

Mineral Uptake and Soluble Carbohydrates of Tomato Plants as Affected by Air Temperatures and Mineral Treatment Levels

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Both low and high temperatures affect plant growth and development at whole plant level, tissue and even cell level through a variety of metabolic changes. Temperature stress is one of frequently occurring problems in greenhouse crops in summer and winter seasons due to the wide-spread year-round cultivation. In the present study, we investigated the extent of the inhibition of growth, macro-element uptake and soluble carbohydrate production, and the effect of extra-supply of minerals as a means of the recovery from temperature damage. Tomato plants were grown five different growth temperatures (15/8, 20/13, 28/21, 33/23 and 36/26°C), and extra-supply of minerals was composed of 1.5- and 2.0-fold stronger than the standard nutrition (1/2 strength of Hoagland's solution). Temperature stress significantly adversely affected tomato growth and mineral uptake, whereas soluble carbohydrate accumulation represented temperature-dependent response, more accumulation at low temperature and more consumption at high temperature. The soluble sugars in leaves and stems were mostly declined with the supply of extra-minerals at low and optimal temperatures, whereas remained unchanged at high temperature. The starch levels also remained unchanged or slightly decreased.

Key words: Tomato, Mineral uptake, Carbohydrates, Temperature stress, Mineral supply

The effect of the extra-supplied nutrients on macro-element uptake.

Temperature (day/night, °C)	Nutrient supply	N	P	K	Ca	Mg
		%				
15/8	x 1.0	54 [†]	68	59	61	67
	x 1.5	54	73	49	52	54
	x 2.0	59	78	53	60	65
28/21	x 1.0	100	100	100	100	100
	x 1.5	104	139	104	95	101
	x 2.0	106	120	111	106	101
36/26	x 1.0	85	89	63	69	83
	x 1.5	77	72	50	70	82
	x 2.0	77	79	55	66	77
F-value						
Temperature		72.41 ^{***}	96.39 ^{***}	142.99 ^{***}	61.16 ^{***}	50.09 ^{***}
Nutrient		0.19	3.46	2.07	0.92	0.72
Temperature x Nutrient		0.74	10.45 ^{***}	1.80	0.74	0.95

Our data report that extra-supply of minerals doesn't play crucial roles to promote macro-element uptake as tomato plants are suffered from temperature stresses. [†]The data indicate a percentage of macro-element uptake when the uptake is defined as 100 in optimal supply (1/2 strength Hoagland's nutrient solution) at optimal temperature condition (28/21°C). The concentration, x 1.0, means the 1/2 strength Hoagland's nutrient solution.

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Introduction

The production of vegetable crops has shown significant yield increases in South Korea since over the last several decades. Transitory or constantly high temperatures cause a variety of morpho-anatomical, physiological and biochemical changes in plants, which affect plant growth and development and may result in a significant reduction in economic yield. At moderately high temperatures, injuries or death to crop plants may occur only after long-term exposure, and it may be derived from a limited photosynthesis, assimilate partitioning, and water and nutrient use efficiency (Kuiper, 1964; Walker, 1969; Ruter and Ingram, 1990). A well-known consequence of elevated temperature in plants is the damage caused by heat-induced imbalance in photosynthesis and respiration; in general, the rate of photosynthesis decreases whereas dark- and photo-respiration rates increase considerably under high temperatures (Nakamoto and Hiyama, 1999). Assimilate partitioning, taking place via apoplastic and symplastic pathways under high temperature, has significant effects on transport and transfer processes in plants although it strongly depends on genotypes (Yang et al., 2002; Taiz and Zeiger, 2006). Mineral uptake by plants in the rhizosphere is directly influenced by soil temperature, and the lower (chilling) and higher (heat) temperatures compared to the optimum lead to a considerable reduction in mineral uptake (Cumbus and Nye, 1984; Raju et al., 1990; Tindall et al., 1990).

