1 Title

2 Effects of relative humidity and nutrient supply on growth and
3 nutrient uptake in greenhouse tomato production

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Abstract

Higher relative humidity under elevated CO₂ conditions increases stomatal conductance and is expected to promote photosynthesis and growth of tomato. However, yield increase under higher relative humidity has been often reported to be unstable, depending on the growing conditions. Therefore, we investigated the effect of relative humidity and nutrient supply on growth and nutrient uptake under elevated CO₂ conditions in greenhouse tomato production. In two greenhouses, we grew tomato hydroponically at two electrical conductivity (EC) levels (low EC treatments: 0.8–1.2 dSm⁻¹, high EC treatments: 1.6–1.9 dSm⁻¹). In one greenhouse, we installed a humidification system. The other was designated as a control. The dry weight (DW) per plant tended to increase with humidification though without significant differences. The leaf area per plant was not affected by humidification, but the high EC treatment increased the leaf area. The average water uptake in the low EC with mist decreased compared with that without mist. Our results suggested that water use efficiency was increased by higher humidity, whereas the nutrient content of leaves was suppressed by mist in the low EC. In both the treatments, supplying higher EC levels of nutrient solutions increased N, K, and P contents but **did not increased** Ca or Mg contents **as well as in low EC without mist**. These results suggest that supplying high EC nutrient solutions cannot increase Ca and Mg contents **sufficiently** in leaves and stems. To stably increase yield of tomato by humidification under elevated CO₂ conditions, it is important to monitor the transpiration rate and carefully control relative humidity.

Keywords

Elevated CO₂ concentration, Misting system, Relative humidity, Nutrient uptake, Fruit growth, Tomato

1. Introduction

Air humidity is a key component of environmental control in greenhouses. But the importance of air humidity to growth and the yield of tomato is insufficiently understood in Japan because high air humidity is believed to increase disease damage. Yabuki and Miyagawa (1970) suggested that the photosynthetic rate increased with an increase in relative humidity because higher relative humidity lowers water stress in the leaf and increases stomatal conductance. Therefore, the CO_2 concentration in the leaf is maintained at higher levels. Talbott et al. (2003) also reported increases in CO_2 uptake rate and stomatal conductance with moderation of drought stress at higher humidity. Bakker (1991a, 1991b) indicated that the photosynthetic rate could be improved at high humidity by increasing stomatal conductance. The yield of tomato is reported to be increased by higher relative humidity (Leonardi et al. 2000; Guichard et al. 2005). Thus, establishing a CO_2 concentration control technique combined with an air humidity control is the key to achieve high yield and productivity in greenhouse tomato production.

The yield of greenhouse tomato per square meter in The Netherlands is more than double of that in Japan (Takakura 2008). Maintaining relative humidity in the greenhouse in a suitable range for photosynthesis is one of the main factors that cause the yield difference between The Netherlands and Japan (Heuvelink and Dorais 2005). Recently in Japan, many researchers and growers have become highly interested in greenhouse environmental control. Some growers have introduced systems for simultaneous control of humidity and CO_2 concentration, consisting of a combination of mist and CO_2 generation. Some have obtained high yields as expected, but others have not. One of the reasons is thought to be short supply of nutrients. Higher humidity and CO_2 in general improve plant growth and plants need more nutrients in response to yields or dry weight increase (Itani et al. 1998). The management of nutrients of tomato in greenhouse that was controlled humidity should be reconsidered. On the other hands, some studies showed that nutrient deficiency was caused by a reduction in transpiration (Bakker 1990; Holder and Cockshull 1990). Another study found that leaf temperatures were raised to an unsuitable range for photosynthesis by low transpiration rate (Ushio 2008). Thus, humidification has many effects on photosynthesis and nutrient absorption; however, only a few reports have discussed these effects together. The cause of yield instability and the relationships among air humidity, nutrient concentration and tomato growth under elevated CO_2 conditions await investigation. We accordingly evaluated the effects of relative humidity and nutrient supply on growth and nutrient uptake under elevated CO_2 conditions in greenhouse tomato production.

