Journal of Agricultural Technology 2010 Vol. 6(3): 543-558
Available online http://www.ijat-rmutto.com
ISSN 1686-9141

Responses of root uptake to high temperature of tomato plants (*Lycopersicon esculentum* Mill.) in soil-less culture

Falah, M.A.F.*, Wajima, T.[2], Yasutake, D. [2], Sago, Y.[3] and Kitano, M.[3]

[1]Faculty of Agricultural Technology, Gadjah Mada University, Sosio Yustisia No 1, Bulaksumur Yogyakarta,55281, Indonesia.
[2]Faculty of Agriculture, Kochi University, Monobe B 200, Nankoku, Kochi, Japan.
[3]Faculty of Agriculture, Kyushu University, 6-10-1 Hakozaki, Higashi-ku, Fukuoka, 812-8581, Japan.

Falah, M.A.F., Wajima, T., Yasutake, D., Sago, Y. and Kitano, M. (2010). Responses of root uptake to high temperature of tomato plants (*Lycopersicon esculentum* Mill.) in soil-less culture. Journal of Agricultural Technology 6(3): 543-558.

In plant production, high temperature stress frequently causes physiological disorders and yield depression, and information about physiological functions of intact roots is essential. However, there have been difficulties in measurement of physiological functions of intact roots in the plant production systems. Effects of high solution temperature on water and nutrients uptake by roots of tomato plants cultivated in the NFT system were analyzed. Dynamic and simultaneous evaluation of water and nutrients uptake by roots was developed in the NFT system. Rates of water and nutrients uptake by roots were evaluated simultaneously on the basis of time courses analyses of water balance and nutrients balance in the systems, and these also enabled estimation of nutrients concentration in root xylem sap. Rates of water and nutrients uptake by roots varied depending on solar radiation. The short-term effect of high solution temperature activated water and nutrients uptake through decrease in water viscosity and affected membranes transport. On the other hand, the long-term effects of high solution temperature caused growth depression and browning in roots, and these resulted in depressed water and nutrients uptake rates. The long-term effects of high solution temperature were considered to relate to the reduced oxygen solubility and the increased enzymatic oxidization of phenolic compounds in root epidermal and cortex tissues. The long-term effect of high solution temperature decreased nutrients concentration in root xylem sap, and the root xylem sap concentrations of N, K and Ca became lower than those in the nutrient solution. This indicates that active processes involved in root uptake of those nutrients were retarded by the long-term treatment with

---

*Corresponding author: Mohammad Affan Fajar Falah; e-mail: affan_ff@yahoo.com

high solution temperature. The short- and long-term effects of high solution temperature on root uptake appeared in different patterns reflecting passive and active processes involved in the transport systems in roots.

Key words: high temperature stress, *Lycopersicon esculentum* Mill.

Introduction

One of the major environmental stress affecting plant growth and productivity is high temperature. In plant production, high temperature stress frequently causes physiological disorders and yield depression, through some physiological and biochemical changes in plant metabolism such as protein denaturation and perturbation of membrane integrity (Levitt, 1980). Primary functions of root systems are uptake of water and nutrients and the anchorage to the ground (Fitter, 1996). Information about physiological functions of intact roots is essential to predict the plant production in global warming for the future and it is necessary to study root responses to high temperature (BassiriRad, 2000). Study of temperature effects on root uptake usually has been due to the ecological relevance, which can be separated into two major problems, the short-term effect with limited ecological relevance and the long-term effect with more ecological significance (Marschner, 1995).

Tomato plants, as a major crop, exposed to a fluctuating temperature regime often suffer no overall loss of yield when compared with those grown in a constant regime having the same temperature (Hurd and Graves, 1984). Fluctuations in temperature may affect the pattern of crop yield, and increasing root temperature up to 12ºC above the ambient of 15 ºC resulted in small reductions in yield and quality of early fruit (Hurd and Graves, 1985). In tomato plants, rise in temperature of rooting systems from 14 to 26ºC increased water uptake by 30% and also increased uptake of some nutrients, but fruit quality and yield were reduced (Hurd and Graves, 1985). However, much less has been known about the effects of the higher root temperatures on water and nutrients uptake by roots (Kramer and Boyer, 1995).

There have been difficulties in measurement of physiological functions of intact roots in the plant production systems and the physiology of roots that affected by temperature has received less attention until recently because roots are usually underground. Changes in root temperature are more flexible in soil-less culture compared with soil culture. Soil-less culture, such as a Nutrient Film Technique (NFT), is often used to simulate and model the experimental system, because this system can provide homogenous root environment with acceptable accuracy and controllable nutrient concentration (Asher, 1983; Graves, 1983).

We conducted the present experiment by using tomato plants that grown in the NFT system to analyze the short-term (diurnal changes) and the long-term (several weeks) effects of high solution temperature on root uptake of water and nutrients (nitrate (NO_3^-), phosphate (PO_4^{3-}), potassium (K^+) and calcium (Ca^{2+}).

