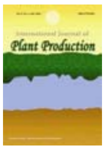

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Effects of climate change on water use efficiency in rain-fed plants

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Abstract

Water use efficiency (WUE) reflects the coupling of the carbon and water cycles and is an effective integral trait for assessing the responses of vegetated ecosystems to climate change. In this study, field experiments were performed to examine leaf WUE (WUE_{leaf}) in response to changes in CO_2 concentration and other environmental variables, including soil moisture and air temperature. We also used yield of maize and soybean, soil water content and precipitation data to calculate water use efficiency at the level of grain yield (WUE_{grain}) in a manner that enabled us to analyze the effects of climatic factors on WUE_{grain}. The results showed that the WUE_{leaf} measurements of maize and soybean plants were negatively correlated with soil moisture and air temperature. At a photosynthetically active radiation (PAR) of 1.600 μmol $m^{-2}s^{-1}$, increasing ambient CO_2 concentrations (from 400 to 800 μmol mol^{-1}) improved WUE_{leaf} by 52.0% and 75.8% for maize (a C_4 species) and soybean (a C_3 species), respectively. Increased annual precipitation stimulated maize WUE_{grain} up to levels of approximately 500-550 mm, although maize WUE_{grain} decreased when annual precipitation exceeded 550 mm. It appears that 400-450 mm is an economical evaportranspiration (ET) for spring maize in Chaoyang area of northeast China. For soybean, more water often reduces WUE_{grain}, and there is a linear relationship between changes in WUE_{grain} and changes in annual temperature. The different responses of WUE_{grain} and WUE_{leaf} to climate change suggest that caution should be taken when attempting to up-scale WUE from leaf to grain or biomass levels.

Keywords: Maize; Soybean; Global warming; Precipitation; Water use efficiency.

Introduction

According to global climate model simulations, by the end of the 21st century, the global average surface temperature will warm 1.8-4.0 ^{o}C and global precipitation regimes will change considerably (IPCC, 2007), which will greatly impact both agriculture and water resources (Guo et al., 2010; Fuhrer, 2003; Yang et al., 2011). Given that photosynthesis and transpiration are often controlled by stomatal conductance at the leaf level, there is a critical link between the carbon and water cycles in vegetated ecosystems (Kuglitsch et al., 2008). Water use efficiency (WUE) is an important index in climate change research and hydrological studies, as it reflects how the carbon and water cycles are coupled and is an effective integral trait for assessing the responses of vegetated ecosystems to climate change. WUE can be calculated in very different ways, depending on the temporal and spatial scales used and the scientific question of interest (Yu et al., 2008; Zhu et al., 2010; Beer et al., 2009; Niu et al., 2011; Li and Yu, 2007). Although various definitions of WUE are applied in different scientific disciplines, a characteristic feature of all of these metrics is that WUE reflects a ratio of carbon gain relative to water loss (ET or transpiration) (Kuglitsch et al., 2008). The rate of CO_2 assimilation may be measured as net CO_2 exchange, increase in dry matter, or economic yield, whereas water use may be measured either as the mass or molar units of water (Bacon, 2004). Agricultural scientists usually determine WUE as a relationship between either yield or biomass to either ET or the total water provided to the crop, including precipitation and the amount of water provided by irrigation (Jones, 2004; Kuglitsch et al., 2008).

In water-limiting environments, WUE is an especially important determinant of crop productivity (Fischer and Turner, 1978; Tanner and Sinclair, 1983) and is strongly influenced by factors that affect transpiration and CO_2 assimilation by leaves and plants (De wit, 1958; Tanner and Sinclair, 1983; Li and Yu, 2007; Cayci et al., 2009). A modeling study suggested that, under both SRES A_2 and B_1 scenarios[1], WUE improved for

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1- The Special Report on Emissions Scenarios (SRES) is a report by the Intergovernmental Panel on Climate Change (IPCC) that was published in 2000. The A_2 scenario describes a very heterogeneous world of high population growth, slow economic development and strong regional cultural identities. B_1 is a rather optimistic scenario assuming "convergent world" and putting an emphasis on global solutions to economic, social and environmental sustainability. The B_1 scenario also assumes high economic growth but with substantial shift to nuclear energy winter wheat, but decreased for maize (Mo et al., 2009). There have been few reports of studies that directly assessed the response of maize or soybean WUE to changes in precipitation and global warming, although research involving controlled irrigation may to some extent reflect the effect of changes in precipitation on WUE. The use of quadratic equations to show the relationships between applied irrigation and WUE in summer maize over different rainfall years (Sun et al., 2010) indicated that the amounts of irrigation needed to optimize WUE in summer maize are less than the greatest level of irrigation tested. The shape of the temperature response curve is determined by different factors at low, moderate and high temperatures (Nicotra et al., 2008; Hikosaka et al., 2006), with critical points varying depending on growth temperatures, plant water status and even time of day (Medlyn et al., 2002). Below a certain temperature threshold, leaf stomatal conductance increased with increasing temperature. More extensive increases in photosynthesis (P_n) than in T_r increase WUE. Once the temperature exceeded the threshold, further increases in temperature reduced WUE as a result of increased rates of evapotranspiration. The temperature threshold differs from the optimal temperature for P_n, and differs between plant species (Wang et al., 2010).

Simulated WUE consistently increases under conditions of elevated CO_2 concentration (Zhu et al., 2011). The major reason for this is that increases in CO_2 concentrations will decrease leaf stomatal conductance (Li et al., 2010). Water flux will therefore be considerably reduced and will decrease ET, as suggested by experimental studies in Chesapeake Bay wetland and tall-grass prairie vegetation (Li et al., 2010; Polley et al., 2008). Under conditions of elevated CO_2, although stomatal conductance is reduced, carbon assimilation can be maintained at levels seen for normal CO_2 availability (Zhu et al., 2011). Given that WUE is expressed as the ratio of yield to ET, it will undoubtedly increase with increased ambient CO_2 concentrations. Increases in leaf surface CO_2 concentration generally enhance photosynthesis and reduce stomatal opening. Therefore, regardless of whether carbon assimilation is assayed in terms of photosynthesis or biomass accumulation, WUE is expected to increase with rising levels of CO_2 in the atmosphere. This has been observed almost universally (Xu and Hsiao, 2004). For C_3 plants grown under conditions of elevated atmospheric CO_2, growth and yield will increase by reducing photorespiration and enhancing photosynthetic CO_2 exchange rates, whereas the effects of elevated atmospheric CO_2 on photosynthesis in C_4 plants remain uncertain (Vu and Allen, 2009; Leakey et al., 2006). In some C_4 plants, WUE responds to increased CO_2 (Ziska and Bunce, 1997; LeCain and Morgan, 1998; Wand et al., 2001), whereas for others it does not (Morison and Gifford, 1984b;Wilsey et al., 1994; Ward et al., 1999; Wand et al., 2001). Unlike the situation for C_3 plants, there is no theoretical basis to expect substantial direct effects of an increase in atmospheric CO_2 on C_4 photosynthesis (Chun et al., 2011; Vu and Allen, 2009; Long et al., 2006).

