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Greenhouse Tomato Growth and Physiological Responses to High Nutrient Solution Electrical Conductivity and Low Substrate Water Content

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ABSTRACT

The ionic concentration of a nutrient solution, shown by its electrical conductivity (EC), has profound effects on tomato plant growth and fruit yield in the greenhouse. However, high EC effects cannot be simply attributed to restricted water uptake by rhizosphere salinity as usual. To understand the differences in effects of high EC and substrate water deficit, tomato plants were grown in peat-moss based substrate with a nutrient solution of high (4.5 dS m^{-1}) or low (2.3 dS m^{-1}) EC under high (95% of capillary capacity) and low (55%) substrate water content (SWC), and examined were the effects on growth, yield, photosynthesis, and plant water relations. Salts were intentionally allowed to accumulate in the substrate for seven weeks by placing the pot in a dish without leaching. Both high EC and low SWC significantly decreased plant growth, dry matter production and fruit yield as well as photosynthesis, leaf water and turgor potentials, stomatal conductance and transpiration. However, blossom-end rot of fruit was more severe in high EC than in low SWC although the leaf Ca content was similar in these two stress treatments. Moreover, soluble protein content and Rubisco activities on a leaf area basis were not decreased by high EC but decreased by low SWC. Results suggested that high EC was different from substrate water deficit in effects on some physiological processes. Further research is needed to elucidate the detailed mechanism of high EC effects.

Keywords: *Lycopersicon esculentum*, salinity stress, transpiration, turgor potential, water stress
Abbreviations: **BER**, blossom-end rot; **DMP**, dry matter production; **EC**, electrical conductivity; **FY**, fruit yield; $\mathbf{g_M}$, mesophyll conductance; $\mathbf{g_S}$, stomatal conductance; **NFT**, nutrient film technique; $\mathbf{P_N}$, net photosynthetic rate; $\mathbf{R_D}$, dark respiration rate; **SWC**, soil water content; **Tr**, transpiration rate; $\mathbf{\Psi_P}$, leaf turgor potential; $\mathbf{\Psi_W}$, leaf water potential

INTRODUCTION

A proper concentration of nutrient solution is usually required for greenhouse production. Because the nutrient solution contains only mineral ions, greenhouse growers and researchers simply use electrical conductivity (EC) to show the concentration of the nutrient solution. High EC of the nutrient solution often reduces yield and quality of greenhouse tomatoes. Much research has been done on growth and yield responses of greenhouse tomato to high EC (Winsor 1984; Ehret and Ho 1986; Charbonneau *et al.* 1988; Adams and Ho 1989; Adams 1991a; Adams and Holder 1992; Signore *et al*. 2008). Charbonneau *et al.* (1988) found that an EC of 4 dS m^{-1} decreases yield under both normal and supplemental lighting conditions, but total plant dry mass of some cultivars under low light conditions is not altered by an EC of 4 dS m^{-1}. In the same experiment of Charbonneau *et al.* (1988), an EC of 6 dS m^{-1} decreased fruit yield and total dry mass of all cultivars up to 37% under both high and low light conditions. Winsor (1984) found significant decreases in fruit number with an EC of 8 and 10 dS m^{-1}. As reviewed by Dorais *et al*. (2001), although increases in EC or salinity limit marketable yield and fruit size, fruit quality and the dry matter content of the fruit are increased by higher ECs. Usually, ECs or salinities higher than 2.3-5.1 mS cm^{-1} result in an undesirable yield reduction, while ECs of 3.5-9.0 mS cm^{-1} improve tomato fruit quality (Cornish 1992; Carvajal *et al*. 1999; Jeong *et al*. 1999; Lee *et al*. 1999; Hao *et al*. 2000; Krauss *et al*. 2006; Gaytán-Mascorro *et al*. 2008). In the above-mentioned studies, only plant growth and fruit yield were examined and no detailed examinations were made on the physiological responses. In all the above-mentioned experiments, blossom-end rot (BER) of fruit was caused by high EC. The negative effects of high EC are simply attributed to the restricted water uptake by rhizosphere osmotic stress. However, no research has shown whether or not a similar water stress caused by substrate water deficit rather than by salinity can cause a similar fruit BER.

The level of EC actually indicates the concentration of the nutrient solution because all the fertilizer molecules are electrolyzed and exist in an ionic state. Because there are no organic molecules in the nutrient solution, EC also indicates the level of osmosis of the nutrient solution. When EC of the nutrient solution reaches a level higher than 2 dS m^{-1}, the amount of nutrients is no more a factor limiting plant growth and physiology and some problems are caused by salinity and ionic toxicity rather than the nutrition level (Papadopoulos 1991). Many reports suggest that salinity causes rhizosphere osmotic stress and decreases Ca content in the fruit and consequently results in BER of fruit (Adams and Holder 1992; Bradfield and Guttrige 1984). However, the mechanism is not clear enough. Ca-deficiency is ultimately attributed to restricted water uptake by rhizosphere salinity, because Ca is usually transported by transpiration water flow to the plant (Adams 1991b). However, there has been no comparative study between the effects of water deficit and salinity, both of which cause plant water stress.

