

Effects of atmospheric and soil water status on photosynthesis and growth in tomato

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ABSTRACT

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The responses of tomato seedlings to different vapour pressure deficit (VPD) under low soil moisture were studied. Plants were grown in greenhouses with low and high VPD, under both well-watered and water stress conditions. Low VPD was effectively maintained below 1.5 kPa with a micro-fog system. Under well-watered conditions, low VPD resulted in reduced transpiration, but this did not affect plant water status or growth. Water stress induced leaf dehydration and inhibition of growth, but the adverse effects were significantly alleviated by a decrease in VPD. Under water stress, no difference in transpiration was observed between plants with or without the VPD regulation, but the whole-plant hydraulic conductance was higher under low VPD. Low VPD increased stomatal conductance in drought-stressed plants because it promoted stomatal development and increased stomatal aperture. Thus, stomatal limitation to photosynthesis was reduced by low VPD under water stress. The reduction in plant growth induced by water stress was moderated by low VPD, partially due to higher photosynthetic rate. These results suggest that decreasing VPD improves plant water status, which ultimately enhances photosynthesis and growth under water stress.

Keywords: atmospheric humidity; gas exchange; vegetable; drought stress; stomata; *Solanum lycopersicum* L.

Water is one of the most important environmental factors and vital to the physiological and biophysical processes in plants. Atmospheric water status can be estimated by vapour pressure deficit (VPD) which is defined as the difference between saturation vapour pressure and actual vapour pressure at a known temperature and relative humidity. High VPD and soil water deficit are difficult to disentangle in most cases. During summer, high VPD-induced drought stress frequently occurs also in greenhouses in the northern China (Zhang et al. 2015). However, fog application can efficiently moderate high VPD. In the soil-plant-atmosphere continuum, atmospheric evaporative demand drives water movement from the soil to

the atmosphere through plants. Thus, plant water status is determined by the soil moisture and VPD and adjustment of plants to dehydration (de Boer et al. 2011).

Stomata play an importance role in the gas exchange. In short-term, low VPD promoted stomatal openness due to low evaporative demand, and water stress induced rapidly stomatal closure to avoid excessive water loss. Stomatal morphology acclimation to long-term low VPD and water stress also occur in opposite directions. Plants have larger stomatal aperture and size under low VPD (Arve et al. 2013), whereas water stress lead to small stomatal aperture and size (Lu et al. 2015). However, the stomatal and photosynthetic responses to decrease VPD under soil

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water deficit are still unknown. Furthermore, it is not clear how the plant water balance is maintained under such conditions.

Tomato (*Solanum lycopersicum* L.) is one of the most economically important vegetable. Much work has been done on the effects of air humidity and soil moisture on tomato growth and physiology (Leonardi et al. 2000, Lu et al. 2015); however, their interactive effects are not well known. Therefore, to improve our understanding of plant responses to atmospheric humidity and soil moisture, the present study was performed in controlled environment to investigate plant water status, photosynthesis, growth and stomatal characteristics.

MATERIAL AND METHODS

Plant material and growth conditions.

Experiments were performed in two identical greenhouses at the Northwest Agriculture and Forestry University (34°15'N, 108°04'E), China from 12 April to 20 May 2016. Both greenhouses were 5 m in length, 4 m in width and 3 m in height. Tomato (*Solanum lycopersicum* L. cv. Difenni) seedlings were transplanted to plastic pots (19 cm × 17 cm, diameter × depth; 8 kg dried soil/pot) at four-leaf stage on 1 April 2016 and watered to near field capacity (FC). After 3 days, a total of 100 pots were equally divided into 4 groups.

The plants were subjected to the following treatments: (1) well-watered nearly to 100% FC (WW) + high VPD (HVPD); (2) WW + low VPD (LVPD); (3) water stress of 55% FC (WS) + HVPD; and (4) WS + LVPD. The treatments were started by withholding water until the soil moisture of the drought stress group reached 55% FC. The VPD was regulated by a micro-fog system as described by Zhang et al. (2015). Briefly, LVPD was maintained below 1.5 kPa by using a micro-fog system, whereas HVPD was obtained without micro-fog application. The total amount of fogging water was recorded with a flow meter. To avoid evaporation from the soil, it was covered with aluminum foil. Pots were weighed and watered to maintain the FC percentages every afternoon. Daily differences in weight were used to calculate cumulative transpiration. To test the effects of atmosphere humidity and soil moisture on tomato plants, data were measured when the seventh true leaf (from bottom to top) was fully expanded. All plants were harvested on 21 May.