Tomato (*Lycopersicon esculentum*) is one of the most popular vegetable crops cultivated commercially around the world and, according to the report (MAFRA statistics, 2013), greenhouses-based cultivation was approximately 6,054ha (the 3rd in vegetable crops) throughout South Korea without big fluctuation year by year. Furthermore, a year round cultivation of tomato often causes unexpected heat (high in summer season) and chilly (low in winter season) stresses, and thus results in deleterious effects on the growth and yield. Although the literature on plant responses to temperatures such as mineral uptake and carbohydrate production is abundant, the information about the effects of extra-supply of minerals is only a very few. From the previous study with lettuce, we have found out several fruitful results about mineral uptake and soluble carbohydrate production under temperature stresses (submitted), and this study aimed to know the extent of a damage of growth, mineral uptake and carbohydrate production under low or high temperature conditions, and to know whether there is any effect of extra-supply of minerals to recover and promote those in tomato plants.

Materials and Methods

Plant materials and growth conditions This study was

performed in an environment-controlled growth chamber, NAAS, RDA, South Korea in 2014. The uniformly grown seedlings of tomato (cv. Seonmyeong, Nongwoo Bio Ltd.) were transplanted into 1 L plastic box filled with pure sand soil, and then fed with 1/2 strength of Hoagland's solution which is composed as follows; 5 mM $\text{Ca}(\text{NO}_3)_2$, 5 mM KNO_3 , 2 mM MgSO_4 , 0.5 mM KH_2PO_4 , 1.5 mM Fe-EDTA, 1 mM NH_4NO_3 , 2 μM H_3BO_3 , 0.2 μM MnCl_2 , 0.01 μM ZnSO_4 , 0.01 μM CuSO_4 , and 0.03 μM H_2MoO_4 . The 1/2 strength of Hoagland's solution, 100 mL per box, was supplied every day during the experiment. Plants were grown in five different temperature conditions, low (15/8°C, day/night), moderately low (20/13°C), optimal (28/21°C), moderately high (33/23°C) and high (36/26°C) temperatures. To investigate the effect of an extra-supply of minerals as a means of mitigating temperature stress, tomato seedlings were grown in three different nutrient conditions, standard (1/2 strength of Hoagland solution), 1.5- and 2.0-fold stronger nutrient solutions. Tomato plants were assigned with the completely randomized two factor factorial design (temperature and nutrient supply) in an environment-controlled chamber and were taken to determine the contents of carbohydrates and mineral elements at 10, 20 and 30 days after treatment (DAT).

Measurement of nutrients The samples (0.3 g) which were at 80°C for 48 h were soaked in 5 mL of 368 mM salicylic acid in 84.7% sulfuric acid (H_2SO_4) for 24 h then digested in a digestion system, heated to 300°C for 3 h, followed by several drops of hydrogen peroxide (H_2O_2). The extracted solution was transferred to 100 mL volumetric flasks and then diluted to 100 mL with deionized water for mineral assays. The N concentration was colorimetrically determined using the automatic flow injection analyzer (BRAN LUBBE, Germany). The P concentration was measured using the molybdate-blue colorimetric method (UV-2450, Shimadzu, Japan) and cation concentrations were determined with ICP-OES (INTEGRA XMP, GBC, Australia).

Measurement of soluble carbohydrates Soluble sugar from dried shoots and roots was determined by the reaction of 1.0 mL of the alcoholic extract with 2.0 mL fresh 0.2% anthrone in sulfuric acid (w/v); the absorbance was read at 630 nm. After the extraction of the soluble fractions, the solid fraction was used for starch analysis. Starch was firstly extracted with 9.3 N (normal concentration) of perchloric acid and followed by 4.6 N. The extracts were combined and starch concentration was determined after reaction with the anthrone reagent. Glucose was used as the standard for soluble sugar.

Statistical analysis This experiment was performed with the completely randomized two factor factorial design (tem-

perature and nutrient level) with three repeats. The analysis of variance (ANOVA) was conducted to find effects of treatments. Least significant difference (LSD) was performed to determine the significance of the difference between the means of treatments. An α error value of 0.05 was chosen to indicate statistical significance. All statistical analysis was performed using version 9.01 of SAS (SAS Institute Inc, Cary, NC).