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This is because the recognition that water deficit usually does not occur in greenhouse production. Actually, short-term mild water stress may occur as a result of the osmotic effects of the high ionic concentrations in the nutrient solution and/or improper irrigation scheduling in hydroponic culture of greenhouse crops such as tomatoes, especially at midday when humidity is low and irradiance is high (Atherton and Rudich 1986; Andersen *et al.* 1995). A high ionic concentration may affect tomato plants by decreasing plant water uptake (Ehret and Ho 1986), but also possibly specific ion toxicity. Reduced transpiration usually results in decreases in Ca translocation towards the upper young leaves by interfering the partitioning process and reduced uptake of some mineral elements such as Mg and K (Adams 1991b). However, if salt accumulation in the substrate is released by some practices like overwatering the substrate once a week, a nutrient solution with an adequately high EC up to 4 dS m^{-1} results in an improvement of fruit quality as reported for greenhouse tomatoes in sand culture (Mizrahi *et al.* 1988) and nutrient film technique (NFT) (Gough and Hobson 1990; Niedziela *et al.* 1993). That is why researchers and greenhouse growers try to find an adequate EC that does not decrease fruit yield but is favorable for fruit quality. Therefore, before searching for an appropriate EC regime for irrigation, it is important to understand the differences in effects on fruit yield and plant physiology between water deficit and high EC.

In this study, the aims are 1) with a series of detailed examinations to ascertain if a high EC of 4.5 dS m^{-1} affects plant growth, fruit yield and some physiological processes such as photosynthesis, transpiration and plant water relations; and 2) in comparison with a similar water stress caused by substrate water deficit, to elucidate the differences in effects between high EC and low SWC. Besides the fruit yield factors, emphases of measurements are focused on photosynthesis and transpiration as well as the related processes such as Rubisco activity and leaf water relations.

MATERIALS AND METHODS

Plant material

Seeds of 'Capello' tomato (*Lycopersicon esculentum* L.) were sown in small rockwool cubes (38 × 36 × 40 mm, Pargro Co., Ltd., Caledonia, Ontario, Canada). Seedlings were transplanted to rockwool blocks (0.1 × 0.1 × 0.1 m) when the third leaf appeared. Five weeks old seedlings were again transplanted to 6.25-L plastic pots filled with peat moss-based substrate (70% sphagnum peat and 30% perlite, v/v, Premier Peat Moss, Riviere-du-lou, Quebec, Canada) in a double-layer polyethylene greenhouse. Hard fertilizers were not added by either the peat moss manufacturer or the experimenters. Temperature was controlled at 21 ± 2°C/18 ± 2°C (day/night). The vapor pressure deficit fluctuated with time of day between 0.6 and 1.0 kPa. When the fifth leaf from the base was fully expanded, treatments were initiated. The experimental design was a randomized block factorial with two levels of EC and two levels of SWC as follows: 1) control – low nutrient solution electrical conductivity (EC) (2.3 dS m^{-1}) and high substrate water content (SWC) (95 ± 5% of the capillary capacity on gravimetric basis); 2) water stress – low EC (2.3 dS m^{-1}) and low SWC (55 ± 8%); 3) salinity stress – high EC (4.5 dS m^{-1}) and high SWC (95 ± 5%); 4) combined stress – high EC (4.5 dS m^{-1}) and low SWC (55 ± 8%). All the solutions were adjusted to pH 5.6. The pH of the tap water used was close to 7 and the EC was 0.3 dS m^{-1}. A nutrient solution EC of 2.3 dS m^{-1} used in this study is normal and often used by growers in Europe and North American (Adams 1991a; Straver 1995). A nutrient solution EC of 4.5 dS m^{-1} is the critical EC to cause yield decreases and fruit BER in some cases (Charbonneau *et al.* 1988). Substrate water content 55 ± 8% is also the critical value of peat-moss to induce a substantial water stress. Our pre-experiment (not shown) showed that water content higher than 65% did not induce a statistically significant decrease in leaf water potential with the exception at midday. This was because the capillary capacity of peat moss was high (1 kg of peat moss absorbs 2.8 kg water).

Table 1 Composition of nutrient solution with low EC (2.3 dS m^{-1}) and high EC (4.5 dS m^{-1}) used in this experiment.

Element	Fertilizer source	Nutrient concentration (mmol L^{-1})	
		Low EC	High EC
N	KNO_3, $Ca(NO_3)_2$	10.1	19.7
P	KH_2PO_4	1.7	3.3
K	KCl, KNO_3, KH_2PO_4	7.2	13.6
Ca	$Ca(NO_3)_2$	3.5	6.8
Mg	$MgSO_4$	1.8	3.5
Fe	EDTA-Fe	0.0726	0.1421
Mn	Mn-Chelate	0.0180	0.0354
Zn	Zn-Chelate	0.0076	0.0149
Cu	Cu-Chelate	0.0016	0.0030
B	Borax	0.0282	0.0510
Mo	$(NH_4)_2MoO_4$	0.0006	0.0011

Each treatment contained five replicate plots. Each plot included 6 plants at a density of 3 plants per m^2. Concentrated solutions were prepared and stored in tanks. Nutrient solutions used for irrigation were prepared using tap water with the fertilizers as shown in **Table 1**. EC of the solution was measured with a portable EC meter and adjusted to the designed levels by adding water or concentrated solutions. Plants were irrigated everyday with the diluted nutrient. Substrate water content was adjusted by weighing and watering the pots with the nutrient solutions twice a day. The substrate water content fluctuated with a deviation of 5 or 8% during the day. Salts were intentionally allowed to accumulate in the substrate by placing a pot in a plastic dish and avoiding overwatering and drainage. In other words, besides those absorbed by plants, all minerals are kept in the substrate.