The northeast part of China is one of the most important agricultural regions for food production in China (Ma et al., 2012; Wu et al., 2008). Spanning an area of 79×10^4 km^2, it includes the three provinces Heilongjiang, Jinlin and Liaoning. As the main food export supply area, the northeastern region of China contributes approximately 22% of the total maize yield and more than 80% of the total soybean yield in China (Zhang et al., 2011). As the northeast territories of China lie within the temperate continental monsoon region, agriculture in this area is already being affected by climate change (He and Zhang, 2011). In the future, evapotranspiration and water use efficiency of crop will alter with climate change (Thomas, 2008; Mo et al., 2007). To ensure that crop systems can adapt to the changing climate, it is important to understand how climate change affects agriculture and WUE (Mo et al., 2010). This study was conducted to investigate the response of WUE to environmental variables at different levels, as well as its underlying mechanisms based on field measurements spanning more than 20 years.

Materials and Methods

Experimental site and field experimental procedure

Jinzhou site

The study site was located in Jinzhou Agricultural Ecosystem Research Station (41^o 09′ N, 121^o 12′ E, 70.2 m above sea level) in the southernmost territories of the northeast of China. The land was under till management and nitrogen-containing fertilizer was applied at a rate of approximately 300 kg of N ha^{-1}. The region has a temperate zone monsoon climate with a mean annual temperature of about 9.5 ^oC and an annual precipitation of about 571 mm (as determined between 1961-2005). The soil type is typical brown soil, with a pH value of 6.3, organic matter content from 0.6% to 0.9% and total nitrogen content of 0.069% (Han et al., 2007). Field experiments were conducted on soybean between 1985-2010 at this site. Rain-fed soybean was sown in early May and ripe at the end of September. According to the records collected between 1985-2010, the average number of days between planting andripeness was 143 days. Plot areas were approximately 1/15 ha.

Chaoyang site

The study site was located approximately 110 km northwest of the Jinzhou site. The selected crop type was rainfed spring maize, which was sown in early May and matured at the mid-September. Field experiments were conducted on maize between 1990-2010 at the Chaoyang site. Plot areas were approximately 1/15 ha. According to the records collected between 1990-2010, the average number of days between planting and ripeness was 126 days. The region has a temperate zone monsoon climate with a mean annual temperature of about 9.0 ^{o}C and an annual precipitation of about 482 mm (as determined between 1961-2005). The total precipitation during 2009 was 295 mm and precipitation between 21 July and 16 August in 2009 was only 0.2 mm. Given that this severe drought killed most of the plants, there is no grain yield data for 2009.

Soil water deficit experiment

Soil water deficit experiment on maize was conducted during the year of 2008 and 2009 at Jinzhou site. A soil water controlling pool was used to grow maize plants under different soil water conditions to obtain photosynthetic rates and transpiration rates under the different soil water conditions. Above the pool, there was a mobile shed which could hold back the rain in rainy days. The motion of the mobile shed was dynamoelectric. There were fifteen 3×5 m plots divided by concrete walls for five soil water content treatments at different growing stages. The walls are 15.0 cm thick and extend 2.0 m beneath the surface. Two kinds of water stress levels were tested for maize during the vegetation and milking stages, and each treatment was replicated three times (Table 1). For each soil water treatment, soil volumetric water contents at the center of each plot were monitored every 3 days in 20 cm increments to a depth of 1.8 m using a section water sensor (TRIME-PICO-IPH).

Tabel 1. Controlled soil moisture level during different growth stages of maize (units: θ / θ_{pc}).

Treatments	Vegetative Tasseling	Cob formation Milk stage
A	0.5~0.6	0.8
B	0.4~0.5	0.8
C	0.8	0.5~0.6
D	0.8	0.4~0.5
E	0.8	0.8

θ : soil water contents; θ_{pc} : soil water contents at field capacity; 0.4~0.5, 0.5~0.6 and 0.8 means the ratio of θ / θ_{pc} .

Measurements

Leaf-level WUE

Leaf gas exchange of maize under the different soil water treatments were measured with a portable photosynthesis system (Li-6400; Li-Cor Inc.) with a 6 cm^2 clamp-on leaf cuvette on clear days (measured every 9 days since June 20). One plant was selected from each plot and the average of three plants was regarded as the value at certain soil water content. During the measurement, leaves were illuminated at the photosynthetic photon flux density (PPFD) of 1,400 μmol $m^{-2}s^{-1}$ using the LED light system (6400-02B LED). We did not control leaf temperature, water vapor or CO_2 concentrations. Leaf level WUE (WUE_{leaf}) was calculated as P_n / T_r.

Photosynthetic rate (P_n) and transpiration rate (T_r) of maize and soybean in response to CO_2 concentration at leaf surfaces were measured at the leaf level be means of a portable photosynthesis system (Li-6400; Li-Cor Inc.) equipped with an halogen lamp (6400-02B LED) positioned on the cuvette and a CO_2 injector to regulate CO_2 concentration. The measurements were taken on clear days (July 18, 2010 for maize and July 19, 2010 for soybean) between 09:00 to 11:00 hours (local time). Leaves were included in a 6 cm^2 leaf chamber and exposed to CO_2 concentration ranging from 1,000 to 0 μmol mol^{-1} in seven steps (1,000, 800, 600, 400, 300, 200, 100, 50 and 0) when leaves were exposed to PPFD at 1,600, 1,400, 1,200 and 1,000 μmol $m^{-2}s^{-1}$. We did not control leaf temperature and water vapor.