Gas exchange and stomatal traits. Leaf gas exchange was measured between 10:00 and 12:00 am on 16 May with a portable system (Li-6400; Li-Cor, Huntington Beach, USA). All measurements were carried out at a CO₂ concentration of 400 μmol/mol, a photosynthetic photon flux density of 1000 μmol/m²/s and a leaf temperature of 30°C. The VPD was set at 1.5 kPa for LVPD and 3.0 kPa for HVPD. After measuring gas exchange, the leaves were used for stomata morphological observation following the method of Xu and Zhou (2008). In brief, the abaxial epidermis of the leaf was cleaned, and then smeared with nail varnish. After 20 min, the thin film was peeled off from the leaf surface. Each treatment included five plants.

Plant water status. Leaf water potential (Ψ_{leaf}) was measured by the balancing pressure technique with a pressure chamber (PMS, Corvallis, USA) in parallel with the measurements of leaf gas exchange. Then, the leaf was immediately packed in aluminum foil and frozen in liquid nitrogen for osmotic potential (Ψ_{π}) measurements as described by Rodriguez-Dominguez et al. (2016). One 7 mm diameter disc per leaf was taken and loaded in a C-52 thermocouple psychrometer chamber connected to a data logger (PSYPRO, Wescor, Inc., Logan, USA). Ψ_{π} was recorded after equilibrium for 30 min. Turgor (Ψ_p) was determined by the difference between Ψ_{leaf} and Ψ_{π} . Predawn leaf water potential was taken as the soil water potential (Ψ_{soil}). Relative water content (RWC) was calculated according to the formula:

$$\text{RWC}(\%) = (\text{fresh weight} - \text{dry weight}) / (\text{saturated weight} - \text{dry weight}) \times 100.$$

Whole-plant hydraulic conductance (K) was calculated according to Martre et al. (2002):

$$K = \text{transpiration rate} / (\Psi_{\text{soil}} - \Psi_{\text{leaf}})$$

The measurements were carried out on fully developed leaves obtained from five plants per treatment.

Growth parameters. Ten plants per treatment were selected to measure plant biomass, plant height and total leaf area. The whole-plant water use efficiency (WUE_p) was calculated as the ratio of total plant biomass to accumulated transpiration. Total water use efficiency (WUE_t) was based on total plant biomass and total input of water, including transpiration and fogging. Total leaf area was determined with a LI-COR 3100 leaf area meter (LI-COR, Inc., Lincoln, USA). The

relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were calculated according a previous method (Yamori et al. 2011).

Statistical analysis. Statistical analyses were performed using the SPSS software version 19.0 (SPSS, Chicago, USA). All data are presented as the mean $\pm$ standard error (SE). Multiple comparisons between all treatments were analysed using a Duncan's test. Differences were considered significant at $P < 0.05$.

RESULTS

Soil water potential and micrometeorological variables. Withholding water induced a decline of Ψ_{soil} . No significant differences were observed in Ψ_{soil} between HVPD and LVPD under WW or WS (Figure 1). The mean VPD reached 2.8 kPa in the no-fogging condition while it was below 1.5 kPa under fog conditions. Fog application caused an increase in relative humidity from 52% to 79%, and temperature decreased by 1.7°C (Figure 1).

Plant water status. Both RWC and Ψ_{leaf} were significantly lower under WS (Figure 2). Plants

grown at LVPD showed significantly higher RWC and Ψ_{leaf} compared with HVPD-treated plants under WS conditions. LVPD eliminated the drop in Ψ_{n} under WS. On the other hand, Ψ_{p} was significantly enhanced by LVPD under WW and WS.

LVPD had no significant effect on K compared to HVPD under WW conditions (Figure 3). However, K in WS + HVPD plants was 47% lower than in WW + HVPD plants, and with LVPD under WS, the decrease in K was only 36%.

Stomatal traits. In WS plants, stomatal density, index and aperture decreased compared to WW plants under HVPD (Table 1). However, under WS conditions, they were generally higher in the LVPD-treated plants than that in the HVPD-treated plants. WS also reduced the stomatal length, but did not affect stomatal width compared to WW under HVPD. There was no difference in stomatal length and width between the LVPD-treated plants and the HVPD-treated plants under WS.