Salts and nutrient concentrations in leaves and in substrate

Thirty days after the beginning of treatments, substrate samples were taken from the pots and dried at 86°C for 48 h and then stored for the nutrient analysis. The fifth leaf from the top was used for leaf tissue analysis. Five whole leaves (including petioles) were randomly sampled from each treatment. The leaves were dried at 65°C for 48 h and then stored in a desiccator for nutrient analysis. Mineral cations and phosphorus in the youngest expanded leaf and in the substrate were determined by an atomic absorption spectrophotometer (Model ICAP 9000, Jarrel-Ash, Waltham, MA, USA). Samples of the substrate were taken from the pots and the concentrations of elements or ions were measured in the same way as for the leaf samples. Plant tissue and soil samples were digested and efficiently ionized by direct injection into a plasmatron formed with argon gas ionized in an applied radio frequency field (Donohue and Aho 1992). Resultant ionic emission spectra are monitored at pre-selected wavelengths. Because each element has a specific emission spectrum when it is ionized, effective multi-element measurement was possible. Standards were first prepared as, for example, no. 1, 1.3 M HCl blank; no. 2, 400 mM P–10 mM Zn–10 mM B; no. 3, 100 mM Al–100 mM Fe; no. 4, 1 M Ca–1 M K–100 mM Mg–10 mM Mn–10 mM Cu. Then, 1.000 ± 0.10 g of dried, ground plant tissue or soil sample was weighed, placed into a ceramic crucible, and dried to ash. The ash was allowed to cool down and then 5 ml concentrated HCl was pipetted into the crucible. The ash was gently stirred to dissolve well. After 30 min of standing, 10 ml deionized water was pipetted in and again 20 min of standing was allowed. Then, 35 ml deionized water was added to make a final volume of 50 ml. The prepared sample was filtered through Whatman #42 filter paper. Then the sample was measured and calibrated with the standard.

$N\text{-}NO_3$ was measured by an automatic colorimeter (TRAACA 800, Bran-Luebbe, Inc., New York, NY, USA) according to Isaac and Johnson Jr. (1992). The plant tissue or soil sample was digested to ammonium compound. The ammonium reacts with phenoxide at the presence of sodium hypochloride to form a green colored complex. Measurement was done automatically and potassium sodium tartrate was added to the sample stream to prevent the precipitation of hydroxides. Electrical conductivity in the substrate solution was estimated from the concentration and solubility

of salts using a method adopted without clear references. The element in concentration of 100 ppm indicates specific EC as follows: N, 0.96 dS m^{-1} (NO_3^- balanced with K) and 0.84 dS m^{-1} (with Ca or Mg); P, 0.73 dS m^{-1} (HPO_4^{2-} with K); K, 0.35 dS m^{-1} (balanced with Cl^-, SO_4^{2-} or NO_3^-) and 0.23 or 0.28 dS m^{-1} (balanced with HPO_4^{2-} or $H_2PO_4^-$); and Mg, 0.97 dS m^{-1} (with NO_3^-) and 0.84 dS m^{-1} (with SO_4^{2-}).

Photosynthesis, transpiration and stomatal and mesophyll conductances

Photosynthesis and transpiration were measured using infrared gas analyzers (ADC-225-MK3, the Analytical Development Co., Ltd., Hoddesdon, England) in an open gas exchange system (Yue *et al.* 1992) five weeks after the beginning of treatments, when the plants and leaves showed clear differences among treatments. The apical leaflet of the youngest fully expanded leaf was placed in an assimilation chamber and the photosynthetic rate was measured at a photosynthetic photon flux of 800 μmol m^{-2} s^{-1}. Air temperature in the assimilation chambers was 23 ± 0.4°C. Leaf temperature was 0.5 to 1.0 higher than air temperature. The vapor pressure deficit (VPD) of the air from the assimilation chamber inlet was controlled at 1.3 kPa. The air inside the chamber was circulated by a fan mounted on one side wall and the VPD varied with the transpiration rate between 1.2 and 0.9 kPa. Stomatal and mesophyll conductances were calculated as described by Jones (1992).

Water potential, turgor potential and water consumption

Five weeks after the beginning of treatments, two youngest fully expanded leaves having 13 leaflets were used for water potential measurement. A leaflet at the middle of the leaf was cut with 12 leaflets left on the plant so that the total photosynthesis in that leaf would not be much affected. The cut leaf was immediately put into a polyvinyl bag and then placed in the pressure chamber (Model 3000, Soilmoisture Equioment Corp., Santa Barbara, CA. USA) for measurement according to Turner (1988). Measurement was made diurnally once an hour from 8:00 to 19:00. Turgor potential was estimated from the pressure-volume curve according to Turner (1988).

