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Spatio-temporal variation in transpiration responses of maize plants to vapor pressure deficit under an arid climatic condition

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Abstract: The transpiration rate of plant is physically controlled by the magnitude of the vapor pressure deficit (VPD) and stomatal conductance. A limited-transpiration trait has been reported for many crop species in different environments, including Maize (*Zea mays* L.). This trait results in restricted transpiration rate under high VPD, and can potentially conserve soil water and thus decrease soil water deficit. However, such a restriction on transpiration rate has never been explored in maize under arid climatic conditions in northwestern China. The objective of this study was to examine the transpiration rate of field-grown maize under well-watered conditions in an arid area at both leaf and whole plant levels, and therefore to investigate how transpiration rate responding to the ambient VPD at different spatial and temporal scales. The transpiration rates of maize at leaf and plant scales were measured independently using a gas exchange system and sapflow instrument, respectively. Results showed significant variations in transpiration responses of maize to VPD among different spatio-temporal scales. A two-phase transpiration response was observed at leaf level with a threshold of 3.5 kPa while at the whole plant level, the daytime transpiration rate was positively associated with VPD across all measurement data, as was nighttime transpiration response to VPD at both leaf and whole plant level, which showed no definable threshold vapor pressure deficit, above which transpiration rate was restricted. With regard to temporal scale, transpiration was most responsive to VPD at a daily scale, moderately responsive at a half-hourly scale, and least responsive at an instantaneous scale. A similar breakpoint (about 3.0 kPa) in response of the instantaneous leaf stomatal conductance and hourly canopy bulk conductance to VPD were also observed. At a daily scale, the maximum canopy bulk conductance occurred at a VPD about 1.7 kPa. Generally, the responsiveness of stomatal conductance to VPD at the canopy scale was lower than that at leaf scale. These results indicate a temporal and spatial heterogeneity in how maize transpiration responses to VPD under arid climatic conditions. This could allow a better assessment of the possible benefits of using the maximum transpiration trait to improve maize drought tolerance in arid environment, and allow a better prediction of plant transpiration which underpin empirical models for stomatal conductance at different spatio-temporal scales in the arid climatic conditions.

Keywords: maize; limited transpiration trait; gas exchange; sap flow; stomatal conductance; vapor pressure deficit

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Agriculture heavily relies on irrigation in the Heixi Corridor area of northwest China (Ji et al., 2006; Kang et al., 2007). Maize is the most important component of local food security. Current agricultural irrigation practices do not promote the sustainable utilization of water resources or the preservation of natural ecosystems in the area (Ji et al., 2006, 2011a). With the prospects of increasing global temperatures and water scarcity in arid regions, efficient agricultural water use is critical (Jones and Thornto 2003; Zhang et al., 2012). Plant characteristics such as enhanced drought tolerance and efficient water use could improve crop productivity (Riar et al., 2015).

One of the key traits to improve maize drought tolerance is to limit transpiration rate under high atmospheric vapor pressure deficit (VPD), which allows a better soil water conservation (Sinclair et al., 2005; Passioura and Angus, 2010; Riar et al., 2015). However, such a restriction on transpiration rate at high VPDs and different spatio-temporal scales has not been documented in maize, especially in arid regions where water is limited; plants and resources that human rely on are scarce, which is a situation commonly found in the arid northwestern China (Chen et al., 2012).

Transpiration through higher-plant stomata is governed by the magnitude of the atmospheric VPD, and by the leaf stomatal conductance (McNaughton and Jarvis, 1991; Jones, 1998; Taiz and Zeiger, 2002). In general, transpiration rates and VPD follow a diurnal pattern, being lowest at sunrise and increasing to maximum around midday (Bunce, 1981; Jarvis and McNaughton, 1986; Jones, 1998; Hirasawa and Hsiao, 1999; Shekoofa et al., 2014). However, the increase of transpiration has limits with a limiting maximum transpiration rate commonly reached at a higher VPD (Grantz, 1990; Franks et al., 1997; Fletcher et al., 2007). The hypothesized mechanism for the limited-transpiration trait is a leaf level hydraulic limitation that results in limited water transport and decreased stomatal conductance at high VPDs (Mott, 2007; Sinclair et al., 2008; Sadok and Sinclair, 2009; Choudhary et al., 2015; Riar et al., 2015). Such limited-transpiration trait at high VPD tends to restrict the photosynthetic rate, thus to increase transpiration efficiency (or water use efficiency), to delay damaging physiological effects of water deficit stress in plant tissues, and to conserve soil water (Sinclair et al., 2005; Yang et al., 2012; Seversike et al., 2013; Shekoofa et al., 2014).

Considerable evidences have confirmed this limited-transpiration trait, even under well-watered conditions in selected genotypes of several crop species including peanut (*Arachis hypogaea* L., Devi et al., 2010; Shekoofa et al., 2013), sorghum (*Sorghum bicolor* L., Sinclair et al., 2005; Gholipoor et al., 2010; Shekoofa et al., 2014; Riar et al., 2015), soybean (*Glycine max* L., Fletcher et al., 2007; Sinclair et al., 2008; Sadok and Sinclair, 2009; Gilbert et al., 2011; Seversike et al., 2013), pear millet (*Pennisetum glaucum* L., Kholová et al., 2010), wheat (*Triticum aestivum* L., Rebetzke et al., 2003), and cowpea (*Vigna unguiculata* L., Belko et al., 2013).

