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Effects of leaf wetting by dew on plant-water relations and gas exchange in dryland crop production

Doctor Thesis by

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Preface

Background

Water scarcity has become an evident concern in the last few decades because of the increased water consumption and the effects of climate change (IPCC, 2013; Mekonnen and Hoekstra, 2016). Drylands, which are the most vulnerable terrain to water scarcity, cover nearly half of the global land surface and are home to more than 38% of the global population (MEA, 2005). Water scarcity is a major limiting factor for agricultural production in drylands, and the risk of water scarcity is predicted to increase with climate change (Huang et al., 2017). Agriculture itself is the most water-intensive sector of society, making up approximately 85% of water consumption by people (Falkenmark and Rockström, 2004). Massive amounts of water are used for irrigation in drylands to compensate for the imbalance between the water supply from precipitation and evaporative demand. Further increases in irrigation are predicted to be required because of climate change (Fischer et al., 2007). Although irrigation improves the crop yield in drylands, the availability of irrigation water is limited. Thus, the water usage of dryland agriculture must be made more efficient.

Rain-fed and irrigated agriculture are the main forms of agriculture in arid and semiarid regions. Hence, rainfall or irrigation water has been regarded as the major or only water source for agricultural production. However, nonmetric water such as dew or fog has also been recognized as a significant water resource for plants in several ecosystems (Martin and von Willert, 2000; Limm et al., 2009; Tomaszkiewicz et al., 2016; Zhang et al., 2019). Particularly, dew occurs in many parts of the world, including arid and semiarid ecosystems (Vuollekoski et al., 2015). Although the importance of dew has been recognized, its significance as a water resource is often evaluated based on “amount,” which might underestimate its relevance since the amount of dew water is much smaller than that of conventional water resources (i.e., irrigation water and precipitation) (Zhang et al., 2015; Zhang et al., 2019). However, the goal of irrigation is to improve plant physiological functions (e.g., photosynthesis, transpiration, stomatal conductance, and water status) and ultimately increase yield. If dew could significantly improve plant physiological functions, dew can be an important water resource regardless of its amount. Therefore, the importance of dew as a water resource should also be evaluated based on its effects on plant physiological functions. In this study, with the combination of long-term field observation of leaf wetting by dew and laboratory experiments, effects of dew on plant physiological functions was comprehensively evaluated.

Summary of this thesis

In this thesis, I addressed a simple yet fundamental question: how leaf wetting by dew affects plant physiological functions? Understanding the plant response to leaf wetting is important as leaf wetting is one of the most common environmental conditions on the earth.

In chapter 1, intra- and inter-annual changes in dew characteristics (i.e., frequency, timing, duration, amount) was observed in a semiarid crop field in northwest China because how leaf wetting by dew affects plant physiological function would differ depending on dew characteristics. Along with the dew characteristics, environmental elements were also observed, and the relationship between dew characteristics and environmental elements was analyzed. The content of chapter 1 was published as Yokoyama et al., 2021 in *Agricultural and Forest Meteorology*.

In chapter 2, nighttime leaf wetting effects on the rehydration process and its subsequent effects on gas exchange and growth were investigated. I have tested the following hypothesis; (1) leaf wetting by dew could be directly absorbed through leaf surface along the water potential gradient when water potential of leaf surface water is higher than that of the inside leaf; (2) if plants are able to rehydrate through the leaves, it would expect that plants can mitigate the reduction in gas exchange and growth under soil water deficit condition. These hypotheses were tested by conducting greenhouse and laboratory experiments. The content of chapter 2 was published as Yokoyama et al., 2021 in *Agricultural Water Management*.

In chapter 3, I explored costs and benefits associated with leaf wetting by dew within a temporal context by testing the following hypothesis. In the early morning, when leaves are still wet, (1) leaf wetting would cover stomata, thereby suppressing transpiration but little effect on photosynthesis under low light conditions. (2) leaf wetting would increase leaf

surface albedo, which reduces photosynthesis. (3) Reduced transpirational water loss during the early morning would benefit photosynthesis after leaf wetting was evaporated. Diurnal changes in gas exchange were measured with a whole plant chamber system; thereby, comprehensive effects of leaf wetting in the diurnal scale were evaluated.

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Chapter 1 Intra- and inter-annual changes in dew characteristics and its environmental control in a semiarid crop field

1.1. Introduction

Rain-fed and irrigated agriculture are the main forms of agriculture in arid and semiarid regions. Hence, rainfall or irrigation water has been regarded as the major or only water source for agricultural production. However, nonmetric water such as dew or fog has recently been recognized as a significant water resource for plants in several ecosystems (Martin and von Willert, 2000; Limm et al., 2009; Tomaszkiewicz et al., 2016; Zhang et al., 2019). Particularly, dew occurs in many parts of the world, including arid and semiarid ecosystems (Vuollekoski et al., 2015). The importance of dew for arid and semiarid ecosystems has been studied from several perspectives. One common approach has been to quantify the proportion of dew in the water balance (Aguirre-Gutiérrez et al., 2019; Gao et al., 2020). Zhang et al. (2015) reported that dew made up 2% of the annual water balance for semiarid farmland in northwest China, whereas Uclés et al. (2014) reported that dew was up to 23% of the annual water input for a coastal steppe ecosystem in Spain. Dew can be harvested with a dew condenser for utilization as a water resource (Maestre-Valero et al., 2015). Harvested dew water can be used for irrigation, which can significantly contribute to reforestation and agriculture in semiarid environments (Tomaszkiewicz et al., 2017).

Dew is not only an essential component of the water balance in an ecosystem but also improves the eco-physiological functions of plants through leaf wetting. Various plants have been reported to absorb water directly from leaf surfaces through a process known as foliar water uptake; it is recognized as an important water acquisition pathway for plants in arid and semiarid ecosystems (Berry et al., 2019; Liu et al., 2020). Martin and von Willert (2000) showed that leaves take up dew via epidermal hydathodes, which improved the water status and consequently increased the photosynthesis for species of *Crassula* from the Namib Desert. Zhang et al. (2019) reported that dew taken up by leaves of *Populus euphratica* could be redistributed in the rhizosphere. Another essential effect of leaf wetting is the suppression of transpiration (Gerlein-Safdi et al., 2018). Leaf wetting changes the microclimate near the leaf surface, which alters the gas exchange between leaf and atmosphere. Leaf wetting by dew reduces evaporative demand in the morning by increasing humidity near the leaf surface and suppresses an increase in leaf temperature (Yasutake et al., 2015). The decrease in evaporative demand reduces transpiration, which is beneficial for maintaining appropriate plant water status and consequently improves photosynthesis (Zhuang and Ratcliffe, 2012; Yasutake et al., 2019; Yokoyama et al., 2019).

Although the significance of dew has been reported in terms of the hydrological and eco-physiological aspects, it is also essential to understand how dew characteristics (occurrence frequency, amount, and duration) are controlled by environmental elements of arid and semiarid crop fields. This is because the timing and frequency of leaf wetting events on both daily and seasonal bases are crucial for evaluating the type or extent of the effect of dew on the eco-physiological functions of plants (Dawson and Goldsmith, 2018). Additionally, understanding the relationship between dew characteristics and environmental elements is important for estimating the dew collection potential (Vuollekoski et al., 2015). The necessary condition for dew formation is that the temperature of the substrate is less than or equal to that of the surrounding atmosphere (Beysens, 1995; Agam and Berliner, 2006). Radiative cooling of the surface (e.g., leaf surface) is required to meet this condition. Radiative cooling has a stronger effect on the surface temperature during calm wind and cloudless nights. The wind mitigates the radiative cooling intensity through two processes. First, wind prevents temperature inversion, which increases the temperature near the surface by mixing the warmer upper layer and cooler lower layer. Second, a stronger wind enhances forced convection through the boundary layer onto the surface, which improves the heat exchange between the surface and ambient air (Kimura et al., 2017). However, moderate wind is also an essential factor for dew formation because wind facilitates the transport of water vapor, which is a source of dew (Jones, 2013). Cloudiness affects the radiative cooling intensity because downward longwave radiation from clouds offsets the upward radiative loss (Madeira et al., 2002). The water vapor concentration is also an essential factor with two opposing effects on dew formation. Water vapor absorbs and emits longwave radiation as well as clouds, so a higher water vapor concentration in the atmosphere suppresses the effect of radiative cooling. Conversely, water vapor is a source of dew, which is important for dew formation (Agam and Berliner, 2006). Several studies have investigated the relationship between dew characteristics and environmental elements such as the wind speed, air or surface temperature, and relative humidity (Besyens et al., 2005; Zhuang et al., 2014; Zhang et al., 2015; Guo et al., 2016; Meng and Whn, 2016; Zhuang et al., 2017; Aguirre-Gutiérrez et al., 2019; Jia et al., 2019a; Fang, 2020). However, only a few studies have evaluated the radiative cooling intensity, which can be evaluated by measuring nighttime net radiation (Aguirre-Gutiérrez et al., 2019). Moreover, although water vapor is an essential factor for dew formation, the relationship between dew characteristics and water vapor has not been well investigated (Zangvil, 1996; Aguirre-Gutiérrez et al., 2019).

Northwest China is a suitable location for research on the relationship between dew characteristics and environmental elements. Most of the region has an arid or semiarid climate, so strong radiative cooling, which plays an essential role in dew formation, is expected to occur frequently. Northwest China is also located at the margin of the Asian summer monsoon, which affects seasonal meteorological variations, especially variations in water vapor (Ma et al., 2014; Chen et al., 2020). This suggests that the water vapor pressure would change seasonally, which would also affect dew formation. Several studies have reported on the relationship between dew occurrence and environmental elements on the basis of field observations in northwest China (Zhuang et al., 2014; Zhang et al., 2015; Meng et al., 2016; Guo et al., 2016; Zhuang et al., 2017; Jia et al., 2019a). However, long-term (>1 year) observations of the nighttime net radiation, wind speed, water vapor concentration, and dew characteristics in crop fields have not been conducted. Therefore, the relationship between seasonal and annual variations in dew characteristics (occurrence frequency, amount, and duration) and environmental elements in crop fields is unexplored.

In this study, we aimed to investigate the relationship between seasonal (from spring to summer) and annual variations in dew characteristics (occurrence frequency, amount, and duration) and environmental elements, including nighttime net radiation and water vapor pressure of a semiarid cornfield during the cultivation period for three years. The results of the present study are expected to advance the understanding of how dew formation is controlled by variations in the environmental elements of semiarid cornfields, which will contribute to improving the utilization of dew as a water resource for agricultural production.

1.2. Materials and methods

1.2.1. Study site and crop growth information

Observations of dew and environmental elements were conducted at a crop field owned by a local farmer in Pingbu Village, Baiyin City, Gansu Province (36°25.5′ N, 104°25.4′ E, 1461 m above sea level), which is located in the monsoon margin of northwest China. The study field is classified as having a semiarid continental monsoon climate. The mean annual air temperature and precipitation from 1951 to 2000 were 8.9℃ and 238.3 mm, respectively. Precipitation is concentrated from July to September. The soil texture in the field is silty loam (14.9% clay, 74.2% silt, and 10.9% sand), and the soil dry density, particle density, and porosity are 1.60 g cm^{-3}, 2.71 g cm^{-3}, and 0.40 cm^3 cm^{-3}, respectively. Corn (*Zea mays* L. cv. Kenyu90) is cultivated in the field from late April to late September at a row spacing of 0.73 ± 0.16 m and plant spacing along each row of 0.42 ± 0.14 m. Irrigation is conducted depending on the local rainfall amount, and the irrigation water is provided by a canal connected to the Yellow River. The plant height was measured on July 26 and 28 in 2008, June 22 in 2009, July 2 in 2014, June 7 in 2018, and June 25 in 2019 (Fig. 1. 1).

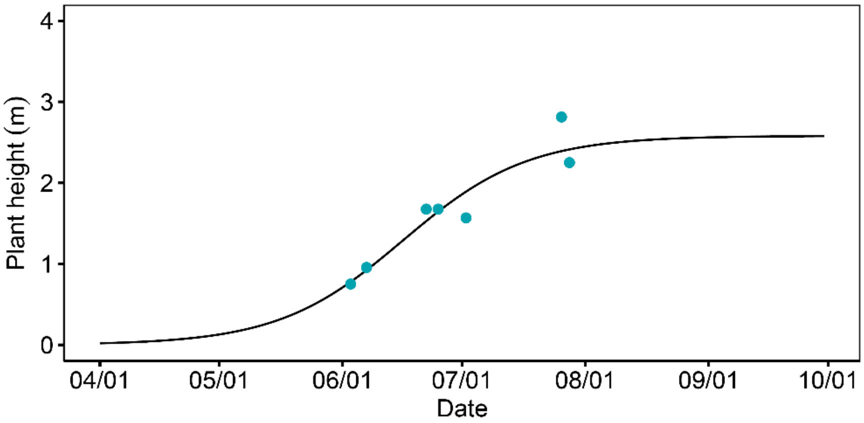

Fig. 1. 1 Changes in plant height during the cultivation periods (late April-late September).

1.2.2. observation and calculation of environmental elements

Fig. 1. 2 Picture of the meteorological station in the study field.

A meteorological station was established in the field (Fig. 1. 2), and environmental elements such as the net radiation (R_n), solar radiation (R_s), air temperature (T_a), relative humidity (RH), wind direction, wind speed, precipitation (i.e., rainfall amount), and canopy surface temperature (T_s) were measured. R_n, R_s, T_a, and RH were measured with a net radiometer (Lite2, Kipp & Zonen, Delft, Netherlands), pyranometer (LP02, Hukseflux, Delft, Netherlands), and temperature–humidity sensor (HMP60, Vaisala, Helsinki, Finland) at the height of 2.0 m. The rainfall amount was measured with a tipping bucket rain gage with a tips at 0.1 mm increments (TE525MM, Campbell Scientific, Logan, UT, USA). T_s was measured with an infrared radiometer sensor (SI-111, Apogee, Logan, UT, USA) that was installed at a height of 3.0 m and tilted 30° downward from horizontal. The wind direction and speed were measured using an anemometer (MODEL 03002, Young, MI, USA) at a height of 4.15 m. All data were sampled every 15 s and recorded every 10 min on average with a data logger (CR1000, Campbell Scientific, Logan, UT, USA).

The saturation water vapor pressure was calculated as follows (Buck, 1981):

$$e_s(T) = 6.11\exp\left(\frac{17.502T}{T + 265.5}\right) \tag{1-1}$$

where $e_s(T)$ (kPa) is the saturation water vapor pressure at a given temperature T (°C) (i.e., T_a in the present study). Then, the vapor pressure was calculated as follows:

$$e_a = e_s \times RH \tag{1-2}$$

where e_a (kPa) is the water vapor pressure.

The wind speed decreases closer to the surface (e.g., soil or canopy). Because we measured the wind speed at a height of 4.15 m ($u_{4.15}$) during our observations, seasonal changes in $u_{4.15}$ would be influenced by an increase in plant height. To exclude this influence, we calculated the wind speed at the height of the canopy surface (Campbell and Norman, 1998):

$$u_s = u_{4.15}\,\frac{\ln\left(\frac{z_1}{z_M}\right)}{\ln\left(\frac{z_2}{z_M}\right)} \tag{1-3}$$

where u_s (m s^{-1}) is the wind speed at the height of the canopy surface, z_1 (m) is the canopy height, z_2 (m) is the measurement height of $u_{4.15}$ (i.e., 4.15 m), and z_M (m) is the surface roughness length (i.e., $0.1 \times z_1$).

1.2.3. Evaluation of dew characteristics

To evaluate dew characteristics such as the dew occurrence frequency, dew duration, and dew amount, a dielectric leaf wetness sensor (PHYTOS 31, METER Group, Inc. Pullman, WA, USA) was installed at a height of 1.0 m at the meteorological station. Data were recorded at intervals of 10 min using a data logger (CR800, Campbell Scientific, Logan, UT, USA). The dielectric constant of water is higher than that of air, so the presence of water from dew or rainfall on the sensor surface can be detected as a change in the output signal (mV). However, although the output signal should only change when the sensor surface is wet, it slightly fluctuated between 255 and 260 mV even when the sensor was dry. Thus, we determined that dew occurred when the output signal was greater than 261 mV. Hence, the dew duration was defined as the period when the output signal was greater than 261 mV. The monthly dew frequency was calculated as the ratio of the number of days that dew occurred to the number of days in a given month. We also defined dew as not occurring during a rain event. Rain event was defined as the value of the rain gauge backet showed larger than 0.1 mm. The dew amount was evaluated according to the method used by Jia et al. (2019b). The accumulated dew amount on the sensor surface at a given time can be estimated from the output signal, which is proportional to the amount of water on the sensor surface. We calculated changes in the dew amount on the sensor surface as follows:

$$\Delta d(t_i) = \begin{cases} D(t_i) - D(t_{i-1}), & D(t_i) > D(t_{i-1}), \quad i \geq 1 \\ 0, & D(t_i) \leq D(t_{i-1}), \quad i \leq 1 \end{cases} \tag{1-4}$$

where $D(t_i)$ is the accumulated water amount on the sensor surface at a given time t_i and $\Delta d(t_i)$ is the change in the dew amount from t_{i-1} to t_i. When $D(t_i) < D(t_{i-1})$, dew condensation was defined as not occurring to exclude dew evaporation on the sensor surface. This definition slightly underestimates the actual dew amount because the condensation and evaporation of dew occur simultaneously. However, evaporative demand should be low because dew usually occurs at night, so the dew evaporation is negligible. Finally, the cumulative dew amount (e.g., daily or monthly) was calculated as follows:

$$d(t_i) = \sum_{k=0}^{i} \Delta d(t_k) \tag{1-5}$$

where $d(t_i)$ is the cumulative dew amount from the initial time (t_0) to a given time (t_i) and t_k is the kth time.

1.2.4. Statistical analysis

Linear regression was used to analyze the relationships between the dew amount and environmental elements. The significance of the correlations between the dew amount and environmental elements was checked with Pearson's correlation test. All statistical analyses were performed using the R. 4.0.1 software.

1.3. Results

1.3.1. Intra- and inter-annual variation of environmental elements

Fig.1. 3 shows the changes in environmental elements during the cultivation periods of 2018, 2019, and 2020. R_s showed similar trends in all 3 years with some variation. R_s was almost constant from April to June and decreased from July to September. R_s in May and June was lower in 2019 (19 and 18 MJ m^{-2} d^{-1}, respectively) than in 2018 (21 and 21 MJ m^{-2} d^{-1}, respectively) and 2020 (21 and 21 MJ m^{-2} d^{-1}, respectively). R_s in September was higher in 2019 (16 MJ m^{-2} d^{-1}) than in 2018 (13 MJ m^{-2} d^{-1}) and 2020 (14 MJ m^{-2} d^{-1}). R_n showed different trends among years. In 2018, R_n increased from April (−52 W m^{-2}) to August (−29 W m^{-2}) and then decreased in September (−35 W m^{-2}). In 2019, R_n increased from April (−46 W m^{-2}) to July (−35 W m^{-2}); these values were higher than the values in 2018 and 2020. R_n then decreased in July and stayed almost constant until September (−45 W m^{-2}). In 2020, R_n showed a similar trend to that in 2018 but with generally lower values. R_n increased from April (−53 W m^{-2}) to August (−34W m^{-2}) and then decreased in September (−44 W m^{-2}).

T_a showed similar trends in all 3 years with some variation. T_a generally increased from April to July and then decreased from August to September. In April, T_a was higher in 2019

(15°C) than in 2018 (13°C) and 2020 (12°C). In May, T_a was lower in 2019 (16°C) than in 2018 (18°C) and 2020 (18°C). T_s showed similar trends in all 3 years with some variation. T_s generally increased from April to July and then decreased from August to September. In May, T_s was lower in 2019 (17°C) than in 2018 (19°C) and 2020 (19°C). In July, T_s was lower in 2019 (21°C) than in 2018 (22°C) and 2020 (22°C).

$u_{4.15}$ showed similar trends for all 3 years with some variation. $u_{4.15}$ was generally constant in April and May, decreased from May to July, and then gradually decreased or remained constant from July to September. In May and June, $u_{4.15}$ was higher in 2020 (1.4 and 1.1 m s^{-1}, respectively) than in 2018 (1.2 and 0.7 m s^{-1}, respectively) and 2019 (1.2 and 0.8 m s^{-1}, respectively). u_s had a different seasonal trend from that of $u_{4.15}$. u_s showed a similar trend in 2018 and 2019, although the values were generally lower from May to July in 2019 than in 2018. u_s increased from April to June, decreased in July, and then was relatively constant from July to September. In 2018, u_s increased from April to May and then continuously decreased until September.