Crop biomass, yield and soil water content

For both of the experimental sites, at the end of the crop growth season, crops were harvested to estimate the yields for maize and soybean. At the

Jinzhou site, since 2001, samples of 20 soybean plants at each growth stage[1] were randomly harvested and the lengths and widths of each leaf were measured manually. The leaf areas of the samples were averaged and combined with plant densities to estimate the LAI for the plot. The plants were then oven-dried (110 °C for 1 h, followed by 80 °C for 2 days) to estimate total biomass. In addition, for the two experiment sites during the growing season, soil water content was measured every 5 days using the drying and weighing method. In this study, daily temperature and precipitation data were obtained from the local meteorological station.

Estimation of water use and WUE

For each year, ET was calculated as follows:

$$ET = CR + I + P + \Delta W - D - R$$

Where CR defines capillary rise, I defines irrigation, P defines precipitation, D defines drainage, R defines runoff, and ΔW (measured in mm) defines the change in soil content at a depth 1.0 m below the soil surface. Owing to the flatness of the land, runoff was negligible. Given that previous observations had indicated that the water table of the two sites was more than 4 m deep, drainage and capillary rise were negligible. Given that rainfed agriculture is prevalent in the northeast of China, it is justified to consider that $ET = P + \Delta W$ under the experimental conditions in this study.

In this study, we defined WUE_{leaf} (μmol mol^{-1}) as moles of CO_2 absorbed per mol of H_2O lost through transpiration. We defined $WUE_{biomass}$ (kg m^{-3}) as biomass produced per unit of H_2O lost through evapotranspiration (ET) during a given period. We defined WUE_{grain} (kg m^{-3}) as the ratio of grain yield to water used throughout the growing season to produce the yield (ET).

Data analysis

We selected the WUE_{leaf} when air temperatures were between 27 and 30 °C to analyze the relationship between WUE_{leaf} and soil water content. Then choose the WUE_{leaf} when soil moisture was between 12% and 19% (v/v) to investigate the relationship between WUE_{leaf} and air temperature. In this study, technique of regression analysis was applied. Regression analysis was used to determine relationships between different variables. The analysis was performed with the SPSS software package.

1- For soybean it refers to three leaves, branching, flowering, milking and maturity stage

Results

Effects of CO_2 concentration and other environmental variables on WUE_{leaf}

Effects of soil moisture and air temperature on WUE_{leaf}

An increase in soil moisture from 12% to 26% increased values of both P_n and T_r of maize by 96.7% and twice, respectively (Figure 1a). A much larger increase in T_r relative to P_n caused a 35.4% reduction of WUE_{leaf} under conditions of increased soil moisture (Figure 1b). Both P_n ($P<0.01$) and T_r ($P<0.1$) of maize showed significantly positive correlations with soil moisture. In contrast, WUE_{leaf} was negatively correlated ($P<0.1$) with soil moisture.

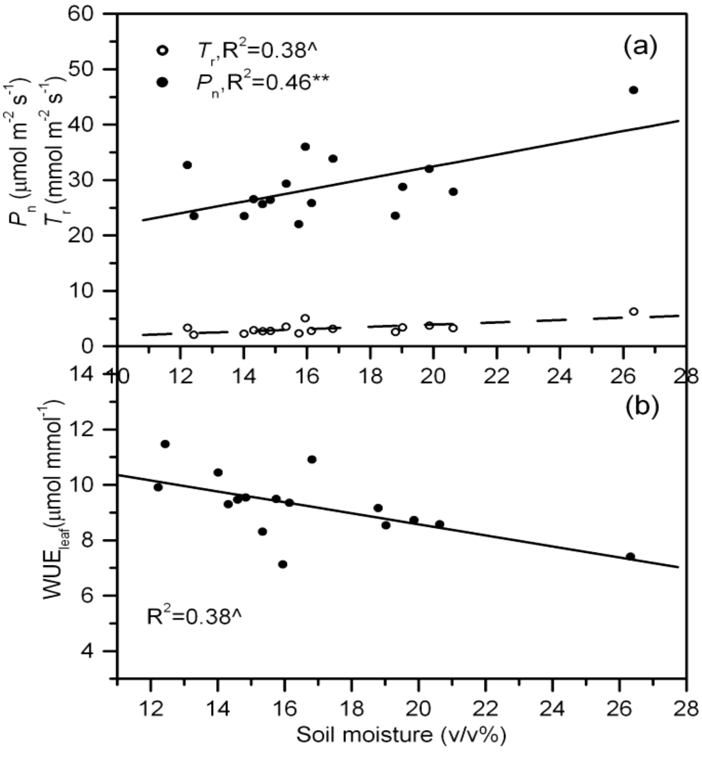

Figure 1. Relationship between soil moisture and photosynthetic rate (P_n), transpiration rate (T_r, a) and water use efficiency (WUE_{leaf}, b) of maize. The PAR was 1,400 μmol $m^{-2}s^{-1}$, and temperatures were between 27 and 30 ^oC. $^{\wedge}$ $P<0.1$; ** $P<0.01$.

Increasing the ambient temperature from 26 to 40 ^oC significantly increased P_n ($P<0.01$) and T_r ($P<0.01$) of maize by 50.2% and 4-fold, respectively (Figure 2a). Likewise, a much greater increase in T_r relative to P_n resulted in a 70.3% reduction in WUE_{leaf} at elevated air temperatures (Figure 2b). Both P_n and T_r of maize showed significantly ($P<0.01$) positive correlations with air temperature. In contrast, WUE_{leaf} was negatively correlated ($P<0.01$) with air temperature.

