiration leading to an increase in WUE_e (Fig. 3a–d). The peaks of NEP, ET and WUE_e usually occurred at the earing stage in late April. In 2003–2006, the maximal WUE_e was 18.2, 21.4, 15.3 and 14.2 $mg\ CO_2\ g^{-1}\ H_2O$, respectively. NEP kept higher before mid grain-filling period (mid-May). Thereafter, it declined and was close to zero at harvest. However, ET remained high until harvest, resulting in a decline of WUE_e from mid-May to early June.

During the growing season of maize, variations of ET were not evident but those of NEP and WUE_e were remarkable (Fig. 3e–h). At the seedling stage, NEP and WUE_e were low under small LAI. NEP and WUE_e rose with the increase in LAI. Except for 2003, WUE_e generally peaked in late July/early August, which was a little earlier than NEP (mid-August). Maximal WUE_e of the maize field was about 25 $mg\ CO_2\ g^{-1}\ H_2O$ for the years 2004–2006. The peak of WUE_e in 2003 (15.6 $mg\ CO_2\ g^{-1}\ H_2O$) was lower than those in the other years mainly because of the smaller peak of NEP. After mid-August, WUE_e decreased gradually with the decline of NEP.

Inter-annual variations of ecosystem water use efficiency

In the main growing season of winter wheat, mean NEP and ET varied largely with years but the inter-annual differences of mean WUE_e were insignificant (Table 1). Seasonal mean WUE_e was 7.4, 7.2, 7.0 and 6.7 $mg\ CO_2\ g^{-1}\ H_2O$ for the years 2003–2006, respectively, lower than the value reported by Baldocchi (1994) (11 $mg\ CO_2\ g^{-1}\ H_2O$) over a closed wheat canopy. Some studies showed

that WUE_e would increase under moderate water stress (Turk and Hall, 1980; Green and Read, 1983; Craufurd et al., 1999). In our experiments, although the precipitation changed greatly over 4 years, seasonal mean soil water content varied less due to sufficient irrigation. It led to similar values of WUE_e in different years.

In the maize field, seasonal mean WUE_e was 8.4, 11.8, 11.2, 12.1 $mg\ CO_2\ g^{-1}\ H_2O$ from 2003 to 2006, respectively. Despite of shortage of rainfall in summer 2003, soil water content and evapotranspiration remained higher due to sufficient irrigation. Owing to the lower solar radiation, NEP and WUE_e of maize in summer 2003 were lower than those in the same periods of other years. In summer 2005, both ET and NEP were low under low soil moisture at surface layer, but WUE_e remained high (Table 1). Our results were close to the values reported by Baldocchi (1994) in an open maize field (11 $mg\ CO_2\ g^{-1}\ H_2O$) and Anderson and Verma (1986) in a sorghum field (6.5–11.9 $mg\ CO_2\ g^{-1}\ H_2O$).

WUE_e of maize was higher than that of wheat, which was chiefly because physiological pathways, as well as leaf structure were different between maize (C_4 crop) and wheat (C_3 crop) (Dengler and Nelson, 1999). C_4 crops have high PEP carboxylase activity (Zhang and Shan, 2002). Theoretically, water use efficiency of plant is the function of leaf-air CO_2 concentration difference and leaf-air water vapor pressure difference (Jones, 1983). Under similar environmental conditions, water use efficiency of C_3 crops is lower than C_4 crops because CO_2 concentration remains higher in C_3

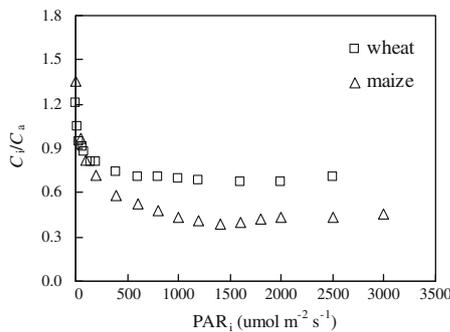


Fig. 4. Light response curves of C_i/C_a for wheat (square) and maize (triangle) leaves.

