A Preliminary Experiment on the Effects of Leaf Wetting on Gas Exchange in Tomato Leaves

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To evaluate the effects of leaf wetting on midday depression of photosynthesis in horticultural crops, we analyzed leaf gas exchange (transpiration rate, stomatal conductance, photosynthetic rate) of tomato plants under two different treatments (the Wet treatment and No-wet treatment as control). The gas exchange was measured at 11:00 (the time at which leaf gas exchange was assumed to be active) and 14:00 (the time at which leaf gas exchange was assumed to be inactive due to midday depression) on the clear days of November 2 to 7, 2016. The gas exchange measurements in the Wet treatment were conducted just after droplets on the leaf surface had evaporated. In the No-wet treatment, transpiration rate, stomatal conductance, and photosynthetic rate at 14:00 were decreased compared to those at 11:00. This suggests that midday depression occurred due to stomatal closure induced by excessive transpirational water loss. In contrast, in the Wet treatment, there was no such depression of leaf gas exchange, suggesting that leaf wetting might contribute to maintaining stomatal aperture through improving leaf water status. Thus, leaf wetting could avoid midday depression of photosynthesis in tomato plants.

Keywords: leaf wetting, midday depression, photosynthetic rate, stomatal conductance, transpiration rate, tomato

INTRODUCTION

On sunny days, plants actively perform photosynthesis using the light energy, however, photosynthetic rate often drops around midday. This reduction in photosynthesis, known as midday depression of photosynthesis, has been frequently observed in plants grown in arid or semi-arid environments (Schulze, 1982; Roessler and Monson, 1985; Raschke and Resemann, 1986). It has also been observed in plants grown in temperate climates with well-watered rhizospheres in both field (Hirasawa et al., 1989; Muraoka et al., 2000) and greenhouse environments (Ayari et al., 2000; He et al., 2007; Allen and Vu, 2009). This means that midday depression of photosynthesis may often occur in crop production, and could be a limiting factor for crop yield. Midday depression would be induced by stomatal closure, because excessive transpirational water loss by high leaf-to-air vapor pressure deficit leads to stomatal closure on sunny days even though plants were well watered (Kitano and Eguchi, 1993; Hu et al., 2009; Yasutake et al., 2016). Although other factors are reported as causes of midday depression, such as photoinhibition (Long et al., 1994; He et al., 2007), and carbohydrate accumulation in leaves (Araya et al., 2006), stomatal closure is one of the major causes of midday depression, or at least partially involved in midday depression.

Yasutake et al. (2015) observed that leaf surface wetting by dewfall contributes to avoid excessive transpirational water loss by decreasing leaf-to-air vapor pressure deficit in the morning in a cornfield of a semi-arid region where plants showed midday stomatal closure owing to soil water stress. Such effects of leaf wetting may provide appropriate water status for plants to maintain stomatal opening (Yasutake et al., 2006). Several researchers also reported similar positive effects of leaf wetting with dew, fog, and intercepted rainfall in natural environments (Martin and Von Willert, 2000; Breshears et al., 2008). Thus, leaf wetting may positively affect plant water status through reducing transpirational water loss and increasing leaf hydration by foliar uptake (Boucher et al., 1995; Limm et al., 2009).

However, in horticultural crops, leaf wetting is generally regarded as an unfavorable status for plants, because leaf wetness duration is related to incidence of plant diseases (Huber and Gillespie, 1992). Therefore, interest in the positive effects of leaf wetting is limited for horticultural crops, despite many reports of these positive effects in natural environments (Limm et al., 2009) and a few reports in horticultural crops (Ozawa, 1988). Leaf wetting may have either positive or negative effects on horticultural crops, depending on plant water status (Cassana and Dillenburg, 2013; Cassana et al., 2016) and leaf morphology (Hanba et al., 2004). Because of the complexity of the effects of leaf wetting on plants, the application of its positive effects to horticultural crop cultivation are not currently fully understood. We hypothesized that leaf wetting could alleviate midday depression of photosynthesis by...
avoiding stomatal closure through improved leaf water status.

In this study, we conducted a preliminary experiment to investigate the effects of leaf wetting on leaf gas exchanges (photosynthetic rate, transpiration rate, stomatal conductance) in tomato leaves using a leaf chamber system in a greenhouse.

MATERIALS AND METHODS

Plant materials and growth conditions

Tomato (Solanum lycopersicum L. ‘Hassu-momotaro’) seeds were sown in plastic pots (diameter 9 cm) filled with vermiculite at the beginning of September 2016. The seeds were germinated and grown in a phytotron glass room with an air temperature of 25°C, and a relative humidity of 70%, which was located at the Faculty of Agriculture, Kyushu University (N 33°37', E 130°25'). The plants were kept moist by tap water until the first leaf was developed, and then grown in nutrient solution with Otsuka-A treatment (Otsuka AgriTechno Co., Ltd., Japan) with an electrical conductivity of 1.5 dS m⁻¹. At the beginning of October, the plants were transplanted to larger plastic pots with a volume of 8 L filled with vermiculite and grown with the nutrient solution in an experimental greenhouse in the Kyushu University.

In the greenhouse, solar radiation (Rs) and air conditions (air temperature Ta and air relative humidity RH) were measured with a radiometer (MS-42, EKO Instruments Inc., Japan) and a temperature-humidity sensor (HMP45A, Vaisala, Finland), respectively, and recorded by a data logger (GL820, Graphtec Corporation, Japan) at 5-min intervals. The air conditions in the greenhouse were 20–27/14–18°C day/night, 35–80% RH and were controlled by a heat pump and ventilation through the roof and side windows.