RH showed similar trends in all 3 years with some variation. *RH* increased from April to July and was almost constant from August to September. In April and May, *RH* was lower in 2020 (30% and 38%, respectively) than in 2018 (41% and 46%, respectively) and 2019 (39% and 50%, respectively). In June, *RH* varied among the years at 55%, 63%, and 49% for 2018, 2019, and 2020, respectively. In July, *RH* was higher in July (76%) than in 2019 (69%) and 2020 (69%). e_a showed similar trends in all 3 years with some variation. e_a sharply increased from April to July, peaked in August, and then decreased in September. In April and May, e_a was lower in 2020 (4 and 12 hPa, respectively) than in 2018 (7 and 15 hPa, respectively) and 2019 (7 and 15 hPa, respectively). In July and August, e_a was higher in

2018 (21 and 21 hPa, respectively) than in 2019 (17 and 17 hPa, respectively) and 2020 (18 and 18 hPa, respectively).

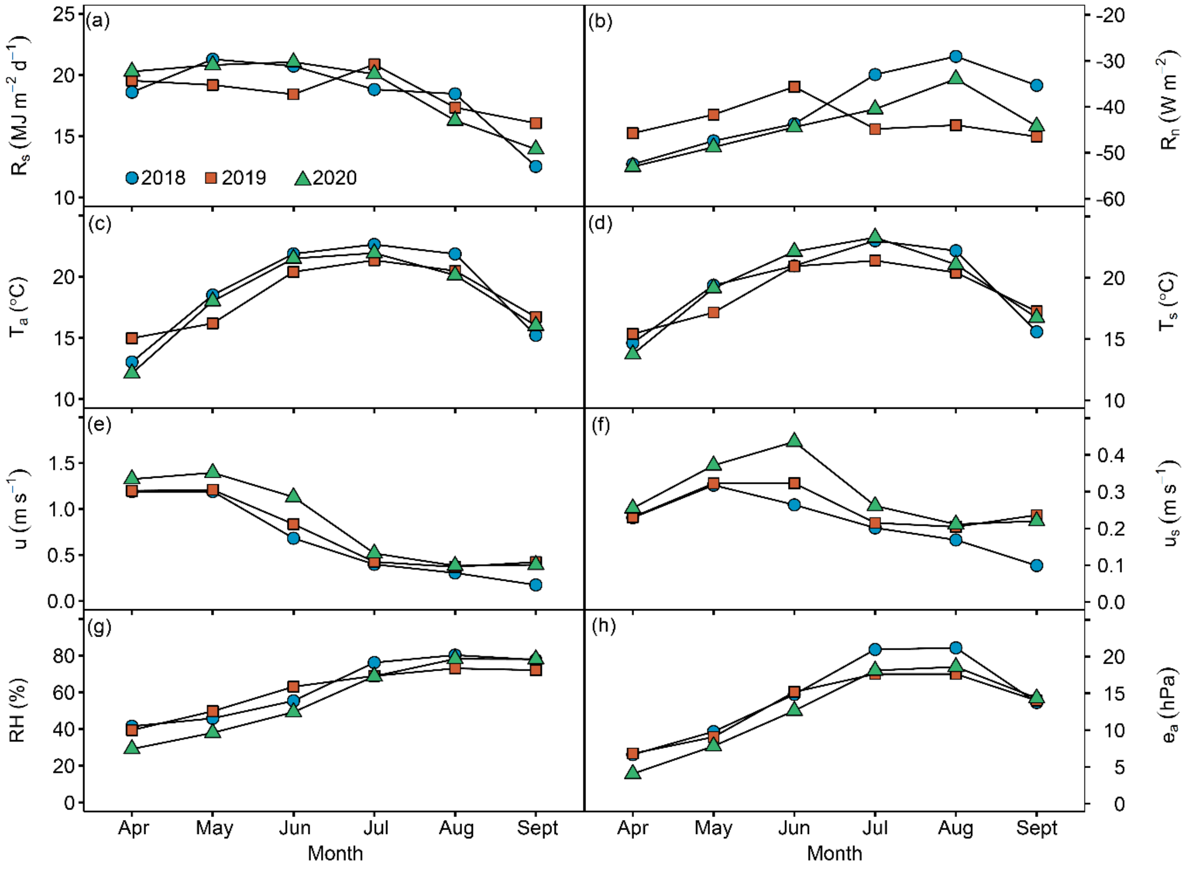

Fig.1. 3 Monthly averages for the (a) daily integrated solar radiation R_s, (b) nighttime net radiation R_n, (c) air temperature T_a, (d) surface temperature T_s, (e) wind speed at a height of 4.15 m $u_{4.15}$, (f) wind speed at the height of the canopy surface u_s, (g) relative humidity RH, and (h) vapor pressure e_a in 2018 (blue circle), 2019 (red square), and 2020 (green triangle) during the cultivation period (April 1–September 30 in 2018 and 2019; April 1–September 16 in 2020). Nighttime is defined as the time when solar radiation is zero.

Fig. 1. 4 shows the wind roses in spring (April, May, and June) and summer (July, August, and September) for 2018, 2019, and 2020. Wind from the northwest (NW) and north (N) directions rarely occurred in all 3 years. In spring 2018, wind predominantly came from the northeast (NE), southeast (SE), south (S), and southwest (SW) directions with occurrence frequencies of 16.8%, 17.5%, 17.4%, and 19.5%, respectively. In summer 2018, the prevailing winds were from the S and SW directions, whereas the frequencies of NE and SE winds decreased to 13.4% and 15.1%, respectively. The frequencies of west (W) and east (E) winds were almost the same in spring and summer for 2018. In spring 2019, the prevailing winds were from the NE, E, SE, and S directions with occurrence frequencies of 16.0%, 17.2%, 16.1%, and 16.7%, respectively. SW and W winds were less frequent at 14.9% and 11.4%, respectively. In summer 2019, SW wind had the highest occurrence frequency at 21.8%. NE, E, and S winds also frequently occurred at 16.6%, 16.7%, and 17.6%, respectively. The frequency of SE wind decreased to 14.5%, and W wind was almost the same in spring and summer. In spring 2020, the prevailing wind was in the NE direction. E, SE, S, and SW winds were also frequent at 17.1%, 16.4%, 16.6%, and 17.6%, respectively. In summer 2020, SE, S, and SW winds frequently occurred at 19.2%, 19.9%, and 18.9%, respectively. NE and E winds decreased to 12.3% and 14.7%, respectively. W wind was almost the same in spring and summer 2020.

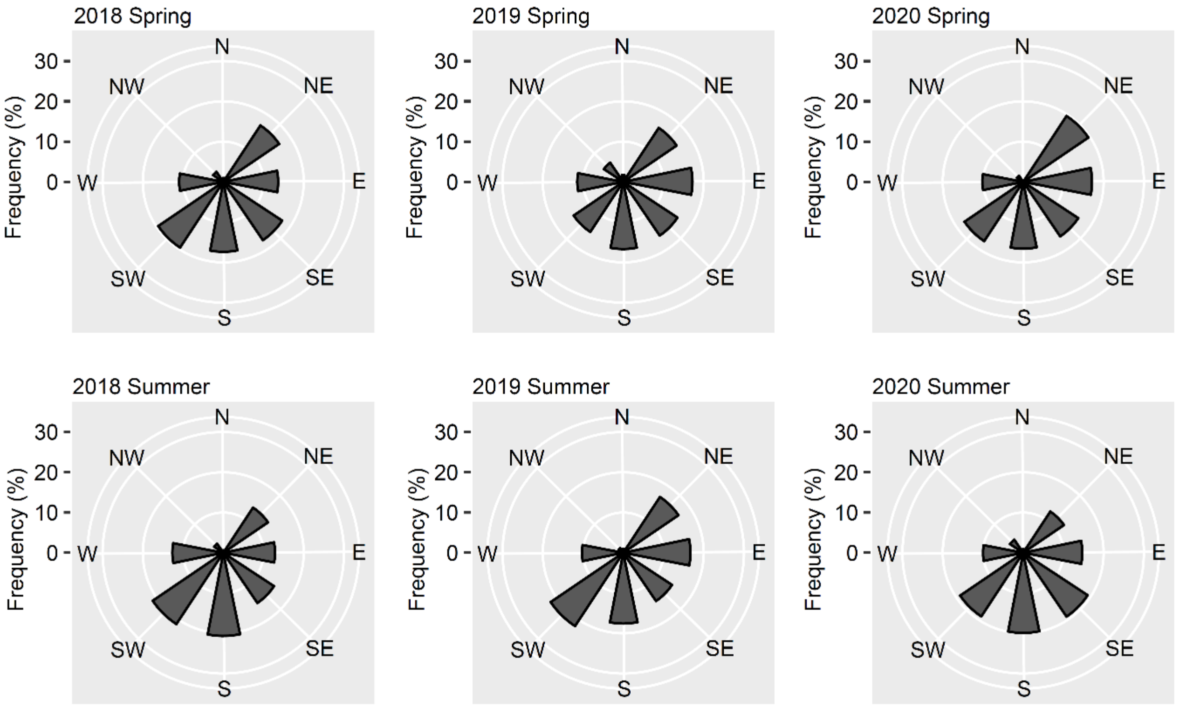

Fig. 1. 4 Wind roses in spring (April–June) and summer (July–September) for 2018, 2019, and 2020.

1.3.2. Intra- and inter-annual variation of dew characteristics

Fig. 1. 5 shows the dew occurrence frequency and duration during the cultivation periods of 2018, 2019, and 2020. The dew occurrence frequency showed a similar trend among all 3 years with some variation. From April to May, the dew occurrence frequency was around 3%–10% in 2018 and 2020 and was exceptionally high at 42% in 2019. In June, the dew occurrence frequency was also exceptionally high in 2019 at 63%, contrary to 2018 (30%) and 2020 (33%). A higher dew occurrence frequency was observed from July to September for all 3 years at 67%–83%. The dew duration showed similar trends among all 3 years. The dew duration increased from April (5–10 h) to August (13–15 h) and was almost constant from August to September (**Fig. 1. 5** and Table. 1. 1).

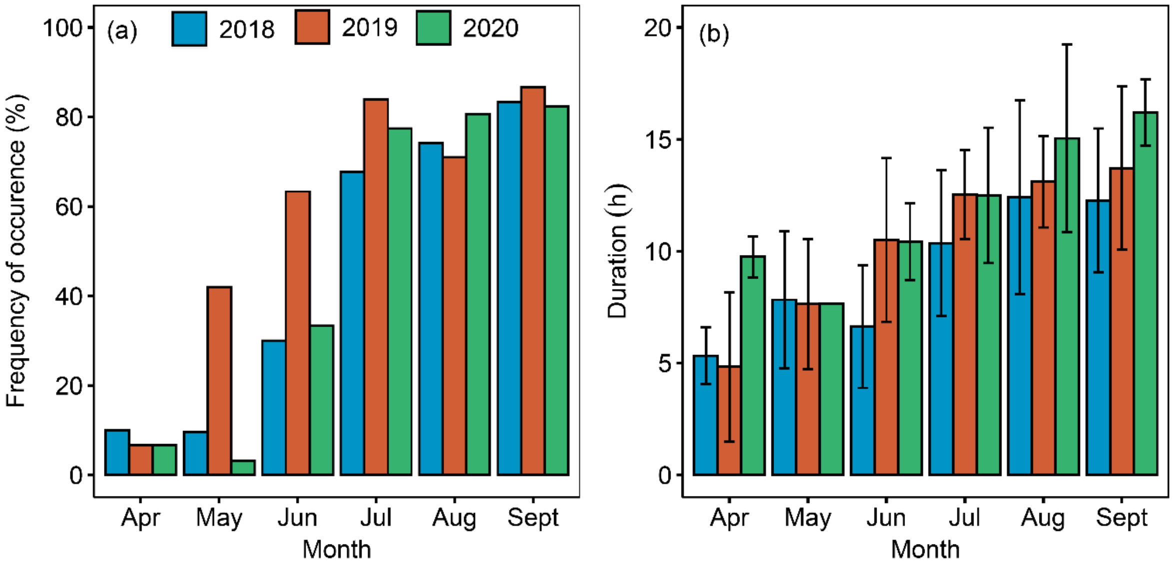

Fig. 1. 5 (a) Dew occurrence frequency and (b) average dew duration for each month of 2018 (blue), 2019 (red), and 2020 (green).

Table. 1. 1 Dew start time, dew disappearance time, and dew duration for each month and the average over the cultivation period (April–September). Data are shown as the average of 3 years (2018, 2019, and 2020) with the standard deviation (SD). Time is Chinese Standard Time (CST).

Month	Dew start (h:min ± SD)	Dew disappearance (h:min ± SD)	Dew duration (h:min ± SD)
April	1:45 ± 2:33	8:21 ± 00:36	6:36 ± 02:44
May	0:24 ± 01:03	8:07 ± 00:36	7:42 ± 00:06
June	0:03 ± 01:27	9:15 ± 01:25	9:11 ± 02:12
July	22:05 ± 01:06	9:51 ± 00:53	11:46 ± 01:17
August	20:19 ± 00:47	9:49 ± 00:35	13:30 ± 01:22
September	19:34 ± 00:54	9:38 ± 01:16	14:03 ± 01:59
Average for April–September	22:42 ± 02:38	09:10 ± 01:04	10:28 ± 03:17

Fig. 1. 6 shows the monthly dew and rainfall amounts during the cultivation periods. The dew amount tended to increase from April to September, although it varied among years. The dew amount was small in April (0.086, 0.042, and 0.057 mm in 2018, 2019, and 2020, respectively). In May, the dew amount was smaller in 2020 (0.004 mm) than in 2018 (0.121 mm) and 2020 (0.149 mm). In June, the dew amount was larger in 2019 (1.0 mm) and 2020 (0.96 mm) than in 2018 (0.29 mm). In July, the dew amount was also larger in 2019 (2.9 mm) and 2020 (2.8 mm) than in 2018 (1.5 mm). In August, the dew amount increased in 2018 (2.2 mm) and 2020 (4.5 mm) but decreased in August 2019 (2.4 mm). The dew amount was larger in 2020 than in 2018 and 2019. The largest dew amount was observed in September at 3.4 and 3.9 mm for 2018 and 2019, respectively. In 2020, the dew amount in September (3.4 mm) was less because the observation period was shorter (September 1–17 in 2020, September 1–30 in 2018 and 2019). However, the average dew amount per dew event in September 2020 was the largest among all the months (Fig.1. 7). The total dew amounts for the cultivation periods in 2018, 2019, and 2020 were 7.64, 10.4, and 11.7 mm, respectively (Table 1).

The rainfall amounts were much larger than the dew amounts with large variation among years. In this region, spring is the dry season and summer is the rainy season. In 2018, the rainfall amount was small in April, May, and June (22.2, 34.1, and 9.9 mm, respectively) and large in July, August, and September (64.9, 83.5, and 52.1 mm, respectively). In 2019, the rainfall pattern was unusual; the rainfall amount was larger in April, May, and June (16.5, 40.7, and 57.5 mm, respectively) than in July, August, and September (17.9, 35.2, and 2.10 mm, respectively). In 2020, the rainfall pattern was similar to that in 2018, except the rainfall amount in September 2020 was much less than that in 2018. The total rainfall amounts in 2018, 2019, and 2020 were 266.7, 169.9, and 162.9 mm, respectively (Table 1).

Fig.1. 8 shows the relative frequency distributions of the dew or rainfall amount for a single event. The dew amount was smaller than the rainfall amount for a single event. The dew amount of a single event was less than 1.0 mm, whereas the rainfall amount of a single event was widely distributed between 0.05–0.1 mm and 20–50 mm. Conversely, dew occurred more frequently than rainfall. In 2018, 2019, and 2020, dew occurred 106, 109, and 76 days, respectively, whereas rainfall occurred 74, 46, and 56 d, respectively (Table1).

Table. 1. 2 Total dew and rainfall days and amounts for the cultivation periods of 2018–2020. The ratios of the total dew amount to the total rainfall amount are also shown.

Year	Dew days (d)	Rainfall days (d)	Dew amount (mm)	Rainfall amount (mm)	Dew amount/ Rainfall amount (%)
2018	106	74	7.64	266.7	2.86
2019	108	46	10.4	169.9	6.14
2020	76	56	11.7	162.9	7.16

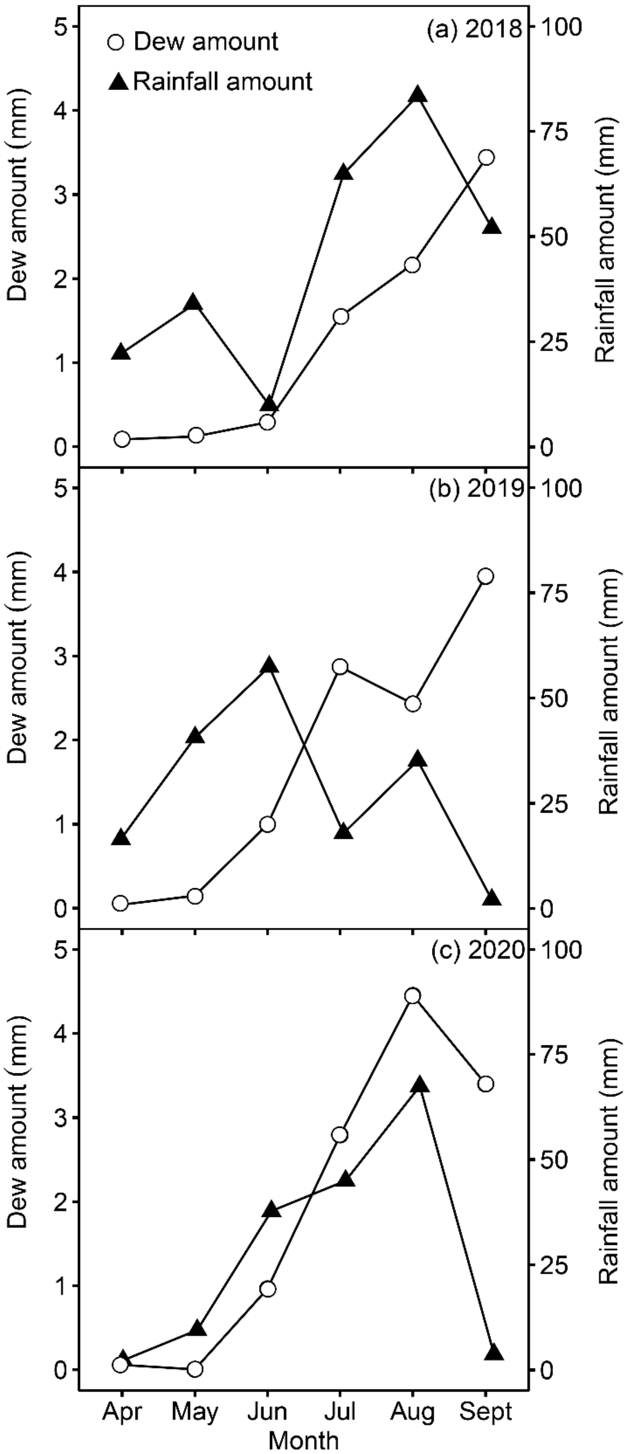

Fig. 1. 6 Monthly dew (open circle) and rainfall (closed triangle) amount during the cultivation periods of (a) 2018, (b) 2019, and (c) 2020. Data in 2018 and 2019 correspond to April 1–September 30, and data in 2020 correspond to April 1–September 17.