Materials and methods

Plant materials and experimental conditions

Seeds of tomato plants (*Lycopersicon esculentum* Mill. cv. Hausu Momotarou) were sown in cell trays filled with vermiculite in a growth chamber. The seedlings were moved into a greenhouse 10 days after sowing. At 45 days after sowing, 25 plants were transplanted to two cultivation beds of the NFT system in the greenhouse and were grown using the standard nutrient solution with an electrical conductivity (*EC*) of 1.0dSm^{-1} at the controlled temperature of 22ºC. For the high root temperature stress treatment, the solution temperature in one of the two beds was increased from 22ºC to 35ºC two weeks after pollination.

The standard nutrient solution based on prescription A from OTSUKA HOUSE (Otsuka Chemical Co. Ltd., Osaka, Japan) with an *EC* of 1.0 dSm^{-1} was used in this experiment. The nutrient solution in the NFT system was refreshed every week. Ion concentrations in the standard nutrient solution (in mg L^{-1}) were 85.2 N-NO_3^-, 42.3 P-PO_4^{3-}, 157.3 K^+, 80.6 Ca^{2+}, 67 SO_4^{2-}, 18.4 Mg^{2+}, 1.0 Fe^{2+}, 0.7 BO_3^{3-}, 0.2 Mn^{2+}, 0.1 Cu^{2+}, 0.03 Zn^{2+} and 0.02 MoO_4^{2-}.

System for evaluation of root uptake of water and nutrient

The NFT system was developed for dynamic and simultaneous evaluation of rates of water and nutrient uptake by intact roots of plant population in the greenhouse (Yasutake *et al*., 2005). Figure 1 shows a schematic diagram of the system. The system was composed of a circulating unit (an NFT bed, a reservoir tank, *etc*.) and a water supply unit (a water supply tank, a solenoid valve, a supply line, *etc*.) for controlling the nutrient solution. A pressure transmitter was installed in the reservoir tank to detect decrease in volume of the nutrient solution caused by root water uptake. The circulation unit was automatically replenished with the fresh nutrient solution from the supply unit by on-off action of the solenoid valve, which was manipulated according to a feedback signal from the water level sensor. Rates of water uptake (Q_W, L d^{-1}) and nutrients uptake (Q_M, g d^{-1}) by roots were evaluated with high the respective accuracy of ± 10% and ± 13% on the basis of accurate analysis of water and nutrient balance in the NFT system (Yasutake *et al.*, 2005). This simultaneous evaluation of rates of water and nutrient uptake by roots enabled evaluation of each nutrient concentration in the root xylem sap ($[M]_{xy}$, g L^{-1}) by dividing the nutrient uptake rate by the water uptake rate. The system was reliable to study the short- and the long-term analysis of root uptake in response to various environmental conditions.

Short- and long-term effects

For analyzing the short-term effect of high temperature, the nutrient solution in the NFT bed was sampled hourly in the daytime and every three hours in the nighttime for evaluating diurnal changes one week after the start of high solution temperature. Then, for analyzing the long-term effect of high temperature, the nutrient solution in the NFT bed was sampled twice a day at 6:00 and 18:00 for four weeks from the start of the high temperature treatment. Changes in concentration of each nutrient (NO_3^-, PO_4^{3-}, K^+ and Ca^{2+}) concentrations was measured by using the soil-plant chemical analyzer (SPCA-6210, Shimadzu, Kyoto, Japan).

Statistical analysis

Dependence of root uptake on solar radiation and dependence of root nutrient uptake on the water uptake were analyzed using statistical software (SPSS, version 10.00, Chicago, USA).

Results

The short-term effects

The diurnal changes in solar radiation and rate of water uptake by roots of tomato plants growing under different root temperatures of 22ºC (Control) and 35ºC (High temp) in the NFT system one week after the start of the high temperature treatment was seen in fig. 2. Root water uptake varied depending on solar radiation, and the high solution temperature enhanced root water uptake. This effect of high solution temperature appeared larger in the higher water uptake in the daytime.The diurnal changes in nutrients (NO_3^-, PO_4^{3-}, K^+ and Ca^{2+}) uptake rates by roots of tomato plants was seen in Fig. 3. Nutrient uptake rate varied depending on water uptake rate, but effects of the high solution temperature were appeared in different pattern among the nutrients. In particular, the uptake rates of NO_3^- and PO_4^{3-} were enhanced as found in water uptake, and the Ca^{2+} in the afternoon depressed under the high solution temperature.

Relationship between water uptake rate and solar radiation and relationship between nutrients (NO_3^-, PO_4^{3-}, K^+ and Ca^{2+}) uptake rate with water uptake rate for daytime analysis in the NFT system was seen in Table 1. High dependence on solar radiation of water uptake rates under the control and the high solution temperature was found. Furthermore, nutrients uptake rate were also high dependence on water uptake rate.