Chlorophyll, soluble protein and Rubisco activities

Leaf discs each with 10 cm^2 were sampled from the youngest expanded leaves on the 38th day after the beginning of treatments, when the photosynthetic measurements were just done. The leaf disc samples were frozen with liquid nitrogen and stored in a –80°C freezer. Chlorophyll was measured using the Arnon method as described by Yoshida (1985). Soluble protein was measured by Bradford method (Bradford 1976). Rubisco activities were determined using ^{14}C isotope method as described in Xu *et al.* (1996) with some modifications. Two leaf discs each with an area of 10 cm^2 were excised as one sample from the top leaflet of the 5th leaf and immediately put into liquid nitrogen. The frozen leaf discs were ground into fine powder in liquid nitrogen and extracted with 5 ml of a buffer solution containing 50 mM Bicine (pH 8.2), 20 mM KCl, 5 mM dithiothreitol (DTT), 0.1 mM sodium ethylenediamine tetraacetate (Na_2-EDTA), 2% (w/v) polyvinyl pyrrolidone (PVP), 0.1 mM phenylmethyl sulphonyl fluouride (PMSF) and 5 μM leupetin. Half of the extract was removed for initial activity. The remainder was used for measurements of total activity. Initial Rubisco activity was measured at 23°C by injecting 50 μl of leaf extract into an assay buffer (400 μL) containing 100 mM Bicine (pH 8.2), 20 mM $MgCl_2$, 5 mM DTT and 200 μM $Na^{14}CO_3$. The reaction was terminated after 30 s by adding 200 μl of 2 M HCl. The samples were dried at 90°C for 3 h and then the acid-stable ^{14}C was determined by liquid scintillation counting. Total Rubisco activity was determined in a similar way except that the assay buffer was incubated at 23°C for 5 min before 50 μl of 20 mM ribulose-1, 5-bisphosphate (RuBP) was added.

Fruit yield and dry matter production

Seven weeks after the beginning of treatments, plants were cut down with shoot, root and fruit separated, and dried at 80°C for three days. Fruit samples were sliced, dried and the dry mass ratio was obtained. The fruit mass was calculated from the fresh fruit weight and the dry mass ratio. Harvest index was expressed as the percentage dry mass ratio of total fruit to the total plant.

RESULTS AND DISCUSSION

Salt accumulation in the substrate

Thirty days after the beginning of treatments, K, Ca, Mg, P and nitrate-N accumulated to a considerable extent in the substrate because of irrigation without leaching (**Table 2**). Except for those absorbed by the plant and leached to the plastic dishes that were placed under the pots, all remaining elements from the irrigated nutrient solution accumulated in the substrate. If the presenting form of the elements was considered as ionic or soluble in the soil solutions, considerable increase in estimated EC resulted from the accumulation of salts, especially in the substrate irrigated with a high concentrated nutrient solution. Because it was not easy to extract soil solution from the dry soil, EC in the soil solution was estimated from the amount of salts. All salts were assumed soluble in the soil solution. Therefore, the real EC value for the soil solution should be lower than that presented in **Table 2** if there were some salts precipitated as insoluble.

The data of the EC at the beginning of the treatments, on the 15th day and on the 30th day showed the developing course of soil salinity (**Table 2**). These data showed clearly that soil salinity became higher and higher as salts accumulated. The consequence of the stress was also shown by the levels of leaf water potential (Ψ_W) at these different stages. However, the substrate water content was maintained the same during this period. The Ψ_W also showed no large changes during this period. This was the difference in stress pattern between high EC and low SWC. At the stage of around 30 days after the beginning of treatments, the strength of water stress shown by Ψ_W became similar to each other between these two treatments.

Photosynthesis, respiration, and chlorophyll content

Five weeks after the beginning of treatments, both salinity

Table 2 Concentrations of K, Mg, Ca, NO_3^- and P, EC in the substrate estimated as well as leaf water potential (Ψ_W) from the salt content on the first and 30th days from the beginning of treatments.

	mmol L^{-1}										dS m^{-1}			MPa		
	K		Mg		Ca		NO_3^-		P		EC			Ψ_W		
	1 d	30 d	1 d	30 d	1 d	30 d	1 d	30 d	1 d	30	1 d	15	30 d	1 d	15 d	30 d
Control	2.2	14.2	0.33	6.3	0.72	8.0	0.35	19.4	0.42	2.9	1.0	3.8	6.6	-0.35	-0.34	-0.98
Water stress	1.8	16.3	0.25	4.7	0.50	10.1	0.32	13.4	0.36	3.4	1.3	4.9	10.8	-0.66	-0.65	-1.21
Salinity stress	2.4	46.1	0.45	14.3	0.80	19.0	0.40	76.7	0.48	9.4	1.2	7.5	19.9	-0.38	-0.62	-1.27
Comb. Stress	2.1	31.2	0.37	11.0	0.62	14.7	0.33	63.4	0.36	7.2	1.5	7.7	22.5	-0.73	-0.85	-1.48
Water stress	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	*	**	**	**
Salinity stress	NS	**	NS	*	NS	**	NS	**	NS	**	NS	**	**	NS	**	**
Water×salinity	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

*, **, and NS mean significance at P≤0.05 and P≤0.01, and no significance according to Waller-Duncan Comparison (These are the same for the following tables).