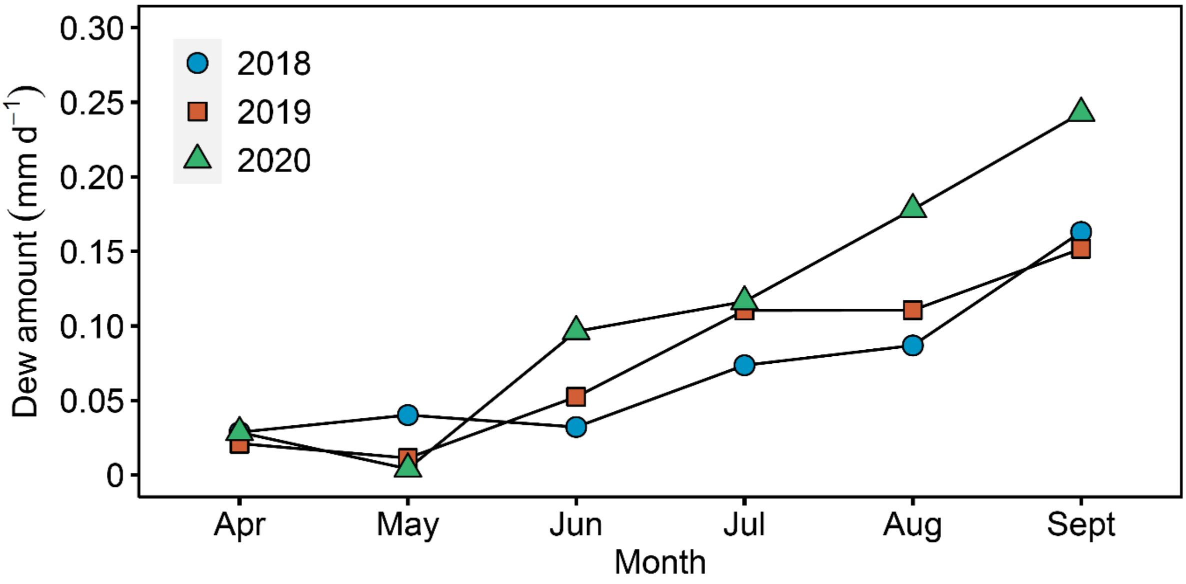

Fig.1. 7 Monthly changes in average dew amount per one dew event in 208, 2019, and 2020.

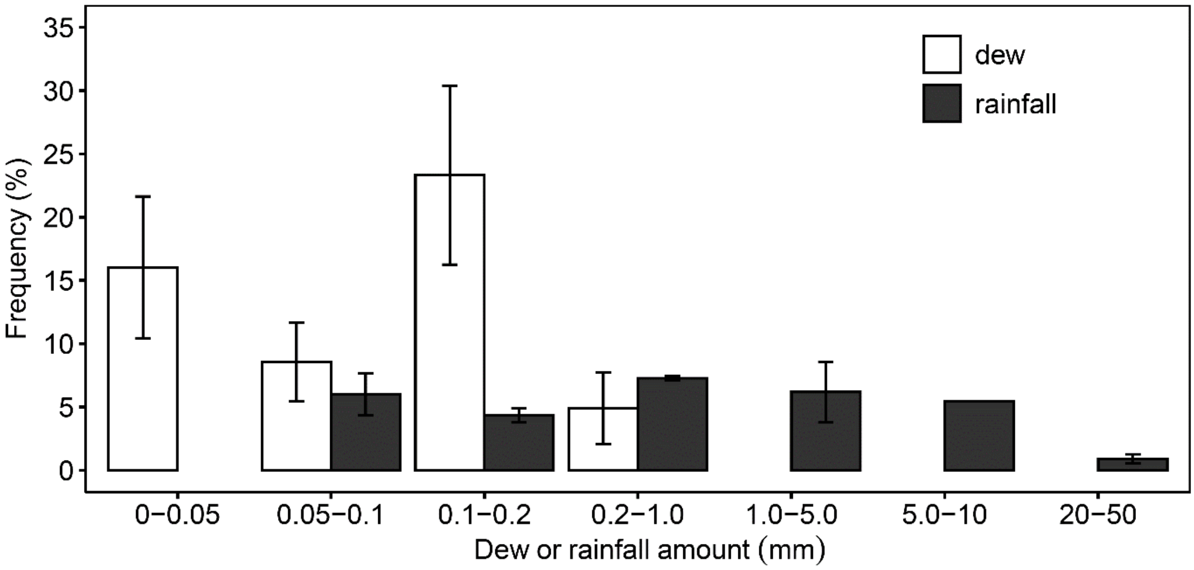

Fig.1. 8 Relative frequency distributions of the dew or rainfall amount for a single event. Means (average of data for 2018–2020) ± SD are shown.

1.3.3. Difference in nighttime environmental condition when dew is present or absent

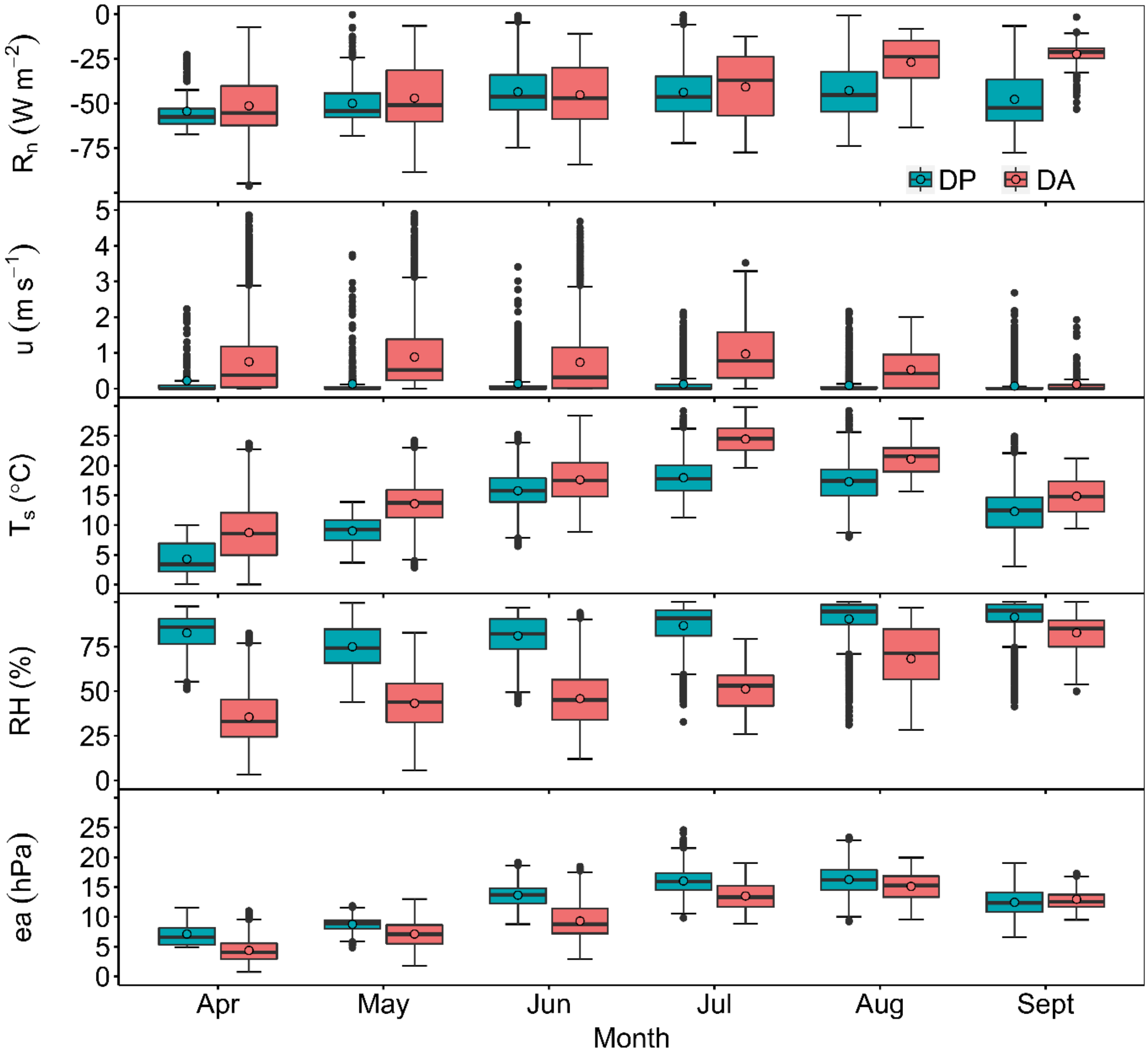

Fig.1. 9 Differences in nighttime (defined as the time when solar radiation is zero) environmental elements when dew is present (DP; gray box) and absent (DA; white box): (a) net radiation R_n, (b) wind speed u, (c) surface temperature T_s, and (d) relative humidity *RH*. Data are shown as the averages for 2018, 2019, and 2020. Data during rainfall are not included. For the box plots, the horizontal line inside the box denotes the median, and the open circle denotes the arithmetic mean. Closed circles denote outliers.

Fig.1. 9 shows differences in nighttime environmental elements when dew is present (DP) or absent (DA). As shown in Fig. 6a, the mean R_n was similar under the DP and DA conditions in April (−54.3 and −51.4 W m^{-2}, respectively) and May (−47.2 and −43.4 W m^{-2}, respectively). However, the DA distribution was wider than the DP distribution. The mean R_n was also similar under the DP and DA conditions in June (−43.3 and −45.2 W m^{-2}, respectively) and July (−43.72 and −40.8 W m^{-2}, respectively). In August and September, the mean R_n was lower under the DP condition (−42.6 and −26.9 W m^{-2}, respectively) than under the DA condition (−36.7 and −22.4 W m^{-2}, respectively).

The mean $u_{4.15}$ was higher under the DP condition than under the DA condition from April to August (Fig. 6b). In September, $u_{4.15}$ was around 0.0 m s^{-1} under both the DA and DP conditions. The first quartile was 0.0 m s^{-1} under both the DA and DP conditions, and the third quartile was 0.02 and 0.10 m s^{-1}, respectively.

The mean T_s was lower under the DP condition than under the DA condition from April to September (Fig. 6c). The mean RH was also higher under the DP condition than under the DA conditions from April to September. From April to July, the mean e_a was higher under the DA condition than under the DP condition, whereas the mean e_a was similar under the DP and DA conditions in August (16.3 and 15.1 hPa, respectively) and September (12.4 and 13.0 hPa, respectively) (Fig. 6e).

1.3.4. Relationships between dew characteristics and environmental elements

Fig.1. 10 shows seasonal changes in the daily averages for e_a and the dew amount in a single night in 2018, 2019, and 2020. The seasonal variations in the dew amount and e_a corresponded for all 3 years. e_a was less than 15 hPa from April to mid-June, and dew rarely occurred or was less than 0.1 mm. e_a sharply increased from mid-June to late June, and a high e_a was observed from June to August with a decrease in September. The dew amount also sharply increased with e_a, and dew occurred frequently during this period. Although the seasonal variations in the dew amount and e_a corresponded, the peaks of the variations did not. e_a decreased in September, but the largest dew amount was observed in that month.

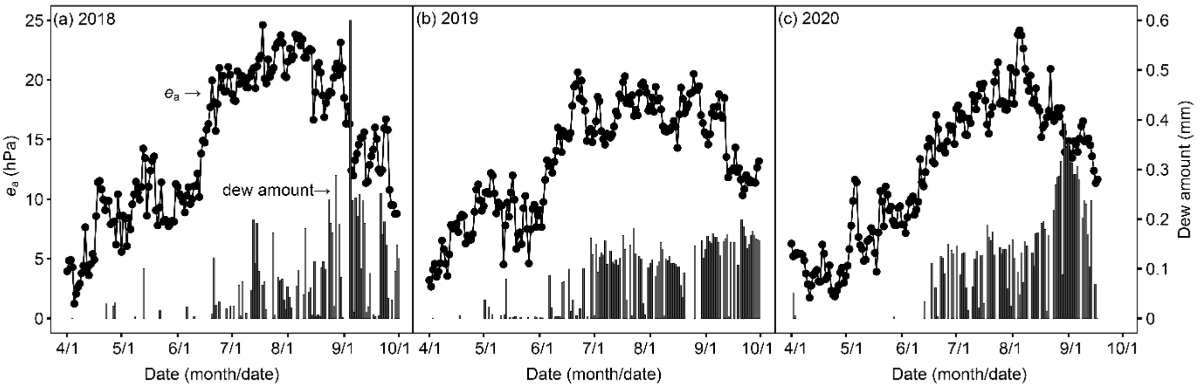

Fig.1. 10 Seasonal variations in the daily average water vapor pressure e_a and daily dew amount in (a) 2018, (b) 2019, and (c) 2020.

Fig.1. 11 shows the relationship between the average nighttime environmental elements when dew occurred and the dew amount of a single night in spring (April–June) and summer (July–September). A significant negative correlation was found between R_n and the dew amount in summer, whereas no significant correlation was found in spring (Fig.1. 11a). No

significant correlation was found between $u_{4.15}$ and the dew amount in both spring and summer (Fig.1. 11b). A negative correlation was found between T_s and the dew amount in summer, whereas no significant correlation was found in spring (Fig.1. 11c). A negative correlation was found between e_a and the dew amount in summer, whereas a significant positive correlation was found in spring (Fig.1. 11d).

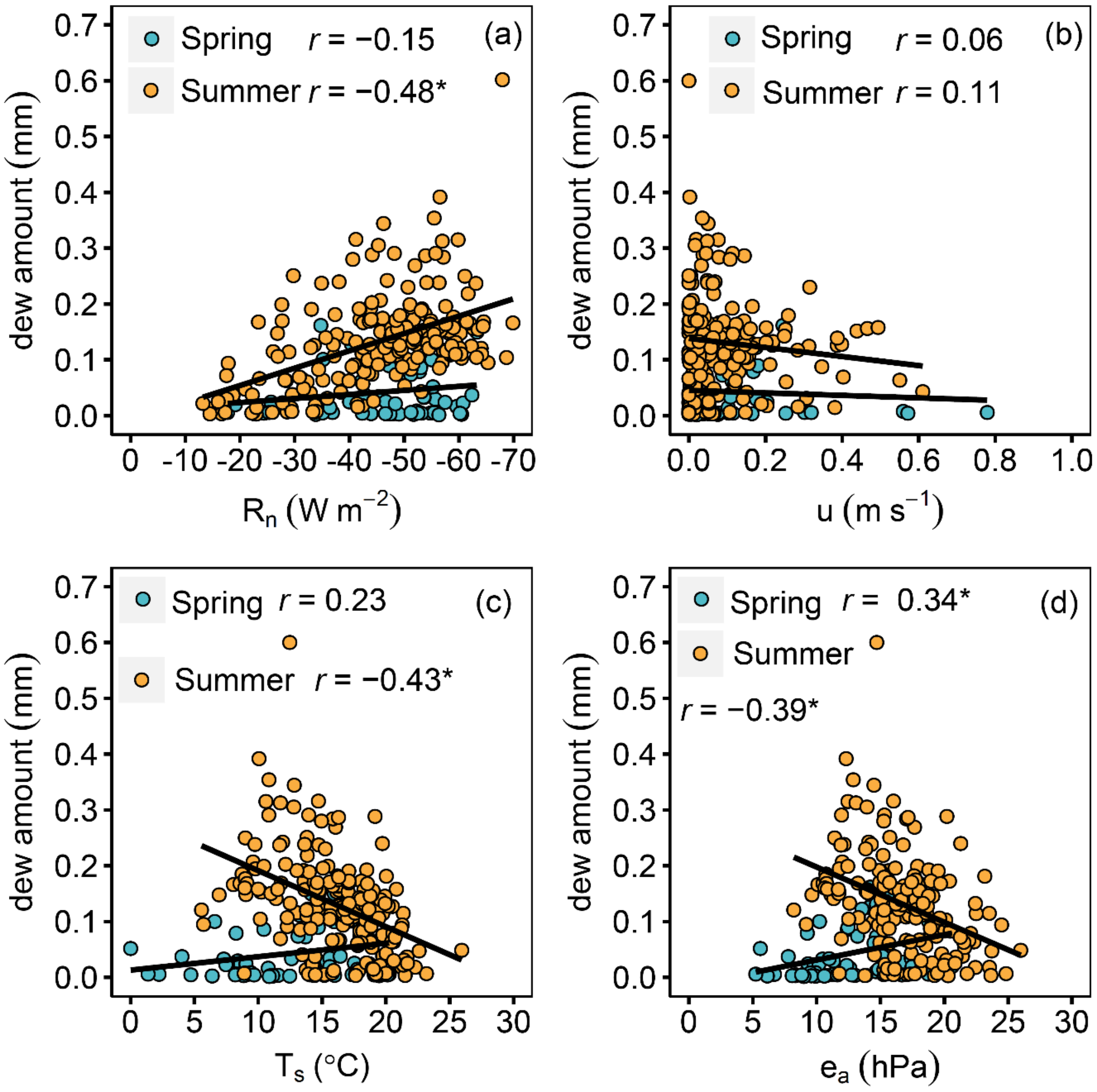

Fig.1. 11 Relationships among the average nighttime meteorological factors for dew occurrence and amount of a single event in spring (April–June) and summer (July–September): (a) net radiation R_n, (b) wind speed u, (c) surface temperature T_s, and (d) relative humidity *RH*. The solid lines represent linear regression. The Pearson correlation coefficients (r) and statistical significance are also shown (*, $p < 0.05$).

1.4. Discussion

1.4.1 Control of dew characteristics by environmental elements

Several studies have evaluated the relationship between dew characteristics and environmental elements on the basis of field observations (Besyens et al., 2005; Zhuang et al., 2014; Zhang et al., 2015; Meng et al., 2016; Guo et al., 2016; Zhuang et al., 2017; Aguirre-Gutiérrez et al., 2019; Jia et al., 2019a; Fang, 2020). One common way to evaluate favorable conditions for dew formation is comparing the differences in environmental elements when dew does and does not occur (Zhuang et al., 2014; Meng et al., 2016; Guo et al., 2016; Zhuang et al., 2017). Previous studies have reported that dew formation occurs when the wind speed and the air or surface temperature are lower and the RH is higher, which was consistent with our results (Fig. 1.9). A lower wind speed indicates temperature inversion, which reduces the air or surface temperature. The drop in temperature increases the RH, which indicates that water vapor is likely to condense. We also observed negative nighttime net radiation (−30 to −55 W m^{-2}), which leads to the conclusion that radiative cooling is an essential factor for dew formation (Beysens, 1995). Interestingly, however, the seasonal trends for the dew characteristics and radiative cooling intensity were opposite (Figs. 1.3, 1.5, and 1.6). In spring, although the radiative cooling intensity was stronger, dew rarely occurred and only in small amounts. Conversely, in summer, dew frequently occurred and in larger amounts despite the lower radiative cooling intensity. Because wind speeds and water vapor pressure are also essential environmental elements for dew formation, we hypothesized that the wind speed and/or water vapor pressure, rather than the radiative cooling intensity, is a dominant influencing factor for dew formation in spring (Agam and Berliner, 2006).

The wind has complex effects on dew formation. The transport of water vapor by wind is regarded as an important factor for dew formation (Jones, 2013), but wind can also weaken the effect of radiative cooling by mixing temperature inversion and facilitating heat exchange between leaf surfaces and ambient air (Kimura et al., 2017). In our study, significant correlation between dew amount and wind speed was not found both in spring and summer (Fig. 1.11). The possible reason is the starting threshold speed of the anemometer (0.5 m s^{-1}). Observed wind speed when dew occurred was mostly less than the starting threshold speed of the anemometer which would have affected the results of correlation analysis. Fang (2020) reported that the rate of dew condensation peaks at a wind speed of 1.2 m s^{-1} and that the condensation rate decreases above and below this wind speed. This result implies an optimum wind speed for dew formation, but dew formation can also be suppressed by different processes regardless of the wind speed. In our study, the observed wind speed at the height of the canopy surface was less than 0.5 m s^{-1} throughout the cultivation period. By contrast, Zhang et al. (2015) reported that dew most frequently occurred at a surface wind speed of 1.5 m s^{-1} in a crop field in northwest China. Thus, the lack of a water vapor supply because of the lower wind speed would have affected the dew formation in our study field.

Although the water vapor pressure is an essential factor for dew formation, the two elements have rarely been considered together (Aguirre-Gutiérrez et al., 2019). Conversely, several studies have used RH as an indicator for the moisture level of the atmosphere when dew occurs. The RH is suitable for predicting whether dew is likely to occur because a higher RH indicates that water vapor is more likely to condense (Sentelhas et al., 2008). However, RH changes with changes in both atmospheric moisture level and temperature. In addition radiative cooling indirectly affects RH through its effects on temperature, and thus RH can be regarded as comprehensive indicator of dew formation rather than a indicator of atmospheric moisture level. Therefore, water vapor pressure is a more appropriate indicator for investigating how dew formation is controlled by the atmospheric moisture level. We found that the trends of the dew amount coincided with those of the water vapor pressure, which was lower in spring and higher in summer (Fig. 1.10). This result is consistent with that of Zangvil (1996), who reported that the trends of dew formation coincided with trends of water vapor pressure rather than nighttime net radiation. In our study, we found a significant positive correlation between the dew amount and water vapor pressure, whereas no significant correlation was found between the dew amount and nighttime negative net radiation in spring (Fig. 1.11). Conversely, significant negative correlations were found between the dew amount and water vapor pressure and between the dew mount and net radiation in summer. The importance of radiative cooling in the summer is further supported by the relationship between surface temperature and dew amount (Fig. 1.11). Surface temperature had significant correlation with dew amount in summer while no significant correlation was found in the spring as well as radiative colling intensity, indicating that decrease in surface temperature by radiative cooling is an important factor for dew formation in the summer. These results indicate that dew formation is limited by the water vapor pressure in spring, whereas the radiative cooling intensity is the dominant limiting factor for dew formation in summer.