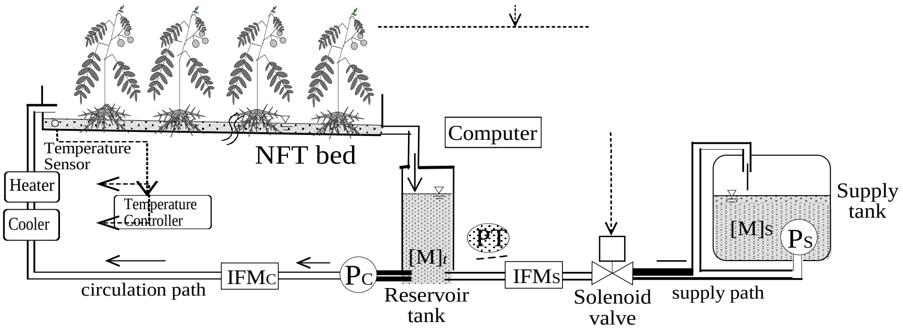

Fig. 1. Schematic diagram of the NFT system developed for dynamic and simultaneous evaluations of water and nutrients uptake rates in roots of plant population. The system is composed of the circulation unit (an NFT bed, a reservoir tank, a water pump and a circulation path, *etc.*) and the supply unit (a supply tank, a solenoid valve, a water pump and a supply path, *etc.*) for controlling the nutrient solution: IFM_c and IFM_s, integrated flow meters on the circulation and supply paths, respectively; $[M]_s$, concentration of nutrient M in the supply tank; $[M]_t$, concentration of nutrient M in the circulation unit at time *t*; PT , pressure transmitter for measuring water level in the reservoir tank; P_c, water pump for circulating the nutrient solution between the reservoir tank and the NFT bed; P_s, water pump for supplying nutrient solution from the supply tank to the reservoir tank; Solid arrows, flow of nutrient solution; broken arrows, flow of electric signals.

The diurnal changes in nutrients (NO_3^-, PO_4^{3-}, K^+ and Ca^{2+}) concentration in the root xylem sap and the nutrient solution were seen in Fig. 4. Different pattern of each nutrient concentration in root xylem sap was found. [NO_3^-] in root xylem sap was constant and high solution temperature was not affected. [PO_4^{3-}] in root xylem sap was almost constant from the daytime, but high solution temperature decreased in the morning.

[K^+] in root xylem sap decreased during higher water uptake, but high solution temperature increased that concentration during higher water uptake and lower concentration of [K^+] in root xylem sap compare with that on control solution temperature was found. [Ca^{2+}] in root xylem sap was relatively stable and higher solution temperature decreased [Ca^{2+}] in root xylem sap compare with that on control solution temperature.

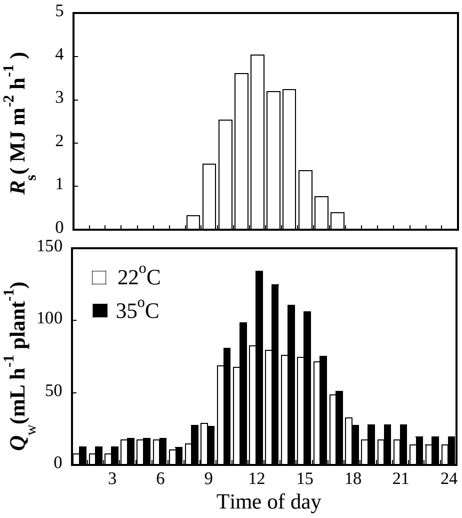

Fig. 2. Diurnal changes in hourly integrated solar radiation (R_s) and water uptake rate (Q_w) in roots of tomato plants at solution temperatures of 22 ºC and 35 ºC in the NFT system on a fine day.

Table 1. Relationship of water uptake rate with solar radiation and relationship of nutrients uptake rate with water uptake rate at solution temperatures of 22ºC and 35ºC in diurnal changes on 6th day after the start of high temperature treatment in the NFT system. Q_w: water uptake rate (mL h^{-1} plant^{-1}); R_s: integrated solar radiation (MJ m^{-2} h^{-1}). Q_{NO3}; nitrate uptake rate (g h^{-1} plant^{-1}); Q_{PO4} : phosphate uptake rate (g h^{-1} plant^{-1}); Q_K : potassium uptake rate (g h^{-1} plant^{-1}) and Q_{Ca}: calcium uptake rate (g h^{-1} plant^{-1}).

	Control	**High temp**
$Q_w = f(R_s)$	$0.004Rs + 22.5$; $R^2 = 0.78$**	$0.007Rs + 24.2$; $R^2 = 0.88$**
$Q_{NO3} = f(Q_w)$	$0.11\ Q_w + 0.19$; $R^2 = 0.99$**	$0.11\ Q_w + 0.055$; $R^2 = 0.99$**
$Q_{PO4} = f(Q_w)$	$0.035\ Q_w + 0.68$; $R^2 = 0.96$**	$0.033\ Q_w + 0.69$; $R^2 = 0.96$**
$Q_K = f(Q_w)$	$0.14\ Q_w + 1.2$; $R^2 = 0.92$**	$0.14\ Q_w - 0.062$; $R^2 = 0.97$**
$Q_{Ca} = f(Q_w)$	$0.088\ Q_w + 0.39$; $R^2 = 0.98$**	$0.063\ Q_w + 0.19$; $R^2 = 0.87$**

