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Reducing the excessive evaporative demand improved photosynthesis capacity at low costs of irrigation via regulating water driving force and moderating plant water stress of two tomato cultivars

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A B S T R A C T

Although atmospheric evaporative demand is increasingly recognized as significant roles in coupling water transport and carbon acquisition, potentials to reduce irrigation demand and improve photosynthesis performance via regulating evaporative demands is highly uncertain. To bridge this gap, plant water status in combination with photosynthetic carbon acquisition under contrasting evaporative demand was examined in two cultivars of tomato (*Solanum lycopersicum* L.). Experiments were conducted from May to August in 2016. Evaporative demand gradients were achieved via regulating vapor pressure deficit (VPD) at two adjacent greenhouses of similar characteristics: High VPD was maintained in natural greenhouse condition without environmental regulation (Control); Moderate VPD was achieved by artificially humidification when evaporative demand exceeded optimal ranges (Humidification). VPD regulation by humidification reduced the excessive driving force for water flow, which efficiently prevented the declines in plant water potential and alleviated hydraulic limitation. Transpiration rate and irrigation demand over experimental period were substantially reduced via reducing evaporative driving force in humidification treatment. Moderation in plant water stress sustained stomatal openness for CO_2 acquisition and utilization. Photosynthetic capacity was significantly improved by humidification, as indicated by the substantial increases in photosynthesis rate(P_n), rubisco carboxylation capacity(V_{cmax}), maximum electron transport capacity (J_{max}) and net assimilate rate (NAR). At long-term scales, fruit yield was increased by 14.6% and 16.7% for two cultivars. Whole plant biomass was increased by 22.6% and 16.9% for two cultivars. Plants irrigation amount in humidification treatment over the experimental period was significantly saved by 16.9% and 17.4% for two cultivars. Taken together, VPD regulation had great potentials to reduce irrigation demand and improve photosynthetic capacity via reducing water driving force and sustaining stomatal function. The present study provided novel information to improve photosynthetic and reduce irrigation demand for sustainable crop production.

1. Introduction

Photosynthesis is the driving mechanism for plant growth and yield production, which is affected by various environmental factors. During photosynthesis, the pathway for CO_2 uptake from the bulk atmosphere to fixation site is determined by a series of diffusion resistance, among which stomatal pores provided a major resistance. Stomata are the "gatekeepers" responsible for all gaseous diffusion, they adjust to external environmental stimuli governing CO_2 uptake and water loss (Lawson and Blatt, 2014). A large body of literature has been published that acquisition and utilization efficiency of CO_2 is modified by various environmental conditions such as soil water status (Pazzagli et al., 2016), light (Soares et al., 2008), temperature and so on. Environmental fluctuation is thought to impact on guard cells of stomatal pores, which profoundly affect the exchange of water loss and CO_2 uptake. Stomatal closure in response to plant water deficit in vascular plants was believed to be a passive process, driven by reduction in turgor of the guard cells (Buckley, 2005). Since turgor pressure was

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directly linked to plant water status, processes of water transport and loss can impact CO_2 diffusion resistance via manipulating the physical and physiological characteristics of guard cells.

The process of water movement through soil-plant-atmosphere continuum (SPAC) determined plant water status and thereby affect stomatal function for photosynthesis. Water movement is a passive process, driven by the free energy gradient between soil and atmosphere (Fricke, 2017). Soil water status has long been recognized as key elements to maintain optimum water driving force and sustain stomatal function. Water-saving irrigation techniques such as controlled alternate partial root-zone irrigation and deficit-irrigation were widely applied for crop production due to the reduced water supply without significant limitation in stomatal function and photosynthesis (Chen et al., 2014; Chen et al., 2013; Ma et al., 2007). In natural condition, soil moisture varies much less than leaf-atmosphere flux, which fluctuates in response to high frequency evaporative demand (Caldeira et al., 2014; Manzoni et al., 2011). High evaporative demand is a major determination for excessive irrigation consumption and photosynthesis limitation, especially for the semi-arid zones which is characterized by "meteorological drought".

Excessive water flux can cause disrupt in water balance between liquid water supply and vapour loss, consequently induce plant water deficit and physiological disorders (Grange and Hand, 1987). The plant water stress under excessive evaporative demand condition would inhibit photosynthesis and plant growth via limiting stomatal function (Brodribb and Holbrook, 2003). While evaporative demand limited stomatal function and photosynthetic carbon gain via regulating water driving force and affecting plant water status, the evaporative demand regulation received far less attention by growers. One possible reason is the difficulty in environmental regulation for field grown crop. The technology of protected horticulture, a new facility to grow plants and facilitates evaporative demand regulation, is growing at an ever-increasing rate (Giacomelli et al., 2007).