Results

Effects of temperature and extra-supplied nutrient on tomato growth The shoot growth of tomato (dry weight-based) from each temperature condition was shown in Fig. 1, and, between temperature conditions, represented significant differences ($p < 0.05$) at 10 and 30 days after treatment (DAT). Tomato growth at the end of the experiment was the highest at

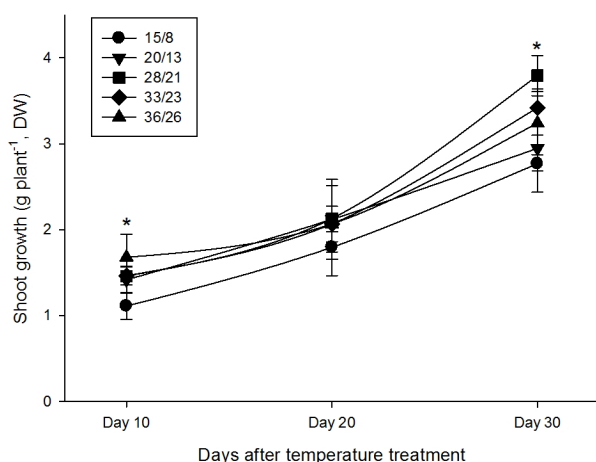


Fig. 1. Effect of temperature stresses on tomato plants grown under 1/2 strength Hoagland's nutrient solution (n=3). Star (*) mark means significant difference in $p < 0.05$.

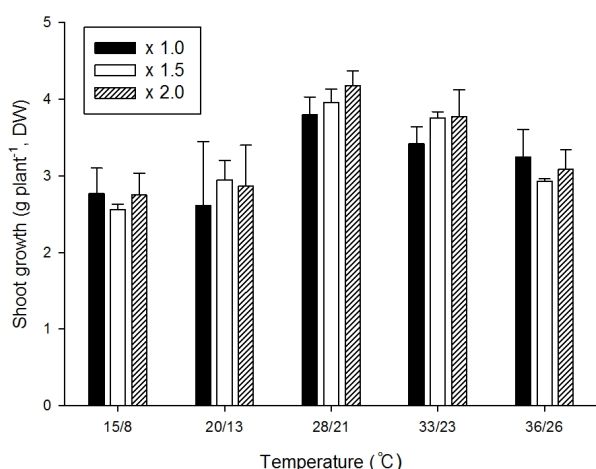


Fig. 2. Effect of an extra-supply of nutrients on tomato plants grown under four different temperature regimes at 30 DAT (n=3). The concentration, x 1.0, means the 1/2 strength Hoagland's nutrient solution.

the optimal (28/21°C) and followed by moderately high (33/23°C), high (36/26°C), low (15/8°C), and moderately low (20/13°C) temperature conditions. The reduction in tomato growth was more significant in low temperature which indicated only 69-73% to the optimal temperature, whereas represented 85-90% in high temperature. The effect of extra-supply of nutrients (1.5 and 2.0 fold stronger) as a means of mitigating the damage from temperature stresses was not observed (Fig. 2).

Effects of temperature and extra-supplied nutrients on concentration and uptake of macro-elements The concentrations of macro-elements in temperature-affected tomato plants resulted in a tendency of the overall decrease except P (unchanged or slight increase at both conditions), N (unchanged at high) and Mg (marked increase at high) in leaves, and except N (slight increase at high) and Ca (slight increase at low) in stems (Table 1). The most significant reduction was K concentration which indicated 70% (leaves) and 85% (stems) at low temperature and 68% (leaves) and 75% (stems) at high temperature. The uptake of macro-elements was greatly affected by the interaction of reduced growth and mineral concentration derived from temperature stresses (Table 2), and the uptake rates at low temperature were ranged from 54 to 68% (Data was only expressed as a mg uptake per shoot on Table) of optimal temperature, and, at high temperature, from 63 to 89% of optimal temperature. In particular, it seemed likely that temperature stress strongly influenced the uptake of cations. The extra supply of nutrients was non-effective to promote the nutrient uptake as tomato plants were exposed extremely adverse temperature conditions although an effect was partially observed for N and P at the double-concentrated nutrient supply at low temperature (Table 3).