2. Material and Methods

2.1 Plant materials and growth conditions

A Japanese tomato cultivar ("Rinka409", Sakata Co., Ltd., Japan) was grown hydroponically

in two greenhouses in Taketoyo, Chita, Aichi, Japan (34°85'N, 136°91'E) from September 2012 to February 2013. The seeds were sown in 72-cell plug trays filled with a commercial substrate (Na Tera, Mitsubishi Plastics Agri Dream Co., Ltd., Japan) on September 24, 2012. These were germinated and grown in a temperature controlled chamber (Nae Terrace, Mitsubishi Plastics Agri Dream Co., Ltd., Japan). The chamber was operated under a CO₂ concentration of 900 ppm, 12 h photoperiod, 25°C/20°C day/night temperature. The trays were subirrigated daily with a commercial nutrient solution (Haitenpo Cu and Haitenpo Ar, Mitsubishi Plastics Agri Dream Co., Ltd., Japan) with an electrical conductivity (EC) of 1.0 dS m⁻¹. Three weeks later, the seedlings were transplanted into rock wool slabs (Grotop Expert, Grodan, The Netherlands) in four rows at 18-cm spacing in a row and 160-cm between rows at a plant density of 2.3 plants m⁻² (four plants per slab) in both greenhouses (8 m × 16 m × 3.6 m; NS-oriented) covered with glass. One greenhouse (the mist greenhouse, G_m) was installed with a humidification system, the other (the control greenhouse, G_c) was designated as a control. Two levels of nutrient solution (low-EC; 0.8–1.2 dS m⁻¹ and high-EC; 1.6–1.9 dS m⁻¹) were evaluated.

In each greenhouse, two alternately arranged rows were selected and designated as low EC treatments. The other two rows were designated high EC treatments. The frequency of supply of nutrient solution was controlled based on the outside weather. The daily draining percentage was maintained at 20%–50% of the total supply of nutrient solution.

2.2 Environmental control

Temperature and relative humidity measurements were recorded with a data logger (TR-72U, T&D Corporation Co., Ltd., Japan) with an aspiration tube radiation shield at 2-m height. The CO₂ concentration was measured at 1.5-m height with a CO₂ Controller (ZFP9AB11, Fuji Electric, Japan) and was automatically recorded with a voltage recorder (VR-71, T&D Corporation Co., Ltd., Japan). The air temperatures at which ventilation and heating began were set at 30°C and 12°C. Vapour pressure deficit (VPD) was calculated from relative humidity and temperature.

Liquefied CO₂ was supplied through perforated plastic tubes placed above the plants to increase CO₂ concentration to 800 ppm between 06:00 and 16:00 h, (when the ventilation windows were opened, CO₂ concentration was at 400 ppm). The CO₂ supplying started from November 20.

In G_m, relative humidity was controlled using a misting system with a binary fluid mist nozzle (BIMV 45 04, Ikeuchi., Japan). Interval spraying (spraying for 1 min, stop for 1 min) was repeated between 08:00 and 15:00 h when the relative humidity was below 75% and room temperature was above 25°C.

A Time course of temperature, relative humidity and CO₂ concentration is shown in Fig. 1.

2.3 Leaf area and dry weight (DW)

Four plants (two plants per row) of each treatment were destructively sampled for DW, and leaf area measurements and for nutrient analyses on 20 February, 2013. The leaf area was measured with an area meter (AAC-400, Hayashi Denko, Japan). Leaves, stems, and immature fruits were separated and oven dried at 100°C for at least 3 days and DW was measured. Mature fruits were weekly harvested from 10 plants per row until 18 February and DW was calculated from fresh weight and DW ratio.

2.4 Water uptake and water use efficiency

To estimate the water uptake, the amount of drainage solution from the rockwool slabs was gathered and subtracted from the amount of supplied solution. The amount of drainage solution was automatically recorded with a flow meter and data logger (RTR-505-P, T&D Corporation Co., Ltd., Japan). We used the data of sunny days (when outside solar radiation was $>10 \text{ MJ/m}^2$) to calculate monthly means of water uptake. The numbers of sunny days in each month were 11 in December, 20 in January, and 18 in February. Water use efficiency was determined as the ratio of total DW to total water uptake during the experiment.

2.5 Mineral nutrient analysis

Dried samples of 50 mg of leaves, stems, and fruits before harvest ripeness were pulverized. N was measured with a CN Corder (JM1000CN, J-Science Lab Co., Ltd., Japan).

Dried samples of 100 mg were also pulverized and digested by wet ashing via dissolution in 5-mL sulfuric acid and 4-mL hydrogen peroxide and heating at 80°C for 6 h.