Gas exchange. P_{n} was suppressed by WS compared to WW under HVPD, and LVPD significantly enhanced the inhibition of P_{n} under WS (Figure 4). G_{s} and C_{i} had similar differences as P_{n} . T_{r} of the WS-treated plants was 20% and 45% lower than

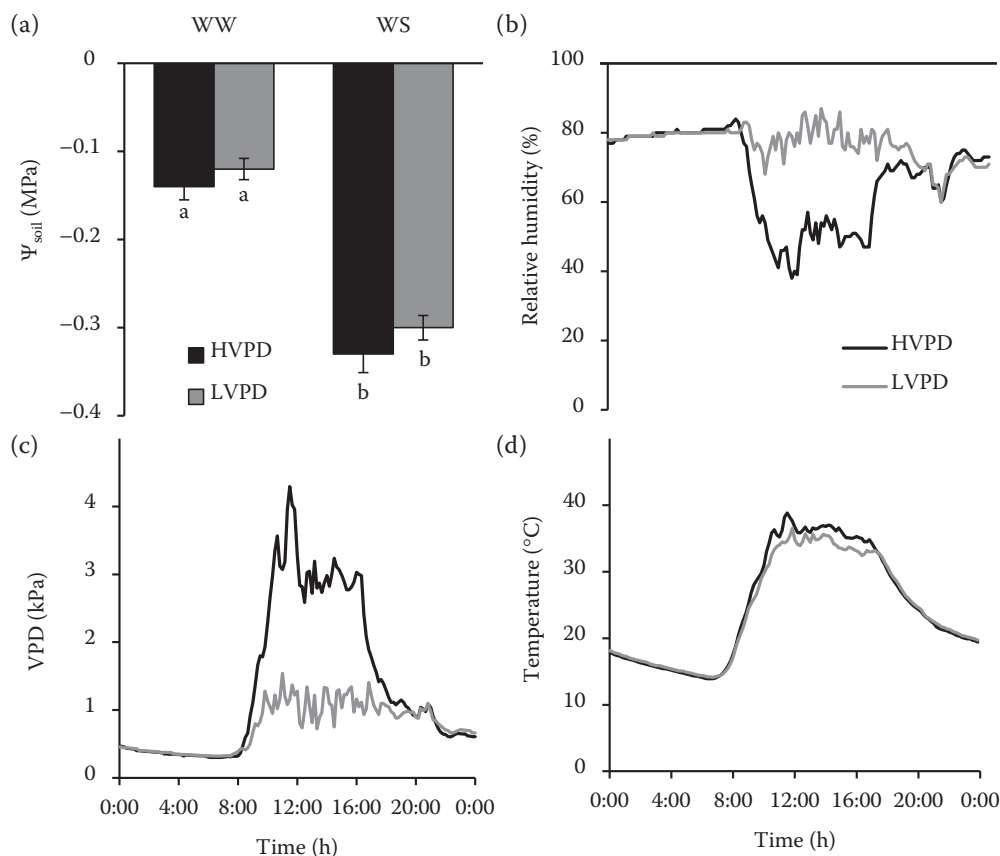


Figure 1. (a) Soil water potential (Ψ_{soil}) (b) and diurnal variation in vapour pressure deficit (VPD); (c) relative humidity and (d) temperature in the different treatments on the measuring day (16 May 2016). WW – well-watered; WS – water stress; HVPD – high VPD; LVPD – low VPD