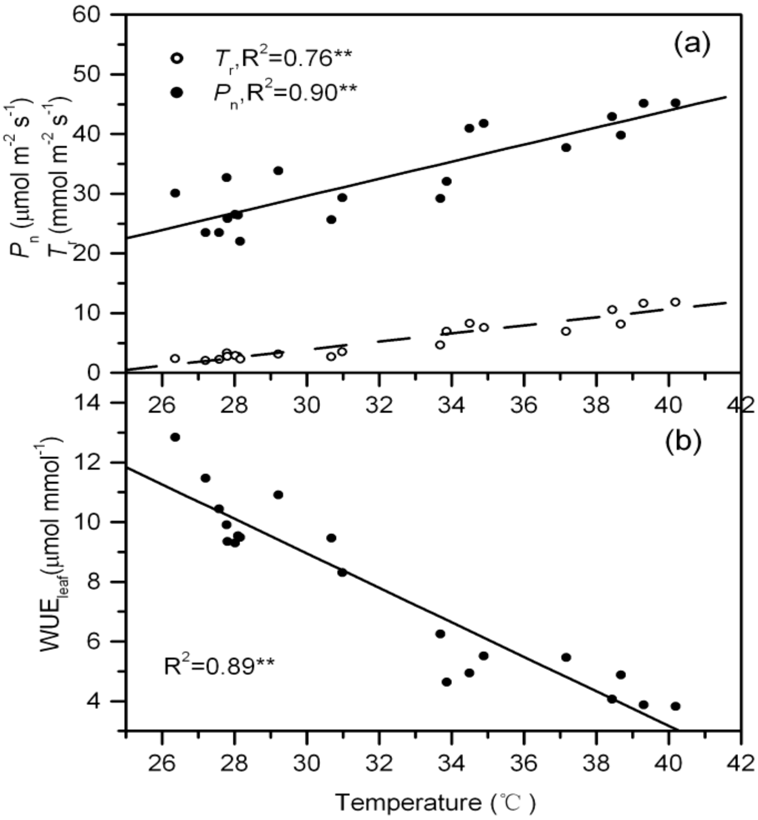

Figure 2. Relationship between air temperature and photosynthetic rate (P_n), transpiration rate (T_r, a) and water use efficiency (WUE_{leaf}, b) of maize. The PAR was 1,400 μmol $m^{-2}s^{-1}$, and soil moisture was between 12% and 19% (v/v). ** $P<0.01$.

Effects of CO_2 concentration on WUE_{leaf}

The effect of CO_2 enrichment on P_n in maize (C_4 species) is weak, with an increase of less than 13% when leaf surface CO_2 concentration was increased (from 400 to 800 μmol mol^{-1}) under a PAR of 1,600 μmol $m^{-2}s^{-1}$ (Figure 3a). Under the same conditions, P_n of soybean increased 46%

(Figure 3b), which is consistent with expectations that a C_3 crop is expected to benefit more from CO_2 enrichment than a C_4 species.

In response to increases in leaf surface CO_2 concentration, leaf transpiration rates (T_r) first increase, and then decrease. The optimal CO_2 concentrations differed between maize and soybean, with an optimum of 100 μmol mol^{-1} observed for maize (Figure 3c), and an optimum of 400 μmol mol^{-1} observed for soybean (Figure 3d). Owing to the substantially larger increase in P_n relative to T_r, as well as the reduction of T_r when leaf surface CO_2 concentrations exceeded optimal levels, WUE_{leaf} values for both maize (Figure 3e) and soybean (Figure 3f) increase with increased ambient CO_2 concentrations. At a PAR of 1,600 μmolm^{-2}s^{-1}, increases in CO_2 concentration (from 400 to 800 μmol mol^{-1}) stimulated WUE_{leaf} by 52.0% and 75.8% for maize (C_4 species) and soybean (C_3 species), respectively.

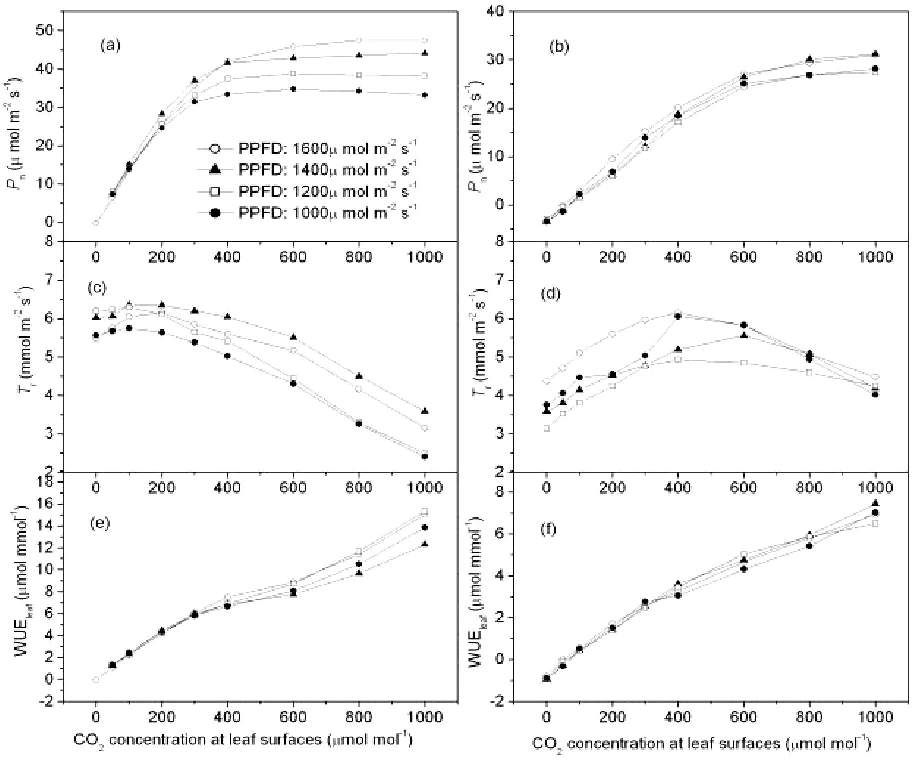

Figure 3. Changes in photosynthetic rate, (P_n, ab), transpiration rate (T_r, cd) and water use efficiency (WUE_{leaf}, ef) of maize (left panel) and soybean (right panel) in response to changes in the CO_2 concentration at leaf surfaces when the leaves exposed to different photosynthetic photon flux densities (PPFD).