Similarly the limited-transpiration trait in response to increasing VPD has been identified in maize. Hirasawa and Hsiao (1999) reported that when VPD was greater than about 3.5 kPa, the epidermal conductance of field-grown maize decreased, possibly in association with a maximum transpiration rate. In pot-grown maize subjected to differing VPD conditions, Ray et al. (2002) found that increase in VPD were not matched by proportional increase in transpiration of young maize plants, indicating essentially a maximum transpiration rate was reached under high VPD conditions. Gholipoor et al. (2013) showed that some maize genotypes exhibited a VPD threshold ranged from 1.7 to 2.5 kPa, above which the transpiration rate was restricted. Comparable findings were observed in similar maize genotypic hybrids (Yang et al., 2012; Choudhary et al., 2015).

The limited-transpiration trait at high VPD could result from the stomata sensing and responding to changes in transpiration, i.e. stomatal closure in response to increased transpiration could be a form of negative feedback that optimizes the rate of photosynthesis (Farquhar, 1978; Mott and Parkhurst, 1991; Monteith, 1995; Bunce, 1996; Jones, 1998; Taiz and Zeiger, 2002). However, multiple mutual influences and feedbacks cause interactions among transpiration, stomatal conductance, and the ambient VPD to be complex and non-linear (Jarvis and McNaughton, 1986; McNaughton and Jarvis, 1991; Jones, 1998). Consequently, the transpiration response varies greatly, both among and within species, in response to a wide variety of environmental variables and across different spatio-temporal scales (Jarvis and McNaughton, 1986; McNaughton and Jarvis, 1991; Oren et al., 1999; Bucci et al., 2004; Barbour and Buckley, 2007; Sinclair et al., 2008; Sadok and

Sinclair, 2009; Mott and Peak, 2010; Gilbert et al., 2011). To demonstrate the interaction of VPD and stomatal conductance in regulating transpiration, it is desirable to measure gas exchange and driving forces simultaneously at both the single leaf and whole plant levels of inquiry (Jarvis and McNaughton, 1986; Collatz et al., 1991; Jones, 1998; Takagi et al., 1998).

The primary objective of the study was to understand the gap in our current understanding of the limited transpiration trait of maize, including the transpiration rate of field-grown maize under well-watered conditions both at the leaf and whole plant level; and to investigate the differences in transpiration responses to ambient VPD at different spatial and temporal scales. This could allow a better assessment of the possible benefits of using the maximum transpiration trait to improve maize drought tolerance in arid environment, and will be of interest to physiologists, plant breeders and water resources managers. This is also important for predicting the plant transpiration by water resources managers, especially for underpinning empirical models for stomatal conductance at different spatio-temporal   scales in arid climatic conditions.

1 Materials and methods

1.1 Site description

The study site is located in the middle section of Hexi Corridor, Gansu province, northwestern China. We made all field measurements at the agricultural experimental field of the Linze Inland River Basin Research Station (39°19′38″N, 100°08′27″E; 1,365 m asl), Chinese Ecosystem Research Network. The site has a typical continental arid climate, dry and hot in summer, cold in winter. The mean annual precipitation is 117 mm, of which 70% falls in July to September. The annual mean air temperature is 7.6°C, with a maximum of 39.1°C in July and a minimum of −27.3°C in January. The soil is sandy loam with 59.0% of sand, 36.3% of silt and 4.7% of clay. Soil organic matter content and pH are 0.72% and 8.86, respectively. The detailed information about the site was presented in Ji et al. (2011a, b).

We conducted the study in a maize field (*Zea mays* L.) planted on 10 April 2011 in 0.45-m row-spacing with a density of about 98,000 plants/hm^2. Throughout the maize growing season, we applied nine flood irrigations for a total of about 1,000 mm of water (approximately 105 mm of water for each irrigation) and fertilized at a rate of 326 kg N/hm^2, 27 kg P_2O_5/hm^2, and 17 kg K/hm^2, respectively. Thus, crop development throughout the growing season did not suffer from nutrient and/or water stresses, but maintained under well-watered conditions.

1.2 Methods and measurement

1.2.1 Meteorological measurements

On a tower (20-m height, six-layer array) within the maize field, we mounted an automatic weather station (IMKO GmbH, Ettlingen, Germany) that continually measured and recorded the 30-minute means of solar radiation, net radiation, air temperature/humidity, air vapor pressure, canopy temperature, wind speed and direction, soil heat flux, soil moisture and temperature, and precipitation throughout the growing season.