P, K, Ca, and Mg were measured by inductively coupled plasma atomic emission spectrometry (SPS7700, Hitachi High-Tech Science Corporation CO., Ltd., Japan) after dilution in distilled water and filtration through a glass fiber filter (GA-100, Advantec Co., Ltd., USA).

2.6 Statistical analysis

Two-way analysis of variance (ANOVA) and *t*-tests were calculated using the statistical software JSTAT version 7.1 (<http://www8.ocn.ne.jp/~jstat/index.html>).

3 Results

3.1 Environments

Changes in temperature, relative humidity and CO₂ concentration in G_m and G_c on January 26, 2013 (left) and February 10, 2013 (right), when the weather consisted of typical sunny days, are shown in Fig. 1. We summarized in Table 1 the climate data in G_m and G_c during the experimental period. The relative humidity was 4–9% higher in G_m than in G_c from 10:00 to 13:00, when the

difference between G_m and G_c was highest. The VPD was lower by 1.2 to 1.9 kPa in G_m than in G_c . Mean temperatures were similar in the two greenhouses. The CO_2 concentrations during November remained at approximately 450 ppm and from December to February at 600 ppm. The control of CO_2 concentration in both greenhouses was kept higher as expected than that of outside and the concentrations in both greenhouses were almost the same level from December to February.

1.1 DW and Leaf area

The DWs of leaves, stems, and fruits are presented in Table 2. The total DW per plant under low EC was higher in G_m than in G_c although the difference was not significant ($P = 0.1352$). The DWs of organs tended to increase with humidification, though without significant differences. The same tendency was observed under high-EC treatments. High-EC treatments significantly increased the DW of leaves and stems in both G_c and G_m . No significant differences in leaf area were found under humidification under low-EC treatment, but under high-EC treatment the leaf area of G_m was significantly greater than that of G_c (Table 2). Leaf area differences caused by nutrient treatments were greater than those caused by humidity treatments.

1.2 Water uptake and water use efficiency

Average monthly amounts of water uptake per plant are shown in Fig. 2A. The average amount of water uptake in low EC of G_m decreased by 9–23% compared with that of low EC of G_c (Fig. 2A). In the high EC treatments, there were no differences in the amount of water uptake per plant between humidity treatments (Fig. 2A). The amount of water uptake per plant in low EC of G_c was the same as that in high EC, although the leaf area under high EC treatment was larger by 40–70%. In addition, the high relative humidity appeared to increase the efficiency of water use in low EC (Fig. 2B).

1.3 Effect of nutrient uptake

Nutrient content (mg per gDW) in leaves, stems, and immature fruits are shown in Table 3–5. In low EC treatment comparison of nutrient contents in G_m and G_c by *t*-tests (Table 3) showed that K and Ca contents of leaves of G_m were significantly decreased, suggesting that higher humidity might be suppressed the absorption and distribution of nutrients by the leaves. Supplying high EC nutrient solution did not increase leaf Ca and Mg contents in G_c but significantly increased N, K and P contents (Table 3). Nutrient contents in stems followed a tendency similar to those in leaves (Table 4). On the other hands in fruits, there were no differences in nutrient contents between G_m and G_c under either nutrient treatment (Table 5). Ca contents were not increased by high EC nutrient solution, although N, K and P contents tended to increase in fruits.

4 Discussion

We investigated the effects of higher humidity level on plant growth and nutrient uptake of tomatoes under elevated CO₂ conditions. In our experiment, the relative humidity in G_c remained at approximately 80%, but was 4.2–9.2% higher from 10:00 to 13:00 in G_m than in G_c. The increase tendency in DW of fruits per plant under high humidity (misting) is in agreement with other reports (Romero-Aranda et al. 2002; Dannehl et al. 2012). DW of leaves, stems, and fruits showed slightly increased tendencies under mist in our experiment (Table 2). Misting has been reported to increase yield under low VPD (Leonardi et al. 2000; Bertin et al. 2000). We considered that higher (more than 80%) relative humidity, which seemed to be high enough to promote photosynthesis, cause the difference in DWs between the humidity treatments no significant ($p>0.05$). Pearce et al. (1993) reported that tomato growth rate was higher during the day than at night under low diurnal stress. Phloem flow was at a maximum during the day and a minimum at night (Guichard et al. 2005). We speculate that a slight increase of DW under higher humidity was promoted during the daytime. Dannehl (2012) reported that although the DW of crops was increased by mist, leaf area expansion was depressed by high humidity because of preferential DW distribution to fruit. Their argument is also applicable to our results. These results confirmed that higher relative humidity increased DW per plant. We speculate that the photosynthetic rate per leaf area was improved by mist.