**, significant level of 0.01.

The long-term effects

The daily integrated solar radiation and water uptake rates by roots of tomato plants growing under different solution temperatures of 22ºC (Control) and 35ºC (High temp) in the NFT system was seen in Fig. 5. Water uptake rate varied with solar radiation. Just after the start of the high solution temperature treatment, water uptake rate was increased, and kept higher rate for one week, and then rates of water uptake were similar between high and control solution temperature during 9-13 days after high solution temperature treatment. However, from 14 days until end of the high solution temperature treatment, rate of water uptake was decreased and lower than that at control solution temperature.

The daily integrated nutrients (NO_3^-, PO_4^{3-}, K^+ and Ca^{2+}) uptake rates under different solution temperatures of 22ºC (Control) and 35ºC (High temperature) for short and long-term effect under different water uptake rate in the NFT system was seen in Fig. 6. Short-term effect of high solution temperature increased uptake rates of NO_3^-, PO_4^{3-}, K^+ and Ca^{2+}, but long-term effect of high solution temperature decreased those uptake rates. These patterns were similar with water uptake pattern and it can be supposed that nutrients uptake rate was highly depending on water uptake rate.

Statistical analysis in the Table 2 shows relationship between solar radiation with water uptake rate and relationship between nutrients (NO_3^-, PO_4^{3-}, K^+ and Ca^{2+}) uptake rates with water uptake rate. Water uptake rate was highly depending on solar radiation on both of control and high solution temperature under short and long-term effect, however water uptake rate under high solution temperature was observed lower dependency than that under control solution temperature for long-term effect. Nutrients uptake rates were highly dependence on water uptake rate, both under conditions of the high and the control solution temperature. But, long-term effect of high solution temperature decreased dependency of nutrients uptake rate with water uptake rate, and these data might explain the patterns of results that mentioned above.

The daily changes in nutrients (NO_3^-, PO_4^{3-}, K^+ and Ca^{2+}) concentration in the root xylem sap and the nutrient solution under different solution temperatures of 22ºC (Control) and 35ºC (High temp) for short and long-term effect under different water uptake rate in the NFT system was seen in Fig. 7. We found different pattern of nutrient concentration in root xylem sap that affected by short- and long term high solution temperature treatment. [NO_3^-], [PO_4^{3-}] and [K^+] in xylem sap were relatively stable, but [Ca^{2+}] in root xylem sap was higher than that in the nutrient solution for short-term effect of high solution temperature. The long-term effect of high solution temperature decreased [NO_3^-], [K^+] and [Ca^{2+}] in the root xylem sap, although their concentrations in the nutrient solution gradually increased with depressing root nutrient uptake. Furthermore, the long-term effect of high solution temperature decreased those concentrations in root xylem sap compare than those in the nutrient solution. However, [PO_4^{3-}] in the root xylem sap were always kept higher compared with that in the nutrient solution.

Table 2. Relationship of water uptake rate with solar radiation and relationship of nutrients uptake rate with water uptake rate at solution temperatures of 22ºC and 35ºC in the short-term (1-9 days after the start of temperature treatment) and the long-term (10-28 days after the start of temperature treatment) in the NFT system . Q_w: water uptake rate (L d^{-1} $plant^{-1}$); R_s: integrated solar radiation (MJ m^{-2} d^{-1}). Q_{NO3}; nitrate uptake rate (g d^{-1} $plant^{-1}$); Q_{PO4} : phosphate uptake rate (g d^{-1} $plant^{-1}$); Q_K : potassium uptake rate (g d^{-1} $plant^{-1}$) and Q_{Ca}: calcium uptake rate (g d^{-1} $plant^{-1}$).

	Control	**High temp**
$Q_w = f(R_s)$		
Short-term	$0.046\ R_s + 0.072$ ($R^2 = 0.78$*)	$0.06\ R_s + 0.093$ ($R^2 = 0.89$*)
Long-term	$0.04\ R_s + 0.112$ ($R^2 = 0.85$**)	$0.015\ R_s + 0.24$ ($R^2 = 0.55$**)
$Q_{NO3} = f\ (Q_w)$		
Short-term	$0.11\ Q_w - 0.012$ ($R^2 = 0.91$**)	$0.112\ Q_w - 0.0124$ ($R^2 = 0.74$**)
Long-term	$0.096\ Q_w - 0.006$ ($R^2 = 0.88$**)	$0.064\ Q_w - 0.0004$ ($R^2 = 0.47$**)
$Q_{PO4} = f\ (Q_w)$		
Short-term	$0.01\ Q_w + 0.026$ ($R^2 = 0.56$*)	$0.022\ Q_w + 0.024$ ($R^2 = 0.53$*)
Long-term	$0.05\ Q_w - 0.001$ ($R^2 = 0.92$**)	$0.054\ Q_w - 0.004$ ($R^2 = 0.84$**)
$Q_K = f\ (Q_w)$		
Short-term	$0.09\ Q_w + 0.006$ ($R^2 = 0.77$**)	$0.15\ Q_w + 0.026$ ($R^2 = 0.86$**)
Long-term	$0.13\ Q_w + 0.019$ ($R^2 = 0.93$**)	$0.138\ Q_w + 0.003$ ($R^2 = 0.65$**)
$Q_{Ca} = f\ (Q_w)$		
Short-term	$0.098\ Q_w + 0.001$ ($R^2 = 0.63$**)	$0.085\ Q_w - 0.0008$ ($R^2 = 0.71$**)
Long-term	$0.035\ Q_w - 0.002$ ($R^2 = 0.48$*)	$0.003\ Q_w - 0.0013$ ($R^2 = 0.31$*)