1.2.2 Leaf transpiration and stomatal conductance measurements

We simultaneously measured the diurnal (24 h) values of leaf-level stomatal conductance and transpiration in the field on two sunny (daytime) and clear (nighttime) days (Julian days 188–189 and 218–219) using a portable steady-state gas exchange apparatus (Li-6400 XP, LI-COR Instruments, Lincoln, NE, USA) at approximately hourly intervals on fully expanded leaves. Before the measurement, we enclosed a 6-cm^2 area of leaf lamina in the instrument chamber and allowed it to equilibrate within the chamber for 60 s and repeated the measurement for three times. We randomly sampled four leaves from the top, middle and bottom layers of the canopy with 12 observations at each sampling time and then averaged the values to estimate the mean instantaneous leaf conductance and transpiration for each sample at a given time. We maintained the natural inclination and azimuth of the leaves during the measurements. Sampling was always done in the central row of five consecutive rows to avoid any border effect. We took all measurements under

ambient conditions and recorded the photosynthetically active radiation, leaf temperature, and relative humidity incident on each leaf. Our measurements at leaf scale were taken at 1-h intervals for 24 hours, from morning (as soon as the foliage was entirely dry) until next morning.

1.2.3 Whole plant transpiration measurements

We measured whole plant transpiration on six representative plants using the stem heat balance approach (Sakuratani, 1981; Baker and Van Bavel, 1987) during the period from Julian days 189 to 252, when maize was entering the peak growth, and the soil surface was fully covered by the maize canopy. We installed sap flow gauges (Models SGB 16, SGB 19 and SGB 25, Dynagage, Dynamax Inc., Houston, TX, USA) and graphed the data to confirm that the temperature differences measured by the gauges remained within reasonable bounds.

1.2.4 Determination of vapor pressure deficit

Vapor pressure deficit (VPD) was calculated using air temperature and relative humidity was measured using the following equation:

$$VPD = \left(1 - \frac{RH}{100}\right)SVP \tag{1}$$

where RH is the relative air humidity (%). The saturation vapor pressure SVP (kPa) is calculated from eq. 2,

$$SVP = 0.6108\exp\left(\frac{17.27T_a}{T_a + 237.3}\right) \tag{2}$$

where T_a is the air temperature (°C).

At the leaf level, we measured the leaf surface air temperature and humidity with LI-6400 XT gas exchange apparatus; for the whole plant/canopy level, we measured the canopy air temperature and the relative canopy air humidity with the HMP45D sensors (Vaisala, Helsinki, Finland) of the IMKO automatic weather station.

1.2.5 Determination of canopy bulk stomatal conductance

We calculated the canopy bulk stomatal conductance (G_c) from micrometeorological and sap flow data using inversion of the Penman-Monteith equation (Monteith and Unsworth, 1990; eq. 3),

$$G_c = \frac{\lambda ET \cdot \gamma \cdot G_a}{\Delta\left(R_n - S\right) + \rho_a C_p VPD \cdot G_a - \left(\Delta + \gamma\right) \cdot \lambda ET} \tag{3}$$

where λ is the latent heat of vaporization of water (MJ/kg); ET is canopy transpiration (mm/s); γ is psychrometer constant (kPa/K); G_a is the aerodynamic conductance (mm/s); Δ is gradient of the water saturation vapor pressure curve (kPa/K); R_n is net radiation (W/m^2); S is soil heat flux (W/m^2); ρ_a is the air density (kg/m^3); and C_p is the specific heat of dry air at constant pressure (MJ/(kg·K)). Assuming neutral stability conditions, G_a can be computed as eq. 4,

$$G_a = \frac{k^2 u}{\ln\left(\left(z - d\right)/\left(h_c - d\right)\right)\ln\left(\left(z - d\right)/z_0\right)} \tag{4}$$

where k is the von Karman constant (0.41); z is the reference height (m); u is the wind speed at the reference height (m/s); h_c is the mean crop height (m); d is the zero plane displacement (m), approximated as 0.67 h_c; and z_0 is the roughness length of the crop relative to momentum transfer (m), approximated as 0.13 h_c.

2   Results

2.1   Seasonal variations in environmental variables

Seasonal variations in the main atmospheric and soil environmental conditions during the period of sap flow measurements are shown in Fig. 1. Solar radiation (R_n) was very high, with a half-hourly maximum value of 941.3 W/m^2 and daily average of 138.8 W/m^2 (Fig. 1a). The daily mean air temperature (T_a) was 21.3°C, and ranged from 14.8 to 27.4°C (Fig. 1b). The relative humidity