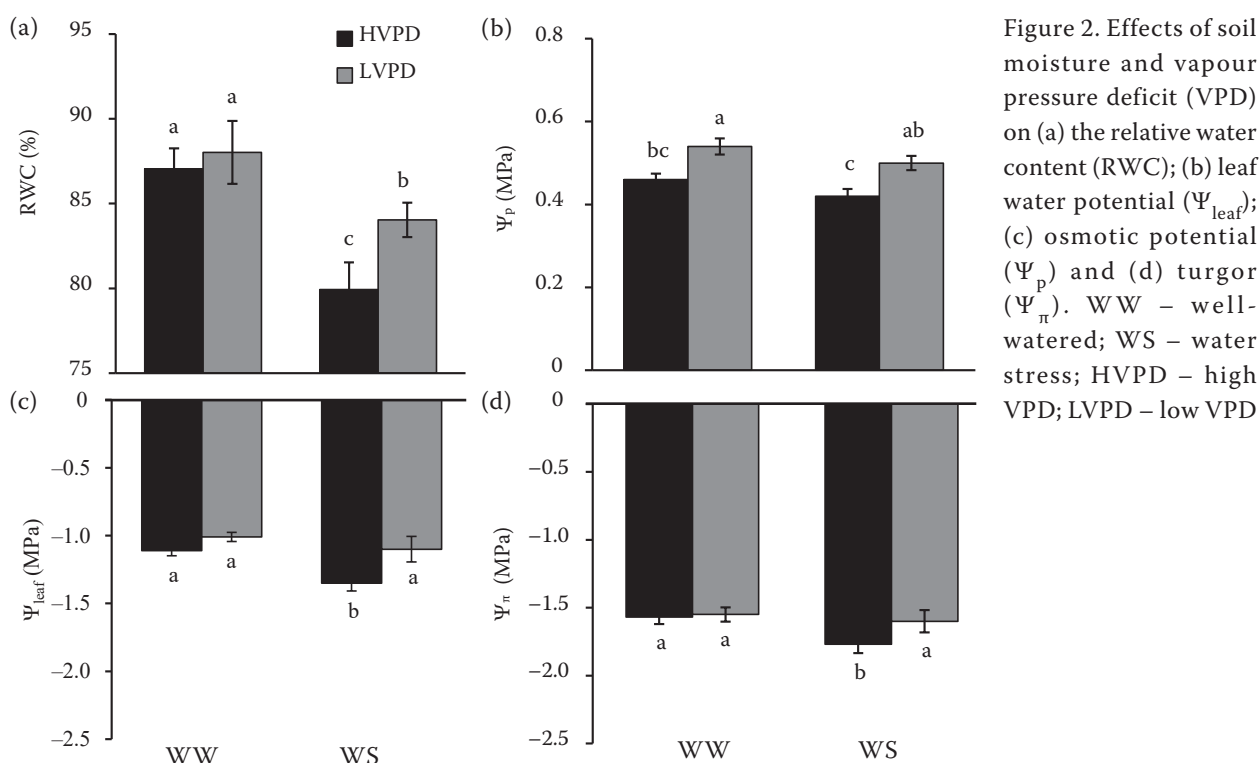


Figure 2. Effects of soil moisture and vapour pressure deficit (VPD) on (a) the relative water content (RWC); (b) leaf water potential (Ψ_{leaf}); (c) osmotic potential (Ψ_p) and (d) turgor (Ψ_{π}). WW – well-watered; WS – water stress; HVPD – high VPD; LVPD – low VPD

for the WW plants under LVPD and HVPD, respectively. However, it was the same in plants with or without VPD regulation under WS.

Plant growth. Compared to plants in WW + HVPD, WS + HVPD severely inhibited plant growth (Table 2). In the LVPD-treated plants, the leaf area and total dry weight were higher by 20% and 18%, respectively, compared with the HVPD-treated plants under WS. No significant difference was observed in plant height between WS + LVPD and WS + HVPD. The root/shoot ratio was significantly higher in WS plants under HVPD, but lower in LVPD than HVPD under WS conditions. Growth analyses showed the changes to RGR and NAR were similar to the total dry weight, whereas the LAR did not change under WS and/or LVPD conditions (Figure 5). Thus, LVPD alleviated plant growth inhibition induced by WS.

Water use efficiency. Compared with WW + HVPD, WUE_p in plants was higher under WS + HVPD or WW + LVPD (Figure 6). Under WW conditions, the WUE_p in LVPD was 1.78-fold higher compared to high-VPD. Furthermore, considering fogging water, no significant difference was observed for WUE_t between fogging and no-fogging treatments under WW or WS when the plant density was 6 plants/m².