**, significant level of 0.01 and *, significant level of 0.05.

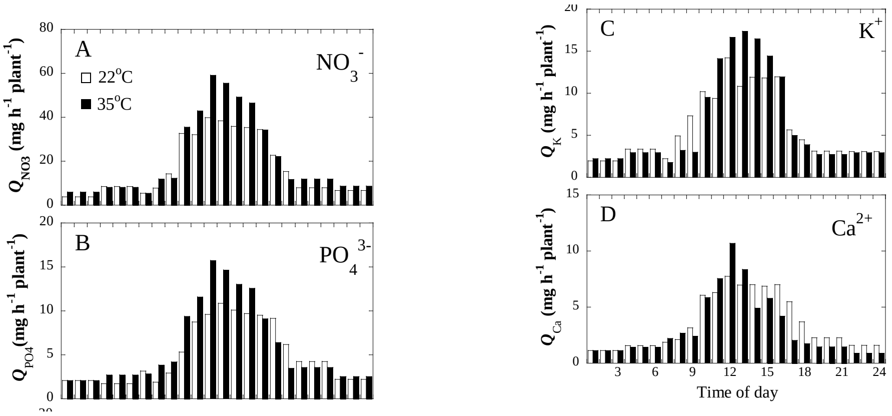

Fig. 3. Diurnal changes in uptake rates of NO_3^-, PO_4^{3-}, K^+ and Ca^{2+} in roots of tomato plants at solution temperatures of 22 ºC and 35 ºC in the NFT system on a fine day. Open symbols indicate data at solution temperature of 22 ºC and closed symbols indicate data at solution temperature of 35 ºC : Q_{NO3}, nitrate uptake rate; $Q_{PO4,}$ phosphate uptake rate; Q_K, potassium uptake rate; Q_{Ca}, calcium uptake rate.

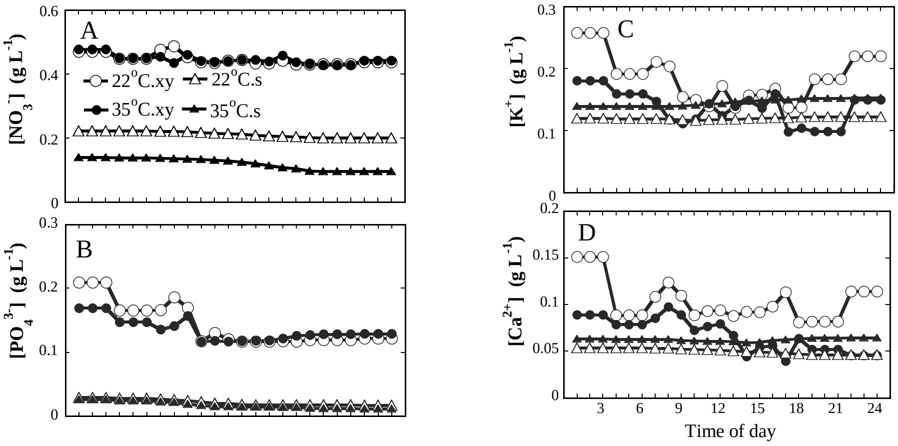

Fig. 4. Diurnal changes in concentrations of root xylem sap of NO_3^-, PO_4^{3-}, K^+ and Ca^{2+} in roots of tomato plants at solution temperatures of 22 ºC and 35 ºC in the NFT system on a fine day. Open symbols indicate data at solution temperature of 22 ºC and closed symbols indicate data at solution temperature of 35 ºC; $[NO_3^-]$, nitrate concentration; $[PO_4^{3-}]$, phosphate concentration; $[K^+]$, potassium concentration ;$[Ca^{2+}]$, calcium concentration; xs and s indicate xylem sap and nutrient solution, respectively.

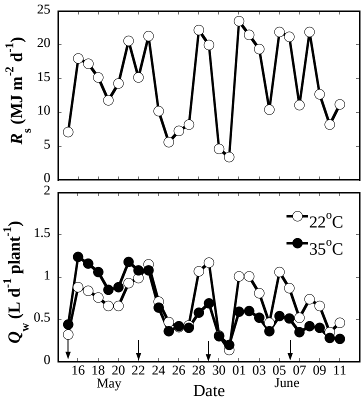

Fig. 5. Time courses of daily integrated solar radiation (R_S) and water uptake rate (Q_w) in roots of tomato plants for four weeks at solution temperatures of 22 ºC and 35 ºC in the NFT system. Arrows indicate refreshment of the nutrient solution in beds of the NFT system.