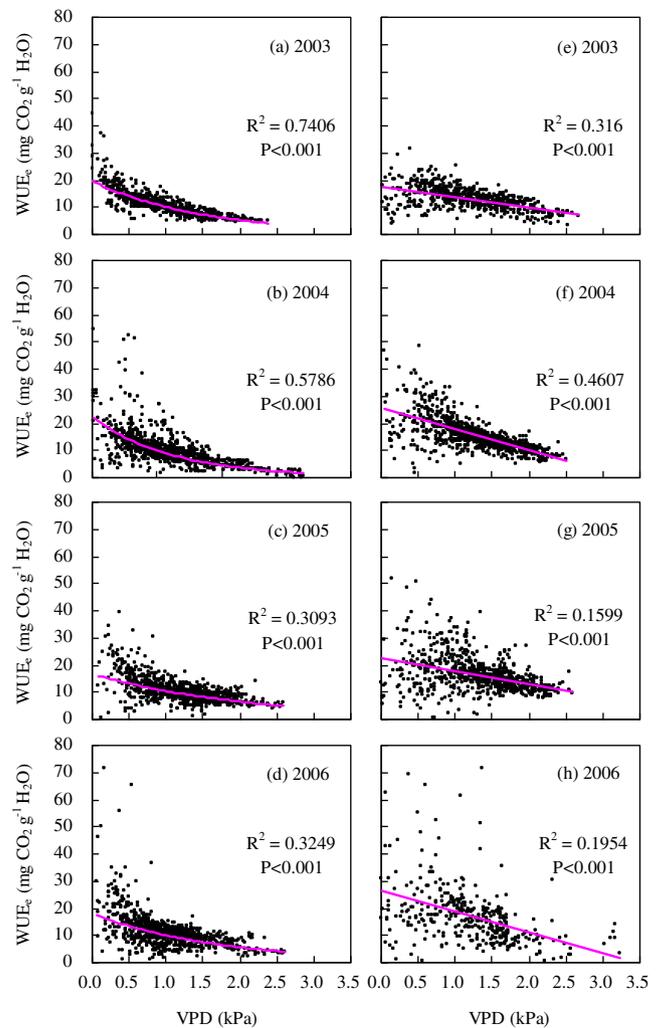


Fig. 5. The relationship between half-hourly WUE_e and the corresponding VPD in wheat (a–d) and maize (e–h) fields.

leaves than in C_4 leaves (Jones, 1983; Pearcy and Ehleringer, 1984). Winter wheat and summer maize grew under different weather conditions. However, the characters of species determined a larger WUE_e for maize than for wheat.

Water use efficiency at leaf and ecosystem levels

Water use efficiency can be studied at different scale. At the leaf scale, water use efficiency is described as the ratio of net photosynthesis to transpiration, and can be described as follow (Farquhar and Richards, 1984; Jones, 1992):

$$WUE_l = \frac{C_a(1 - C_i/C_a)}{1.6VPD} \quad (4)$$

where C_i/C_a is the ratio of internal to ambient CO_2 partial pressure. The factor 1.6 is the ratio of the diffusivities of water vapor and CO_2 in laminar boundary over leaf surface. Under small PAR, C_i/C_a decreased significantly with the increase in PAR. When PAR was higher than a critical value (nearly $500 \mu mol m^{-2} s^{-1}$ for wheat and $1000 \mu mol m^{-2} s^{-1}$ for maize), C_i/C_a was approximately constant at 0.69 for wheat and 0.42 for maize (Fig. 4), very close to the reported values for C_3 plants (0.7) (Tanner and Sinclair, 1983) and maize (0.4) (Wong et al., 1979), respectively.

At the ecosystem scale, water use efficiency is defined as the ratio of net ecosystem productivity to evapotranspiration and Eq. (4) can be revised as:

$$WUE_e = \frac{C_a(1 - C_i/C_a)(1 - \Phi_w)}{1.6VPD(1 + \Phi_c)} \quad (5)$$

where Φ_c is the ratio of apparent soil respiration (R_s) to NEP, Φ_w the ratio of evaporation to evapotranspiration. Except for raining days and dewing mornings, canopy evaporation can be ignored in the

daytime and Φ_w is approximate to the proportion of soil evaporation (E) to evapotranspiration (ET). In winter wheat and maize fields, daily E and ET could be determined by large-scale weighting lysimeter and micro-lysimeter, separately (Liu et al., 2002). NEP was measured using eddy covariance technique, and R_s were measured using close chamber method (Tong, 2007). Without water stress, Φ_w had negative correlation with LAI (Brisson et al., 1992; Liu et al., 2002; Kang et al., 2003; Kato et al., 2004). Similar relationship could be found between Φ_c and LAI. Theoretically, it is possible to transform water use efficiency between leaf and ecosystem levels in a simple way.