The importance of water vapor pressure and radiative cooling for dew formation can be inferred from annual differences in the dew characteristics and environmental elements. Our results showed that variations in the dew characteristics coincided with those for rainfall in spring. The lowest dew amounts in May (2020) and June (2018) coincided with the lowest rainfall amounts. Dew occurred more frequently in May and June of 2019, which also had a higher rainfall amount than the other years. Zhang et al. (2015) reported an increase in the dew amount after rainfall, which indicates that an increase in water vapor due to rainfall facilitates dew formation. Guo et al. (2016) also found a significant positive correlation between the daily rainfall amount and dew amount on the first day after rainfall. These results suggest that the water vapor supply from precipitation facilitates dew formation in spring. However, our results showed that rainfall had different effects on dew formation in July–September. During these months, the rainfall amount was higher in 2018 than in 2019 and 2020, but the dew amount was lower in 2018 than in 2019 and 2020. Thus, the dew formation in summer is limited by the radiative cooling intensity. A larger rainfall amount indicates an increase in cloud cover and water vapor pressure, which weaken the radiative cooling intensity and thus limit dew formation.

1.4.2 Seasonal changes in water vapor pressure

We found a large seasonal variation in the water vapor pressure that predominantly controlled the dew formation in spring (Fig. 1.10). One possible reason for the increase in water vapor is an increased supply from transpiration. We found that plant growth is most active from June and July, which suggests that the leaf area increased and thus would increase canopy transpiration (Fig. 1.1). However, an increase in transpiration may not be the only factor. This is because the increase in water vapor pressure was too rapid considering the growth rate of plants. For example, the water vapor pressure increased by approximately 10 hPa in 10 d in 2018.

Another possible reason is the effects of large-scale meteorological variations. Although our results represent local meteorological conditions that are affected by local conditions such as the topography and vegetation, we found that the patterns of water vapor pressure and wind direction corresponded to large-scale meteorological variations reported by other studies. Ma et al. (2014) reported that westerlies and the Asian summer monsoon have a dominant role in large-scale water vapor transport in Lanzhou, which is 66 km away from our study field. In Lanzhou, westerlies have a constant effect, whereas the water vapor transport by the monsoon is prominent from June to August. Chen et al. (2020) also reported on the importance of the Asian summer monsoon for the transport of water vapor in Lanzhou and showed that the amount of precipitable water increases in summer. In our study, the water vapor pressure increased in July and decreased in September. Moreover, wind from the south direction occurred more frequently in summer than spring, which may indicate the influence of the Indian and East Asian monsoons (Fig. 1.4). These results suggest the possible importance of large-scale meteorological variations to dew formation, which is yet to be explored. Investigating the relationship between dew formation and the East Asian summer monsoon index, which represents the strength of the summer Asian monsoon (Wang et al., 2008), may be one way to explore the effects of large-scale meteorological variations on dew formation.

1.4.3 Implication of dew effects on semiarid crop production

The effects of dew on crop production must be evaluated quantitatively and in terms of eco-physiology. In our study, the ratios of the total dew amount to the total rainfall amount in 2018, 2019, and 2020 were 2.9%, 6.1%, and 7.2%, respectively (Table 1.2). This result is similar to those of other studies, which reported ratios of 5.9% (Zhang et al., 2019) and 11.2% (Meng and Wen, 2016) for crop fields in northwest China. Given that crop fields are generally irrigated in arid and semiarid regions, the dew amount accounts for only a small portion of the water balance. Despite the small amount, our results implied that the frequent occurrence of dew (approximately 50% of days during the cultivation periods) has significant effects on crop production in arid and semiarid regions through its influence on the eco-physiological functions of plants. This is because the frequency, timing, and duration rather than the dew amount are essential factors for evaluating how or to what extent dew affects the eco-physiological functions of plants (Dawson and Goldsmith, 2018). We found that dew started around 22:42 at night and continued for more than 10 h before evaporating at around 9:10 in the morning of the next day (Table 1.1). Guzmán-Delgado et al. (2017) reported that leaf rehydration by foliar water uptake takes over 150 and 300 min for *P. dulcis* and *Q. lobata*. Although corn is mainly cultivated in our study field, 10 h would be enough for the leaves to be rehydrated by foliar water uptake. Foliar water uptake is also more important under saline conditions, which is often observed for irrigated crop fields (Schilfgaarde, 1994) because dew water has low salinity (Lekouch et al., 2010). Another essential eco-physiological effect of dew is reducing transpirational water loss by increasing humidity near the leaf surface and suppressing an increase in leaf temperature (Gerlein-Safdi et al., 2018). During our observations, sunrise started around 6:00 in the morning, so transpirational water loss could be reduced at least 3 h after sunrise. Given that leaf wetting by dew was observed approximately 50% of the day during the cultivation period, the effect of reduced transpiration would not be negligible. However, quantifying the transpiration rate of wet leaves has not been investigated closely because it is impossible to measure the evaporation of leaf wetting and transpiration separately with the conventional gas exchange method. One method to quantify the transpiration rate of wet leaves was proposed by Yasutake et al. (2019), who separately evaluated the evaporation of leaf wetting and transpiration under steady-state conditions by combining the stem heat balance and chamber methods. Overall, dew represents a small amount of the water balance for a crop field yet would have a significant impact on crop production because of its influence on the eco-physiological functions of plants.

1.5. Conclusion

We examined the seasonal and annual variations in the dew characteristics (i.e., occurrence frequency, amount, and duration) of a semiarid cornfield during the cultivation period (April–September) and analyzed how they are affected by variations in environmental elements. The dew amount was smaller than the rainfall amount at 5.4% on average over the 3 years studied (2018–2020). However, dew occurred more frequently than rainfall at 53% of the days during the cultivation period on average. Additionally, the average duration of leaf wetting over the cultivation periods was about 10 h. Our findings indicated the

importance of dew for its eco-physiological effects on leaf wetting in a semiarid crop field. Dew showed a clear seasonal variation; it rarely occurred in spring and only in small amounts, whereas it occurred almost every day in summer and in large amounts. The seasonal variation of dew coincided with that of water vapor pressure, which was identified as an essential influencing factor. In spring, dew formation is limited by the low water vapor pressure, which is the source of dew. In summer, the water vapor pressure is high, so dew formation is predominantly limited by the radiative cooling intensity. Our study presents important findings on how variations in dew characteristics are controlled by environmental elements, which should contribute to improving the utilization of dew as a water resource for agricultural production.

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Chapter 2 Effects leaf wetting by dew on nighttime rehydration process

2.1. Introduction

Water is an essential resource for agricultural production; however, recent studies have predicted that the risk of water shortage will further increase in the near future (IPCC 2013). The risk of water shortage is high in arid and semi-arid regions, which are home to approximately 38% of the global population (Huang et al., 2016). Therefore, a more efficient use of water in agricultural production is required to sustain the food supply, especially in arid and semi-arid regions where crop yields are strongly dependent on the availability of water resources (Fischer et al., 2007).

It was previously considered that precipitation and irrigation were the only means of water input to agricultural production. However, it has more recently been recognized that non-metric water inputs such as dew and fog serve as essential water sources for plants in many ecosystems (Zhuang and Ratcliffe, 2012; Baguskas et al., 2017; Eller et al., 2017). Dew is a widely observed meteorological phenomenon, and its potential significance as a water resource in arid and semi-arid ecosystems has been reported (Vuollekoski et al., 2015; Zhang et al., 2015; Zhang et al., 2019). Aguirre-Gutiérrez et al. (2019) reported that dew accounted for up to 10.2% of the annual water input and 33.6% of the total dry season precipitation in a continental semi-arid grassland. Dew harvesting, using a dew condenser, has been reported as a means of utilizing dew as a water resource (Maestre-Valero et al., 2015). Tomaszkiewicz et al. (2017) showed that irrigation with harvested dew could significantly increase soil water content and could be utilized in reforestation and the growing of crops in arid and semi-arid environments. Although the importance of dew has been recognized, its significance as a water resource is often evaluated based on “amount”, which might underestimate its relevance since the amount of dew water is much smaller than that of conventional water resources (i.e., irrigation water and precipitation) (Zhang et al., 2015; Zhang et al., 2019). Nevertheless, dew can have significant effects on crop production through leaf wetting and subsequent effects on plant physiological functions. Direct water absorption from the leaf surface, known as foliar water uptake, is one of the important effects of leaf wetting on plant physiological functions (Martin and von Willert, 2000; Simonin et al., 2009; Eller et al., 2013). Subsidiary to root water uptake, foliar water uptake can be a significant water acquisition pathway that contributes to improvements in plant–water relations and consequently mitigates decrease in photosynthetic rate, increasing a plant’s chances of survival under drought conditions (Martin and von Willert, 2000; Simonin et al., 2009; Eller et al., 2013). Leaf wetting can also improve plant–water relations by mitigating excessive transpirational water loss. Leaf wetting increases humidity near the leaf surface and suppresses increases in leaf temperature, which leads to a decrease in evaporative demand and can contribute to limiting a midday depression in photosynthesis (Yasutake et al., 2015; Yokoyama et al., 2019). Overall, these studies suggest that leaf wetting by dew would have significant effects on agricultural production through its effects on plant physiological functions, even though the amount of dew present is small. Therefore, the potential of dew as a water resource should also be evaluated in terms of its effects on plant physiological functions.

Although recent studies have reported the positive effects of leaf wetting, it has also been considered to negatively affect photosynthesis. This is because the presence of water droplets or a water film on a leaf surface occludes the stomata, causing a physical barrier to CO_2 uptake since CO_2 diffusion in water is much slower than that in air (Ishibashi and

Terashima, 1995; Hanba et al., 2004). In contrast, Berry and Goldsmith (2020) reported that leaf wetting decreases photosynthetic rate only for leaf surfaces without stomata, indicating that the blockage of CO_2 uptake by leaf surface water is not the only factor involved in the short term photosynthetic response to leaf wetting. How leaf wetting affects gas exchange is still not well understood; however, it is likely that the photosynthetic rate tends to decrease when the leaf surface is covered with water (Aparecido et al., 2017; Berry and Goldsmith, 2020).

Based on recent studies, leaf wetting affects plant physiological functions both positively and negatively depending on environmental and plant physiological conditions. Leaf wetting may temporarily decrease the photosynthetic rate when a leaf is wet. However, at the same time, transpiration rate can also decrease with leaf wetting. A reduction in transpiration rate would be beneficial to plants in terms of mitigating water stress at times of high evaporative demand (Yokoyama et al., 2019). Consequently, leaf wetting would increase the photosynthetic rate in the long term by mitigating water stress. In addition, leaf wetting by dew at nighttime contributes to improving plant–water relations owing to foliar water uptake, which indirectly affects daytime gas exchange. Overall, to assess the effects of dew on plant physiological functions, a comprehensive investigation with consideration of the tradeoff between carbon and water relations is needed (Dawson and Goldsmith. 2018).

Northwest China is an appropriate location for studying the effects of dew on agricultural production as it is an important agricultural region of China. Moreover, the region has a mostly arid and semi-arid climate, and the imbalance between the supply and demand of water resources is a serious problem. Agricultural production accounts for about 90% of the total water consumption; therefore, measures to address water resource issues in agricultural production are needed (Shen et al., 2013). It has been reported that dew frequently occurs in this region and its importance to the water balance in the region has been reported in several studies (Zhuang and Zhao, 2014; Zhang et al., 2015; Meng and Wen, 2016; Jia et al., 2019). However, there are few studies investigating the effects of leaf wetting by dew on plant physiological functions in this region (Zhang et al., 2012). In particular, there is a lack of information on how leaf wetting by dew affects plant physiological functions in crops and its potential significance for agricultural production.

The overall aim of this study was to investigate the impact of leaf wetting by dew on crop production in a semi-arid environment in terms of its effects on plant physiological functions. The specific aims are (1) to evaluate the effects of leaf wetting by dew on plant physiological functions such as plant-water relations and gas exchange by greenhouse experiments, and (2) to investigate the effects of leaf wetting by dew on plant water used efficiency by greenhouse experiments.

2.2. Materials and methods

2.2.1. Plant materials and growth conditions

Maize (*Zea mays* L.) cultivar 'P2307' was used as the plant material. The seeds were germinated and grown in a phytotron glass room (air temperature of 25°C, relative humidity of 70%) located at the Faculty of Agriculture, Kyushu University, Japan. The plants were grown using a standard nutrient solution (Otsuka AgriTechno Co. Ltd., Japan) with an electrical conductivity of 2.0 dS m^{-1}. The nutrient solution contained 17.1 mmol (NO^{3-}) L^{-1}, 1.1 mmol (PO_4^{3-}) L^{-1}, 1.6 mmol (SO_4^{2-}) L^{-1}, 8.4 mmol (K^+) L^{-1}, 1.5 mmol (Mg^{2+}) L^{-1}, and 3.9 mmol (Ca^{2+}) L^{-1}. At the third to fourth leaf stage, the plants were transplanted to larger plastic pots (8-L volume) filled with soil (6.7% clay, 14.7% silt, 78.6% sand). After transplanting, the plants were moved to an experimental greenhouse (area; 90 m^2) at Ito

Plant Experimental Fields & Facilities, Faculty of Agriculture, Kyushu University. A ventilation fan was operated when T_A exceeded 20°C, and the side windows of the greenhouse were kept open during the cultivation period. Environmental conditions in the greenhouse, i.e., solar radiation (R_S), photosynthetic photon flux density (*PPFD*), air temperature, relative humidity, and CO_2 concentration, were measured using a pyranometer (CAP-SP-110, Apogee Instruments, Logan, UT, USA), quantum sensor (CAP-SQ-110, Apogee Instruments, Logan, UT, USA), and a datalogger-integrated temperature–humidity–CO_2 sensor (TR-76Ui, T&D Corporation, Matsumoto, Japan), respectively. The data from each instrument were recorded by a datalogger (GL820, Graphtec Corporation, Yokohama, Japan) at 10-min intervals.

2.2.2. Plant-water relations and gas exchange measurements

The control experiment was conducted using a randomized design consisting of the cross of two factors: two different soil water conditions (well-watered [ww] and water - stressed [ws]) and two types of leaf wetting condition (no-wetting [nowet] and wetting [wet]). For this experiment, maize plants at the 10th leaf stage were used. The plants were divided into two groups, and the water-stress treatment was imposed on one group by gradually reducing the water supply approximately 10 days before the measurements. Volumetric soil water content (*SWC*) was monitored daily using a moisture sensor (EC-5, METER Group, Inc. Pullman, WA, USA) with a sensor read-out device (Procheck, METER Group, Inc. Pullman, WA, USA). The water potential of the soil was estimated from the soil water characteristic curve, which was determined by centrifuge and hanging column method (Fig.2. 1). Soil water potential (Ψ_{Soil}) in the water-stressed plants was set approximately −0.35 MPa, which was around the temporary wilting point of the soil. Each of the well-watered and water-stressed plants was further separated into two groups, with one group subjected to leaf wetting and the other maintained under normal conditions (no leaf wetting). Leaf wetting was conducted manually using a mist sprayer (Maista-726, Maruhachi Industrials, Tokyo, Japan). Both sides of the leaves were fully wetted, resulting in coverage of approximately 99.9 g m^{-2}. Leaf wetness duration was set according to the measured dew duration in July in the field (see table 1.1 in Chapter 1) since the growth stage of the plant materials used in this experiment approximately corresponded to growth stage of plants in July in the field. Leaf wetting was performed only on the day of measurement.

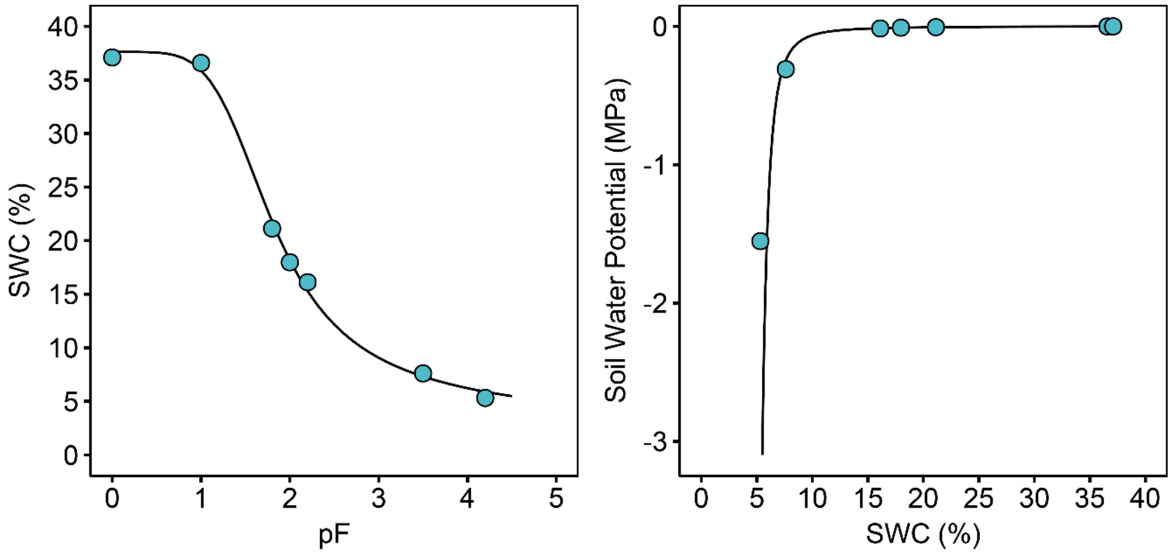

Fig.2. 1 Soil water characteristic curve and the relationship between soil water potential and volumetric soil water content (*SWC*) of the soil used in the greenhouse experiment.

To evaluate how leaf wetting affects plant−water relations, we measured leaf potential after sunset (Ψ_{AS}) and pre-dawn (Ψ_{Pd}) using a pressure chamber (Pump-Up Chamber, PMS Instruments, Albany, OR, USA). The measurements were conducted on April 25 and 26, 2018 on five plants in each treatment plot. In addition, to investigate the relationship between Ψ_{Pd} and *SWC*, with and without leaf wetting. The measurements were performed on September 13 and November 22, 5, and 6, 2018.

The gas exchange measurements were carried out in fully expanded, recently mature leaves a few hours after the Ψ_{Pd} measurement (from 9:00−15:00) on plants that had been subjected to the same treatments as the plants used for the leaf water potential measurements during the night. Note that plants used in the gas exchange measurement were not used for leaf water potential measurements in order to avoid influencing gas exchange with destructive methods used to measure leaf water potential. Added water on the leaves was allowed to completely evaporate before the gas exchange measurements were performed. Photosynthetic rate (A_{N}) and stomatal conductance (g_{S}) were measured with a portable leaf chamber system (LI-6400XT, LI-COR Biosciences, Lincoln, NE, US) under constant conditions of PPFD (1500 μmol m^{-2} s^{-1}) and CO2 concentration (400 μmol mol^{-1}). Air temperature and relative humidity were allowed to follow natural conditions. The gas exchange measurements were performed on April 26, 2018.

2.2.3. Growth and water consumption measurements

To investigate how leaf wetting affects the growth and water consumption of maize, we conducted a follow-up greenhouse experiment for 12 days (June 4–16, 2019) that had a similar experimental design to the plant–water relations and gas exchange studies. The experimental plots consisted of the cross of two factors: two different soil water conditions (well-watered [ww] and water-stressed [ws]) and two types of leaf wetting treatment (no-wetting [nowet] and wetting [wet]). Each plot consisted of five plants, with the *SWC* of each plot monitored using a moisture sensor (EC-5, METER Group, Inc. Pullman, WA, USA) and recorded by a datalogger (Em50, METER Group, Inc. Pullman, WA, USA). All treatments were initiated on Jun 4, when the plants were at the seventh leaf stage. Water stress was imposed by gradually decreasing water supply. When the *SWC* decreased to close to the primary wilting point, the water supply was adjusted to keep the *SWC* at this level. In order to replicate nighttime leaf wetting by dew, leaf wetting was performed using a misting system (MS028M-A, MARUYAMA MFG. CO., INC., Tokyo, Japan). The operation of the misting system was controlled by a timer and was switched on every 30 min for 3 min each time.