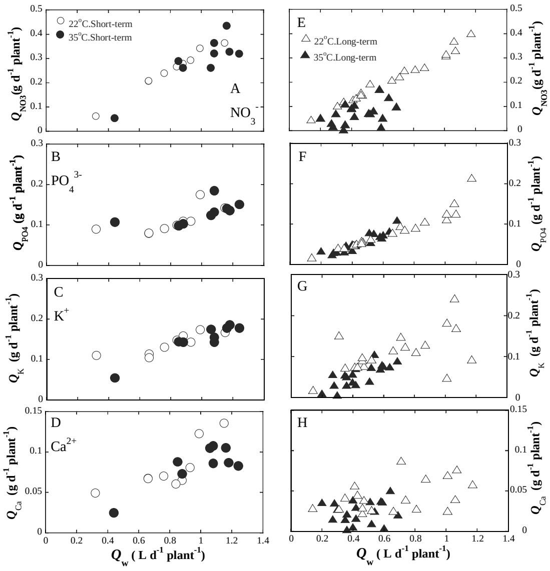

Fig. 6. Relationship between uptake rates of NO$_3^-$, PO$_4^{3-}$, K$^+$ and Ca^{2+} and water uptake rate in roots of tomato plants at the solution temperatures of 22ºC and 35ºC for short-term (A-D, 1-9 days after the start of the temperature treatment) and long-term (E-F,10-28 days after the start of the temperature treatment) in the NFT system. Q_w, water uptake rate; Q_{NO3}, nitrate uptake rate; $Q_{PO4,}$ phosphate uptake rate; Q_K, potassium uptake rate; Q_{Ca}, calcium uptake rate.

Discussion

The study showed water uptake rate varied and highly dependence on solar radiation for the short-term effect (Fig. 2 and Table.1). According to Kramer and Boyer (1995) and Nobel (1991), high intensity of solar radiation during the daytime can increase rate of water uptake that was driven by transpiration stream. The short-term effect of the high solution temperature increased rate of water uptake through decreasing viscosity of water in the nutrients solution. Kramer and Boyer (1995) concluded that the high temperature enhanced water uptake through decrease in viscosity of water, which brought the lower hydraulic resistances and accelerated water transport in roots 1.4 times. The viscosity of a fluid indicates a resistance to flow; decrease in the viscosity of water as the temperature rises reflects breaking of hydrogen bonds and also lessening the attractive forces accompanying the greater thermal motion of molecules (Nobel, 1991).

Our findings in the long-term effects of high solution temperature showed the daily water uptake rate varied and highly dependence on solar radiation, although at the high solution temperature lower dependence of water uptake rate on solar radiation was found compare than that at control solution temperature (Fig.5 and Table.2). This lower dependence of water uptake rate on solar radiation in the long-term treatment of high solution temperature can be supposed through the growth depression of root. Root growth was affected as a function of temperature (McMichael and Burke, 1996) and roots formed at high temperatures are thinner than those produced at optimum temperature for growth (Nielsen, 1974).

Decrease in water uptake rate under the long-term effect of high solution temperature can also be caused through decrease in root hydraulic conductance. From the high temperature pre-conditioning in tomato that grown in soil (Morales *et al*, 2003), root hydraulic conductance in tomato plants under the long-term treatment with the high temperature is expected to be lower than that at the control temperature. Root hydraulic conductance for the long-term treatment with high root temperature in woody plants (Graves *et al.*, 1991) and pepper (Dodd *et al.*, 2002) were also decreased. Other scientists also found decreased water uptake rate under the high temperature caused by various reasons, such as increased suberization or the deposition of secondary cell wall materials behind the zone of elongation (Boyer, 1985), decreasing xylem vessel diameter increases the axial resistance to water uptake (Oosterhuis, 1983) and increased un-saturation in membrane fatty acid associated with increased resistance to root water uptake (Markhart *et al.*, 1980).

Pattern of nutrient uptake rate in the NFT system were increased just after the start of high solution temperature, and decreased several days after treatment with high solution temperature (Figs. 3 and 6). The observed high dependence of nutrient uptake on water uptake can be considered brought through the apoplastic mass flow, because the apoplastic transport of ion is driven by the mass flow with water (Kramer and Boyer, 1995), although ion transport in roots involves apoplastic, symplastic and membrane transports (Nissen, 1996; Maathuis and Sanders, 1999). We supposed that short and long-term effect of the high solution temperature also affected membrane transport, because composition and integrity of membranes are affected by environmental factors (light intensity, temperature, water deficit, air pollutant, and also deficiency of nutrients), and high temperature can lead cells to reorganize membrane fluidity, bi-layer stability and permeability (Levitt, 1980; Marschner, 1995; Leone *et al.*, 2003) and also changing fluidity of the fatty acids in plasmalemma affect nutrient uptake capacity (Clarkson *et al.*, 1988).