The influencing factors on water use efficiency

Humidity

In the well-watered cropland, the influence of soil moisture on water use efficiency was indistinctive because soil water content remained high and satisfied for crop growth during the main growing season. However, the effects of air humidity on water use efficiency were significant. Many studies indicated that WUE_e had a strong negative correlation with VPD at leaf (Steduto et al., 1997; Moriana et al., 2002) and canopy (ecosystem) levels (Baldocchi et al., 1985; Verma et al., 1992; Baldocchi, 1994; Verhoef et al., 1996; Steduto et al., 1997; Berbigier et al., 2001; Law et al., 2002; Ponton et al., 2006). Similar phenomena were found in our experiments. WUE_e declined obviously with the increase in VPD in wheat and maize fields (Fig. 5). During main growing seasons of wheat and maize, LAI was generally greater than two (Fig. 1d) and WUE_e was mainly controlled by stomatal factors. Stomata adjusted gas exchange between leaves and the atmosphere and trended to keep a constant C_i/C_a under various weather conditions (Wong et al., 1979, 1985a, 1985b; Ehleringer and Cerling, 1995),

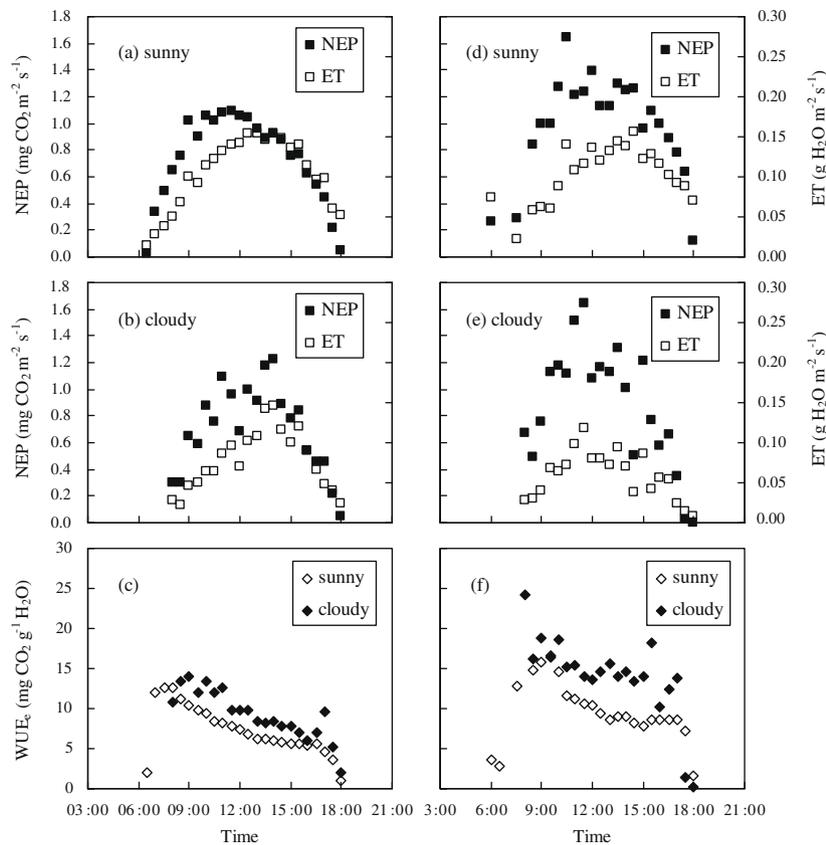


Fig. 6. Diurnal courses of NEP, ET and WUE_e on the sunny days and the cloudy days (a–c): wheat field, May 1 and 3, 2003; (d–f): maize field, August 11 and 12, 2003.