Table 3 Effects of EC and soil water content on the net photosynthetic rate (P_N), Stomatal (g_S) and mesophyll (g_M) conductances, dark respiration rate (R_D), chlorophyll content (Chl), leaf transpiration rate (Tr_L), plant transpiration rate (Tr_P), leaf water potential (Ψ_W) and turgor potential (Ψ_P) at predawn (P) and at midday (M) of tomato plants at the stage of 35 days after beginning of treatments.

Treatment	P_N	g_S	g_M	R_D	Chl	Tr_L	Tr_P	$\Psi_{W(P)}$	$\Psi_{W(M)}$	$\Psi_{P(P)}$	$\Psi_{P(M)}$
	$\mu mol\ m^{-2}\ s^{-1}$	$mm\ s^{-1}$		$\mu mol\ m^{-2}\ s^{-1}$	$mg\ m^{-2}$	$mg\ m^{-2}\ s^{-1}$	$Kg\ d^{-1}$	MPa			
Control	16.3	5.1	2.1	0.43	378	38	1.74	-0.34	-0.98	0.97	0.48
Water stress	14.2	3.2	1.8	0.37	396	29	1.12	-0.53	-1.21	0.68	0.21
Salinity stress	13.8	3.5	1.9	0.54	439	30	1.12	-0.57	-1.27	0.72	0.23
Comb. Stress	12.4	2.4	1.4	0.51	484	23	0.86	-0.76	-1.48	0.53	0.14
Water stress	*	*	*	NS	NS	**	**	**	**	**	**
Salinity stress	*	*	NS	*	**	**	**	**	**	**	**
Water×salinity	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	*

Fig. 1 Plant (top) and leaf (bottom) appearances of tomato plants grown under control, water stress, salinity stress, and combined stress conditions five weeks after the beginning of treatments.

stress caused by salt accumulation and low SWC significantly decreased net photosynthetic rate (P_N) (**Table 3**). The effects of high EC and low SWC were simply additive on P_N without interactions. However, in a previous experiment, when substrates were overwatered every week to wash out the accumulated salts, a high EC of 4.0 to 5.5 dS m^{-1} did not decrease photosynthesis (Xu *et al.* 1995). Adams (1991a) reported that tomato plants could tolerate relatively high levels of EC if there is no salts accumulation in hydroponic systems. Salinity can cause water stress, osmotic stress and specific ionic toxicity. However, here, we cannot separate these stresses.

Both high EC and low SWC significantly decreased stomatal conductance but mesophyll conductance was only slightly decreased by low SWC but not by high EC (**Table 3**). Here this was a difference in effect manner on photosynthesis between high EC and low SWC. Dark respiration was not decreased by low SWC but significantly increased by high EC. The reason for the differences in effect of respiration between high EC and low SWC was not clear. There are also many suggestions and conclusions concerning water stress effects on respiration. Usually, a mild stress promotes respiration and severe stress depresses respiration activity (Jones 1992). However, in this study, respiration was increased by high EC even under conditions of substrate water deficit. According to common concepts of water stress physiology, under mild stress, adaptation processes such as osmotic adjustment occur in response to the stress. These processes require more energy expenditure by maintenance of respiration (McCree 1986) and may account for the increase in respiration under high EC conditions. However, this respiration increase was not observed for low SWC. There might be some other reasons accounting for respiration increase by high EC. Chlorophyll concentration was increased slightly by low SWC, but largely by high EC under both high and low SWC. This result can also be observed from the leaf color as shown by the photographs in **Fig. 1**. Thus, chlorophyll was not a factor limiting photosynthesis in the present experiment. In leaves under combined stress, a synergistic interaction effect was shown on the chlorophyll concentration.

Leaf water potential, turgor potential and water consumption

After 5 weeks of treatment, leaf water potential (Ψ_W) and turgor potential (Ψ_P) at both predawn and midday were lower in water and/or salinity stressed plants than in control plants (**Table 3**). Significant decreases in Ψ_W were observed around midday in all treatments (**Fig. 2**). Under water deficit conditions, photosynthetic rate is associated with Ψ_P. Maintenance of Ψ_P, even to a partial extent, keeps stomata open and enables photosynthesis to continue (Kramer 1983; Jones 1992). Turgor potential is, in turn, associated with Ψ_W. Apparently, decreases in photosynthesis by high EC and low SWC were attributed to decreases in Ψ_W and Ψ_P. Water consumption based on both whole plant per day or transpiration rate per unit of leaf area was decreased by water and salinity stress, especially at midday (**Fig. 2**). Even in plants of control, the Ψ_W was quite low at midday because the measurements of Ψ_W diurnal changes were made on a typical shiny hot day. Many researchers have pointed out that the short-term water stress at midday may cause some problem in pollination and fruit setting (Ehret and Ho 1986; Adams 1991a). Decreases in Ψ_W at midday showed clearly that water stress did occur in the control plots. This phenomenon is often observed in normal cases of greenhouse production and experiments (Holder 1990; Sánchez-Blanco *et al.* 1991). Holder (1990) has found that not only does the leaf water potential decrease but also leaf size is reduced at midday. This stress extent increases as the salinity increases or the humidity decreases. That is why some researchers have tried to develop an evapotranspiration-dependent automatic system and combine with washing the salts out of substrates, in order to avoid the midday water stress (Papadopoulos 1991; Norrie *et al.* 1994).