Effects of temperature and precipitation on WUE_{grain}

Maize

The WUE_{grain} of maize seems low during both dry years and wet years, peaking when the annual precipitation is approximately 500-550 mm (Figure 4a). The relationship between WUE_{grain} and precipitation from planting to ripeness fits a quadratic function, although the relationship is not significant ($P>0.05$), unless data obtained during 2000 and 2002 are excluded (Figure 4b). As shown in Figure 4c, WUE_{grain} of maize increased with increases in amount of ET, but reached a plateau when the ET was around 450 mm. The relationship between WUE_{grain} and ET fits a quadratic function and was significant at the level of $P<0.05$ (data obtained during 2000 and 2002 are excluded).

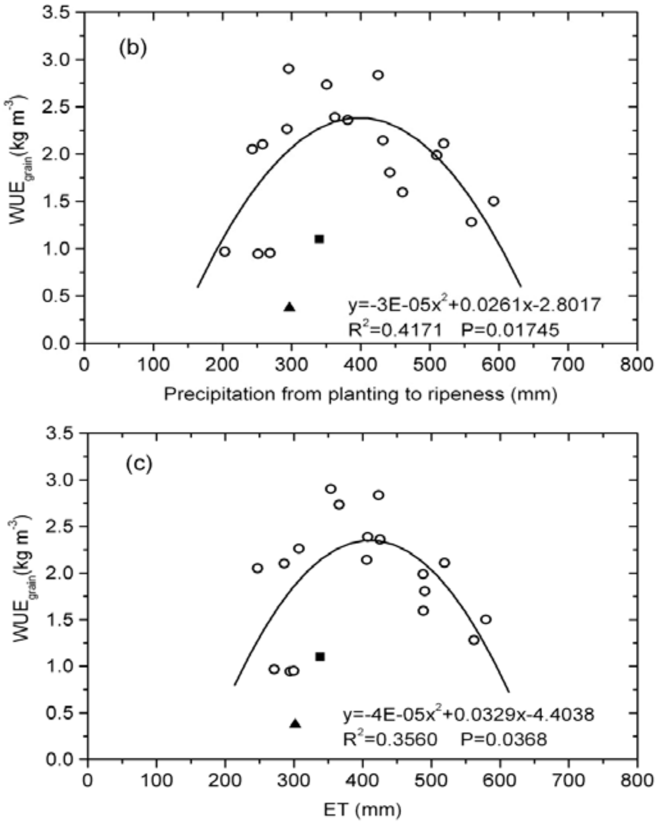

Figure 4. Relationship between annual precipitation, precipitation from planting to ripeness, ET and water use efficiency at the level of maize yield (WUE_{grain}) at the Chaoyang site in Northeast China between 1990-2010. The solid triangle and square represent the years 2000 and 2002, respectively.

Analysis of the effect of ET on grain yield over the 20 years monitored showed a limited increase in grain yield when ET exceeded 400-450 mm (Figure 5). The WUE_{grain} also started to decrease after this critical rate of evapotranspiration (Figure 4c). The observation that both grain yield and WUE_{grain} achieved their maximum levels when ET was 400-450 mm suggests that 400-450 mm was an economical ET for spring maize in Chaoyang site of northeast China.

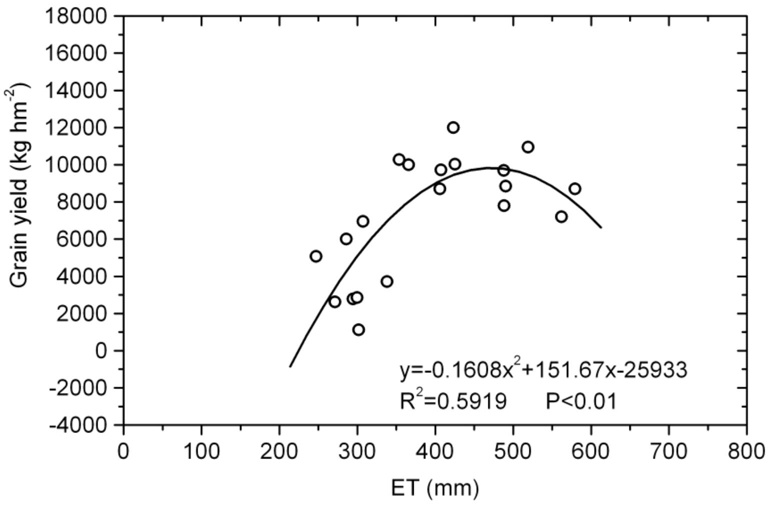

Figure 5. Relationship between grain yield and ET at the Chaoyang site in northeast China between 1990-2010.

Throughout the 20 years over which data was collected, since the relations between WUE_{grain} and temperature were not significant at the level of $P<0.05$, the variations of WUE_{grain} of maize showed no obvious relationship with temperature (Figure 6).

Soybean

Soybean WUE_{grain} was negatively correlated with annual precipitation, ET as well as precipitation from planting to ripeness (Figure 7). The relationship was significant ($P<0.01$) when data during 1989 and 2010 were excluded.

Soybean WUE_{grain} was positively correlated with annual temperature as well as mean temperature from planting to ripeness and the relationship was significant ($P<0.05$) when data during 1989 and 2010 were excluded (Figure 8).