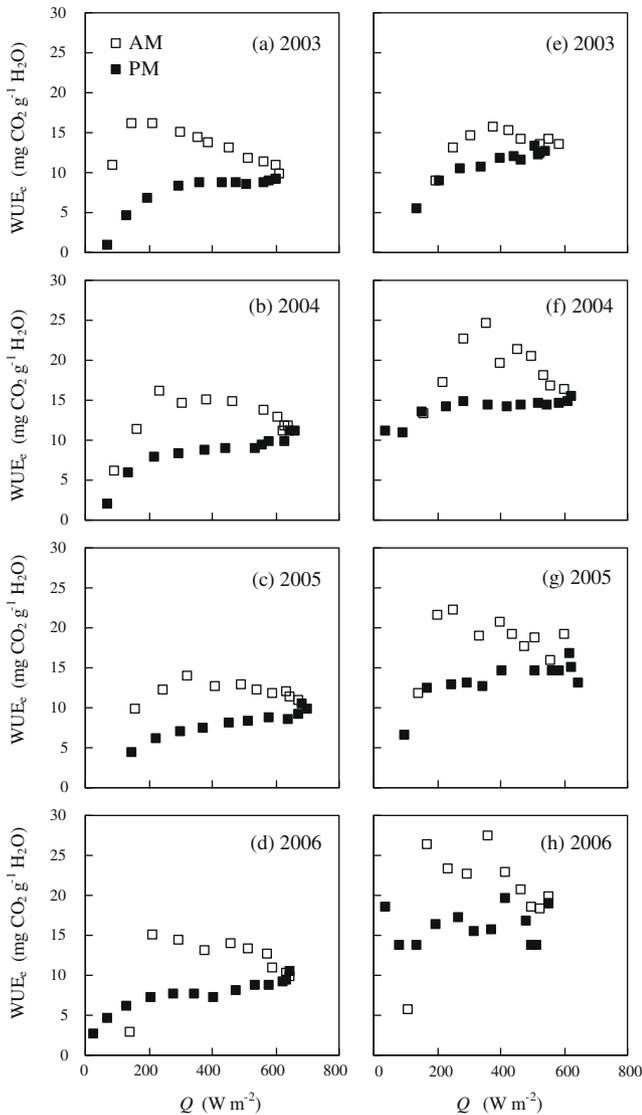


Fig. 7. Monthly mean diurnal WUE_e responded to Q in April and August for wheat (a–d) and maize (e–h) fields, respectively (□: morning; ■: afternoon).

involving different CO_2 concentrations, leaf ages, nutrient conditions and slight water stress (Brodrribb, 1996). Eq. (5) emphasizes the role of VPD in determining WUE_e in different climates. The non-linear relationship between WUE_e and VPD for wheat field

was likely related to low air humidity and soil moisture, in contrast to maize field, where soil and air were wet due to much precipitation during maize growing period.

Solar radiation

As the driving factor of photosynthesis and transpiration, solar radiation is one of important factors affecting water use efficiency. Based on harvesting biomass, some studies showed canopy water use efficiency was negative proportional to solar radiation (Kumar et al., 1996; Roupael and Colla, 2005), which was possibly due to high evapotranspiration under strong radiation (Monteith, 1989). Using the cuvette method and canopy model, Tenhunen et al. (1990) obtained greater water use efficiency on the overcast days than on the clear days. Similar phenomena were found in our measurements using the EC technique when LAI was large (Fig. 6). Generally, photosynthetic rate of wheat was lower on the cloudy days than the value on the sunny days. On the cloudy days, both NEP and ET in wheat field declined but ET decreased more than NEP. Nevertheless, photosynthesis of maize remained high on the cloudy days. In the maize field, NEP changed less but ET dropped markedly on the cloudy days. It resulted a higher WUE_e for both wheat and maize on the cloudy days than on the sunny days (Fig. 6). Canopy structure of maize is sparser than that of wheat and benefits light penetration. When LAI was large, there was more diffuse radiation received by the maize leaves at the lower layers. The light distributed more equally in the canopy and the assimilate rate of shadow leaves increased (Gu et al., 2003). That is the reason why photosynthesis of maize kept larger on the cloudy days.

In the monthly mean diurnal course, WUE_e enlarged firstly and then declined under increasing Q in the morning. It kept on decreasing with the decline in Q in the afternoon (Fig. 7). The diurnal peak of WUE_e appeared when solar radiation arrived to a critical value. The critical light intensity was about 200 W m^{-2} for wheat and 300 W m^{-2} for maize. At the same Q , WUE_e in the morning was higher than that in the afternoon. It was mainly due to low feedback inhibition of photosynthesis in the morning. Carbohydrate was almost used out during the whole night. Consequently, only less carbohydrate was kept in leaves. Photosynthetic rate was strong even under low light intensity. Strong photosynthesis and weak evapotranspiration led to a maximal WUE_e in the morning. In the afternoon, photosynthetic production cumulated gradually in leaves for the delayed transportation. The feedback inhibition of photosynthetic production led to lower photosynthetic rate in the afternoon than in the morning. However, evapotranspiration was usually higher in the afternoon than that in the morning due to higher temperature and VPD. It resulted a higher WUE_e in the morning than in the afternoon at the same light intensity.