Plant height and whole plant leaf area were measured every three days (Jun 4, 7, 10, 13, and 16, 2019). The measurements were con- ducted in five plants per treatment. Leaf area was estimated as follows (Nomiyama et al., 2012):

$$\mathrm{LA} = 0.807 \times (\mathrm{L} \times \mathrm{W}) - 10.684 \tag{2-1}$$

where *LA* is the leaf area of a single leaf (cm^2), *L* is the length of the leaf, and *W* is the width of the leaf. In order to estimate an increase in above- ground dry weight in a non-destructive manner, regression equations were estimated based on a preliminary experiment. The dry weights of the leaves and stem were estimated as a function of leaf area and plant height, respectively (Fig.2. 2) At the end of the experiment, all plants were separated into leaves and stems and oven-dried at 80°C for 72 h to determine the final dry weight of the leaves and stems (above-ground DW_{final}).

To evaluate the effects of leaf wetting on plant–water consumption, transpiration rate (*Tr*) was evaluated by changes in pot weight. The weight of each pot was measured every day after sunset prior to watering (M_{i}). Then, plants were watered according to their treatments, and the weight of the water supplied to the plants was also recorded (M_{water}). Tr was calculated as follows:

$$Tr = (M_{\mathrm{i}} + M_{\mathrm{water}}) - M_{\mathrm{i+1}} \tag{2-2}$$

where M_{i+1} is the weight of the pot measured the day after M_i. Note that we assumed pot weight changed only due to transpiration since the pot surface was covered with plastic film to prevent soil evaporation. Tr was normalized by leaf area, with leaf area between the measurement days (measured only every three days) estimated by linear interpolation. Plant–water use efficiency during the experimental periods was calculated using the ratio between changes in above-ground dry weight and the total amount of transpired water (Tr_{total}) during the experimental periods.

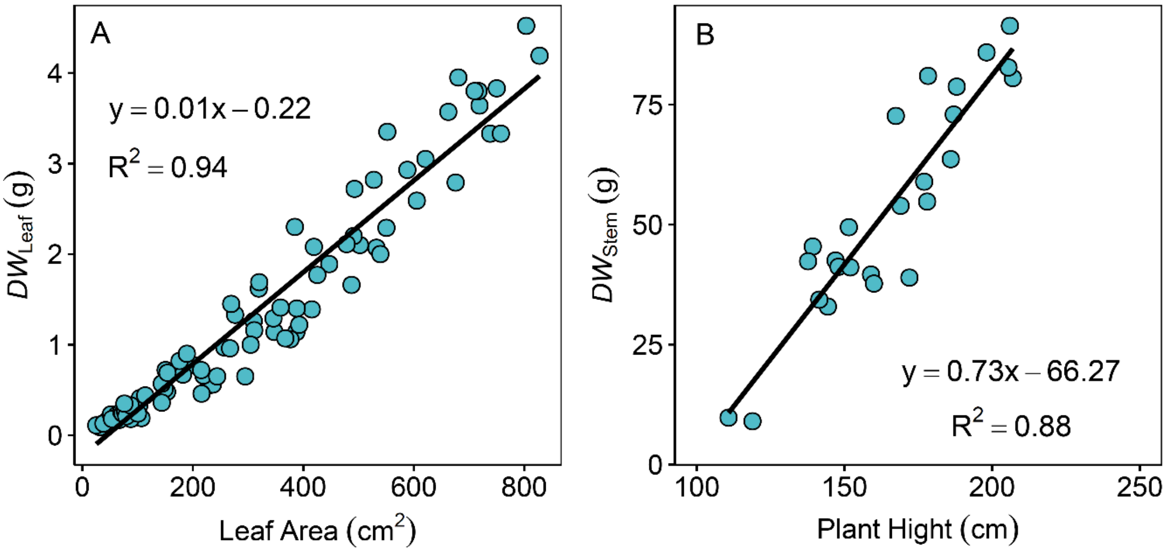

Fig.2. 2 Leaf dry weight (DW_{leaf}) as a function of leaf area (A), and stem dry weight (DW_{stem}) as a function of plant height (B).

2.2.4. Foliar water uptake measurement

In order to investigate the relationship between foliar water uptake (FWU) and plant–water status, FWU was measured in leaves with different leaf water potentials (Ψ_L). A range of Ψ_L was established by setting up various soil water conditions. Initially, Ψ_L was measured with a pressure chamber (Pump-Up Chamber, PMS Instruments, Albany, OR, USA). Then, the capacity for FWU by the maize leaves was measured based on changes in mass before and after leaf submergence, as proposed by Limm et al., (2009). The cut section was immediately sealed after Ψ_L measurement, and the initial mass of the leaf (M_1) was recorded. The leaf was submerged in distilled water for 10 h. After submergence, moisture was removed with a paper towel and the leaf was reweighed (M_2). To minimize errors resulting from residual water on the leaf surface, the leaf was dried naturally for 5 min before the mass was measured again (M_3). The leaf was then momentarily submerged again, after which the moisture was removed with a paper towel before a final weighing (M_4). This instantaneous rewetting did not allow sufficient time for FWU, and thus any increase in mass related to rewetting represented the residual water on the leaf surface. FWU normalized by leaf area was calculated as follows:

$$FWU = \frac{(M_2 - M_1) - (M_4 - M_3)}{LA} \tag{2-3}$$

2.2.5. Statistical analysis

Data normality was checked by the Shapiro–Wilk's test. The effects of soil treatment (well-watered and water-stressed), leaf wetting treatment (with and without leaf wetting), and their interaction on soil water potential, leaf water potential, above-ground dry weight at the end of the experiment, cumulative transpiration rate during the experiment, and water use efficiency were tested using two-way analysis of variance (ANOVA). We used the Tukey–Kramer test ($p < 0.05$) to detect any significant differences among plots. All statistical analyses were conducted using the statistical program R (ver. 3.2.4).

2.3. Results

2.3.1. Effects of leaf wetting by dew on leaf water potential during nighttime

Results of ANOVA showed that there were significant differences in Ψ_{Soil}, Ψ_{As}, Ψ_{Pd}, and $\Psi_{\mathrm{As}}-\Psi_{\mathrm{Pd}}$, between the two soil treatments (well-watered and water-stressed) (Table 2. 1). Significant differences in Ψ_{Pd} and $\Psi_{\mathrm{As}}-\Psi_{\mathrm{Pd}}$ were observed between the two leaf wetting treatments (with and without leaf wetting). Since (i) leaf wetting was commenced after the measurement of Ψ_{As} and (ii) we tried to avoid added water dripping onto the soil, the effects of leaf wetting on both Ψ_{Soil} and Ψ_{As} were not significant. The interactive effect of soil and leaf wetting on Ψ_{Pd} was significant. For the ws-nowet and ws-wet treatments, Ψ_{Soil} was significantly lower than that for the ww-nowet and ww-wet treatments (Fig.2. 3A). Owing to lower soil water availability, Ψ_{As} values for the ws-nowet and ws-wet were significantly lower than those for the ww-nowet and ww-wet treatments (Fig.2. 3B). After the leaf wetting treatment through the night (from 22:00–8:30), Ψ_{Pd} in the ws-nowet treatments was significantly lower than that in the other three plots (ww-nowet, ww-wet, and ws-wet), and no significant differences were found between these three plots (Fig.2. 3C). $\Psi_{\mathrm{As}}-\Psi_{\mathrm{Pd}}$ values for the ww-nowet and ws-wet treatments were much larger than those for the ww-nowet and ww-wet treatments (Fig.2. 3D). No significant difference in this parameter was found between the two well-watered plots (ww-nowet and ww-wet). Also, there was no significant difference in $\Psi_{\mathrm{As}}-\Psi_{\mathrm{Pd}}$ between the two water-stressed plots (ws-nowet and ws-wet).

Fig. 2.4 shows relationship between Ψ_{Pd} and *SWC* of leaves with and without leaf wetting treatments. The difference in Ψ_{Pd} between the wet and no-wet treatments was larger when *SWC* was smaller, while the difference become smaller as *SWC* increase. Fig.2. 5 shows relationship between *FWU* and Ψ_{L}, which showed a significant linear relationship ($p < 0.001$). *FWU* was greater when the Ψ_{L} value taken before the *FWU* measurement was lower.

Table 2. 1 Results of two-way ANOVA for effects of soil treatment, leaf wetting treatment, and their interactions. Soil water potential: Ψ_{Soil} [MPa] ($n = 5$), leaf water potential measured at after sunset: Ψ_{As} [MPa] ($n = 5$), pre-dawn leaf water potential: Ψ_{Pd} [MPa] ($n = 5$), changes in leaf water potential before (i.e. after sunset) and after (i.e.

Parameters	Soil treatment			Leaf wetting treatment			Soil × Leaf wetting		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Ψ_{Soil} [MPa]	1	26.9	<0.001	1	0.159	0.696	1	0.163	0.692
Ψ_{As} [MPa]	1	70.2	<0.001	1	0.0710	0.793	1	0.0240	0.878
Ψ_{Pd} [MPa]	1	19.7	<0.001	1	5.29	<0.05	1	4.63	<0.05
$\Psi_{\mathrm{As}} - \Psi_{\mathrm{Pd}}$ [MPa]	1	64.3	<0.001	1	5.36	<0.05	1	2.55	0.130

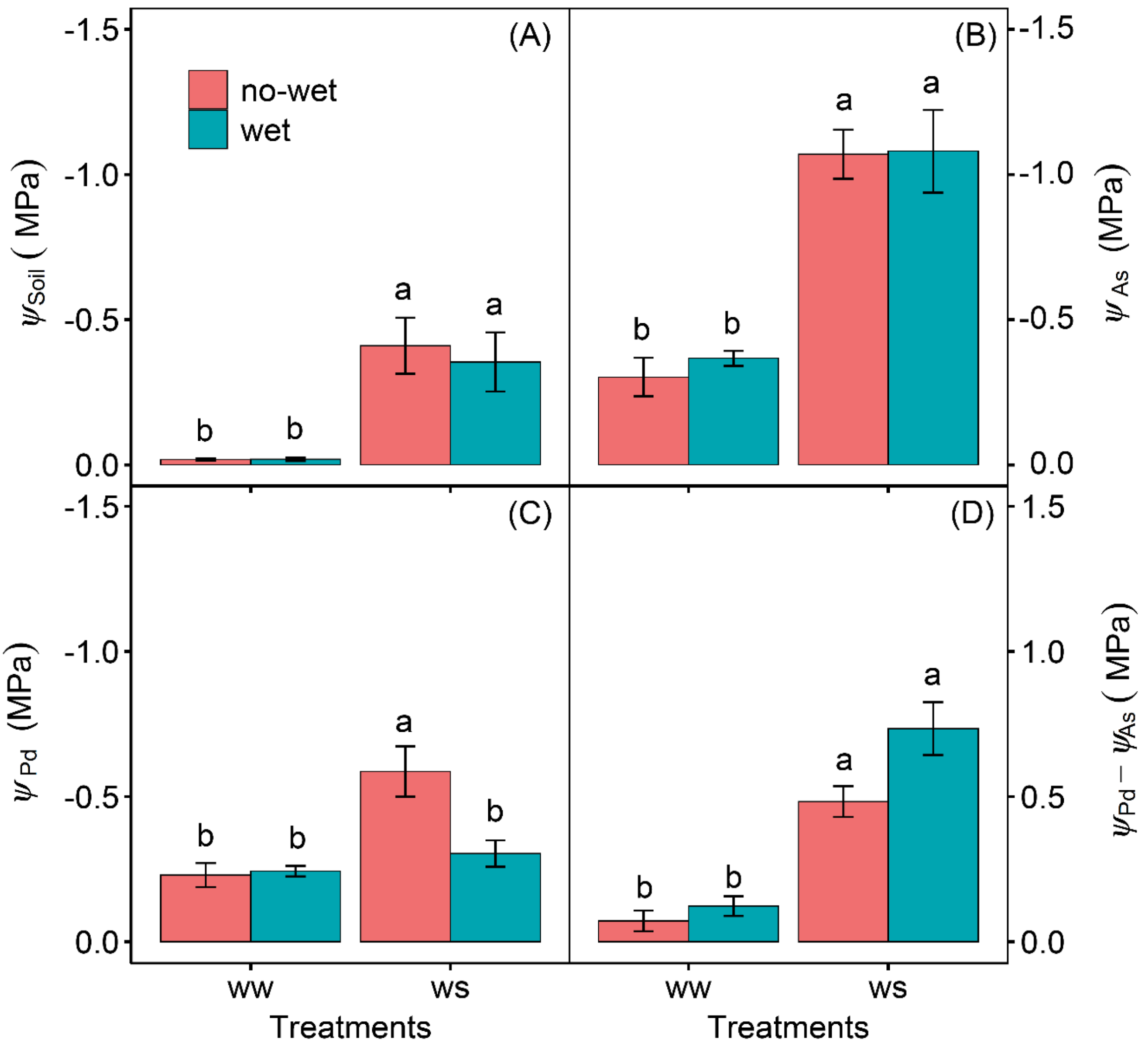

Fig.2. 3 Soil water potential (A: Ψ_{Soil}), leaf water potential measured after sunset (B: Ψ_{As}), pre-dawn leaf water potential (C: Ψ_{Pd}), and changes in leaf water potential before (i.e., after sunset) and after (i.e., pre-dawn) leaf wetting events (D: $\Psi_{\mathrm{Ast}}-\Psi_{\mathrm{Pd}}$) under well-watered (ww) and water-stressed (ws) treatments in maize with (wet) and without (non-wet: nowet) leaf wetting. Means ± SE (n = 5) are shown. Differing lower case letters denote significant differences among treatments ($p < 0.05$). The measurements were conducted on April 25 and 26, 2018.

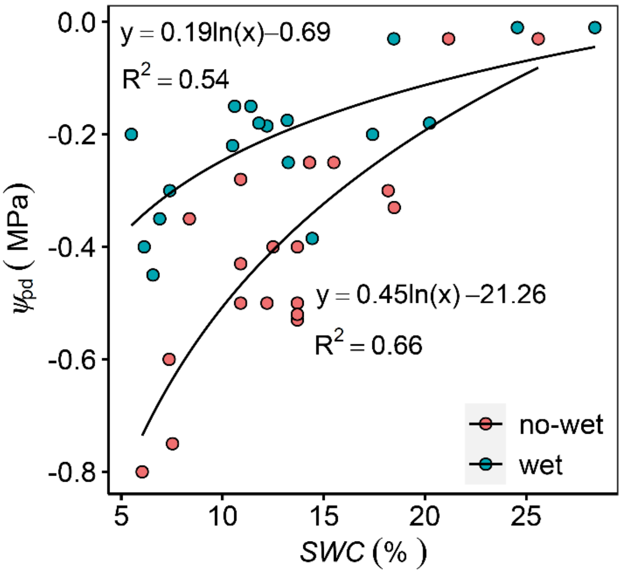

Fig.2. 5 Pre-dawn leaf water potential of wetted (filled circles) and non-wetted (open circles) leaves in relation to volumetric soil water content (*SWC*).

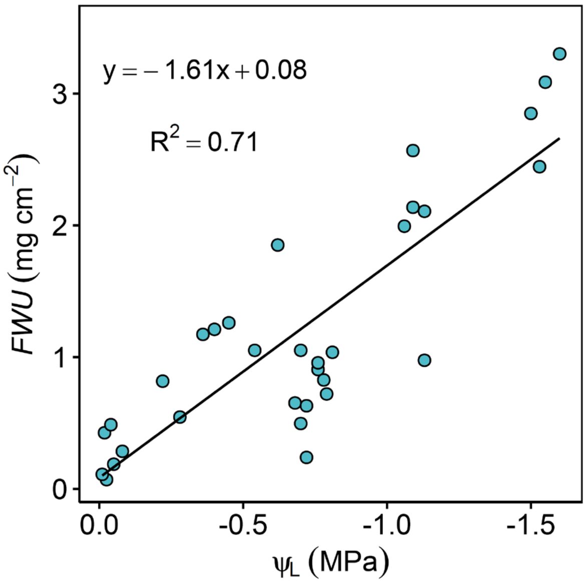

Fig.2. 4 Relationship between foliar water uptake per unit leaf area (*FWU*) and leaf water potential (Ψ_L). Note that leaf water potential was measured before evaluating the foliar water uptake.

2.3.2. Effects of nighttime leaf wetting on daytime gas exchange

Fig. 2.6 shows the diurnal variations in photosynthetic rate (A_N) and stomatal conductance (g_S) in each plot. In the morning (soon after nighttime leaf water had evaporated), both A_N and g_S in all the plots showed almost the same values; this trend continued until 10:00. At 11:00, A_N and g_S in the ws-nowet treatment decreased, while the other plots (ww-nowet, ww-wet, ws-wet) maintained relatively high A_N and g_S values. P_N and g_S for the ws-wet treatment decreased to the same value as that for the ws-nowet treatment. In the well-watered plots (ww-nowet and ww-wet), A_N and g_S were maintained at higher values than in the water-stressed plots (ws-nowet and ws-wet) through the afternoon.

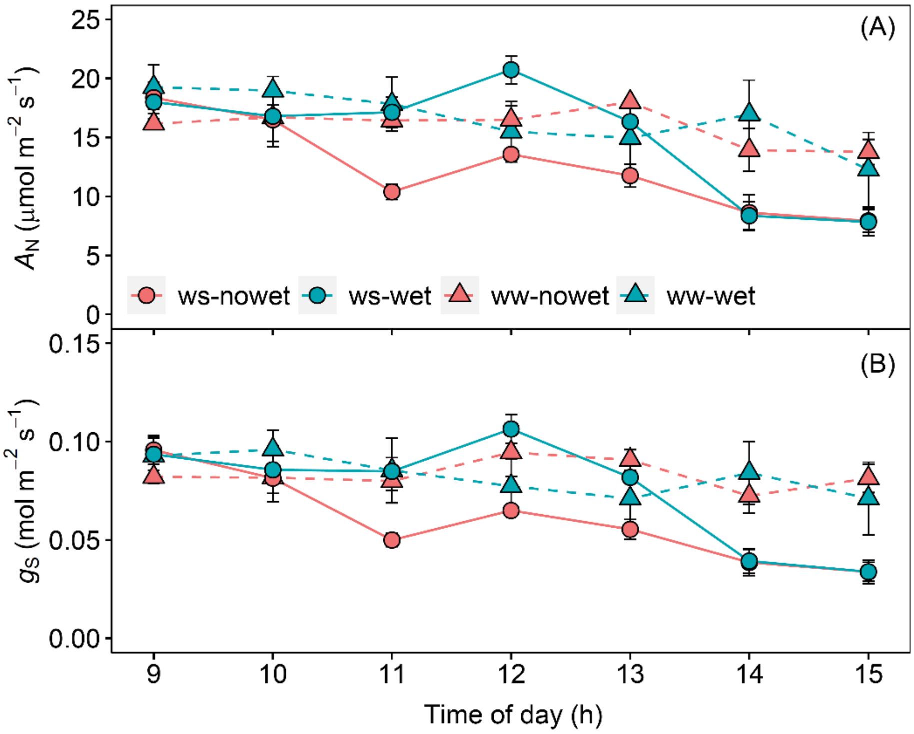

Fig.2. 6 Diurnal variation in photosynthetic rate (A; A_N) and stomatal conductance (B; g_S) per unit leaf area measured under well-watered (circles; ww) and water-stressed triangles; ws) treatments in maize with (blue; wet) and without (red; nowet) leaf wetting. Means ± SE ($n = 3$) are shown.

2.3.3. Effects of leaf wetting on plant growth and water use efficiency

To assess how leaf wetting affects plant growth and water consumption, we conducted a follow-up greenhouse experiment for 12 days. Fig.2.7 shows changes in daily integrated solar radiation (R_S), volumetric *SWC*, and daily transpiration rate (*Tr*) during the experimental periods. *Tr* in the well-watered plots (ww-nowet and ww-wet) followed changes in R_S. On the other hand, *Tr* in the water-stressed plots (ws-nowet and ws-wet) followed the daily changes in R_S until around Jun 7, although *Tr* was suppressed as *SWC* decreased. Fig.2.8 shows the percent increase in plant growth characteristics (leaf area, plant height, above-ground *DW*) from the beginning of the experiment. No clear difference was seen in the percent increase in leaf area, although leaf area in the ws-nowet treatment showed a slightly lower percent increase (compared with the other treatments) in the late periods of the experiment. The percent increase in plant height showed a more distinct difference among the treatments toward the end of the experiment. Plant height in the two well-watered plots (ww-nowet and ww-wet) showed a higher percent increase compared with the two water-stressed plots (ws-nowet and ws-wet). Also, the percent increase in plant height in the ww-nowet treatment tended to be higher than that in the ww-wet treatment, and the percent increase in plant height in ws-wet was higher than that in ws-nowet in the late periods of the experiment. The percent increase in above-ground *DW* in the ww-nowet and ww-wet treatments showed a higher percent increase compared with those of ws-nowet and ws-wet. There was no clear difference between the percent increase in above-ground *DW* in the ww-nowet and ww-wet treatments, whereas the percent *DW* increase in ws-wet tended to be higher than that in ws-nowet.