The benefits of high humidity in a greenhouse lie not only in increasing dry matter production but also in saving water. In this study, we observed decreased water uptake per plant with mist compared to that without mist in the low EC treatment because of a decrease in the transpiration rate (Fig. 2A). Thus, water use efficiency under the low EC treatment with mist was higher than that without mist (Fig. 2B). Sánchez-Guerrero (2009) also compared the water use efficiency of cucumbers with and without CO₂ treatment and found that water use efficiency with CO₂ was improved, given that DW had increased with CO₂ supply. In our experiment, water use efficiency was enhanced similarly to their study (Sánchez-Guerrero, 2009), with total DW under misting being slightly increased (Table 2).

Irrigation water was reduced by an estimated 0.1 L/plant/day and water consumption by the misting nozzle was estimated to be 0.05 L/plant/day in misting under the low EC treatment. Thus, the amount of water saved by misting was, on average, 0.05 L/plant/day. A misting system is not necessary for humidification. Methods that control relative humidity without mist are available in practice, including the use of lower ventilation rates or higher temperature setting for the start of ventilation. In the high EC treatment, the amount of water uptake did not differ between G_m and G_c (Fig. 2A). Leaf area per plant was greater in the high EC treatment. Thus, the water uptake per leaf area was lower in the high EC than that in the low EC treatment. High EC nutrient solution (more than 3.5 dS m⁻¹) reduces the water potential in the root zone and reduces water uptake (Li and

Stanghellini 2001; Jokinen et al. 2011; van de Sanden and Veen 1992). In our experiment, in the high EC treatment, low water potential in the root zone reduced water uptake in both G_m and G_c and cause the difference to be less.

In low EC, K, and Ca contents in leaves and stems tended to decrease with mist compared with those without mist (Tables 3, 4). These results are in agreement with those of previous studies (Adams 1991; Choi et al. 1997). Because of the reduction of water uptake by mist (Fig. 2A), the distribution of some nutrient element to leaves was insufficient. In particular, Ca, which plants cannot readily take up and retranslocate easily (Bloom 2006), are known as immobile elements. Our results show the risk of Ca deficiency in leaves when tomatoes are grown under higher relative humidity.

In immature fruits, nutrients contents including Ca did not differ with and without mist (Table 5). Ca content is usually lower in fruit than in other organs (Ho 1989; de Freitas et al. 2011). Ca is carried in xylem water driven by transpiration. Because the numbers of stomata are lower in fruits than in leaves, the transpiration rate of fruit is low and the amounts Ca moved into fruit are also small. We attribute the low effect of humidification on fruit Ca content to this low fruit transpiration rate.

In high EC, N, K, and P contents in all organs on a per-plant basis were increased (Table 3, 4, 5). These elements are known as mobile elements (Bloom 2006). However, Ca and Mg contents in leaves and fruits were not increased by the high EC nutrient solution (Table 3, 5). We conclude that supplying a high EC nutrient solution will not lead to an increase in nutrient contents in leaves.

5 Conclusions

In this study, we showed benefits and disadvantages of the humidification technique combined with elevated CO_2 conditions. We confirmed that dry matter production was increased with misting, whereas nutrient content was decreased.

Even when tomatoes are grown under conditions that increase fruit yield, including higher relative humidity and elevated CO_2 conditions, the risk of deficiency of nutrients caused by reduced transpiration rate is present.

Supplying a high EC nutrient solution will not always lead to an increase in the nutrient content in leaves. To increase tomato yield stably by humidification under elevated CO_2 conditions, it is important to monitor the transpiration rate and carefully control relative humidity.

Water use efficiency of tomatoes were also increased with misting.

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Footnotes

Author contributions: M.S., K.S., H.H., and Y.I. designed the study; M.S., H.U., Y.K., D.A., and Y.I. performed the experiments; and M.S. and Y.I. wrote the manuscript.