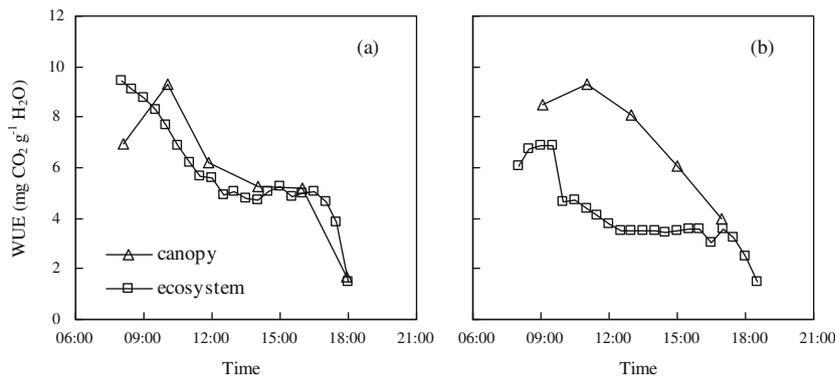


Fig. 8. Diurnal courses of water use efficiency at canopy and ecosystem levels (a) wheat field, April 16, 2003, LAI = 3.50; (b) maize field, July 22, 2004, LAI = 0.79.

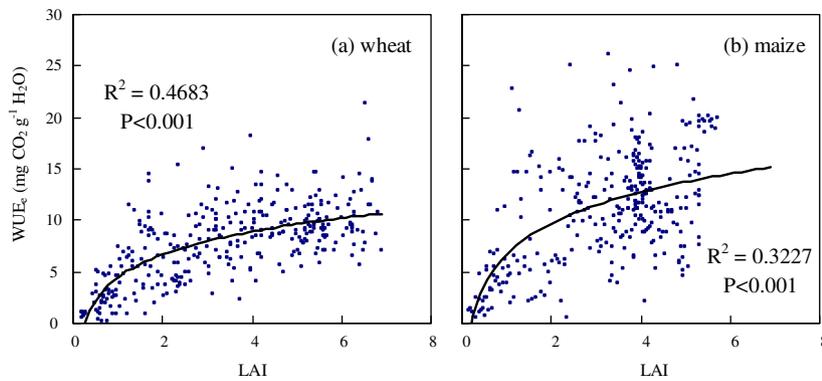


Fig. 9. Relationship between daytime average WUE_e and LAI in wheat (a) and maize (b) fields.

Leaf Area Index

To evaluate how much WUE_e represents actual crop water use, water use efficiencies were compared between ecosystem and canopy levels. The results showed that WUE_e was close to WUE_c under large LAI (3.50) but much lower than WUE_c under small LAI (0.79) (Fig. 8). When LAI was small, WUE_e could not represent actual crop water use because the effect of nonstomatal factors (soil respiration and evaporation) on WUE_e was significant. When LAI was great, the influence of nonstomatal factors on WUE_e was small and could be neglected. WUE_e was mainly determined by stomatal factors (photosynthesis and transpiration) and could be used to express the real status of crop water use.

With the increase in LAI, WUE_e enlarged rapidly under small LAI but slowly under large LAI (Fig. 9). When LAI was larger than one, the scattered values of WUE_e implied other factors rather than LAI influenced WUE_e more evidently. The factors influencing WUE_e include stomatal and nonstomatal parts. Which one will dominate WUE_e is mainly due to LAI. With the change of LAI, the allocation of energy between canopy and soil varied. So did partitioning of water vapor and CO_2 flux between plant canopy and soil. Under low LAI, Φ_c and Φ_w diminished significantly with the increase in LAI. When LAI was larger than two, Φ_c and Φ_w became constants (Liu et al., 2002), which meant the weak influence of LAI on WUE_e .

Conclusions

During the main growing seasons of wheat and maize, WUE_e varied diurnally and seasonally. Daily maximal WUE_e appeared in the morning. WUE_e generally peaked in late April in wheat field and in late July/early August in maize field. From 2003 to 2006, seasonal mean WUE_e for wheat was 7.4, 7.2, 7.0 and 6.7 $mg\ CO_2\ g^{-1}\ H_2O$, respectively, and for maize 8.4, 11.8, 11.2, 12.1 $mg\ CO_2\ g^{-1}\ H_2O$, respectively.

WUE_e was much lower than WUE_c under small LAI but very close to WUE_c under large LAI. With the increase in LAI, WUE_e enlarged rapidly under low LAI but slowly when LAI was higher than 1. WUE_e was greater on the cloudy days than that on the sunny days. Under the same Q , WUE_e was higher in the morning than in the afternoon. C_i/C_a significantly decreased with the increase in PAR when PAR was lower than critical values (around 500 and 1000 $\mu mol\ m^{-2}\ s^{-1}$ for wheat and maize, respectively). Beyond critical PAR, C_i/C_a was approximately constant at 0.69 for wheat and 0.42 for maize. Thereby, when LAI and solar radiation was large enough, WUE_e was negative proportional to VPD in both of irrigated wheat and maize fields.

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