Furthermore, growth depression and browning in roots occurred several weeks after the high solution temperature treatment can also be considered to cause lower uptake of nutrient. The high solution temperature can reduce oxygen solubility of the nutrient solution and then increasing enzymatic oxidization of phenolic compounds that produces brown substance in root epidermal and cortex tissues (Hurd, 1978 ; Fukuoka and Enomoto, 2001; Wells and Eissenstat, 2003).

The major difficulty in sampling xylem sap directly is the negative pressure in the xylem of transpiring plant in the field, and it has proved impossible to determine nutrient concentration in the xylem under condition of negative pressure (Schurr, 1998). One of the approximations to calculate the nutrient concentrations in the xylem sap is the mass flux to the xylem. The mass flux to the xylem is equivalent with rate of transpiration, where water uptake rate during the daytime depend on the transpiration stream and xylem concentrations of nutrient are low because the incoming water dilutes the xylem solution during the daytime (Kramer and Boyer, 1995; Herdel *et al.*, 2001). Our experiment used similar approximation to calculate nutrient concentrations in the root xylem sap, where nutrient concentration in the root xylem sap can be estimate by dividing the respective nutrient uptake rates by the water uptake rate.

$[NO_3^-]$, $[PO_4^{3-}]$, $[K^+]$ and $[Ca^{2+}]$ in root xylem sap were higher than those in the nutrient solution during diurnal analysis at high solution temperature, while lower [K^+] and [Ca^{2+}] at high solution temperature were also observed in root xylem sap (Fig. 4). This indicates that at lower nutrients concentration in the NFT system, the active processes in those nutrients transport play an important role (Chrispeels *et al.*, 1999; White, 2001; Glass *et al*. 2002; Shaul, 2002). And, the long-term effect of high solution temperature decreased [NO_3^-], [K^+] and [Ca^{2+}] in root xylem sap , although those concentrations in the nutrient solution were gradually increased with the depressed nutrient uptake rate (Fig. 7). Nutrient concentrations in root xylem sap became remarkably lower than those in the nutrient solution at the long-term treatment of high solution temperature, and this result indicate that the active processes involved in the transport of NO_3^-, K^+ and Ca^{2+} in roots are significantly retarded by the long-term treatment with high solution temperature. On the other hand, affect of high solution temperature on [PO_4^{3-}] in the root xylem sap was not found, because [PO_4^{3-}] in root xylem sap kept higher as compared with that in the nutrient solution.

We conclude that the short-term effects of the high solution temperature enhanced water and nutrient uptake and it brought through the physical processes such as the apoplastic mass flow in roots that it accelerated by decrease in viscosity with temperature rise and affected membrane transport. On the other hand, the long-term effects of the high solution temperature depressed water and nutrient uptake and they were brought through the physiological processes such as the root browning and the active transport in membranes which are affected by the lower oxygen availability under the higher solution temperature. The long-term effect of the high solution temperature decreased nutrient concentration in root xylem sap, and the root xylem sap concentrations of N, K and Ca became lower than those in the nutrient solution. This indicates that active processes involved in root uptake of those nutrients were retarded by the long-term treatment with the high solution temperature.

These results showed that unfavorable effect of the high solution temperature influenced water and nutrient transport in roots and be considered to result in the deterioration of root physiological functions. The effects of the high solution temperature on root uptakes of water and nutrient appeared in different patterns reflecting the passive and active processes involved in the respective transport systems in roots.