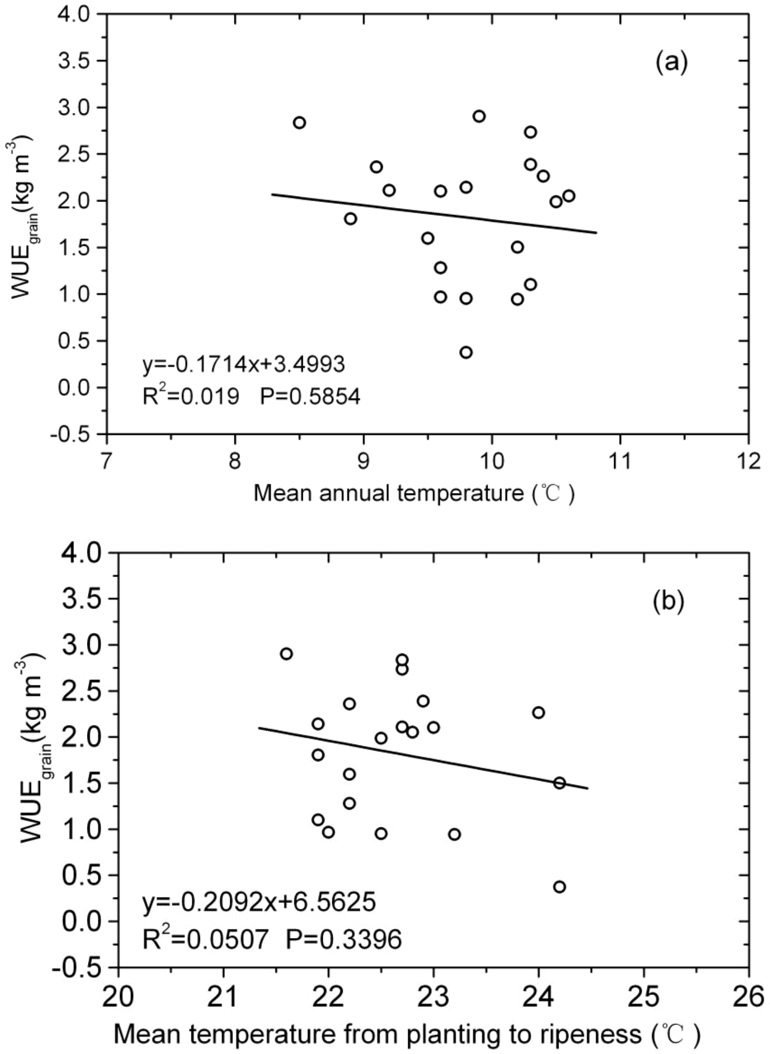

Figure 6. Variations in water use efficiency at the level of maize yield (WUE_{grain}) with changes in mean annual temperature and mean temperature from the time of planting to the time of ripeness.

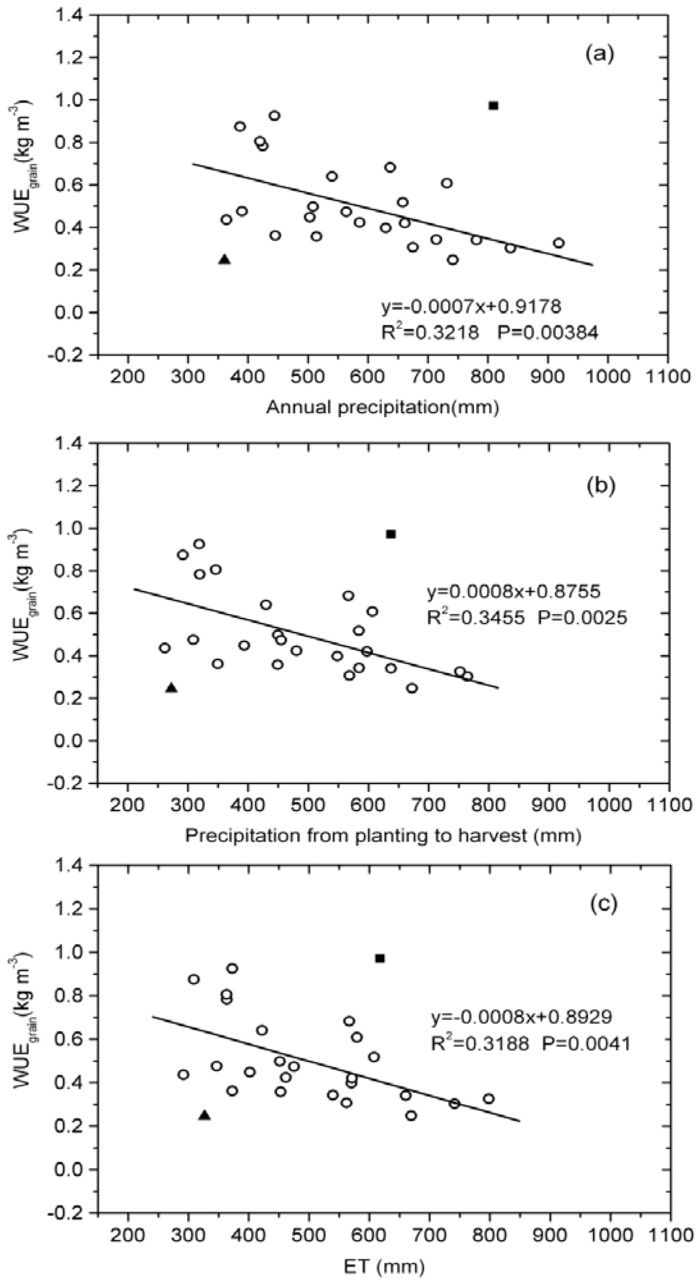

Figure 7. Relationship between annual precipitation, precipitation from planting to ripeness, ET and water use efficiency at the level of soybean yield (WUE_{grain}) at the Jinzhou site in Northeast China between 1985-2010. The solid triangles and squares represent the years 1989 and 2010, respectively.