Although the diurnal change pattern was similar to each other for high EC and low SWC treatments, the diurnal pattern of Ψ_W was somewhat different between these two treatments. In the morning and late afternoon, Ψ_W was lower in high EC than in low SWC although the initial value in the early morning and that at midday were the same. This phenomenon might be attributed to some different characteristics in the rhizosphere conditions of these two treatments.

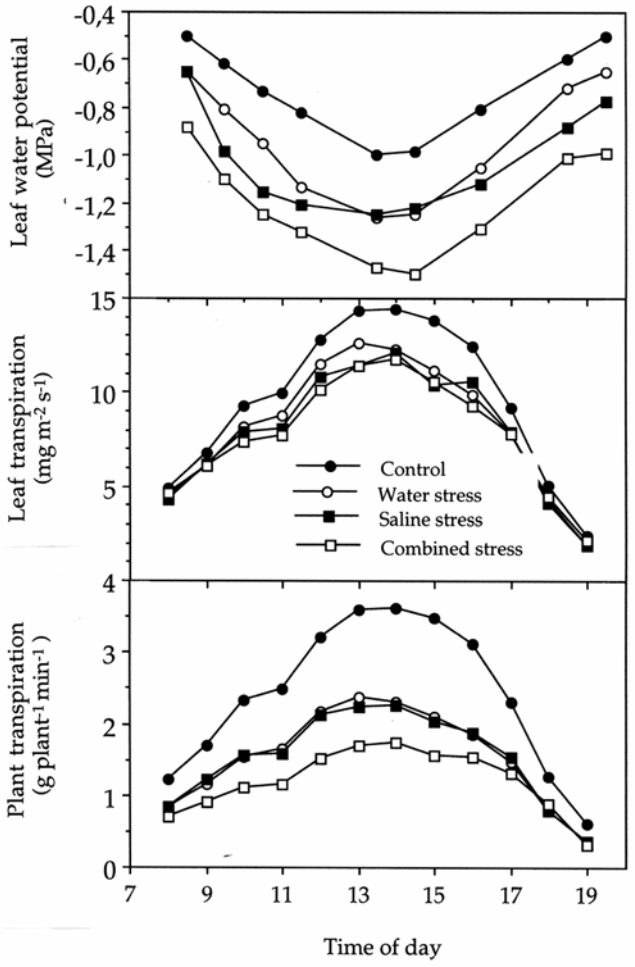

Fig. 2 Diurnal changes in leaf water potential, leaf transpiration rate and plant water consumption of tomato plants for different treatments measured five weeks after the beginning of treatments.

Soluble protein content and Rubisco activities

Soluble protein content is a measure of the amount of Rubisco because 50-75% of soluble protein in C_3 plant leaves is Rubisco (Hartman and Harpel 1994). Soluble protein content was decreased by low SWC, but not affected by high EC (**Table 4**). Both initial and total activities of Rubisco were not decreased by high EC. This suggested that the reduction in photosynthesis by high EC was not attributable to reduced carboxylation activity. Rubisco activities were lower in tomato leaves under low SWC conditions. This was attributed to low enzyme content since the specific activity based on protein amount was not low. The results are consistent with many other reports (Castrillo and Calcagno 1989; Majumdar *et al.* 1991), where the Rubisco activity on leaf dry mass basis was depressed by water stress, while the protein content changes in parallel with the Rubisco activity. Usually, researchers just present the Rubisco activity based on either leaf area or unit of enzyme protein. In these cases, it is not easy to know whether the overall depression in Rubisco activity is attributed to a protein content decrease, a decrease in enzyme activity itself, or both. In our study, the Rubisco activity was presented on bases of both leaf area and unit of protein, so that the attribution was made clear. Rubisco activities were not depressed by the EC of 4.5 dS m^{-1} treatment. The possible explanation may be that the nutrition conditions are different from the cases of salinity treatment caused by NaCl or sulfate additions and also different from the cases of just water deficit. In the present experiment, a high EC in the nutrient solution was adjusted by increasing concentrations of all nutrient elements in parallel. The EC build-up in the substrate is caused by accumulations of most elements that appear in the nutrient solution therapy, although the accumulation was not in parallel. The salinity caused by high EC in the present study is different in nutrient balance from the cases of salinity treatments by adding one or two ions, such as NaCl (Adams and Ho 1989), as well as field cases caused by excessive application or accumulation of sulfates (Papadopoulos 1986; Martinez *et al.* 1993). One of the typical characteristics of the tomato leaves grown under high EC was the deep green color (**Fig. 1**), which was reflected by the relatively high chlorophyll concentration (**Table 3**) and relatively high concentrations of N and Mg (**Table 5**). However, these results can not be found in the cases of salinity caused by NaCl and sulfates. The differences between high EC and low SWC in effects on Rubisco content and activities might be attributable to some unclear reasons.