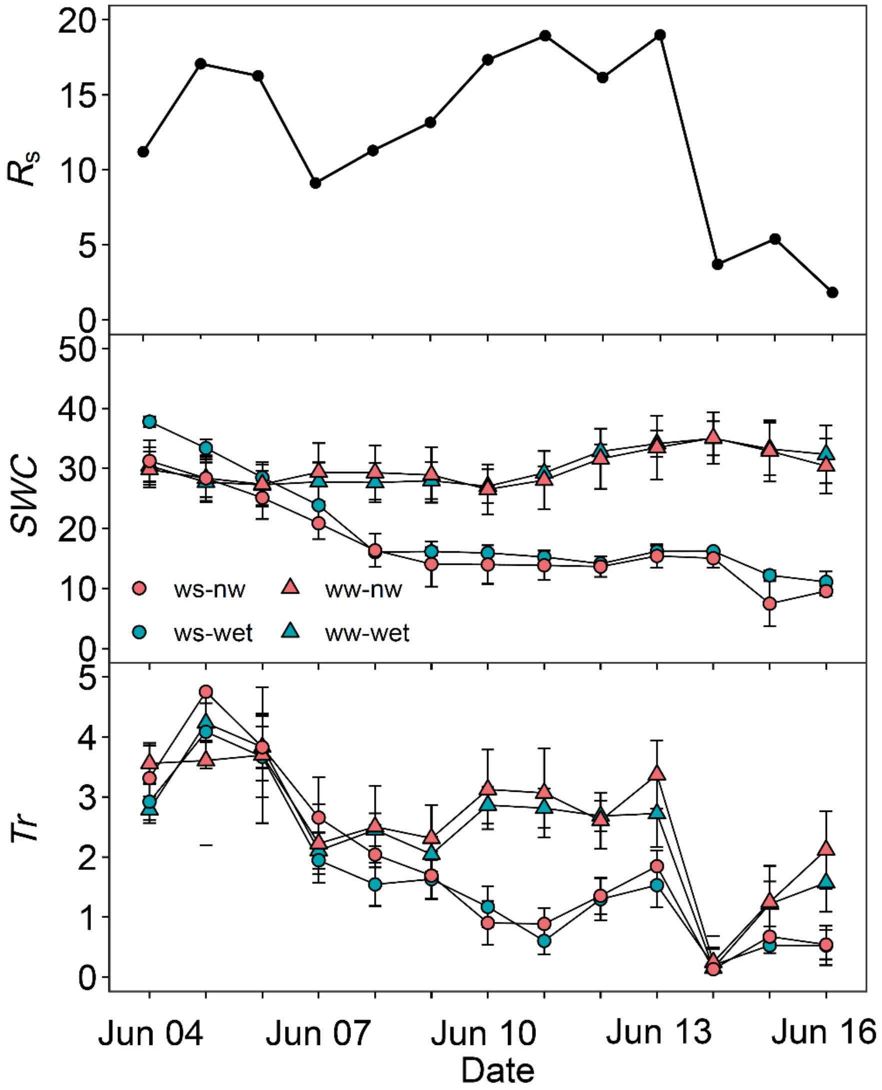

Fig. 2.7 Temporal changes in daily integrated solar radiation (A; R_S), volumetric soil water content (B; *SWC*), and transpiration rate (C; *Tr*) measured under well-watered (triangles; ww) and water-stressed (circles; ws) treatments in maze with (filled symbols; wet) and without (open symbols; nowet) leaf wetting during the experimental periods (June 4–16). Means ± SE ($n = 5$) are shown.

Soil treatment (water-stress treatment) had a significant effect on above-ground DW_{final}, Tr_{total}, and *WUE* (Table 2.2). Leaf wetting had a significant effect on Tr_{total} and *WUE*, but not on above-ground DW_{final}. The interaction effects on *WUE* was also significant. Above-ground DW_{final} values in the well-watered plots (ww-nowet and ww-wet) were significantly higher than those of water-stressed plots (ws-nowet and ws-wet). However, there was no significant difference in above- ground DW_{final} between the same soil treatment groups, indicating that leaf wetting had no effect on above-ground DW_{final}. Tr_{total} values of the well-watered plots (ww-nowet and ww-wet) were significantly higher than those of the water-stressed plots (ws-nowet and ws-wet). Within the same soil treatment groups, Tr_{total} in ww-nowet was significantly higher than that in ww-wet, whereas no significant difference was found between ws-nowet and ws-wet. WUE in the ws-wet treatment was significantly higher than that in the other three plots (ww-nowet, ww-wet, and ws-nowet).

Table 2.2. Results of two-way ANOVA for effects of soil treatment, leaf wetting treatment, and their interactions. Above-ground dry weight at end of the experiment: above-ground DW_{total} [g] (n =5), cumulative transpiration rate over experimental periods: Tr_{total} [mm d^{-1}] (n =5), water use efficiency derived from changes in above-ground dry weight divided by cumulative transpiration rate during the experimental periods: *WUE* [mmol mol^{-1}] (n =5).

Parameters	Soil treatment			Leaf wetting treatment			Soil × Leaf wetting		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Above-ground DW_{final} [g]	1	25.5	<0.001	1	0.034	0.856	1	0.592	0.453
Tr_{total} [mm d^{-1}]	1	570	<0.001	1	10.7	<0.01	1	0.526	0.478
WUE [mmol mol^{-1}]	1	15.9	<0.01	1	10.2	<0.01	1	6.37	<0.05

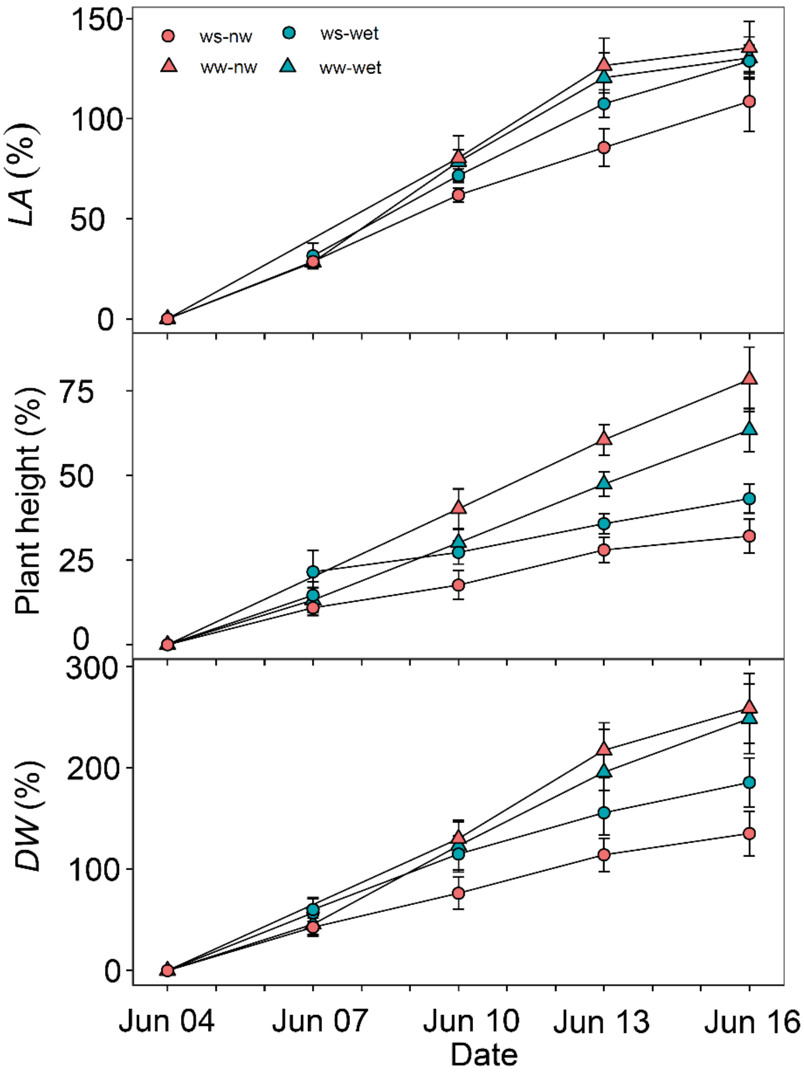

Fig. 2.8 Temporal changes in percent increase of leaf area (A), plant height (B), and above-ground dry weight (C; above-ground *DW*) measured under different soil water conditions (triangles; ww and circles; ws) in maize with (filled symbols; wet) and without (open symbols; nowet) leaf wetting during the experimental periods (June 4–16, 2018). Means ± SE (n = 5) are shown.

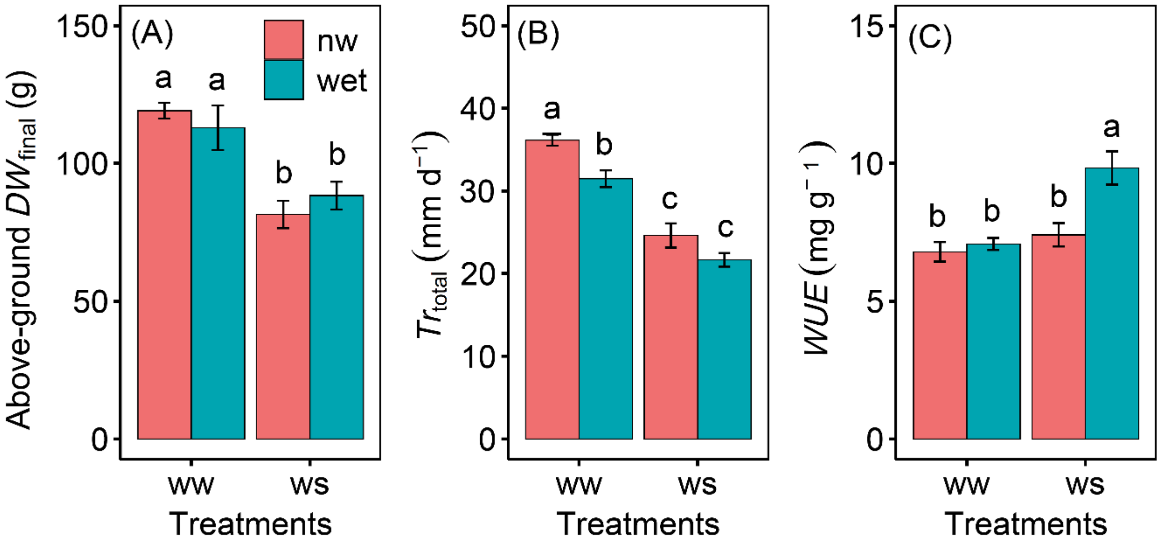

Fig. 2.9 Above-ground dry weight at the end of experimental period (A; above-ground DW_{total}), transpiration rate integrated over experimental periods (B; Tr_{total}), and water use efficiency (C; *WUE*) under well-watered (ww) and water-stressed (ws) treatments in maize with (wet) and without (no-wet: nowet) leaf wetting. Means ± SE (n = 4) are shown. Differing lower case letters denote significant differences among treatments (p

2.4. Discussion

2.4.1. Effects of leaf wetting by dew on nighttime rehydration process

FWU is a common phenomenon across many plant species, and it is known as an important water acquisition pathway subsidiary to root water uptake (Dawson and Goldsmith, 2018). The present study showed that maize leaves also have the capacity for *FWU* (Fig. 2.5). Maize is one of the major crops in northwestern China (Tan and Zheng, 2017) and leaf wetting by dew frequently occurs in this region (Zhang et al., 2015; Meng and Wen, 2016; Zhuang and Zhao, 2017). This suggests that *FWU* is likely a common phenomenon is agricultural fields of the region and has a large impact on the water cycle.

Our results show that *FWU* increases as Ψ_L decreases, indicating that the water potential gradient between the interior of the leaf and dew water on the surface of the leaf is the driving force of *FWU*. Therefore, rehydration by *FWU* may be more effective when water stress becomes more severe (Fig. 2.4). Absorbed water through *FWU* would be transferred along the water potential gradient inside the plant and re-enter the atmosphere through transpiration. However, a few studies have reported that absorbed water from leaf surfaces could also redistributed to the soil via the plant (Eller et al., 2013; Zhang et al., 2019, 2019b). Although the *FWU* of leaf wetting by dew can positively affects plant-water status, it may have little effect on plant-water relations when plants have sufficient soil water availability. This is probably because of the higher resistance of the *FWU* pathways compared with the rood water uptake pathway (Guzmán–Delgado et al., 2018).

2.4.2. Subsequent effects of nighttime leaf wetting on daytime gas exchange and plant growth

Leaf wetting by dew can both directly and indirectly affect plant gas exchange. At nighttime, leaf wetting by dew would improve plant-water status by *FWU* and consequently contributes to improving daytime photosynthesis under water-stress conditions (Simonin et al., 2009; Eller et al., 2013). Leaf wetting by dew also affects plant gas exchange after sunrise, decreasing transpirational water loss by decreasing evaporative demand (Yasutake et al., 2015). Such a decrease in transpiration would mitigate a decrease in photosynthesis by stomatal closure due to excessive transpirational water loss (Yokoyama et al., 2019). However, as reported in several studies, leaf wetting could also decrease photosynthesis by blocking CO_2 uptake through stomata (Ishibashi and Terashima, 1995; Hanba et al., 2004) In addition, photosynthesis can decrease under leaf wetting conditions for reasons other than stomatal blockage due to a water film (Berry and Goldsmith, 2020). In this study, leaf wetting contributed to the maintenance of A_N and g_S under water-stress conditions (ws-ww treatment). Whereas plant without leaf wetting (ws-nowet) showed a rapid decrease in A_N and g_S under water-stress conditions (Fig. 2.6). On the other hand, no clear difference was found between the gas exchange parameters of ww-nowet and ww-wet. In our study, the gas exchange measurement started after leaf moisture was evaporated since it is impossible to evaluate some important gas exchange parameters (i.e., *Tr* and g_S) when leaves are wet. Therefore, we could not evaluate gas exchange under leaf wetting conditions. However, it can be assumed that there is a tradeoff between carbon gain and water loss under leaf wetting conditions. A longer leaf wetting duration may suppress photosynthesis for a longer time, yet reduced water loss by transpiration may consequently increase future photosynthesis and may offset the reduction in photosynthesis by leaf wetting after sunrise. Our findings show that plant-water status is a key factor in whether leaf wetting benefits plant gas exchange. Leaf morphological traits such as leaf water repellency may also be important factors in determining how leaf wetting affects plant gas exchange. Leaves with lower water repellency would hold a larger amount of water, and a larger proportion of the leaf area would be covered with a water film, which may result in lower photosynthesis and transpiration under leaf wetting conditions (Hanba et al., 2004; Urrego-Pereira et al., 2013).

The results of this study showed that leaf wetting by dew would have significant effects on plant physiology under water-stress conditions, which may consequently affect plant growth characteristics. As reported in several studies, leaf wetting suppresses transpirational water loss by reducing evaporative demand. Specifically, leaf wetting increases vapor pressure near the leaf surface and suppresses an increase in leaf temperature (Yasutake et al., 2015; Yokoyama et al., 2019). Such effects may be beneficial in terms of water relations but are not always so for photosynthesis. Therefore, we here propose *WUE* as a suitable candidate for evaluating the physiological significance of leaf wetting. Several studies have reported the positive effects of leaf wetting by dew or fog on plant growth through its effects on plant–water relations under both well-watered and water-stressed conditions (Cassana and Dillenburg, 2013; Eller et al., 2013; Zhang et al., 2019). Further studies have reported that the positive effects of leaf wetting on plant–water relations not only contribute to higher photosynthesis but also facilitate turgor-driven growth, which would increase growth rate (Steppe et al., 2018; Schreel et al., 2019). In our study, the effect of leaf wetting on above-ground DW_{final} was not statistically significant; however, based on the trend in growth parameters and the physiological significance of leaf wetting under water stress, we assume that leaf wetting would have positive effects on plant growth under water-stress conditions. In terms of water consumption, no significant difference was found between Tr_{total} of the ws-nowet and ws-wet treatments because transpiration in the ws-nowet treatment was strongly inhibited by stomatal closure due to water stress. Contrary to previous studies, growth rate in the ww-wet treatment was lower than that of ww-nowet. One possible explanation for this is that if plants have sufficient water, the positive effects of leaf wetting on photosynthesis would be very small because the positive effects of leaf wetting on photosynthesis occur via its effects on plant–water relations (Simonin et al., 2009; Eller et al., 2013). On the other hand, the negative effects of leaf wetting on photosynthesis would be maintained (Ishibashi and Terashima, 1995; Hanba et al., 2004; Berry and Goldsmith, 2020). Therefore, the negative effects of leaf wetting would become relatively strong under well-watered conditions, resulting in a lower growth rate. One interesting finding is that the manner in which leaf wetting affects plant physiology changes depending on plant–water status, which resulted in different *WUE* values among experimental plots.

2.5. Conclusion

This study was conducted to investigate the impact of leaf wetting by dew on crop production in a semiarid environment in terms of its effects on plant physiological functions. Specifically, 1) we investigated the frequency and duration of leaf wetting by dew through the maize cultivation periods, and its effect on the leaf water potential in the maizefield of northwest China, and 2) evaluated the effects of leaf wetting by dew on plant physiological functions based on the greenhouse experiments. Our results showed that although the amount of dew may be much smaller than that of conventional resources, it could have a significant impact on agricultural production in arid and semiarid climates through its effects on plant physiological functions in maize. When plants had sufficient water, neither positive nor negative effects of leaf wetting on plant physiological function and growth were found. However, when plants were under water-stressed conditions, the dew on leaves was directly absorbed from the leaf surface of maize during nighttime, contributed to an improvement in plant water potential and consequently increased photosynthesis during the daytime. As a result, dew had significantly increased plant water use efficiency under water-stressed conditions. Our study indicates that plant–water status is one of the key factors determining how leaf wetting affects plant physiological functions. The question raised by this study is the extent of water stress that maximize water use efficiency while avoiding yield loss. A limitation of our study is that the water-stressed treatment imposed in the experiment was relatively severe, which resulted in lower plant growth, indicating lower crop yield. An ideal outcome is that increasing water use efficiency under leaf wetting condition while keeping crop yield under some extent of water stress. Therefore, the investigation of the “optimum” extent of water stress under leaf wetting condition would help us to establish better water management of agriculture in an arid and semiarid region.

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Chapter 3 Effects of leaf wetting by dew on daytime gas exchange

3.1. Introduction

Leaf wetting occurs in nearly all ecosystems on earth not only by precipitation but also by dew and fog (Beysens et al., 2005; Baguskas et al., 2018; Steppe et al., 2018), and thereby leaves experience considerable time under wet conditions (Dawson and Goldsmith, 2018) indicating that importance of understanding the effects of leaf wetting on plants. The effects of leaf wetting on plants have been studied from several perspectives. The relationship between leaf wetting and pathogen infection has been well-studied because the duration of leaf wetting is a dominant factor for the incidence of plant disease (Carisse et al., 2000; Uddin et al., 2003). In contrast, leaf wetting is also regarded as a positive factor because water on the leaf surface can be directly absorbed by leaves and contributes to rehydration (Steppe et al., 2018; Binks et al., 2019). To date, at least 233 species and spanning 77 plant families have been identified to have the capacity for absorbing water from leaves (Berry et al., 2019). These two topics related to leaf wetting (i.e., plant disease and foliar water uptake) have been intensively studied in recent years. However, understanding the relationship between gas exchange and leaf wetting has not been well investigated as only a few studies have reported the effects of leaf wetting on leaf gas exchange in the last 10 years (Aparecido et al., 2017; Gerlein-Safdi et al., 2018; Berry and Goldsmith, 2020). Understanding the effects of leaf wetting on gas exchange is critical for modeling ecosystem primary production and also for agricultural production, as gas exchange is one of the fundamental physiological processes for crop production.