Effects of temperature and extra-supplied nutrients on soluble carbohydrates production The contents (glucose equi.) of soluble carbohydrates greatly differed with both temperature conditions and a type of soluble carbohydrates (Fig. 3). The levels of soluble sugars were the highest at low temperature regardless of tissue (leaves and stems) and time points, and followed by optimal and high temperatures. The level of soluble sugars in leaves and stems at low and high temperatures represented 172 ($5.45 \pm 0.14 \text{ mg g}^{-1} \text{ DW}$), 120 ($5.64 \pm 0.23 \text{ mg g}^{-1} \text{ DW}$), 74 ($2.34 \pm 0.17 \text{ mg g}^{-1} \text{ DW}$) and 30 ($1.42 \pm 0.10 \text{ mg g}^{-1} \text{ DW}$) %, respectively, at 30 DAT. An accumulation of starch was differed from soluble sugars, and was in order of low, high and optimal temperatures. The level of starch in leaves and stems at low and high temperatures represented 235 ($4.43 \pm 0.11 \text{ mg g}^{-1} \text{ DW}$), 147 ($2.98 \pm 0.23 \text{ mg g}^{-1} \text{ DW}$), 124 ($2.35 \pm 0.16 \text{ mg g}^{-1} \text{ DW}$) and 95 ($1.93 \pm 0.13 \text{ mg g}^{-1} \text{ DW}$) %, respectively, at 30 DAT. The extra supply of nutrients on the contents of soluble carbohydrates greatly

Table 1. The range of macro-element concentrations in temperature-affected tomato plants.

Tissue	Temperature (day/night, °C)	N	P	K	Ca	Mg
		%, DW				
Leaves	15/8	3.20 ~ 4.20 [†] (84)	0.48 ~ 0.59 (105)	3.75 ~ 5.97 (70)	2.04 ~ 2.69 (70)	0.67 ~ 0.83 (93)
	28/21	4.06 ~ 5.04 (100)	0.47 ~ 0.60 (100)	6.80 ~ 7.65 (100)	3.05 ~ 3.61 (100)	0.72 ~ 0.91 (100)
	36/26	4.34 ~ 5.06 (101)	0.48 ~ 0.56 (100)	4.75 ~ 5.19 (68)	2.84 ~ 3.22 (91)	0.90 ~ 1.03 (114)
Stems	15/8	2.81 ~ 3.45 (93)	0.32 ~ 0.50 (74)	7.61 ~ 9.39 (85)	2.09 ~ 2.95 (105)	0.63 ~ 0.76 (82)
	28/21	3.09 ~ 3.49 (100)	0.39 ~ 0.58 (100)	9.16 ~ 9.79 (100)	2.29 ~ 2.86 (100)	0.77 ~ 0.88 (100)
	36/26	3.58 ~ 3.67 (111)	0.30 ~ 0.40 (69)	6.45 ~ 7.53 (75)	1.29 ~ 1.54 (56)	0.54 ~ 0.66 (75)

[†]Data indicate the range of the concentrations measured at three sampling points, 10, 20 and 30 DAT, and the data within the parenthesis represent a concentration index of macro-elements when the concentrations are defined as 100 in optimal temperature condition (28/21°C).

Table 2. The shoot uptake of macro-elements in temperature-affected tomato at 30 DAT.

Temperature (day/night, °C)	N	P	K	Ca	Mg
	mg shoot ⁻¹ , DW				
15/8	94.3 ± 13.9b [†]	12.0 ± 1.2b	177.9 ± 28.8b	71.4 ± 11.6b	21.3 ± 2.3c
28/21	173.8 ± 10.3a	17.6 ± 0.6a	299.3 ± 12.8a	117.4 ± 5.7a	32.0 ± 0.8a
36/26	147.8 ± 15.1a	15.6 ± 1.5a	187.9 ± 18.7b	80.9 ± 8.4b	26.7 ± 3.1b
F-value	27.98 ^{***}	17.38 ^{**}	30.37 ^{***}	25.93 ^{**}	16.11 ^{**}

[†]Data indicate the uptake of macro-elements of tomato shoots at three different temperature conditions at 30 days after treatment, and tomato plants were grown under the 1/2 strength Hoagland's nutrient solution. The letters mean significant differences from LSD test (n=3).