(*RH*) ranged from 10.9% to 95.7% with a mean value of 59.7% (Fig. 1c), and was strongly influenced by the precipitation and irrigation events. The mean wind velocity (*u*) was 1.35 m/s and usually under 5 m/s (Fig. 1d). Soil moisture (*θ*) (within the upper 50 cm of soil) varied considerably (ranged from 0.21 to 0.37 m^3/m^3) throughout the measurement period (Fig. 1e), responding to irrigation events. Throughout the measurement sap flow period (Julian days 189 to 252), however, we maintained well-watered conditions for the maize. Total precipitation for the measurement period was 13 mm (three rainfall events). During the measurement period, we irrigated the field three times with a total of about 315 mm.
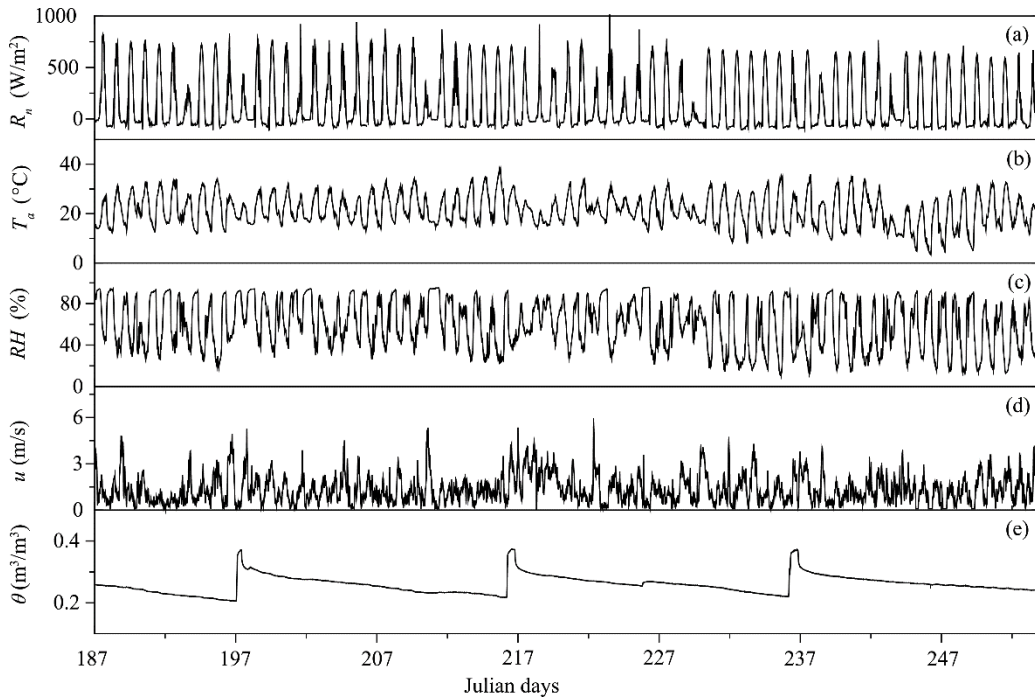

Fig. 1 Half-hourly time series of net radiation (R_n; a), air temperature (T_a; b), relative humidity (*RH*; c), wind speed(*u*; d), and soil moisture (*θ*; e) during the measurement period

2.2 Diurnal patterns of transpiration at leaf scale

Diurnal time courses of transpiration (T_1) and leaf-to-air VPD from the gas exchange apparatus at the leaf level on Julian days 188–189 and 218–219 are presented in Figs. 2a and b, respectively.
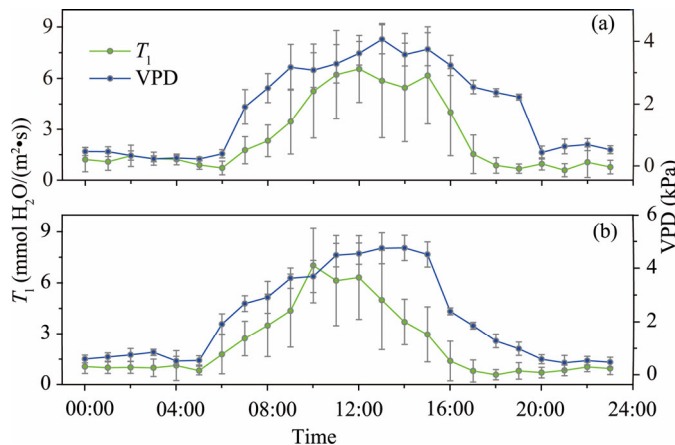

Fig. 2 Averaged diurnal course of transpiration T_1 and leaf-to-air vapor pressure deficit (VPD) at leaf level on Julian days of 188–189 (a) and 218–219 (b). Error bars represent the standard deviation of replicate measurements on different leaves.

The average hourly leaf transpiration rate and VPD exhibited a similar daily patterns, being lowest at sunrise and increasing to a maximum at around 12:00 (local time, hereinafter referred to as same). Gas exchange measurements at leaf level, however, indicate a temporal lag between transpiration and VPD, suggesting that stomata regulate transpiration to some extent at higher VPD in the daytime, and weak midday stomatal closure (at higher VPD) seems to have occurred on both measurements.

Moreover, the magnitude of transpiration occurring during the nocturnal hours (20:00−06:00) remained relatively stable throughout the nighttime, and was considerably lower than that during the daytime (06:00−20:00). The mean nighttime transpiration rate (0.99±0.44 mmol H_2O/(m^2·s)) was about 27% of the daytime rate (3.71±1.78 mmol H_2O/(m^2·s)). This can be partly explained by the evidence that the nighttime VPD (0.56±0.17 kPa) was much lower than the daytime VPD (3.18±0.40 kPa).