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Tables

Table 1 Daytime mean temperature, relative humidity (between 10:00 and 13:00 h), and CO₂ concentrations (between 8:00 and 16:00 h) in greenhouses with mist (+M), and without mist (−M).

		Nov.		Dec.		Jan.		Feb.	
		−M	+M	−M	+M	−M	+M	−M	+M
Temp. (°C)	10:00–13:00	23.4	23.0	19.4	20.0	22.6	22.3	22.1	21.6
RH (%)	10:00–13:00	56.3	60.8	78.1	87.4	82.5	86.7	79.3	84.5
VPD (kPa)	10:00–13:00	12.6	11.0	4.9	3.0	4.8	3.6	5.5	4.0
CO ₂ (ppm)	8:00–16:00	449.6	443.2	663.5	686.4	639.1	566.8	626.6	670.0

Table 2 Dry weights (DW) of senescent leaves, leaves, stems and fruits, including fruits before harvest–ripe stage and harvested fruits, per plant, and leaf area per plant under low EC or high EC nutrient solution and with mist (+M) or without mist (–M) 130 days after transplanting.

EC	Humidity	DW (g/plant)					Leaf area (m ²)	
		Senescence leaves	Leaves	Stems	Fruits	Total		
Low EC	–M	16.8 ± 0.4	45.6 ± 3.0	34.3 ± 2.4	218.0 ± 15.4	314.7 ± 20.2	0.930 ± 0.094	
	+M	17.2 ± 0.9	46.2 ± 2.2	37.4 ± 0.6	245.9 ± 15.2	346.6 ± 16.9	0.915 ± 0.055	
	p-value ^x	0.3415	0.4335	0.1486	0.1229	0.1352	0.4483	
High EC	–M	18.7 ± 0.8	72.6 ± 5.4	46.4 ± 2.5	233.0 ± 16.3	370.8 ± 21.5	1.534 ± 0.117	
	+M	18.9 ± 1.9	68.3 ± 6.8	46.3 ± 3.8	253.1 ± 10.6	386.6 ± 19.0	1.260 ± 0.057	
	p-value ^x	0.4731	0.3202	0.4918	0.1704	0.3	0.0403	
Two-way	Humidity (A)	n.s. ^z	n.s.	n.s.	n.s.	n.s.	n.s.	
ANOVA	EC (B)	n.s.	**	**	n.s.	*	**	
	(A)×(B)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	

Values represent the means of four tomato plants ± standard errors.

^x Probability value of Student's *t*-test between –M and +M in the same EC treatment.

^y *: Significant difference by Student's *t*-test between –M and +M in the same EC treatment at $P < 0.05$. n.s.: Not significantly different at $P < 0.05$.

^z *, **: Significantly different by two-way ANOVA between EC and humidity treatments at $P < 0.05$, 0.01 as determined by Bonferroni correction. n.s.: Not significantly different at $P < 0.05$.

Table 3 Nutrient concentrations per DW (mg per g) in leaves under low EC or high EC treatment and with mist (+M) or without mist (–M) 130 days after transplanting.

EC	Humidity	Nutrient concentrations (mg/g)				
		N	K	P	Ca	Mg
Low EC	–M	40.83 ± 0.78	37.62 ± 1.68	7.20 ± 0.59	20.01 ± 1.9	4.42 ± 0.53
	+M	41.85 ± 1.00	31.92 ± 1.62	5.96 ± 0.41	15.17 ± 1.2	3.65 ± 0.37
	p-value ^x	0.225	0.025	0.066	0.038	0.139
High EC	–M	44.29 ± 0.80	54.04 ± 3.22	8.69 ± 0.67	14.15 ± 0.6	3.37 ± 0.28
	+M	42.38 ± 0.87	48.33 ± 4.41	7.63 ± 0.72	16.71 ± 1.4	4.04 ± 0.23
	p-value ^x	0.079	0.168	0.163	0.153	0.058
Two-way	Humidity (A)	n.s. ^z	*	*	n.s.	n.s.
ANOVA	EC (B)	*	**	**	n.s.	n.s.
	(A)×(B)	n.s.	n.s.	n.s.	*	n.s.

Values represent the means of four tomato plants ± standard errors.

^x Probability value of Student's *t*-test between –M and +M in the same EC treatment.

^y *: Significant difference by Student's *t*-test between –M and +M in the same EC treatment at $P < 0.05$. n.s.: Not significantly different at $P < 0.05$.