Leaf wetting treatments

The plants were divided into two different treatment groups in the same greenhouse. One was the Wet treatment and the other was the No-wet treatment. In the Wet treatment, the adaxial surfaces of all leaves were fully wetted once an hour from 10:00 to 14:00 with distilled water using a sprayer (Maista-726, Maruhachi Industrials, Japan). The amount of water adhered to each leaf was 144 ± 32 g m⁻², which was the maximum adhesion amount of water per unit leaf area of the tomato plants. As a control, plants were not wetted but remained in normal conditions in the No-wet treatment. These treatments were conducted on the clear days of November 2 to 7, 2016.

Gas exchange measurements

The gas exchange measurements were carried out in fully expanded, recently matured leaves of the 10th leaf stage tomato plants (n=3) at 11:00 (the time at which leaf gas exchange was assumed to be active) and 14:00 (the time at which leaf gas exchange was assumed to be inactive due to midday depression) using a portable leaf chamber system (LI-6400, Licor, USA) on the measurement days. Transpiration rate (Tr), stomatal conductance (Gs), and photosynthetic rate (A) of the leaves for two different treatments were measured under constant conditions of light intensity (photosynthetic photon flux density of 1.000 μmol m⁻² s⁻¹), air temperature (25°C), relative humidity (40%), and CO₂ concentration (400 μmol mol⁻¹) in the leaf chamber. The gas exchange of the Wet treatment was measured once the droplets on the leaf surface had evaporated (approximately 15 min after wetting treatment).

Statistical analyses

Statistical analyses of leaf gas exchange characteristics (Tr, Gs, and A) between different measurement times and treatments were performed using the Tukey-Kramer test at P<0.05.

RESULTS AND DISCUSSION

Greenhouse environment in the morning and afternoon

Figure 1 shows boxplots of Rs, Ta, and RH in the greenhouse during measurement periods of the morning (9:30–11:00) and the afternoon (12:30–14:00). Distribution and median values (approximately 360 W m⁻²) of Rs were very similar in both the morning and afternoon measurement periods. Ta showed similar fluctuation in both morning and afternoon measurement periods, although the median value of Ta in the morning (28.8°C) was slightly higher than that in the afternoon (27.4°C). This is because the environmental control systems (the heat pump and ventilation systems) in the greenhouse were operated automatically in the afternoon. Contrary to the similarity of the morning and afternoon Ta profiles, the fluctuation of RH values was different between the morning and afternoon periods. RH showed wider fluctuation in the morning than in the afternoon because of the high relative humidity of nighttime to early morning and the on-off operation of the heat pump, whereas in the afternoon, RH was almost constant at 37–40% because the greenhouse was kept ventilated and the heat pump was operating throughout the afternoon. However, the mean RH values for both morning (43.9%) and afternoon (39.0%) periods were similar.

Leaf wetting effects on gas exchanges

Figure 2 shows the Tr, Gs, and A at 11:00 and 14:00 under the No-wet and Wet treatments. In the No-wet treatment, Tr was decreased by 32% at 14:00 compared to that at 11:00, which could be the result of stomatal closure. In fact, Gs was decreased by 28% at 14:00 compared to that at 11:00. The depression of Gs in the afternoon could be due to high leaf-to-air water vapor pressure deficit (Nonami et al., 1990), as this could induce plant water deficit through excessive transpirational water loss (Kitano and Eguchi, 1993; Yasutake et al., 2016). As a result, A was decreased by 21% at 14:00 compared to that at 11:00. Thus, midday depression of photosynthesis was observed with the decrease in all gas exchange parameters.

In contrast to the No-wet treatment, there was no significant decrease in gas exchange parameters in the Wet treatment at 14:00 compared to those at 11:00. Leaf wetting can decrease the leaf-to-air vapor pressure deficit by decreasing leaf temperature and increasing humidity near the leaf surface (Yasutake et al., 2015). Therefore, the Tr
LEAF WETTING EFFECTS

under a wetted leaf should be low. However, $Tr$ in the Wet treatment was similar to the No-wet treatment at 11:00, but higher than the No-wet treatment at 14:00. This is because the gas exchange measurements were conducted just after droplets on the leaves had evaporated, and high $Tr$ in the Wet treatment at 14:00 could be due to high evaporative demand in the afternoon.

The $Gs$ at 14:00 in the Wet treatment was 58% higher than that in the No-wet treatment. This could potentially be the result of maintaining moderate water status by leaf wetting. Infiltration of water into leaves and decreasing leaf-to-air vapor pressure deficit are assumed to be major processes that affect plant water status. Infiltration of water causes a rapid increase in the turgor pressure of epidermal cells, which may become excessively turgid, and stomata may close through a hydropassive process (Zeiger, 1983; Ishibashi and Terashima, 1995). In this study, there was no such reduction in $Gs$ observed in the Wet treatment. It can be assumed that, in an environmental condition in which midday depression occurs, high evaporative demand could contribute to preventing the epidermal cells being turgid. In addition, leaf wetting may contribute to maintaining stomatal aperture by decreasing leaf-to-air vapor pressure deficit (Yasutake et al., 2015). In this study, at 14:00 when midday depression should occur, $A$ in the Wet treatment was 33% higher than that of the No-wet treatment. This is because of high $Gs$ at 14:00 in the Wet treatment. Thus, leaf wetting could be effective for avoiding midday depression of photosynthesis due to maintaining stomatal aperture.

In conclusion, leaf wetting may improve gas exchange in the afternoon through avoidance of midday stomatal closure. However, it is difficult to measure the gas exchange of wetted leaves using the portable leaf chamber. Thus, the mechanisms of stomatal behavior under wetted leaves have not yet been fully understood. Therefore, further investigations, including gas exchange measurements of wetted leaves and the effects of leaf wetting on plant water status, are needed.

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