2.3   Diurnal patterns of whole plant transpiration

Figure 3 shows the average half-hourly diurnal patterns of whole plant transpiration rate (J_s) from sap flow measurement (i.e., averaged across the sampled six plants±one standard deviation) (Fig. 3a) and air VPD (Fig. 3b) at the top canopy during the measured period from Julian day 189−252. J_s in maize and the ambient VPD had distinct diurnal variations which were triggered mainly by solar radiation (greater solar radiation resulting in higher VPD and greater J_s). However, the diurnal VPD trend lagged clearly behind J_s by about 2 h. For example, J_s increased gradually after 06:00, peaked (75.21±24.90 g/h) at about 11:30, then gradually decreased until 18:30, and stabilized over night from about 19:00 to 06:00 next day; in contrast, VPD peaked (2.74±1.02 kPa) at about 14:00, decreased linearly until 18:00, and then gradually dropped to its lowest level (0.32±0.25 kPa) before predawn (at about 05:00) next day.
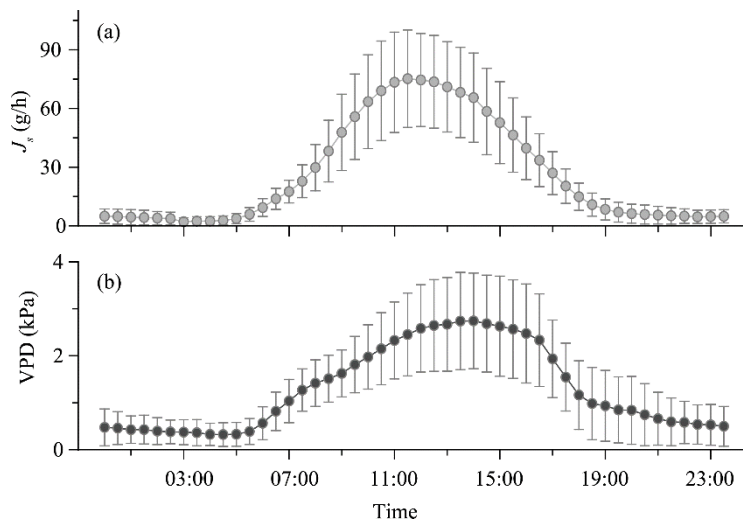

Fig. 3   Averaged diurnal course of whole plant transpiration rate (J_s; a) and vapor pressure deficit (VPD) at the top of canopy (b) during the observed period from Julian days 189 to 252. Error bars represent the standard deviation of replicate measurements on different leaves.

Whole plant transpiration rate (J_s) was generally much lower at night (mean value of 4.66±3.60 g/h), only about 10% of the values during the daytime (45.12±16.67 g/h), but the magnitude of cumulated transpiration at night was not trivial (about 0.5 mm in height), exceeded 8% of the daytime value. The corresponding nighttime VPD averaged 0.52±0.41 kPa and was approximately 27% of the daytime value (1.95±0.77 kPa).

2. 4   Responses of daytime transpiration and stomatal conductance to VPD

We analyzed the daytime data by plotting the instantaneous transpiration/stomatal conductance against leaf-to-air VPD at the leaf level for both measurements and found that the response of leaf

transpiration (T_{ld}) to increasing leaf-to-air VPD could be described as two linear regressions, indicating a significant positive response of T_{ld} to VPD (R^2=0.51; P<0.05) at lower VPD (<3.5 kPa) (Fig. 4a) and a negative response at higher values (≥3.5 kPa) (Fig. 4b). The transition point (the limiting maximum transpiration rate reached at a VPD of 3.5 kPa) divided the response of T_{ld} to VPD into two distinct groups, suggesting that, to a large extent, the 'patchy' stomatal closure (i.e. feedforward response) (Farquhar, 1978; Bunce, 1996) appeared when leaf-to-air VPD was greater than about 3.5 kPa. This conclusion is consistent with the leaf level observations of Hirasawa and Hsiao (1999), and Ray et al. (2002).
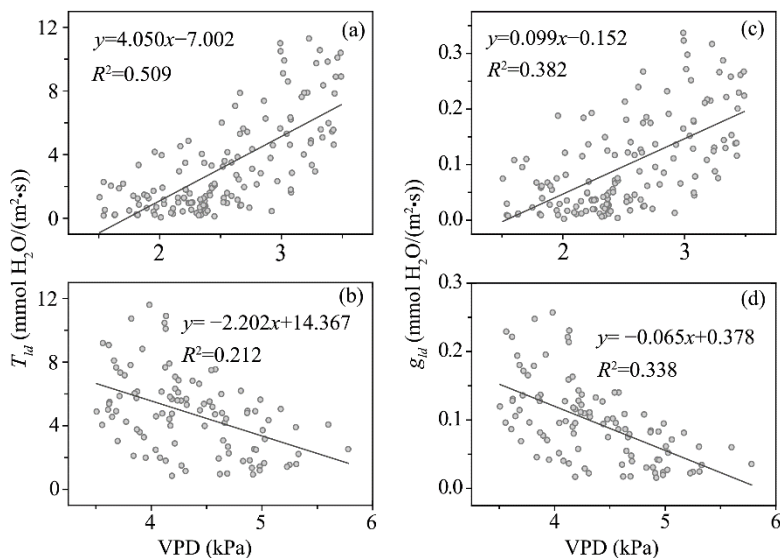