DISCUSSION

Soil drought stress induces water deficit in plants due to limitation of water supply in soil and high atmospheric evaporative demand (Sperry and Love 2015). In this study, RWC and Ψ_{leaf} were significantly lower in drought conditions, and both of these values increased after fogging (Figure 2). Biomass distribution is a good predictor that indicates the most growth-limiting resource (Sellin

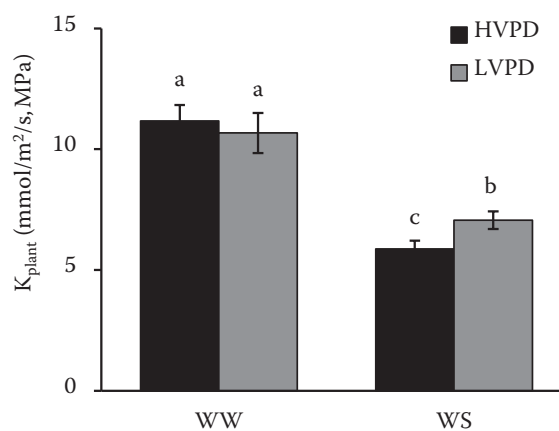


Figure 3. Effects of soil moisture and vapour pressure deficit (VPD) on the whole-plant hydraulic conductance (K). WW – well-watered; WS – water stress; HVPD – high VPD; LVPD – low VPD

Table 1. Effects of soil moisture and vapour pressure deficit (VPD) on stomatal traits

Treatment	Stomatal density (m/m ²)	Stomatal index	Stomatal length	Stomatal width	Stomatal aperture
			(μm)		
WW + HVPD	108.90 ± 3.01 ^b	0.238 ± 0.004 ^b	31.82 ± 0.62 ^a	20.56 ± 0.53 ^b	1.49 ± 0.13 ^c
WW + LVPD	151.96 ± 3.88 ^a	0.255 ± 0.005 ^a	32.17 ± 0.54 ^a	25.66 ± 0.43 ^a	5.82 ± 0.24 ^a
WS + HVPD	96.21 ± 2.10 ^c	0.184 ± 0.004 ^d	27.97 ± 0.38 ^b	20.13 ± 0.28 ^b	0.98 ± 0.08 ^d
WS + LVPD	113.76 ± 2.06 ^b	0.208 ± 0.004 ^c	29.30 ± 0.46 ^b	20.56 ± 0.35 ^b	3.15 ± 0.22 ^b

Data represent means ± standard error ($n = 15$ for stomatal density and index; $n \geq 40$ for stomatal length, width and aperture). Different letter within a column indicate significant difference ($P < 0.05$) between treatments. WW – well-watered; WS – water stress; HVPD – high VPD; LVPD – low VPD

et al. 2015). Water deficit in plants induces a large root/shoot ratio. A decline in root/shoot ratio was found in WS + LVPD compared to WS + HVPD. These results indicated that LVPD alleviated the water deficit in plants that was induced by WS.

Inhibition of transpiration rates was previously reported under WS or LVPD (Leonardi et al. 2000, Zhang et al. 2015). This was also confirmed in this study. Although no differences in T_r were found between low and HVPD under WS, LVPD significantly reduced the reduction of K induced by WS (Figure 3). Therefore, the improvement of water status in plants grown at LVPD can mainly be explained by improvement of water transport under WS. Additionally, no significant difference

was observed in plant height between LVPD and HVPD under WS. Low plant height would favour the maintenance of the whole-plant hydraulic conductance under WS (McDowell et al. 2002).

Stomatal conductance is a crucial parameter for plant-atmosphere gas exchange. G_s was lower under WS, but LVPD eliminated the drought-induced reduction in G_s (Figure 4). This result may be ascribed to the responses of stomata morphology to atmosphere water status, as G_s is dependent on anatomical features (Lawson and Blatt 2014). WS caused a reduction in stomatal aperture, but lower VPD promoted stomatal opening in WS plants. Moreover, G_s also can be regulated by stomatal aperture that is mediated by turgor (McAdam