Table 3. The effect of the extra-supplied nutrients on macro-element uptake.

Temperature (day/night, °C)	Nutrient supply	N	P	K	Ca	Mg
		%				
15/8	x 1.0	54 [†]	68	59	61	67
	x 1.5	54	73	49	52	54
	x 2.0	59	78	53	60	65
28/21	x 1.0	100	100	100	100	100
	x 1.5	104	139	104	95	101
	x 2.0	106	120	111	106	101
36/26	x 1.0	85	89	63	69	83
	x 1.5	77	72	50	70	82
	x 2.0	77	79	55	66	77
F-value						
Temperature		72.41 ^{***}	96.39 ^{***}	142.99 ^{***}	61.16 ^{***}	50.09 ^{***}
Nutrient		0.19	3.46	2.07	0.92	0.72
Temperature x Nutrient		0.74	10.45 ^{***}	1.80	0.74	0.95

[†]The data indicate a percentage of macro-element uptake when the uptake is defined as 100 in optimal supply (1/2 strength Hoagland's nutrient solution) at optimal temperature condition (28/21°C). The concentration, x 1.0, means the 1/2 strength Hoagland's nutrient solution.

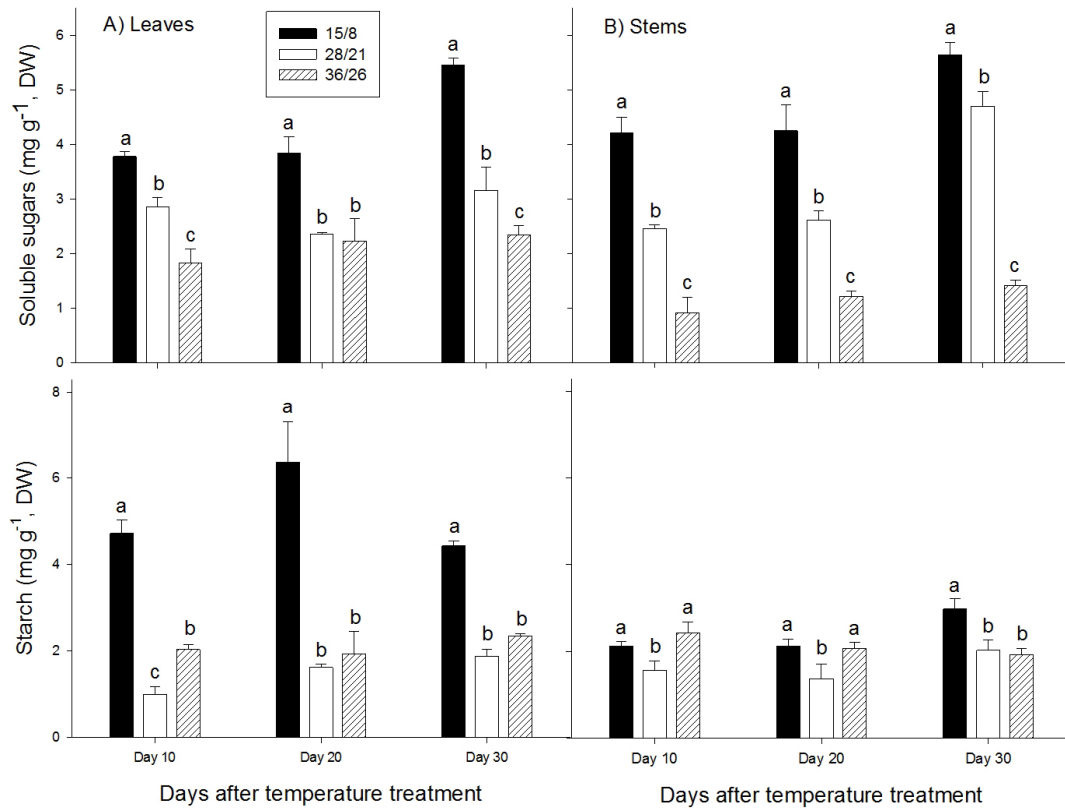