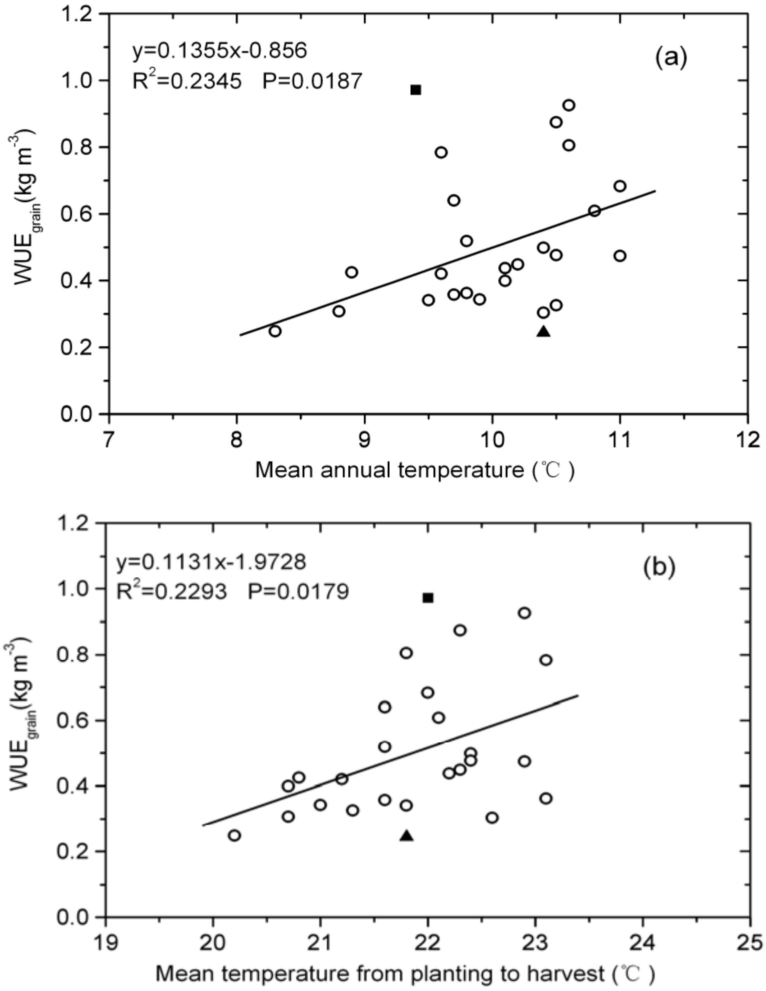

Figure 8. Variations in soybean water use efficiency at the level of yield (WUE_{grain}) with differences in mean annual temperature and mean temperature from planting to ripeness. The solid triangle and square represent the years 1989 and 2010, respectively.

Discussion

The effects of climatic variables and CO_2 concentration on WUE

The WUE_{grain} parameter is widely used in agricultural research (Qiu et al., 2008; Karam et al., 2005; Du et al., 2010). The overall mean WUE_{grain} (1.0-2.9 kg m^{-3}) of spring maize during the growing season in the southernmost territories of Northeast China observed in this study is consistent with that seen for summer maize planted in the North China Plain (1.6-2.3 kg m^{-3}, Guo et al., 2010) and with spring maize planted in northwest China (1.1-2.9 kg m^{-3}, Du et al., 2010). The WUE_{grain} (0.31-0.92 kg m^{-3}) of soybean observed in this study exceeds that reported for soybean grown in Lebanon (0.39-0.54 kg m^{-3}, Karam et al., 2005).

As observed in previous studies (e.g., Katerji et al., 2008; Mo et al., 2009), maize (a C_4 species) is characterized by larger average WUE_{grain} and WUE_{leaf} values than those observed for the C_3 species soybean (Figure 3, Figure 4 and Figure 7). These differences are explained by the relationship between photosynthesis and stomatal conductance realized on the leaf scale, and they are specific for each species. They can also be explained by seed composition: corn contains starch essentially, while soybean contains 16% oil and 35% protein. The biosynthesis of lipids and protein is more expensive than starch (Katerji et al., 2008).

Any analysis of the effects of environmental modification on WUE should discriminate between the effects related to ambient CO_2 concentrations, temperature, and water resources, as well as the interaction of these parameters in the context of agriculture. As reported previously (Rogers et al., 1983; Amthor, 1995; Kimball et al., 2002), this study revealed that elevated CO_2 has the potential to enhance plant WUE in plants with either C_3 or C_4 photosynthetic systems. This increase in WUE associated with elevated CO_2 content is largely attributed to decreases in stomatal conductance and transpiration (Woodward, 1992; Ghannoum et al., 2001; Prior et al., 2010; Chun et al., 2011). In C_3 plants, both increased photosynthesis and reduced transpiration contribute to increased WUE (e.g., Figure 3b, 3d and 3f), whereas decreased transpiration accounts primarily for any contribution seen in C_4 plants (e.g. Figure 3a, 3c and 3e) (Rogers and Dahlman, 1993). Under conditions of both water deprivation and an adequate supply of water, approximately 13-35% less water was used under conditions of elevated CO_2 than under the ambient CO_2 conditions. This suggests that under the increased CO_2 concentrations generally predicted for the future, maize plants will require less water than they do today (Chun et al., 2011).

When annual precipitation was less than 530 mm, any increase in precipitation increased maize WUE_{grain} (Figure 4a). There is no obvious relationship between WUE_{grain} and temperature (Figure 6), which suggests that water is the most important limiting factor for WUE of maize grown at our experimental site. The WUE_{grain} started to decrease after the precipitation exceeded 530 mm. Although few studies have investigated the response of maize WUE_{grain} to precipitation, a deficit irrigation study concluded that 450 mm was an economical ET for spring maize in northwest China, enabling WUE_{grain} values as high as 2.9 kg m^{-3} (Du et al., 2010). Our results are consistent with this conclusion. In present study, WUE_{grain} was peaked when levels of precipitation were 500-550 mm and the growing season ET was about 400-450 mm (Figure 4a and 4c).

For soybean, more water often reduces WUE_{grain} owing to the fact that an increase in precipitation has little effect on grain yield of soybean, whereas it increases ET. The linear relationship between ET and precipitation was significant at the level of $P<0.01$ (Figure 9). For soybean, increases in WUE_{grain} were positively correlated with increases in annual temperature, apparently owing to the fact that the grain yield of soybean increases with mean annual temperature and that there is no obvious relationship between ET and temperature (Figure 10). Katerji (2008) concluded that an increase in temperature modified WUE both by (i) reducing the crop cycle, which reduces water consumption (Perarnaud et al., 2002), and (ii) increasing daily rates of evapotranspiration, owing to the increase in vapor pressure deficit as a result of the increase in temperature (Ragab, 2003). In this study, based on a long term (26 years) investigation, with the increases of mean annual temperature the reducing water consumption and increasing daily rates of ET seems counteract and increasing grain yield become a determinant of WUE_{grain}.