^z *, **: Significantly different of by two-way ANOVA between EC and humidity treatments at $P < 0.05$, 0.01 as determined by Bonferroni correction. n.s.: Not significantly different at $P < 0.05$.

Table 4 Nutrient concentrations per DW (mg per g) in stems under low EC or high EC treatment and with mist (+M) or without mist (–M) 130 days after transplanting.

EC	Humidity	Nutrient concentrations (mg/g)				
		N	K	P	Ca	Mg
Low EC	–M	21.67 ± 0.82	28.61 ± 2.42	4.68 ± 0.41	8.61 ± 0.38	2.28 ± 0.05
	+M	21.56 ± 0.65	24.81 ± 0.98	4.36 ± 0.16	6.87 ± 0.44	1.99 ± 0.19
	p-value ^x	0.4602	0.0976	0.249	0.0124	0.0915
High EC	–M	24.63 ± 0.92	35.59 ± 1.25	6.89 ± 0.10	6.35 ± 0.12	1.83 ± 0.06
	+M	22.92 ± 0.37	34.69 ± 1.68	6.52 ± 0.22	7.03 ± 0.29	2.11 ± 0.05
	p-value ^x	0.0665	0.3414	0.0862	0.0386	0.006
Two-way	Humidity (A)	n.s. ^z	n.s.	n.s.	n.s.	n.s.
ANOVA	EC (B)	**	**	**	**	*
	(A)×(B)	n.s.	n.s.	n.s.	*	*

Values represent the means of four tomato plants ± standard errors.

^x Probability value of Student's *t*-test between –M and +M in the same EC treatment.

^y *, **: Significant difference by Student's *t*-test between –M and +M in the same EC treatment at $P < 0.05, 0.01$. n.s.: Not significantly different at $P < 0.05$.

^z *, **: Significantly different by two-way ANOVA between EC and humidity treatments at $P < 0.05, 0.01$ as determined by Bonferroni correction. n.s.: Not significantly different at $P < 0.05$.

Table 5 Nutrient concentrations per DW (mg per g) in fruits before harvest–ripe stage under low EC or high EC and with mist (+M) or without mist (–M) 130 days after transplanting.

EC	Humidity	Nutrient concentrations (mg/g)				
		N	K	P	Ca	Mg
Low EC	–M	16.27 ± 0.34	26.48 ± 0.82	3.90 ± 0.20	1.69 ± 0.27	1.36 ± 0.04
	+M	16.49 ± 0.41	26.26 ± 1.34	3.83 ± 0.17	2.06 ± 0.31	1.47 ± 0.09
	p-value ^x	0.3488	0.448	0.3962	0.2024	0.1553
High EC	–M	17.76 ± 0.47	29.82 ± 1.12	4.42 ± 0.07	1.52 ± 0.14	1.27 ± 0.03
	+M	16.96 ± 0.38	28.43 ± 0.63	4.25 ± 0.11	1.53 ± 0.19	1.38 ± 0.08
	p-value ^x	0.1174	0.1602	0.1161	0.4936	0.1199
Two-way	Humidity (A)	n.s. ^z	n.s.	n.s.	n.s.	n.s.
ANOVA	EC (B)	*	*	**	n.s.	n.s.
	(A)×(B)	n.s.	n.s.	n.s.	n.s.	n.s.

Values represent the means of four tomato plants ± standard errors.

^x Probability value of Student's *t*-test between –M and +M in the same EC treatment.

^y *: Significant difference by Student's *t*-test between –M and +M in the same EC treatment at $P < 0.05$. n.s.: Not significantly different at $P < 0.05$.

^z *, **: Significantly different by two-way ANOVA between EC and humidity treatments at $P < 0.05$, 0.01 as determined by Bonferroni correction. n.s.: Not significantly different at $P < 0.05$.

Fig. 1

Figure 1 Time course of relative humidity (black line), temperature (gray line) and CO₂ concentration (bold pale gray line) in G_m (solid line) and G_c (dotted line) on January 26, 2013 (left) and February 10, 2013 (right).

Fig. 2

Figure 2 Effect of electrical conductivity levels of nutrient solution and relative humidity on water uptake and water use efficiency. Average (from December 1 to February 19) daily amount of water uptake per plant on sunny days (A). Water use efficiency (total DW per unit of water uptake) (B).