One of the greatest challenges when investigating the effects of leaf wetting on plant gas exchange is the difficulties of measuring key gas exchange parameters, i.e., transpiration rate and stomatal conductance, of wet leaves. Generally, the leaf gas exchange of a plant is measured by the open chamber method (Nomura et al., 2020). In the open chamber method, transpiration rate is measured by the H_2O gas balance inside the chamber. Because transpiration from the leaf is the only source that affects H_2O gas balance when the leaf is not wetted, whereas both evaporation of water on the leaf surface and transpiration affects H_2O gas balance when the leaf is wet. Thus, it is difficult to separately evaluate evaporation of leaf surface water and transpiration of leaf when a leaf is wet. In order to overcome this challenge, we proposed a new method for measuring the transpiration of wet leaves (Yasutake et al., 2018). In this method, evapotranspiration of leaf surface water and leaf transpiration can be measured by the chamber method, and transpiration can be measured by the stem heat balance method. However, this method had only been tested under steady-state conditions, and thus testing the method under dynamic conditions is the next step of the research.

Recent evidence suggests that leaf wetting is likely to have negative effects on photosynthesis (Ishibashi and Terashima, 1995; Hanba et al., 2004; Gerlein-Safdi et al., 2018). One of the major effects of leaf wetting on photosynthesis is the decrease in photosynthetic rate due to stomata covered by water film. Since CO_2 is 10000 times slower in water than air, CO_2 uptake through stomata could be suppressed (Ishibashi and Terashima, 1995). In addition, Berry and Goldsmith (2020) reported a decrease in photosynthetic rate when wetting the abaxial side of the leaf, which only has stomata on the adaxial side. However, Berry and Goldsmith (2020) also found a decrease in photosynthetic rate when wetting the adaxial side of the leaf, which only has stomata on the abaxial side. These results suggest that the photosynthetic rate would be decreased when leaves are wet, but not only due to stomatal blockage by water film. One reason for decrease in photosynthetic rate is effects of leaf wetting on leaf temperature. This is because, activity of photosynthetic enzyme increase as the leaf temperature increase within the optimum range (Bernacchi et al., 2001; Bernacchi, 2003). Another possible reason for decrease in photosynthetic rate is changes in light condition received by leaf surface. Brewer and Smith (1991) reported that the lensing effects of water droplets on leaf surfaces increased incident sunlight by over 20-fold at the focal point, which would damage the photosynthetic light-harvesting systems and subsequently reduce photosynthetic rate.

In the natural environment, leaf wetting by dew occurs in the nighttime and continues to a few hours after sunrise, suggesting that both negative and positive effects of leaf wetting by dew on photosynthesis change along the diurnal cycle (Yokoyama et al., 2021). During the nighttime, leaf wetting would have positive effects on plant water relations through foliar water uptake or reducing nighttime transpiration (Carisse et al., 2000; Dawson and Goldsmith, 2018), which would subsequently have positive effects on photosynthesis after the evaporation of leaf wetting by dew. During the early morning, photosynthetic rate may be reduced because of the occlusion of stomata by leaf wetting, reduced leaf temperature, and the lensing effect (Brewer et al.,1991; Bernacchi, 2003; Hanba et al., 2004). At the same time, leaf wetting would reduce transpirational water loss during the early morning, which has positive effects on plant water status, and subsequently have positive effects on photosynthesis after evaporation of leaf wetting by dew. Therefore, it is important to evaluate the effects of leaf wetting by dew on photosynthesis with consideration of dynamic changes in the effects of leaf wetting by dew.

In this study, I explored costs and benefits associated with leaf wetting by dew within a temporal context by testing the following hypothesis. In the early morning, when leaves are still wet, (1) leaf wetting would cover stomata, thereby suppressing transpiration but little effect on photosynthesis under low light conditions. (2) leaf wetting would increase leaf surface albedo, which reduces photosynthesis. (3) reduced transpirational water loss during the early morning would benefit photosynthesis after leaf wetting was evaporated. Diurnal changes in gas exchange were measured with a whole plant chamber system; thereby, comprehensive effects of leaf wetting in the diurnal scale were evaluated.

3.2. Materials and methods

3.2.1. Plant materials and growth conditions

Maize (*Zea mays* L.) cultivar 'P2307' was used as the plant material. The seeds were germinated and grown in an experimental greenhouse (area; 90 m^2) at Ito Plant Experimental Fields & Facilities, Faculty of Agriculture, Kyushu University, Japan. The plants were grown using a standard nutrient solution (Otsuka AgriTechno Co. Ltd., Japan) with an electrical conductivity of 2.0 dS m^{-1}. The nutrient solution contained 17.1 mmol (NO^{3-}) L^{-1}, 1.1 mmol (PO_4^{3-}) L^{-1}, 1.6 mmol (SO_4^{2-}) L^{-1}, 8.4 mmol (K^+) L^{-1}, 1.5 mmol (Mg^{2+}) L^{-1}, and 3.9 mmol (Ca^{2+}) L^{-1}. At the third to fourth leaf stage, the plants were transplanted to larger plastic pots (8-L volume) filled with soil (6.7% clay, 14.7% silt, 78.6% sand). A ventilation fan was operated when T_A exceeded 20°C, and the side windows of the greenhouse were kept open during the cultivation period. Environmental conditions in the greenhouse, i.e., solar radiation (R_S), photosynthetic photon flux density (*PPFD*), air temperature, relative humidity, and CO_2 concentration, were measured using a pyranometer (CAP-SP-110, Apogee Instruments, Logan, UT, USA), quantum sensor (CAP-SQ-110, Apogee Instruments, Logan, UT, USA), and a datalogger-integrated temperature–humidity–CO_2 sensor (TR-76Ui, T&D Corporation, Matsumoto, Japan), respectively. The data from each instrument were recorded by a datalogger (GL820, Graphtec Corporation, Yokohama, Japan) at 10-min intervals.

3.2.2 Evaluation of gas exchange response in wet leaves

In order to evaluate the influence of stomatal blockage by leaf wetting, gas exchange was measured in leaves with surface coated with Vaseline. First, the gas exchange (photosynthetic rate: A_N and stomatal conductance: g_S) of the untreated leaf (gas exchange of both adaxial and abaxial sides) was measured with a portable leaf chamber system (LI-6400XT, LI-COR Biosciences, Lincoln, NE, US). Then, either the adaxial or abaxial surface of the leaf was coated with Vaseline, and gas exchange was measured again. Finally, both sides of the leaf surface were coated with Vaseline, and gas exchange was measured. When both sides of the leaf surface were coated with Vaseline, the gas exchange rate was almost zero, showing that Vaseline is able to block gas exchange. All the gas exchange measurement was conducted in fully expanded leaves under conditions of PPFD at 1500 and 300 μmol m^{-2} s^{-1}, CO_2 concentration at 400 μmol mol^{-1}, block temperature at 25 °C, and relative humidity at 40−60%.

When either adaxial or abaxial leaf surface is coated with Vaseline, the reduction in gas exchange may be determined by the number of stomata in each side of the leaf, and thus the number of stomata in adaxial and abaxial leaf surface and stomatal ratio. Stomatal impression was obtained using celluloid plates and amyl acetate. Briefly, amyl acetate solution was applied to the celluloid plate, and the celluloid plate was pressed on either adaxial or abaxial leaf surface for 3 min. The number of stomata was counted by microscope

(B120C-E1, Amscope, Irvine, CA, US), and the stomatal ratio was calculated as a ratio of adaxial to abaxial stomatal number.

In order to investigate how changes in leaf temperature induced by leaf wetting affect leaf photosynthesis, the temperature-photosynthetic response curve was measured with a portable leaf chamber system (LI-6400XT, LI-COR Biosciences, Lincoln, NE, US). Photosynthetic rate (A_N) was measured at the leaf temperature (T_L) of 12°C, 15°C, 20°C, 25°C, and 30°C. PPFD and reference CO_2 concentration were maintained at 300 μmol m^{-2} s^{-1} and 400 μmol mol^{-1}, respectively.

To investigate whether presence of water on leaf surface changes light conditions perceived by leaf surface, reflectance, transmittance, and absorbance of a maize leaf was measured with and without leaf surface wetting. For the measurement of leaf reflectance, transmittance, and absorbance, we developed an integrating sphere by using 3D printer (Davinchi Jr. Pro X+, XYZprinting Japan, Tokyo, Japan). ABS (acrylonitrile butadiene styrene) filament was used as a printing material for the integrating sphere. The integrating sphere has diameter of 6 cm and has three ports on top (4 cm^2), bottom (1 cm^2), and side (0.03 cm^2). When measuring the reflectance of a leaf, the leaf was placed between the integrating sphere (top) and a optical black sheet (bottom), and light was provided with a custom made LED , which has spectral distribution from 400 nm to 1000 nm through the top port of the integrating sphere. The reflectance was measured with a spectroradiometer (BIM-6002A-10-S03L00F05G02,Yixi Intelligent Technology, Shenzhen, China), which can detect spectral distribution between 400 nm and 1000 nm. The spectroradiometer was inserted from the side port of the integrating sphere and fixed at the degree of 60° from the horizontal leaf surface. For the measurement of transmittance, leaves were placed top of the integrating sphere and a hollow cylindrical cube. Light was provided with the LED from the top of the hollow cylindrical cube, and the bottom port of the integrating sphere was closed with a same materials used for the integrating sphere. The transmittance of leaf was also measured by the spectroradiometer inserted from the side port (fixed horizontal to the leaf surface). The absorbance was calculated as the residual of reflectance and transmittance.

3.2.3. Measurement of leaf wetting effects on diurnal changes in gas exchange

Gas exchange measurements were conducted using the whole–plant chamber system described by Yasutake *et al*. (2018), which can independently evaluate the transpiration and evaporation rates of leaf surface water by combining stem heat balance method and chamber method when the plants are wetted (Fig. 3.1). The transpiration rate (Tr) of wetted plants were measured with a sap flow sensor (SGB–10WS, Dynamax, Houston, TX, USA) attached to the stem base. Evapotranspiration (transpiration from a plant and evaporation of leaf surface water) rate was evaluated by the gas balance of inflowing and outflowing H_2O gas concentration. H_2O gas concentration was calculated from T_A and RH measured with a temperature-humidity sensor (HMP155, Vaisala, Helsinki, Finland). When plants were not wetted, Tr was measured by both the sap flow sensor and the gas balance of the chamber (Fig. 3.2). Photosynthetic rate (A_N) was evaluated by the gas balance of CO_2 gas concentration which was measured with an infrared gas analyzer (LI–820, LI-COR Biosciences, Lincoln, NE, US). Vapour pressure near the leaf surface (e_A) was calculated from T_A and RH measured at 3 cm above the leaf surface with three temperature–humidity sensors (HMP60, Vaisala, Helsinki, Finland). Leaf temperature (T_L) was measured with a copper-constantan thermocouple at three different leaves and used for calculating leaf vapor pressure (e_L). Leaf to air vapor pressure deficit ($\mathrm{VPD_L}$) was evaluated as e_L–e_A and Stomatal conductance (g_S) was evaluated as $Tr\cdot P/(e_L-e_A)$ where P is the atmospheric pressure (because inside of the chamber was well circulated by stirring fans, boundary layer conductance was negligible). All data were recorded with a program data logger (CR–1000, Cambell Scientific Inc. Logan, UT, US).

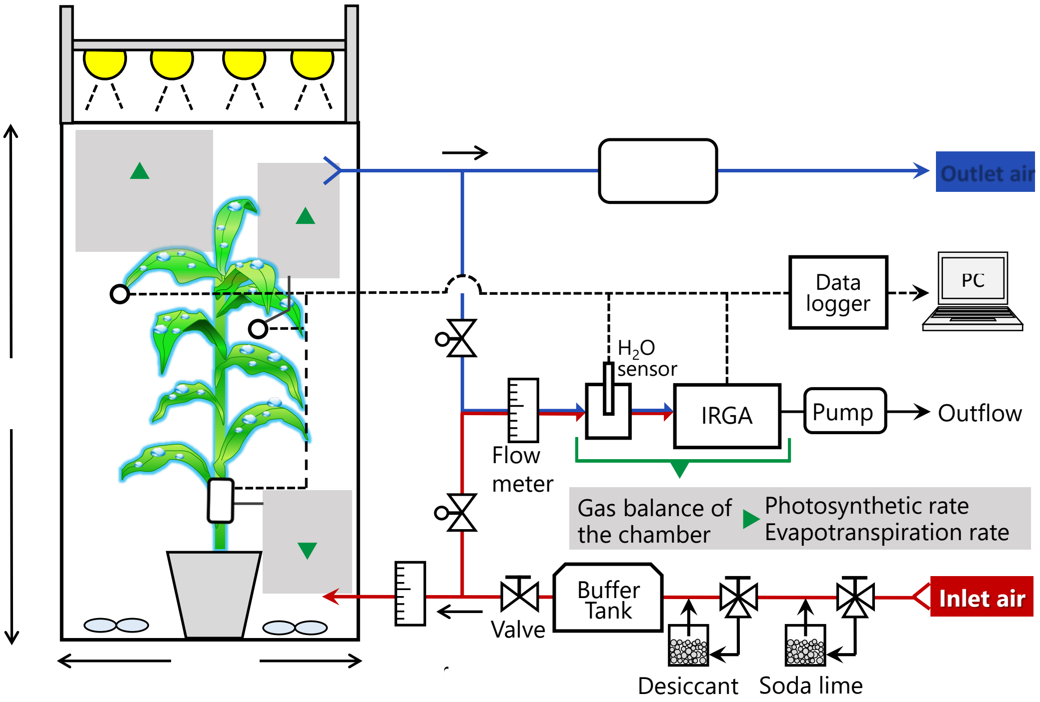

Fig. 3.1 Schematic diagram of a whole plant chamber system for analyzing the gas exchange of a whole-plant.

The chamber was placed in a laboratory room in Kyusyu University. Twelve LED (LLM031, Stanley Electric Co. Ltd, Tokyo, Japan) bulbs were used as the light source. The wavelength of LED is 400 – 800 nm and two peaks in light intensity at 450 and 550 nm. More detailed characteristics of the LED is described in Hidaka et al. (2013). The CO_2 concentration was maintained at 421.8 ± 1.7 μmol mol^{-1}. Average horizontal distribution of *PPFD* at the height of 20, 40, 60, 100 cm from the ceiling of the chamber (chamber height

120 cm) was approximately 1554, 1551, 1121, 535 μmol m^{-2} s^{-1}, respectively (Fig. 3.3). Environmental conditions such as light intensity, air temperature, and vapor pressure during the gas exchange measurements were controlled by LED and air conditioning units to replicate a dryland environment (Fig.3.4). Before the gas exchange measurement, water stress was slowly imposed on the plants by gradually reducing the amount of watering. Finally, Soil water content was adjusted to around 8.3% to replicate the water stress condition of dryland in both treatments. After that, the plants were divided into two treatment groups, consisting of wet treatment and no-wet treatment. In the wet treatment, leaves were fully wetted from 22:00 to 8:00 by misting equipment (MS028M-A, MARUYAMA MFG. CO., INC., Tokyo, Japan) to replicate the leaf wetting by dew. In the no-wet treatment, plants were not wetted but remained in normal conditions.

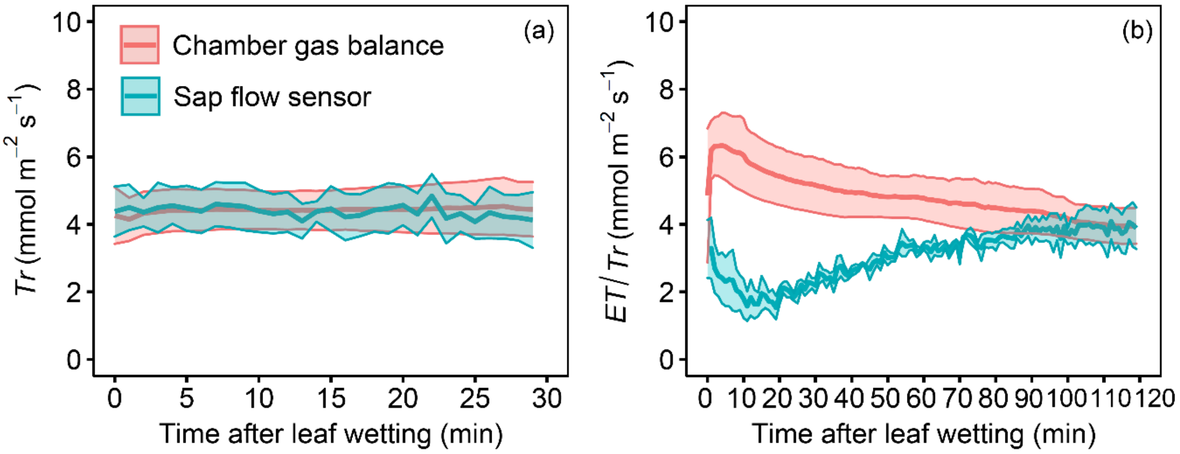

Fig. 3.2 Time course changes of transpiration rate (*Tr*) and evapotranspiration rate (*ET*) measured by gas balance of a chamber and a sap flow sensor without (a) and with (b) leaf wetting. the solid lines denote mean values and the shaded parts denote standard error (mean ± SE).

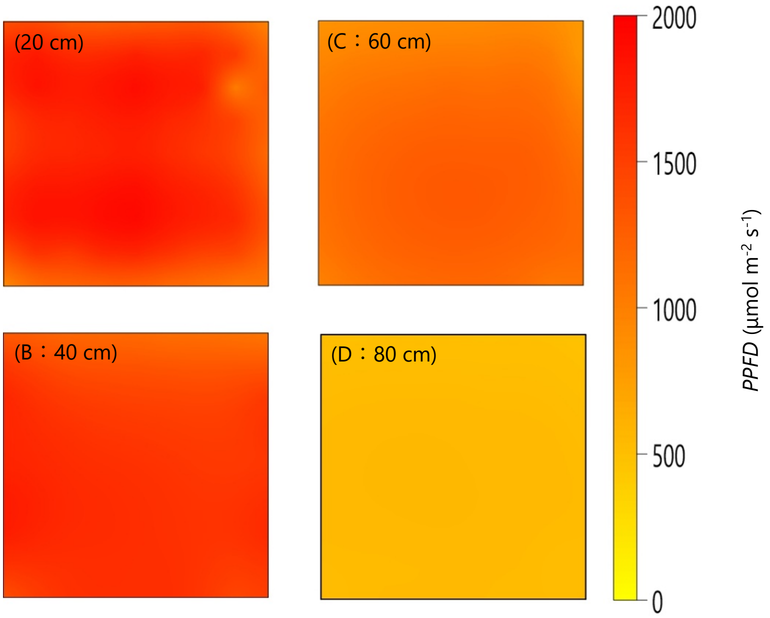

Fig. 3.3 Horizontal distribution of photosynthetic photon flux density at different height (20, 40, 60, 100 cm from celling of the chamber).

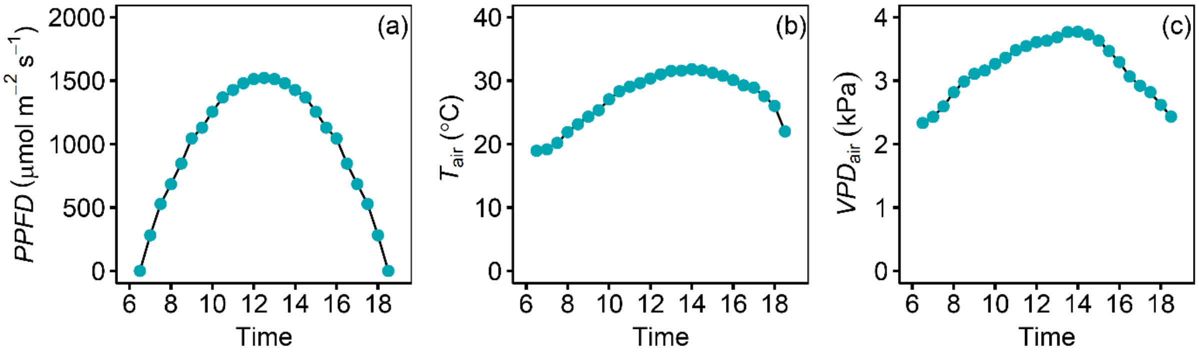

Fig. 3.4 Diurnal changes in photosynthetic photon flux density (*PPFD*), air temperature (T_A), vapor pressure deficit (VPD) during the measurement periods.