Fig. 3. Effect of temperature stresses on the accumulation of soluble sugars and starch in the shoot of tomato plants grown under 1/2 strength Hoagland’s nutrient solution at 30 DAT (n=3). The letters above vertical bars mean significant differences from LSD test.

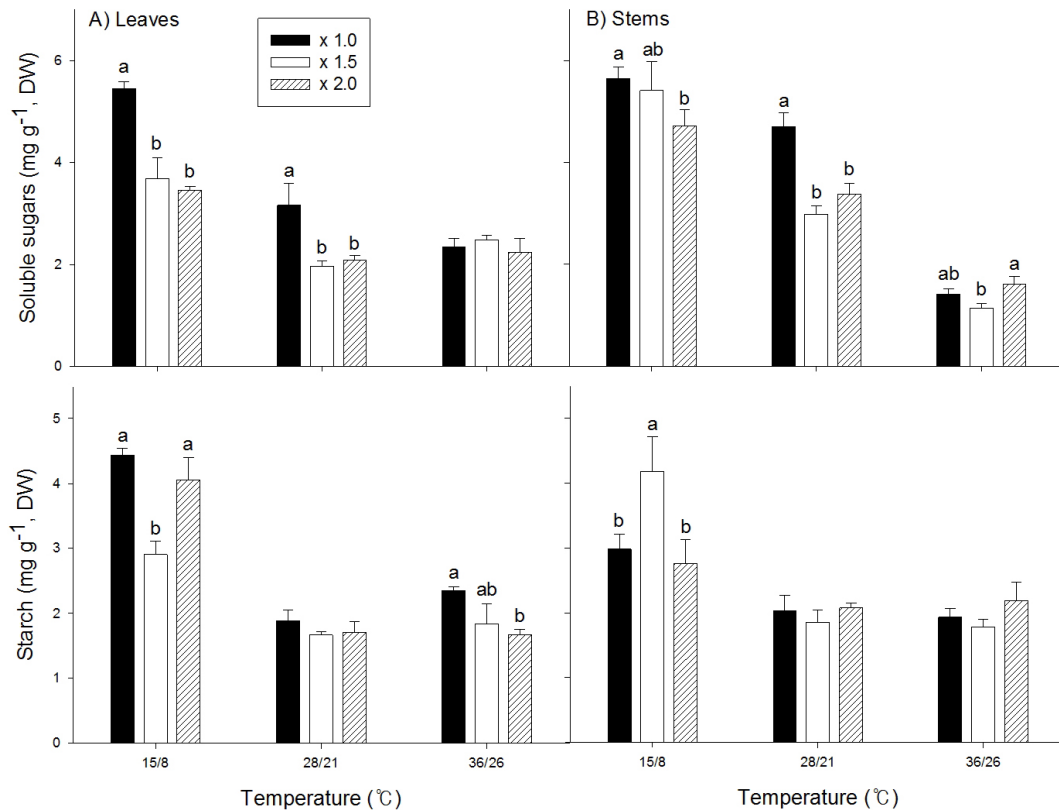


Fig. 4. Effect of an extra-supply of nutrients on the accumulation of soluble sugars and starch in the shoot of tomato plants grown under three different temperature conditions at 30 DAT (n=3). The concentration, x 1.0, means the 1/2 strength Hoagland’s nutrient solution. The letters above vertical bars mean significant differences from LSD test.

depended on temperature conditions and a type of carbohydrates (Fig. 4). The soluble sugars in leaves and stems mostly declined with an increase in mineral supply at low and optimal temperatures whereas remained unchanged at high temperature. The starch levels also remained unchanged or slightly decreased although 1.5-fold stronger mineral supply led to a decrease in leaves and an increase in stems at low temperature.