Fig. 4   Daytime leaf transpiration rates (T_{ld}; a, b) and stomatal conductance (g_{ld}; c, d) of maize in response to leaf-to-air VPD when VPD was below 3.5 kPa (a, c), and above 3.5 kPa (b, d), respectively

The data from the gas exchange apparatus measurements also showed that the response of leaf stomatal conductance (g_{ld}) to leaf-to-air VPD was consistent with transpiration response observed during the daytime, the T_{ld} and g_{ld} both increased linearly as VPD increased at values lower than approximately 3.5 kPa (Fig. 4c), and by contrast, both decreased as VPD increased at higher values (≥3.5 kPa) (Fig. 4d). The similar responses of T_{ld} and g_{ld} to VPD further demonstrated that the traditional evidence of a 'feedforward' response worked properly through stomatal regulation, in which transpiration and stomatal conductance decreases with increasing VPD (Farquhar, 1978; Bunce, 1996).

In comparison with the transpiration to VPD at leaf level, however, we observed a strong and significant positive linear relationship (R^2=0.765; P<0.05) between whole plant transpiration (J_{sd}) and air VPD across a wide range throughout the daytime (Fig. 5a). There was no statistical transition point of transpiration response to VPD. Moreover, there was no statistically significant
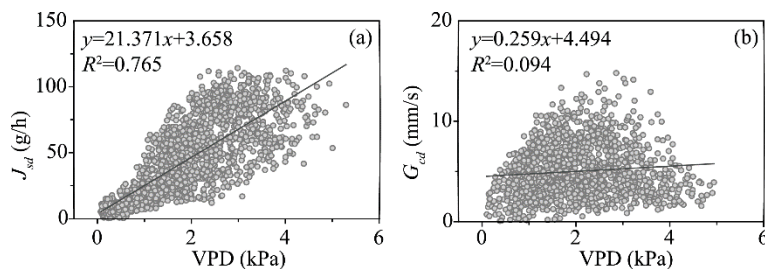

Fig. 5   Daytime half-hourly whole plant transpiration rates (J_{sd}; a) and canopy bulk stomatal conductance (G_{cd}; b) of maize in response to air VPD at top of canopy

relationship between canopy conductance (G_{cd}) and VPD (Fig. 5b). It is important to note, however, that a limiting maximum G_{cd} was commonly reached at a VPD of about 3.0 kPa, above which there was a general trend of decreased daytime G_{cd} with increased VPD (Fig. 5b). The evidences showed that whole plant transpiration was more responsive to VPD, and conversely, the corresponding G_{cd} was relatively unresponsive to changes in VPD, indicating that the canopy transpiration was strongly VPD-dependent, although other limiting factors (environmental and physiological) played a significant role in J_{sd} (Bunce, 1996), in conjunction with stomata regulation.

2.5   Responses of nighttime transpiration and stomatal conductance to VPD

We investigated the role of VPD in driving nighttime maize transpiration at both leaf (T_{ln}) and whole plant (J_{sn}) levels. The information presented here clearly demonstrates that nighttime leaf transpiration (Fig. 6a) was more responsive to leaf-to-air VPD than daytime leaf transpiration (Fig. 4a). Changes in VPD can explain about 69% and 64%, respectively, of the nighttime variations in transpiration at the leaf (Fig. 6a) and whole plant levels (Fig. 7a).
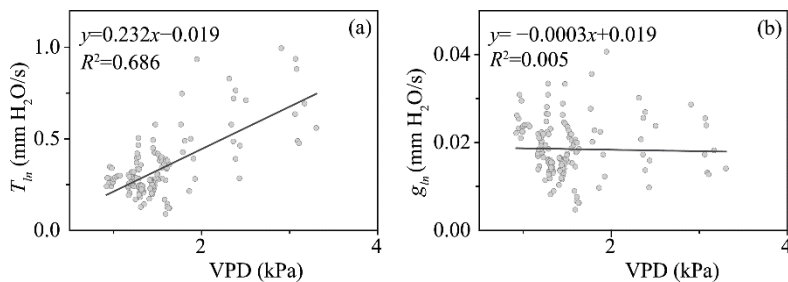

Fig. 6   Nighttime leaf transpiration rates (T_{ln}; a) and leaf stomatal conductance (g_{ln}; b) of maize in response to leaf-to-air VPD

We also found that stomatal conductance at both the leaf (g_{ln}) and canopy (G_{cn}) levels were quite insensitive to changes in VPD (Figs. 6a and 7b). Therefore, we can conclude that the nighttime transpiration of maize depends, to a large extent, on the driving vapor gradient between the leaf and the atmosphere (i.e. VPD), and that nighttime stomatal conductance scattered against VPD on both scales, which was probably associated with circadian rhythms (Barbour and Buckley, 2007) or boundary layer mixing (Collatz et al., 1991).
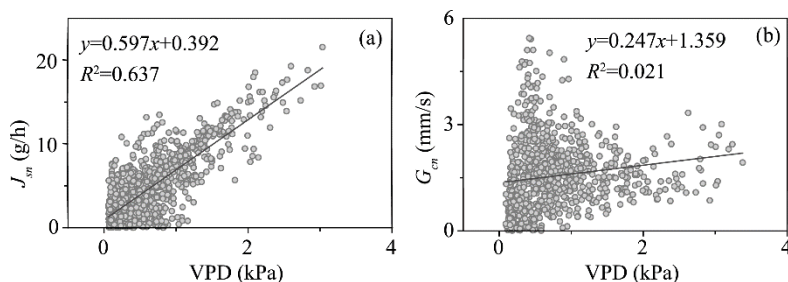