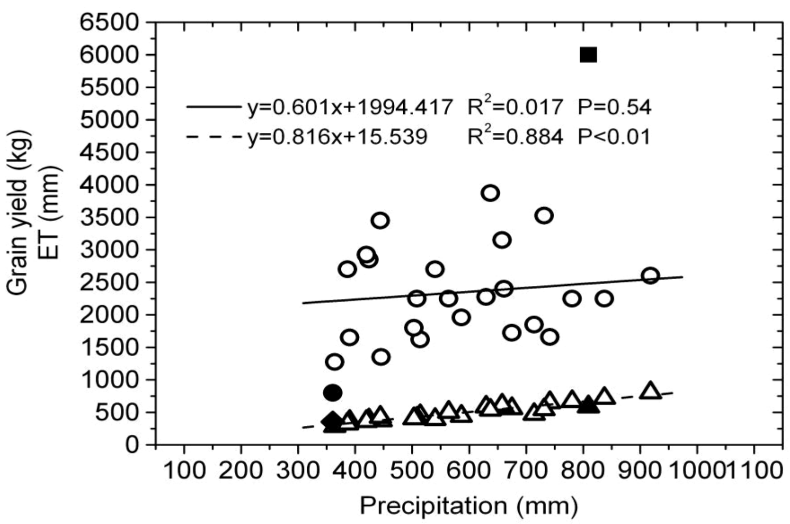

Figure 9. Relationships between grain yield, ET and precipitation of soybean at the Jinzhou site in northeast China between 1985-2010. Quadrate and triangle points represent grain yield and ET during 2010. Circular and rhombic points represent grain yield and ET during 1989.

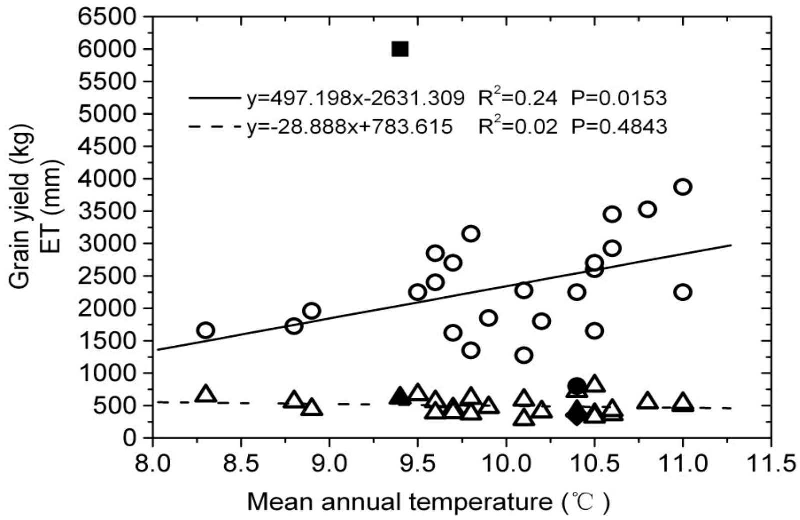

Figure 10. Relationships between grain yield, ET and mean annual temperature of soybean at the Jinzhou site in northeast China between 1985-2010. Quadrate and triangle points represent grain yield and ET during 2010. Circular and rhombic points represent grain yield and ET during 1989.

WUE at different scales responds differently to environmental variables

In this study, we examined WUE of maize and soybean and their responses to environmental variables. Our results showed that for maize (a C_4 species), a more extensive increase in rates of transpiration relative to increases in rates of photosynthesis (Figures 1 and 2) resulted in decreased WUE_{leaf} under conditions of elevated soil moisture and temperature. The reason why the WUE_{leaf} value primarily reflects stomatal regulation of leaf photosynthesis and transpiration and their response to environmental variables is that WUE_{leaf} reflects near instantaneous variables that describe the behavior of single leaves (Hsiao, 1993). Similar conclusions that WUE_{leaf} generally decreased with increased frequency of irrigation were obtained for wheat (Qiu et al., 2008) and soybean (Chen et al., 1993; Liu et al., 2005), both of which are C_3 species. Our results showed that the response of WUE_{grain} to precipitation was dramatically different from the response of WUE_{leaf} to soil moisture (Figures 1 and 4). WUE_{grain} usually shows little relation to WUE_{leaf}, since WUE_{grain} differed from WUE_{leaf} not only by the night respiration, but also by the fact that WUE_{grain} was dependent on the partitioning of carbon between plant organs (Hsiao, 1993).

Both WUE_{grain} and $WUE_{biomass}$ can describe the long-term behavior of a plant population, with WUE_{grain} being a function of $WUE_{biomass}$ over the life of the crop. The results of Qiu et al. (2008) indicated that higher seasonal $WUE_{biomass}$ of winter wheat could contribute to higher WUE_{grain}, which ultimately contributed to an increased final yield. Based on the data collected for maize over a 10-year period, WUE_{grain} showed no obvious relationship with seasonal $WUE_{biomass}$ (Figure 11) and this result needs verification by long-term observation across geographical sites.

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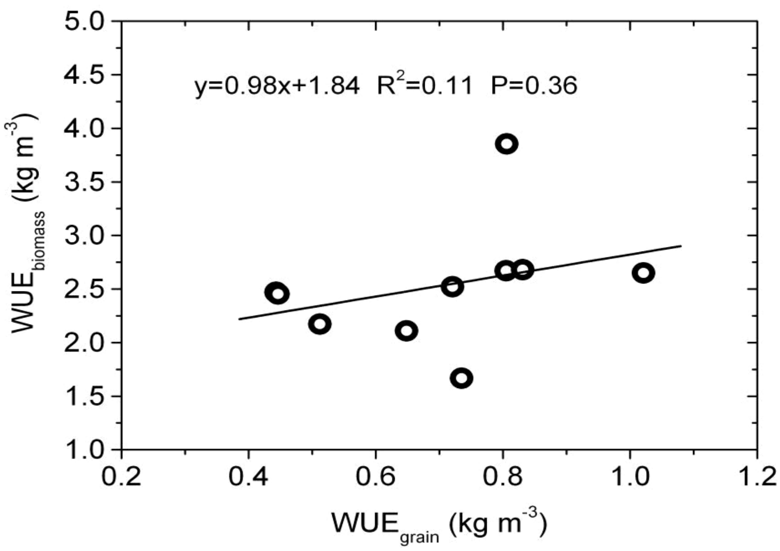

Figure 11. Relationship between WUE at the levels of grain yield (WUE_{grain}, kg m^{-3}) and biomass ($WUE_{biomass}$, kg m^{-3}) for maize.

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