3.3. Results

3.3.1 Influence of stomatal blockage by leaf wetting on gas exchange

A_N and g_S significantly decreased by coating the leaf surface by Vaseline under both low (PPFD at 300 μmol m^{-2} s^{-1}) and high light condition (PPFD at 1500 μmol m^{-2} s^{-1}) (Fig. 3.4). In the low light condition, no significant difference was found between adaxial and abaxial gas exchange parameters (A_N and g_S). Compared to both sides A_N, adaxial and abaxial A_N decreased 17% and 16%, respectively. Both adaxial and abaxial g_S decreased 31% compared with both sides g_S. In the high light condition, significant difference was found between adaxial and abaxial gas exchange parameters (A_N and g_S). Compared to both sides A_N, adaxial and abaxial A_N decreased 56% and 34%, respectively in the high light condition. Both adaxial and abaxial g_S decreased 69% and 50%, respectively, compared with both sides g_S. The stomatal density of maize leaves were 77.3 ± 2.46 on the adaxial sides and 106.9 ± 2.79 on the abaxial sides, respectively, which resulted in stomatal ratio of 0.72.

Fig. 3.7 shows photosynthetic-temperature response curve of maize leaves. A_N increased as the leaf temperature (T_l) increase between 15°C and 25°C. A_N was almost constant between the T_l of 12°C and 15°C, and 25°C and 30°C, respectively.

The spectral distribution of the reflectance, transmittance, and absorbance of the leaves with and without leaf wetting showed similar pattern with slight difference (Fig. 3.8). The reflectance of the leaf surface was slightly higher in leaves without leaf wetting than with leaf wetting. The difference of reflectance between without and with leaf wetting was around 2% in the visible region (400 nm to 700 nm) and around 3–4% in the NIR region (700 nm to 1000 nm). The transmittance of leaves with and without leaf wetting was almost same between 400 nm and 500 nm, while transmittance in leaves with leaf wetting was slightly higher (around 2%) between 500 nm and 1000 nm, except around 680 nm. The absorptance of leaves with leaf wetting was higher from 400 nm to 500 nm and from 600 nm to 700 nm. The difference of absorbance between with and without leaf wetting was not found around the wavelength at 560 nm.

Table 3.1. Stomatal density, number of adaxial or abaxial stomata / total number of stomata, and stomatal ratio of maize leaf.

	Adaxial		Abaxial
Stomatal density	77.3 ± 2.46		106.9 ± 2.79
Number of adaxial or abaxial stomata / total number of stomata	0.58		0.42
Stomatal ratio		0.72	

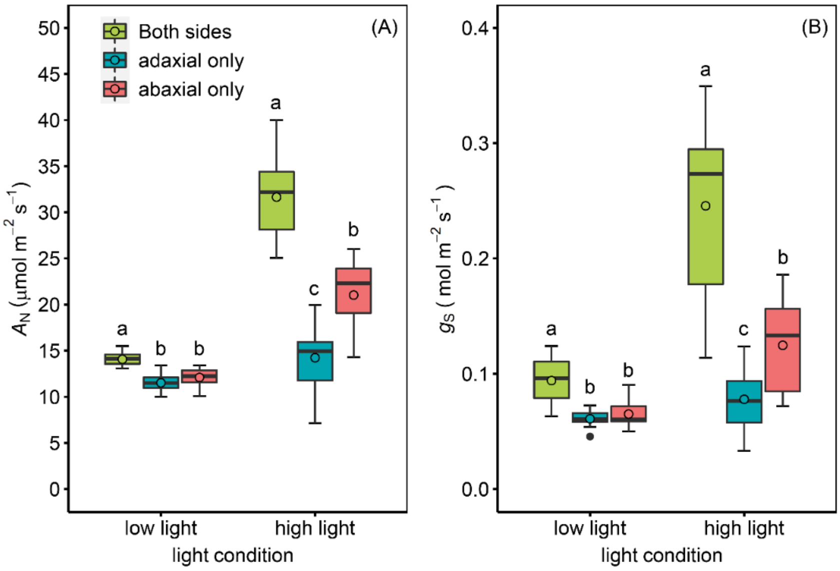

Fig. 3.5 Adaxial, abaxial, and both sides of leaf photosynthetic rate (A_N) and stomatal conductance (g_S) under low light (PPFD of 300 µmol m^{-2} s^{-1}) and high light (PPFD of 1500 µmol m^{-2} s^{-1})

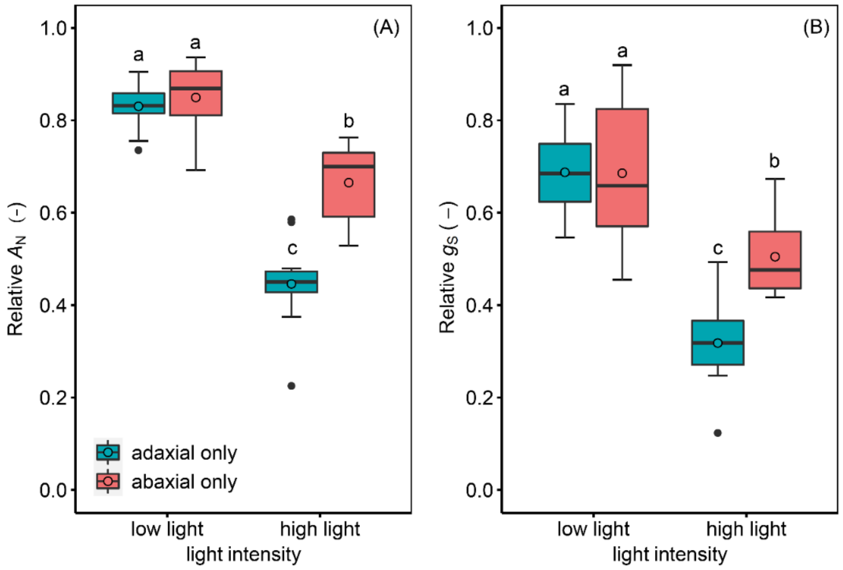

Fig. 3.6 Adaxial and abaxial leaf photosynthetic rate (A_N) and stomatal conductance (g_S) relative to photosynthetic rate of both sides of leaf under low light (PPFD of 300 µmol m^{-2} s^{-1}) and high light (PPFD of 1500 µmol m^{-2} s^{-1}).

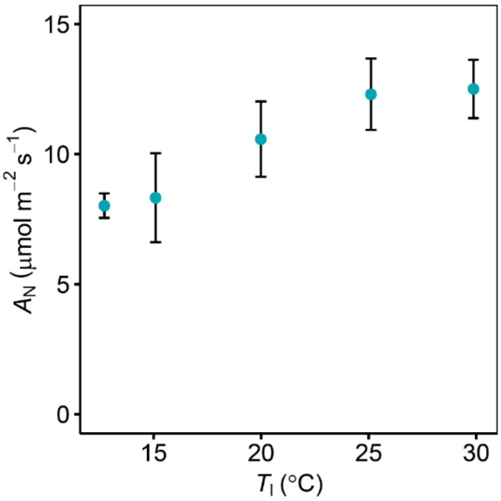

Fig. 3.7 Temperature-photosynthetic rate response curve of maize leaf.

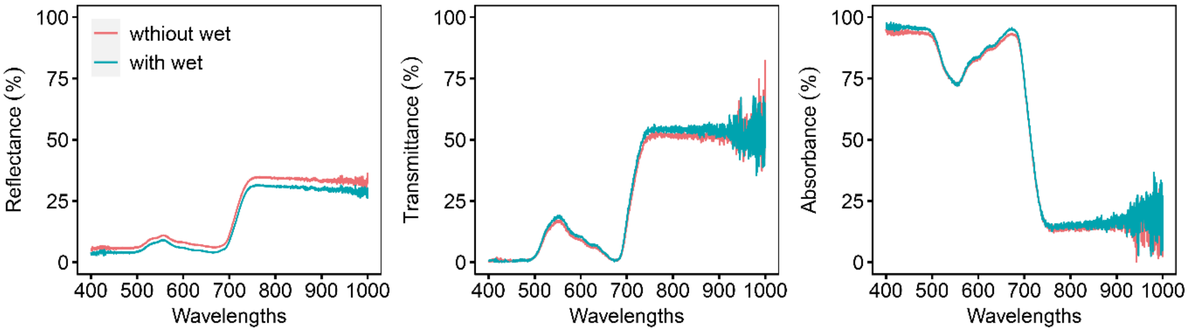

Fig. 3.8 Spectral distribution of reflectance, transmittance, and absorbance in leaves without and with leaf wetting. Average of five measurement was shown (n = 5).

3.3.3 Diurnal changes in gas exchange with and without leaf wetting

Fig. 3.9 shows time-course changes in photosynthetic rate (A_N), transpiration rate (Tr), stomatal conductance (g_S), vapor pressure deficit (VPD_{leaf}), leaf temperature (T_{leaf}), and water use efficiency (WUE) in the nowet and wet treatments. A_N and g_S in the nowet and wet increased as the light intensity increased, yet increase in A_N and g_S in the nowet were faster than those in wet. A_N and g_S in the nowet showed the highest value around 9:30 and then rapidly decreased thereafter. In the wet treatment, A_N and g_S showed the highest value around 11:00, and then decreased but showed higher value compared with those of nowet treatment. Tr in the nowet treatment increased as the light intensity increased, and then gradually decreased. In the wet treatment, Tr showed lower value than that in the nowet during 7:00 to 11:00, and then decreased thereafter. T_{leaf} in the wet treatments was relatively lower than that in the nowet treatments throughout the experiments. The largest difference in T_{leaf} between the treatments (around 4°C difference) was found during 7:00–8:00. After that difference in T_{leaf} between the treatments were relatively small (0.5°C–2.0°C). VPD_{leaf} in the wet treatment was also relatively smaller than that of the nowet treatment. WUE in the wet treatment was relatively higher than that in the nowet treatment.

Fig. 3.9 shows cumulative photosynthetic rate (ΣA_N), transpiration rate (ΣTr), and water use efficiency (ΣWUE) calculated as $\Sigma WUE = \Sigma A_N / \Sigma Tr$. ΣA_N and ΣWUE in the wet treatment was significantly higher than that of the nowet treatment, while no significant difference was found between the treatments in ΣTr.

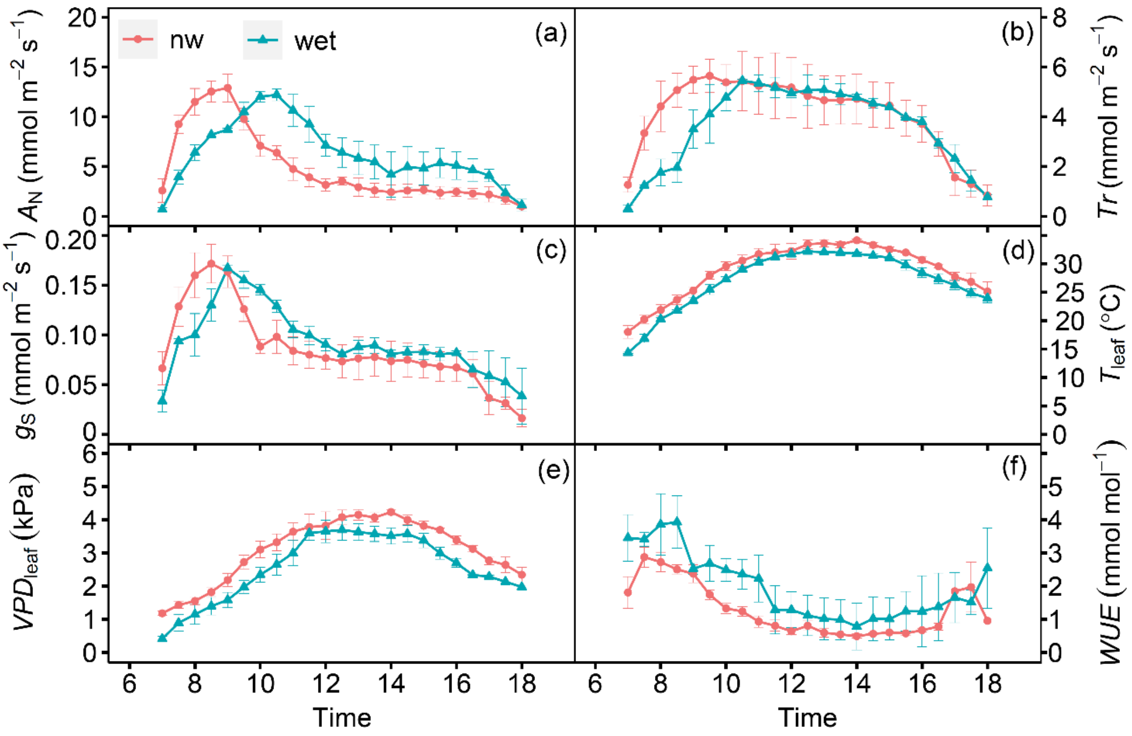

Fig. 3.9 Photosynthetic rate (A_N), Transpiration rate (Tr), stomatal conductance (g_S), water use efficiency (WUE), leaf temperature (T_L), and leaf-to-air vapor pressure deficit (VPD_L) in the wet (plants were wetted during night from 22:00– 6:00) and nowet plants.

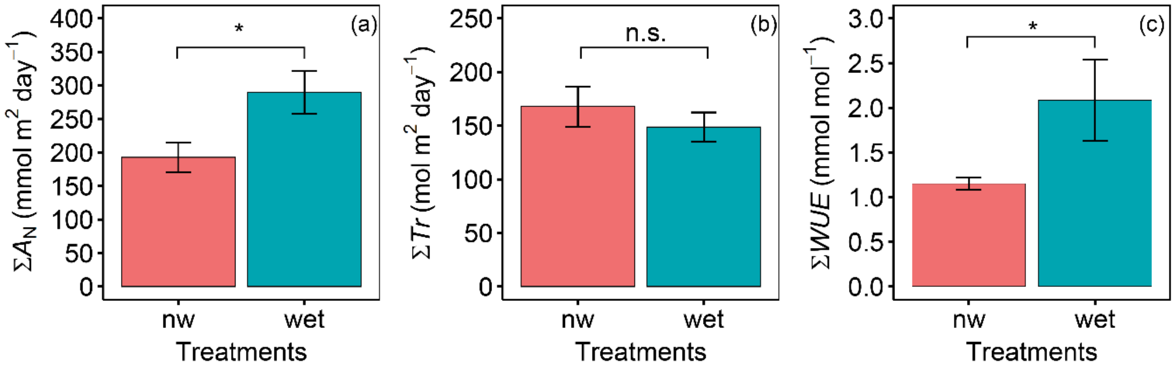

Fig. 3.10 cumulative photosynthetic rate (ΣA_N), transpiration rate (ΣTr), and water use efficiency (ΣWUE) calculated as $\Sigma WUE = \Sigma P_N / \Sigma Tr$ in the wet (plants were wetted during night from 22:00– 6:00) and nowet (plants were not wetted but remained in normal

3.4. Discussion

Leaf wetting occurs not only by precipitation but also by dew or fog, and thus leaf wetting is one of the most common environmental conditions on earth. However, because of the difficulty of measuring the gas exchange of wet leaves, the effects of leaf wetting on plant gas exchange is unclear. Here, we developed the new measurement systems to investigate the effects of leaf wetting on gas exchange(Yasutake et al., 2018; Yokoyama et al., 2019). Compared to the nowet treatment, P_N of the wet treatment was lower during leaves were wet. Several reasons were proposed for the decrease in P_N under leaf wetting conditions. One reason is a decrease in CO_2 uptake rate due to stomatal blockage by leaf water on the leaf surface (Ishibashi and Terashima, 1995). In our study, covering stomata by Vaseline significantly decreased P_N showing that stomatal blockage would be a major factor for the decrease in P_N under leaf wetting conditions. However, the photosynthetic rate is generally limited by the lowest process of either CO_2 uptake or light absorption (Farquhar et al., 1980). Therefore, a decrease in P_N by leaf wetting would be small when light intensity is small. Another reason for the decrease in leaf wetting is the decrease in leaf temperature (Gerlein-Safdi et al., 2018). As the activity of photosynthetic enzymes increases with an increase in leaf temperature within the optimum temperature regime (Bernacchi et al., 2001; Bernacchi, 2003), lower leaf temperature leads to a lower photosynthetic rate. In our study, the photosynthetic rate of maize leaf increased around 2 μmol m^{-2} s^{-1} for the increase in leaf temperature of around 5°C. The difference in leaf temperature during leaf wetting conditions was around 2°C suggesting that lower leaf temperature due to leaf wetting would be decreased photosynthetic rate, yet its effect was small. The transpiration rate also decreased by leaf wetting. Leaf wetting suppresses temperature rise and increases vapor pressure near leaf surface, which results in a decrease in leaf-to-air vapor pressure deficit (Yasutake et al., 2015). A decrease in *Tr* by leaf wetting would be beneficial for plants under water stress conditions as it contributes to maintaining appropriate plant water status under water stress conditions (Simonin et al., 2009). Consequently, reduced transpiration by leaf wetting contributes to maintaining a higher photosynthetic rate under water stress conditions. Although leaf wetting reduces photosynthetic by several processes, leaf wetting also indirectly contribute to improving photosynthetic rate under water stress condition, which offsets the negative effects of leaf wetting.

3.5. Conclusion

In this study, the potential costs and benefits of leaf wetting by dew on gas exchange were evaluated in the diurnal scale. During the early morning, the photosynthetic rate of wet leaves was lower than that of no-wet leaves. The possible reasons for the decrease in photosynthetic rate under leaf wetting conditions were investigated. By mimicking the stomatal occlusion by water film using Vaseline, a large decrease in photosynthetic rate was found in the high light condition but a smaller decrease in the low light condition. The temperature response curve also showed that lowered leaf temperature reduces the photosynthetic rate. Changes in the reflectance, transmittance, and absorptance were also observed yet, the detailed mechanism behind the changes in the reflectance, transmittance, and absorptance were still unclear. At the same time, the transpiration rate also decreased by leaf wetting because of the reduced evaporative demand by leaf wetting. After leaf wetting was evaporated, the photosynthetic rate was higher in the wet leaves than no-wet leaves since leaf wetting decreased photosynthetic rate but also improved plant water relations when the leaf was wet. As a result, leaf wetting improved water use efficiency on the diurnal scale. This study presents the importance of the leaf wetting by dew on gas exchange, and also provided the necessity of further research to understand the detail mechanism of how leaf wetting affects plant gas exchange.

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General conclusion

In this thesis, in order to evaluate the significance of leaf wetting by dew as a water resource in dryland crop production, I addressed a simple yet fundamental question: how leaf wetting by dew affect plant physiological functions? To assess how leaf wetting affects plant physiological functions, characteristics of dew formation was observed in a semiarid crop field of northwest China. By analyzing intra- and inter annual variation of dew characteristics and its relationship with environmental elements, importance of dynamics of water vapor pressure and radiative cooling intensity on the dynamics of dew characteristics was revealed. The observed dew amount was much smaller than that of precipitation, yet dew occurred more than half of the cultivation periods. In addition, leaf wetting by dew continued for more than 10 h on average, suggested that leaf wetting by dew would have large effects on dryland crop production through its effects on plant physiological functions. Based on the observation data of dew characteristics in the dryland crop field, I investigated nighttime leaf wetting effects on the rehydration process and its subsequent effects on gas exchange and growth were investigated. I have tested the following hypothesis; (1) leaf wetting by dew could be directly absorbed through leaf surface along the water potential gradient when water potential of leaf surface water is higher than that of the inside leaf; (2) if plants are able to rehydrate through leaves, it would expect that plants can mitigate the reduction in gas exchange and growth under soil water deficit condition. Leaf wetting by dew was directly absorbed from leaf surface along with the water potential gradient between leaf surface water and inside the leaf, which significantly improved leaf water potential, and thereby mitigated decrease in photosynthetic rate due to water stress. However, although plant water status was improve by leaf wetting, no significant difference was found between the growth (above-ground dry weight) of plants with and without leaf wetting by dew. These results motivated me to investigates how leaf wetting affects plant gas exchange (i.e., photosynthesis and transpiration) as photosynthesis is one of the important physiological processes for plant growth. In order to evaluate how leaf wetting affects plant gas exchange, I developed a whole plant chamber system, which can evaluate the gas exchange of wet leaves. By using this system, I explored costs and benefits associated with leaf wetting by dew within a temporal context. Although leaf wetting by dew had negative effects on photosynthesis when leaves under wet condition, higher photosynthetic rate was observed after leaves were dried, and thereby offset reduction in photosynthesis under wet conditions. Moreover, leaf wetting significantly reduced transpirational water loss, and thus improved water use efficiency.

I believe my research had advance our understanding of how leaf wetting affects plant physiological functions, and thus will contributed to improving dryland crop production in the near future.

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