Table 4 Soluble protein content and Rubisco activities of tomato leaves at the stage of 35 days after beginning of treatments.

Treatment	Protein g m^{-2}	Rubisco activities (μmol O_2 s^{-1})				Activated ratio (%)
		Per m^2 of LA		Per g of protein		
		Initial	Total	Initial	Total	
Control	2.7	37.9	57.5	14.0	21.3	65.9
Water stress	2.3	33.7	52.6	14.7	22.9	64.2
Salinity stress	2.9	36.3	57.7	12.5	19.9	62.8
Comb. stress	2.8	34.4	55.4	12.2	19.7	61.5
Water stress	*	*	*	NS	NS	NS
Salinity stress	NS	NS	NS	NS	NS	NS
Water×salinity	NS	NS	NS	NS	NS	NS

In the present study, treatments of high EC and low substrate water content were compared with the control designed as described in this report. The accumulated salts were not washed out of the substrate and salt accumulation also occurred in the substrate of control. This lowered the stress difference between the control and other stress treatments. This might be one of the reasons why no depressions of Rubisco activities were found for the high EC treatment. However, depressions of photosynthesis and leaf water potential were obvious in leaves of tomato plants under high EC conditions. In this sense, it could be suggested that depressions of photosynthesis by high EC was mainly attributed to decreases in leaf water potential, which caused low stomatal conductance, rather than to depressions of Rubisco content and activities.

Leaf nutrition

Leaf Ca and Cu concentrations in water- or salinity-stressed plants were lower relative to the control (**Table 5**). Boron and Fe concentrations were also lower in water-stressed

Table 5 Mineral concentration in the fully expanded leaf of tomato plants at the stage of 35 days after beginning of treatments.

Treatment	mg g^{-1}					μg g^{-1}				
	N	P	K	Ca	Mg	B	Zn	Fe	Mn	Cu
Control	42	53	8.7	20	5.0	64	29	124	210	25
Water stress	41	53	7.8	17	5.3	57	28	90	208	10
Salinity stress	42	53	8.0	16	4.7	67	42	112	184	16
Comb. Stress	46	60	7.8	14	5.5	67	53	126	169	13
Water stress	NS	NS	NS	*	NS	*	NS	**	NS	*
Salinity stress	NS	NS	NS	**	NS	NS	*	NS	NS	*
Water×salinity	NS	NS	NS	NS	NS	NS	**	NS	*	*

Table 6 Effect of EC and substrate water content on plant growth and dry matter production of tomato plants at the stage of 35 days after beginning of treatments.

Treatment	Plant growth				Dry matter production				Partitioning	
	Height	Leaf number	Leaf area	Specific weight	Fruit	Shoot	Root	Total	R/S[z]	FHI[y]
	-m-		-m^2-	-g m^{-2}-	g $plant^{-1}$				%	
Control	2.2	33	4.180	23.7	241	130	6.4	377	4.9	64
Water stress	1.9	30	3.144	24.4	154	91	6.2	251	6.8	61
Salinity stress	2.0	32	3.265	26.2	160	116	7.9	284	6.8	57
Comb. Stress	1.6	30	2.489	28.1	105	83	6.3	194	7.6	54
Water stress	*	*	**	*	**	**	NS	**	*	*
Salinity stress	*	*	**	**	**	*	*	**	NS	
Water×salinity	NS	NS	NS	*	NS	NS	*	*	NS	NS

[z] Root/shoot ratio; [y] fruit harvest index (fruit dry mass/total dry mass ratio).

Table 7 Effect of EC and substrate water content on fruit yield of tomato plants.

Treatment	Total fruit			Marketable fruit			Small and abnormal fruit		
	Number	Yield	Average weight	Number	Yield	Average weight	Small	Cracked	Rot
		g $plant^{-1}$	g $fruit^{-1}$		g $plant^{-1}$	g $fruit^{-1}$	% of total weight		
Control	21	2952	141	15	2793	188	4.4	0.9	0.0
Water stress	21	1881	90	12	1653	140	10.6	1.2	0.0
Salinity stress	23	1966	86	11	1615	139	14.8	2.2	0.9
Comb. Stress	18	1280	71	9	1037	110	14.1	2.8	2.1
Water stress	NS	**	**	**	**	**	*	NS	NS
Salinity stress	NS	**	**	**	**	**	**	**	NS
Water×salinity	*	NS	*	NS	*	NS	*	NS	*

plants, but not affected by high EC. Manganese concentration was decreased by the combination of high EC and low SWC. High EC increased leaf Zn concentration. We found a positive relation ($y=8.8+6.556x$, $r^2=0.95$) between plant water consumption (x, L $plant^{-1}$ d^{-1}) and leaf Ca concentration (y, mg g^{-1}). The decrease in Ca concentration of leaves of tomato plants grown under high EC and low SWC might be the result of low transpirational water flow. A similar result was found in tomato plants with low transpiration under low vapor pressure deficit (Adams 1991b). The direct cause of BER is the limited Ca import into and accumulation in the rapidly developing/enlarging tomato fruit (Ho and Adams 1995; Ho *et al.* 1996). BER was also observed in the present experiment for high EC-treated plants. Low leaf Ca concentration caused by salinity-induced low transpiration may be indirectly associated with BER. In the present experiment, all nutrients were doubled in high EC treatment compared to the control. However, this did not increase the nutrient levels very much in the leaf and some elements like Ca were even decreased. This means that the concentration of a nutrient solution is no more a factor that limits plant nutrition when it reaches a level higher than that shown by an EC of 2.3 dS m^{-1}.