Fig. 7   Nighttime half-hourly whole plant transpiration rate (J_{sn}; a) and canopy bulk stomatal conductance (G_{cn}; b) of maize in response to air VPD

2.6   Responses of daily transpiration and canopy conductance to VPD

Over the long term (the period of sap flow measurement from Julian day 189 to 252), the averaged half-hourly whole plant transpiration (J_{sm}) from six sap flow measurements varied commonly in concordance with the fluctuation of air VPD (Fig. 8). The averaged half-hourly J_s varied from 8.45 to 43.00 g/h with a mean value of 25.73 g/h during the measurement period, whereas their corresponding air VPD ranged from about 0.45 to 2.55 kPa with a mean of about 1.26 kPa. The fluctuations of J_s and VPD are mainly attributed to lower solar radiation associated with rainfall events or cloudy days.
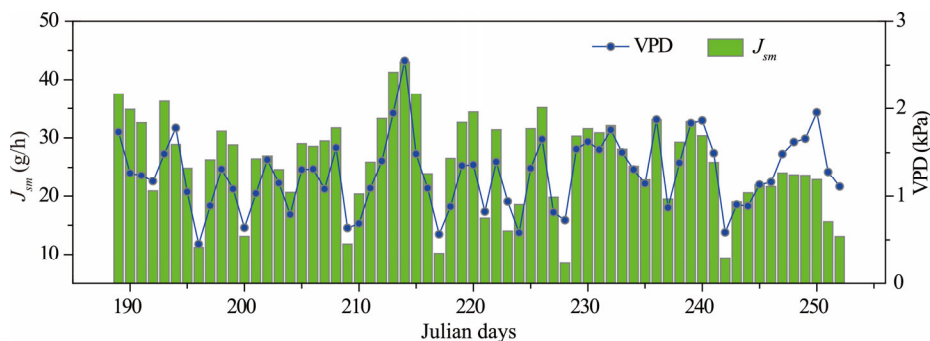
Fig. 8   Daily variations in average half-hourly whole plant transpiration rate (J_{sm}) and their corresponding air VPD

We analyzed the relationship between the daily average whole plant transpiration (J_{sm}) and mean daily VPD across the sap flow measurement periods. A strong and significant linear relationship ($R^2 \approx 0.78$; $P<0.05$) appeared between J_{sm} and VPD (Fig. 9a), suggesting that the J_{sm} was highly responsive to variation in VPD at a daily scale. In contrast, no linear relationship was found between daily canopy bulk conductance (G_{cm}) and VPD (Fig. 9b). However, there were two roughly distinguished trends for increased G_{cm} with increased *VPD* when VPD increased to about 1.7 kPa, and decreased G_{cm} with increased VPD when VPD was above 1.7 kPa. It is possible that that the negative feedbacks work by stomatal patchy closure at a daily scale when the mean daily VPD was higher than approximately 1.7 kPa.
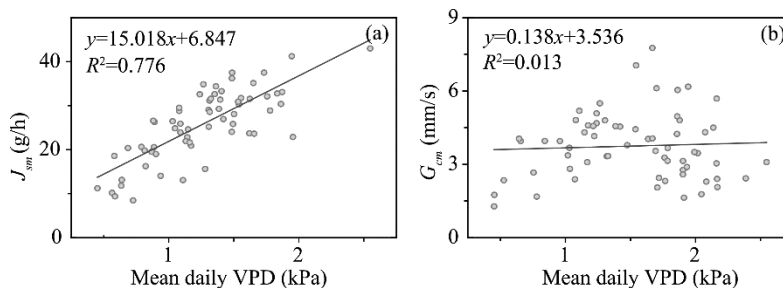

Fig. 9   Averaged daily transpiration (J_{sm}; a) and mean canopy bulk stomatal conductance (G_{cm}; b) in response to mean air VPD

3   Discussion

The rate of transpiration is governed by the magnitude of the vapor pressure deficit between the leaf and the surrounding air, and is also regulated by the leaf stomatal conductance (Jones, 1998; Taiz and Zeiger, 2002). A number of studies have shown that the response of plant transpiration to VPD falls into one of three categories (Grantz, 1990; Monteith, 1995; Franks et al., 1997; Oren et al., 1999; Fletcher et al., 2007; Mott and Peak, 2010; Shekoofa et al., 2014): at low VPD values, as VPD increases, stomatal conductance is high and transpiration increase; at intermediate VPD values, as VPD increases, transpiration remains relatively constant because stomatal conductance declines with increasing VPD; and at high VPD values, as VPD increases, stomatal conductance is more extreme and transpiration declines with increasing VPD. Furthermore, McNaughton and Jarvis (1991), and Mott and Peak (2010) demonstrated that increasing scale leads to an increase in the number of negative feedback paths that stabilize the system and diminish the sensitivity of transpiration to the changes in VPD.