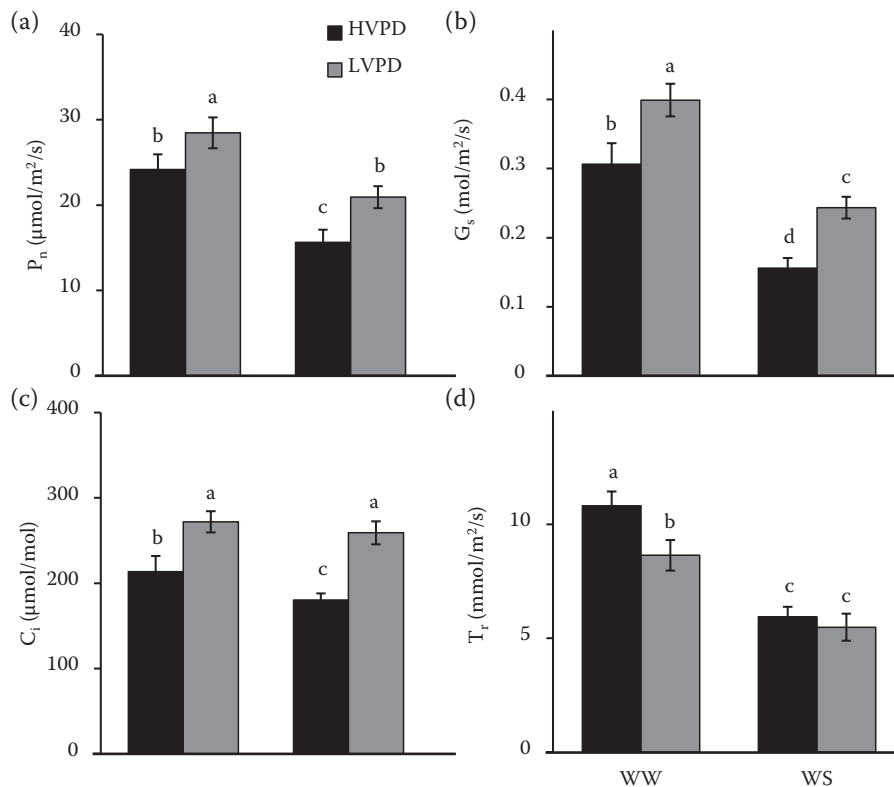


Figure 4. Effects of soil moisture and vapour pressure deficit (VPD) on (a) the photosynthetic rate (P_n); (b) stomatal conductance (G_s); (c) intercellular CO_2 concentration (C_i), and (d) transpiration rate (T_r). WW – well-watered; WS – water stress; HVPD – high VPD; LVPD – low VPD

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Table 2. Effects of soil moisture and vapour pressure deficit (VPD) on plant growth

Treatment	Leaf area (m ²)	Total dry weight (g)	Plant height (cm)	Root/shoot
WW + HVPD	0.30 ± 0.02 ^a	44.62 ± 1.65 ^a	79.9 ± 2.4 ^a	0.17 ± 0.01 ^b
WW + LVPD	0.31 ± 0.01 ^a	45.70 ± 2.31 ^a	83.3 ± 3.9 ^a	0.10 ± 0.01 ^c
WS + HVPD	0.21 ± 0.01 ^c	29.62 ± 1.21 ^c	67.3 ± 2.4 ^b	0.24 ± 0.02 ^a
WS + LVPD	0.25 ± 0.02 ^b	34.83 ± 1.36 ^b	69.3 ± 2.5 ^b	0.17 ± 0.01 ^b

Data represent means ± standard error ($n = 10$). Different letter within a column indicate significant difference ($P < 0.05$) between the treatments. WW – well-watered; WS – water stress; HVPD – high VPD; LVPD – low VPD

and Brodribb 2016). For adaptation to dehydration, plants tend to maintain turgor by osmotic adjustment (Blum 2017). In this study, stomatal aperture and Ψ_p decreased due to leaf dehydration under

drought stress, and Ψ_π was reduced to maintain turgor. Thus, stomatal aperture in LVPD-treated plants was maintained by higher turgor under WS because the water status in drought-stressed plants was improved under lower VPD. Under water deficit, photosynthesis was primarily dependent on the stomatal regulation (Varone et al. 2012). Stomatal conductance increased under LVPD, resulting in increased gas exchange through stomata, which contributed to CO₂ supply for carboxylation (Flexas et al. 2016). This was supported by higher intracellular CO₂ concentration under LVPD (Figure 4).