Discussion

Temperature stresses (low and high temperatures) are the major environmental factors affecting plant growth and development, and also induce morphological, physiological and biochemical changes in plants. It is well known that crop growth rates are significantly reduced by temperature stresses as results of a decrease in metabolic processes and photosynthesis (Sharkova, 2001; Wise et al., 2004; Waraich et al., 2012), shoot and root growth inhibition, and leaf senescence (Vollenweider and Gunthardt-Goerg, 2005), however the growth reduction in the present study was only observed at low temperature, and this differed from the result of our previous study with lettuce (submitted). An extra-supply of minerals to promote tomato growth did not have any effect at both low and high temperature stresses (Fig. 2), and even was not observed at optimal temperature condition. Waraich et al (2011) reported that N fertilization mitigated the adverse effects of temperature stresses which induced the reduction in photosynthesis and growth by photo-oxidative damage. Increasing K supply also alleviated the damage of leaf and stem and decrease in crop yield (Grewal and Singh, 1980; Hakerlerler et al., 1997), however the effect mentioned above was not observed in the present study. The concentration and uptake of macro-elements were strongly influenced by temperature conditions. Certainly, temperature stresses led to substantial decrease in the uptake of macro-elements, which ranged from 54 to 89% compared to optimal temperature. This suggests the existence of a controlling mechanism in plant, particularly root, which is mediated by physiological responses such as transpiration, mineral absorption, and leaf and root growth. Marked reduction in mineral concentration has been considered as a factor responsible for temperature stresses (Ali et al., 1998; Tindall et al., 1990; Engels and Marschner, 1996; Du and Tachibana, 1994). The extra-supply of minerals as a means of promoting mineral uptake was not noticeable, but rather resulted in marked reduction except N and P fed with 2 fold-stronger mineral nutrient at low temperature (Table 3), and this result was similar to the previous study with lettuce (submitted), which induced P uptake under temperature stresses. Temperature condition affected differently the levels of soluble sugars and starch in tomato shoots (Fig. 3); low temperature induced a significant

accumulation of soluble carbohydrates, whereas high temperature resulted in a marked reduction in soluble sugars and a slight accumulation of starch. More carbon losses due to increased respiration and the shortage of non-structural carbohydrate have long been considered as factors responsible for the growth inhibition under various temperature stresses (Youngner and Nudge, 1968; Canmore-Neumann and Kafkafi, 1983), consistent with our observation although it was not at low temperature. Starch metabolism (diurnal fluctuation) is very sensitive to changes in the environment, and soluble sugars that accumulate in response to stress can function as osmolytes to maintain cell turgor against adverse environments, particularly temperature stresses (Madden et al., 1985; Todaka et al., 2000; Kaplan and Guy, 2004; Basu et al., 2007; Kempa et al., 2008). In the present study, the accumulation of soluble carbohydrates at low temperature might be possibly closely associated with reduced mineral uptake, whereas the decrease in soluble carbohydrates at high temperature could be predicted the loss of carbon source by the increased respiration rather than reduced photosynthesis. In order to clarify carbohydrate metabolism and mineral uptake against adverse temperature conditions, further study is needed. The extra-supply of minerals play a role to improve carbohydrate metabolism, particularly soluble sugars at low and optimal temperatures, and it is suggested that soluble sugars were used as a source of the production of organic compounds and respiratory energy as being consistent with a slight increase in mineral uptake, particularly N and P, with 1.5- and 2.0-fold stronger minerals at low and optimal temperatures. In conclusion, temperature stresses caused significant reduction in crop growth, mineral uptake and carbohydrate production while macro-element concentrations in tomato plants seemed likely to be a temperature-dependent response. Moreover, extra-supply of minerals did not play crucial roles to promote an adverse damage caused by temperature stresses. Further research should be included on the effect of extra-supply of minerals when plants are recovered from low or high temperature stress, and metabolic interaction such as mineral uptake and carbohydrates between shoot and root.

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