Water stress can be induced as a secondary stress by salinity even though the water supply is sufficient. Sometime it is difficult to tell the difference in the water stress effects caused by water deficit and salinity. However, some specific symptoms can be induced by ion toxicity and antagonism against uptake of other elements. For example, high salinity leads to an antagonism against uptake of Ca and consequently causes symptoms of the BER and/or crack on the fruit (**Table 7**). This kind of problem or symptom is smaller for water stressed plants than salinity stressed plants. As having been described in the above paragraphs, a high EC of the nutrient solution was adjusted by increasing the concentration of total elements rather than that of one or two ions. Consequently, nutrition conditions in both substrate and leaf tissue were better for high EC treated than for plants treated with only substrate water deficit (**Table 5**) and for plants treated with NaCl addition (Adams and Ho 1989).

Plant growth, fruit yield and total dry matter production

Both water deficit and salinity stress decreased plant height, leaf number and total leaf area per plant (**Table 6**). However, the leaf specific weight was increased by both water and salinity stresses with a synergistic interaction. This means that leaves were thicker in stressed plants (not shown). Water and salinity stresses decreased dry matter of both shoot and fruit (**Table 6**). However, root dry matter was increased by high EC under high SWC but not under low SWC. Fruit harvest index was lower in plants under salinity stress. Both decreased fruit size and increased abnormality (cracked and BER) contributed to the reduced marketable fruit yield associated with high EC and low SWC (**Table 7**). Fruit harvest index is further lower in high EC than in low SWC. This might be due to the restricted fruit growth by the problem of BER in high EC.

It is logical that the decrease in photosynthesis results in a decrease in fruit yield and total dry matter production if the leaf area and harvest index are not increased. Another main reason for the decreased yield was reduced leaf area. Leaf area might be more important for yield formation than photosynthetic capacity. We also found a positive relation ($y=0.281+1.85x$, $r^2=0.98$) between transpirational water consumption (x, L $plant^{-1}$ d^{-1}) and fruit yield (y, kg $plant^{-1}$). This phenomenon has also been observed in grain sorghum (Faci and Fereres 1980), grain legumes (Lawn 1982), corn (Musick and Dusek 1980) and sunflower (Stegman and Lemert 1981). Decreases in tomato fruit yield with low transpiration have also been found under conditions of low vapor pressure deficit in greenhouses (Bakker 1990; Holder 1990).

Our results suggest that the effect of salinity caused by high EC (4.5 dS m^{-1}) of the nutrient solution is not negligible. It is necessary to develop an irrigation system with appropriate scheduling to avoid and release water and/or salinity stresses, thus maintaining photosynthesis and transpiration at maximum rates. Water deficit is not a factor considered in greenhouse productions because water source is not limited. However, in some cases, water stress can be induced by insufficient irrigation in combination with rhizosphere salinity and/or in interactions with low humidity, high irradiation and high temperature. In our study, we designed a substrate water deficit treatment. The objectives were not only to see the effects of water deficit on greenhouse tomato growth and physiology, but also aimed at comparisons between high EC and substrate water deficit. Our data showed clear differences between high EC and substrate water deficit in effects on leaf nutrition, fruit BER,

photosynthetic enzyme protein content and activities, diurnal pattern of leaf water potential, and even the fruit harvest index. However, our data cannot explain the mechanisms that account for the differences. For example, why was the fruit BER more severe in high EC than in low SWC even if the leaf Ca content was the same? Several similar questions can be posed from the different effects between high EC and low SWC. Therefore, further researches are needed to clarify the mechanism for the problems caused by high EC such as fruit BER, nutrient absorption, plant water relations and photosynthetic responses.

Using an EC of 2.3 dS m^{-1} as the normal for the control in the present experiment, we examined effects of a high EC as 4.5 dS m^{-1} and the build-up in substrate in details of growth and physiology. However, the results of the present experiment do not provide solutions to these stresses such as optimal irrigation volume, leaching fraction and critical EC in substrate. From this research we cannot know the effects of a constant EC because EC was built-up as salts accumulated in the present experiment. If the substrate was washed once a while, the negative effects might be avoided or diminished. Successive experiments on micro-environment-dependent variable EC and nutrient solution recycling to improve fruit quality and avoid salinity stress have been conducted and some results are reported elsewhere (Norrie *et al.* 1994; Xu *et al.* 1995; Zekki *et al*. 1996).

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