Atmospheric vapor pressure deficit (VPD) is a good indicator of evaporative demand, which can be used to identify healthy air moisture conditions for plant production, while taking into account different temperature levels (Bouchabk et al., 2006; Medina and Gilbert, 2016; Parent et al., 2010; Prenger and Ling, 2001). It has been suggested that effect of humidity is best given in terms of VPD between the leaf and bulk air, which is a more appropriate variable for describing plant physiological responses to air moisture (Peak and Mott, 2010). In greenhouse production, the increasing sophistication of mechanical devices and computer programs can be applied for greenhouse atmospheric moisture regulation. Mechanical systems of heating, ventilation, heat pumps, and air circulation could be applied for increasing VPD. Evaporative cooling methods such as pad-and-fan and fogging systems facilitated VPD decreasing (Katsoulas et al., 2009; Leyva et al., 2015; Max et al., 2009; Romero-Aranda et al., 2002). Large evidence was provided that optimal control of VPD improved plant growth and increased yield of horticultural crop in greenhouse production (Zhang et al., 2015). Although VPD mediated stomatal function for water and CO_2 exchange, the potentials to reduce irrigation demand and improve photosynthesis through regulating VPD was highly uncertain.

VPD control was hypothesized to perform significant roles in reducing irrigation demand, moderating plant water stress and thereby sustaining stomatal function for CO_2 utilization in the present study. The purpose of this research was to identify the potential mechanisms linking VPD regulation to irrigation demand and photosynthetic capacity from a hydraulic perspective. Considering the spatial and temporal variation in carbon and water balance, two main components were highlighted in the present study: plant productivity process- photosynthesis, plant growth, biomass and yield production; water transport process-stomatal and hydraulic regulation, transpiration and irrigation demand. Plant water status and stomatal function were exemplified as the central elements in coupling and balancing two processes.

2. Materials and methods

2.1. Plant materials and growth conditions

The experimental site is an experimental station of Northwest Agriculture and Forestry University, located in the Yangling demonstration zone, Shaanxi Province of northwest China (N34°15′, E108°04′, altitude 443.6 m). Experiments were conducted in two adjacent greenhouses in similar characteristics (15 m in length, 10 m in width and 3 m in height, North-South oriented). Variability in environmental factors between two greenhouses was examined prior to experiments. Minor differences in environmental factors were observed between two greenhouses. Two tomato cultivars were examined: JinPeng NO.1 (heat sensitive, CV1 hereafter; JinPeng&Co., Ltd., China) and FenGuan (heat tolerant, CV2 hereafter; ZhongYa &Co., Ltd., China). Plants were grown in plastic cultivation bed (200 cm in length, 45 cm in width and 18 cm in height) and white-colored pots (40 cm in diameter and 30 cm in height), filled with same amount of substrate. Plants were transplanted at four-leaf stage and cultivated with three truss, four fruits were retained in each truss. The planting density is 4 plants per m^2. The apical part of shoot was pinched after the third flower truss started blooming. Soil moisture was maintained uniformly at 90–95% field capacity. Cultivars of CV1 and CV2 were examined under spring-summer climatic condition from May to August in 2016.

2.2. Experimental design

Two experimental greenhouses were controlled in same growth condition but contrasting VPD condition: high VPD was maintained in natural greenhouse condition without environmental control, served as control area; moderate VPD was achieved by artificially humidification when evaporative demand exceeded physiological favourable condition, served as humidification treatment. Misting systems (Spray pressure: 2–6 MPa, droplet size: 25.8–46.2 μm; Huawei Instruments Co., Ltd., China) was automatically activated when the greenhouse VPD exceed 1.2 KPa, considering the recommend values for tomato cultivation in greenhouse (Bakker, 1990; Iraqi et al., 1995). The misting system operated continuously and turned off until VPD below the set point. There were five blocks per treatment, with ten plants in each block.

2.3. Determination of daily transpiration and cumulative irrigation amount

Potted plants were used for transpiration and irrigation estimation. Soil surface was covered with circular polythene sheet to prevent soil water evaporative. Plant transpiration was measured by a standardized gravimetric approach of daily pot weighting with an electronic balance, as described by previous research (Kadam et al., 2015). Weight of pots was weighted at about 0800 h. Daily plant transpiration was estimated as the difference of pot weightings. Daily water loss due to transpiration was replenished by adding an exact amount of water to bring back the moisture content to the desired target. Irrigation amount during the whole growing season was estimated from the sum of the daily transpiration.

2.4. Measurements of leaf gas exchange

Leaf gas exchange parameters were measured with portable photosynthesis systems (LI-6400, Li-Cor, Inc., Lincoln, NE, USA) every 10 days after leaf appearance (during 9:00 a.m.–12:00 a.m.).