The effects of spatial scale on VPD control of transpiration and the limited transpiration rate under a high VPD have been reported for maize under different environments (Hirasawa and Hsiao, 1999; Ray et al., 2002; Yang et al., 2012; Gholipoor et al., 2013; Choudhary et al., 2015), which were confirmed by our study that the response of maize transpiration to VPD differs considerably at different spatial and temporary levels under arid environmental climate and well-watered

conditions. At the leaf level, the maize plant exhibits a breakpoint (about 3.5 kPa) in the transpiration response to VPD. In contrast, there is no defined breakpoint at the whole plant level, indicating that the mechanism of the limited transpiration trait gradually vanishes at an increasing spatial scale under conditions that are not water-limited. We attributed these disparities in the transpiration responses to VPD at different spatial scales to two possible causes. First, the micrometeorological conditions (i.e. VPD, boundary layer mixing, etc.) in the leaf cuvette of LI-6400 gas exchange system differed generally from those in whole plant or canopy, resulting in variations in gas exchange properties between the leaf level and whole plant level under field conditions. Second, the individual leaves from canopy top to bottom were exposed to vastly different environmental conditions, which apparently triggered highly varied transpiration responses. With respect to temporal scales, the responsiveness of transpiration to VPD increased to some extent as the temporary scale was broadened. The reasons for this are similar to the variability in transpiration responses to VPD at different spatial scale.

It is noteworthy, however, that the maize also had a breakpoint in the stomatal conductance response to VPD at different spatial levels during the daytime, likely stemming from the discrepancies between the stomatal conductance and canopy conductance, and between leaf boundary-layer conductance and surface-layer conductance (Collatz et al., 1991; McNaughton and Jarvis, 1991; Monteith, 1995; Takagi et al., 1998; Mott, 2007; Yang et al., 2012; Choudhary et al., 2015). While during the period of nighttime, transpiration at night is theoretically controlled by atmospheric VPD and is free of stomatal conductance regulation (Jarvis and McNaughton, 1986; Jones, 1998). However, our results demonstrated there are nighttime stomatal conductance of maize was unresponsive to VPD across spatial and temporal scales. Also, nighttime stomatal conductance shifted decreasingly from small spatio-temporal level to large one, indicating the transpiration of maize under well-watered conditions can be limited by low stomatal conductance at high VPD. These results are similar to the findings of Barbour and Bucklay (2007) for *Ricinus communis* plant, but differ from the findings of Mott and Peak (2010) for *Tradescantia pallida* and Bucci et al. (2004) for tropical savanna woody species, mostly due to differences in the response of transpiration to VPD, or stomatal conductance to VPD for different species under different environment conditions.

The clear message from the above discussions is that the limited transpiration rate of the maize plant is spatio-temporal dependent because of the complex interactions among transpiration, stomatal conductance and the ambient VPD. These interactions are non-linear because of multiple mutual influences and feedback at different spatio-temporal scales (McNaughton and Jarvis, 1991; Jones, 1998). So we highly recommend that the effects of spatial and temporal scales on the response of transpiration to VPD must be taken into account to quantify the limited-transpiration trait of the maize plant at high VPD.

4   Conclusions

The maize transpiration at leaf, whole plant and canopy scales were measured independently *in situ* under arid climatic and well-watered conditions. The responses of transpiration to VPD at different temporal scales (i.e. instantaneous, half-hourly and daily scales) for different spatial scales were discussed. Our results demonstrate that the maize transpiration response to VPD is -dependent.

For spatial scale, the transpiration response to VPD shows an apparent breakpoint at approximately 3.5 kPa VPD, mostly due to partial stomatal closure at high VPD (negative feedback) in the daytime; while maize transpiration is not virtually restricted under high VPD at the whole plant level and canopy scales. However, the limiting canopy bulk stomatal conductance occurred at VPD values of approximately 3.0 kPa and 1.7 kPa at half-hourly and daily scales, respectively, although good correlation could not be established between the canopy conductance and VPD, indicating maize transpiration is controlled by stomatal conductance at high VPD under even well-watered conditions in the arid environments. The temporal responses of maize transpiration are similar to those at spatial scales.

In reality, the maize transpiration is linked to the combined influences of climate-driven variables that a crop may experience in the field and by stomatal regulation and a better understanding of the

mechanism of transpiration regulation is needed to account for the effect of spatio-temporal scales in practice. Our results provide an improved understanding of this phenomenon, which could assist physiologists, plant breeders and water resources managers to better take advantage of maize's transpiration restriction trait, and to better estimate plant transpiration using the empirical models for stomatal conductance at different spatio-temporal scales, and then in the effort to improve the understanding of the combined influences of VPD and stomatal regulation in arid environment. A restricted transpiration at high VPD may be linked to anatomical, physiological, or ecological features and these proximate controls deserve further studies.

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