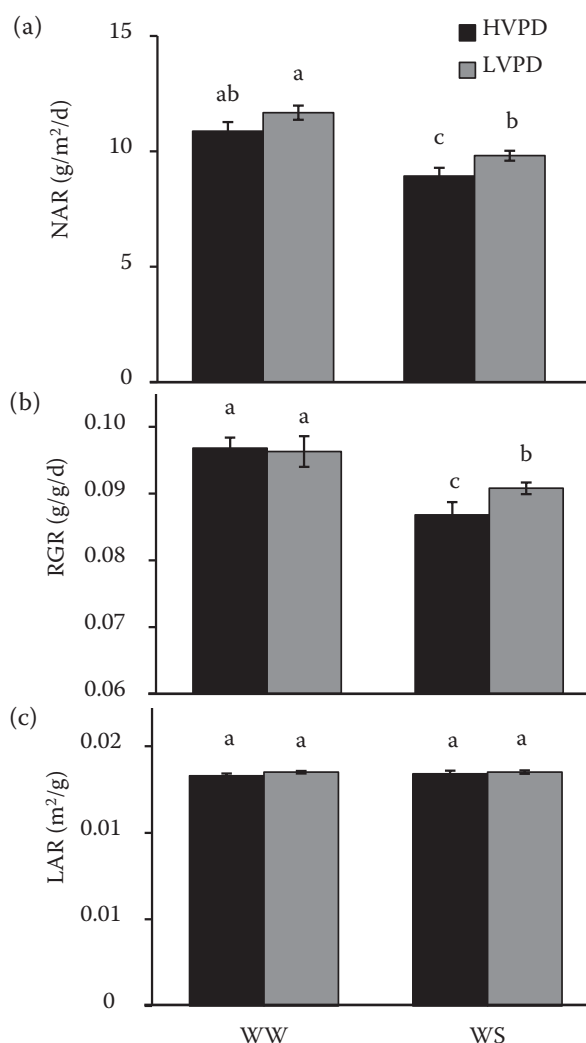


Figure 5. Effects of soil moisture and vapour pressure deficit (VPD) on (a) the net assimilation rate (NAR); (b) relative growth rate (RGR), and (c) leaf area ratio (LAR). WW – well-watered; WS – water stress; HVPD – high VPD; LVPD – low VPD

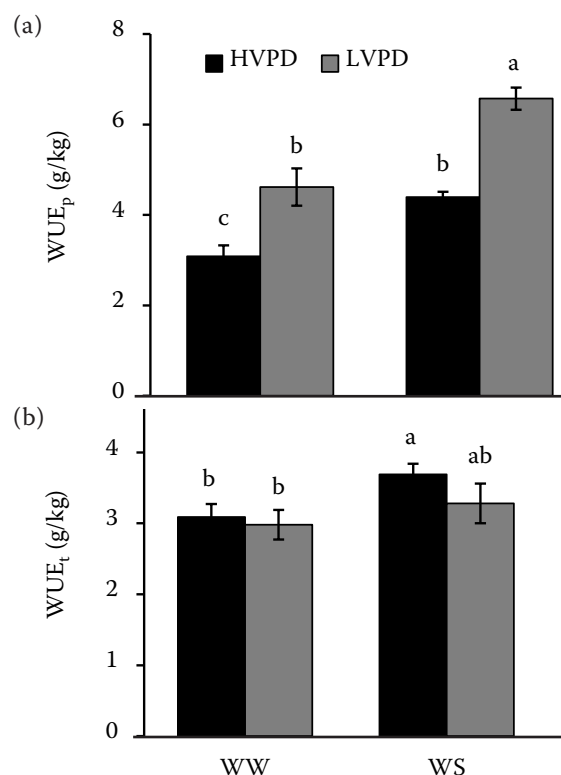


Figure 6. Effects of soil moisture and vapour pressure deficit (VPD) on (a) the whole-plant water use efficiency (WUE_p) and (b) total water use efficiency at 6 plants/m² (WUE_t). WW – well-watered; WS – water stress; HVPD – high VPD; LVPD – low VPD

Plant growth was severely inhibited by water deficit. However, under WS, total dry mass, RGR and NAR in LVPD-treated plants were higher than that in HVPD-treated plants (Table 2, Figure 5). That may to some extent be attributed to an increase in photosynthetic rate caused by fog treatment. Evidence that plant biomass is strongly correlated with photosynthesis was widely demonstrated, as photosynthesis provides carbohydrate for plant growth. Leaf area was also increased in LVPD-treated plants under WS, which may be the result of turgor maintenance (Devi et al. 2015). Moreover, the interception of light for photosynthesis is increased by a larger leaf area (Poorter et al. 2009).

VPD regulation improved WUE by reducing water loss and enhancing carbon production under WS (Figure 6). In addition to transpiration, agricultural water consumption also included fogging water for VPD regulation. Considering the trade-off between water input and carbon production, fog application is recommended for relatively high plant densities (≥ 6 plants/m²) in greenhouses during summer.

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