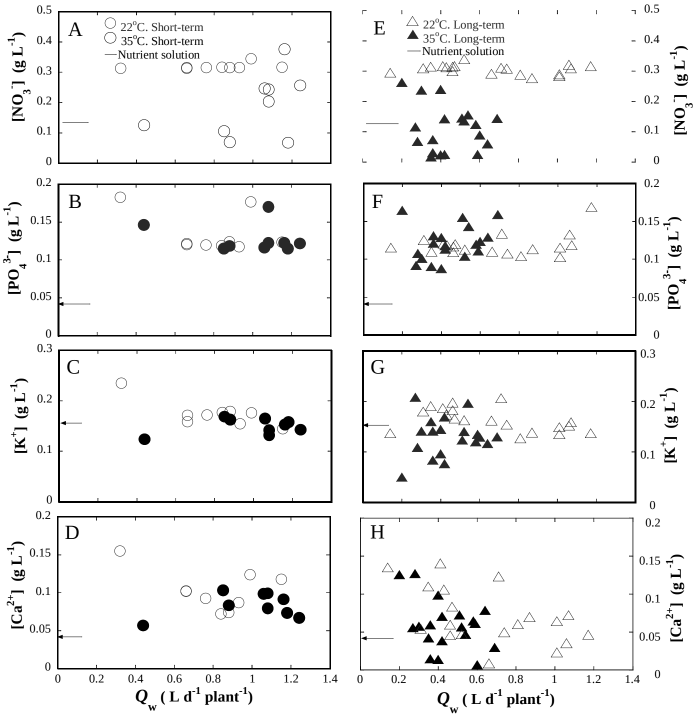

Fig. 7. Relationship between nutrients concentrations of NO_3^-, PO_4^{3-}, K^+ and Ca^{2+} and water uptake rate in root xylem sap of tomato plants at different solution temperatures of 22°C and 35°C for short-term (A-D, 1-9 days after the start of the temperature treatment) and long-term (E-F, 10-28 days after the start of the temperature treatment) in the NFT system. Q_w, water uptake rate; $[NO_3^-]$ nitrate concentration; $[PO_4^{3-}]$ phosphate concentration; $[K^+]$ potassium concentration and $[Ca^{2+}]$ calcium concentration. Arrows indicated ion concentration in the nutrient solution just after refreshment.

Acknowlwdgements

This study was supported by The Japanese Ministry of Education, Culture, Sports, Science and Technology (MONBUKAGAKUSHO) with a Grant-in-Aid for Scientific Research (No.14360154). First author would like to make a deeply thank to Faculty of Agricultural Technology for support publication of this paper.

References

Asher, C.J., and Edwards, D.G. (1983). Modern solution culture technique. In : Lauchli A, Bieleski RL, eds. Inorganic Plant Nutrition, *Vol. 15A*. Tokyo: Springer-Verlag, p.94-115.

BassiriRad, H. (2000). Kinetics of nutrient uptake by roots: responses to global change. New Phytologist 147: 155-169.

Boyer, J.S. (1985). Water transport. Annual Review Plant Physiology 36: 473-476. Chrispeels, M.J., Crawford, N.M. and Schroeder, J.I. (1999). Protein for transport of water and mineral nutrients across the membrane of plant cells. The Plant Cell 11: 661-675.

Clarkson, D.T., Earnshaw, M.J., White, P.J. and Cooper, H.D. (1988). Temperature-dependent factors influencing nutrient uptake: an analysis of responses at different levels of organization. In : Long SP, Woodward FI, eds. Plants and temperature, Vol 42. Symposium of Society for Experimental Biology. Cambridge, UK: The Company of Biologist Limited . p. 281- 309.

Dodd, I.C., He, J., Turnbull, C.G.N., Lee, S.K. and Critchley, C. (2002). The influence of supra-optimal root-zone temperatures on growth and stomatal conductance in *Capsicum annuum* L. Journal of Experimental Botany 51: 239-248.

Fitter, A. (1996). Characteristics and functions of root systems. In : Waisel Y, Eshel A, Kafkafi U, eds. Plant Roots : The Hidden Half. New York : Marcel Dekker, p. 1 – 17.

Fukuoka, N. and Enomoto, T. (2001). The Occurrence of internal browning induced by high soil temperature treatment and its physiological function in *Raphanus* root. Plant Science 161: 117-124.

Glass, A., Dev, P.M., Brent, T.B., James, N.K., Hebert, R.K., Anshuman, J.K., Mamoru, K., Suman, O.R., Siddiqi, M.Y., Shiela, E.U. and Joseph, .JV. (2002). The regulation of nitrate and ammonium transport systems in plants. Journal of Experimental Botany 53: 855-864.

Graves, C.J. (1983). The Nutrient film technique. In Janick J, ed. Horticultural Reviews Vol. 5. Connecticut : Avi Publishing Company.p. 1 – 33.

Graves, W.R., Joly, R.J. and Dana, M.N. (1991). Water use and growth of honey locust and tree-of heaven at high root zone temperature. HortScience 26: 1309-1312.

Herdel, K., Schmidt, K., Feil, R., Mohr, A. and Schurr, U. (2001). Dynamics of concentrations and nutrients fluxes in the xylem of Ricinus communis- diurnal course, impact of nutrient availability and nutrient uptake. Plant, Cell and Environment 24: 41-52.

Hurd, R.G. (1978). The roots and its environment in the nutrient film technique of water culture. Acta Horticulturae 82: 87-98.

Hurd, R.G. and Graves. C.J. (1984). The influence of difference temperature patterns having the same integral on the earliness and yield of tomatoes. Acta Horticulturae 148: 547-554.

Hurd, R.G. and Graves. C.J. (1985). Some effects of air and root temperatures on the yield and quality of glasshouse tomatoes. Journal of Horticultural Science 60: 359-371.

Kramer, P.J. and Boyer, J.S. (1995). Water relations of plants and soils. San Diego : Academic Press. 495 p.

Leone, A., Perrotta, C. and Maresca, B. (2003). Plant tolerance to heat stress : current strategies and new emergent insights. In : Toppi LSD, Pawlik-Skowronska B, eds. *Abiotic Stresses in Plants.* Dordrecht: Kluwer 1-19.

Levitt, J. (1980). Responses of plants to environmental stresses, Vol. 1 Chilling, freezing and high temperature stresses. New York : Academic Press. 447 p.

Maathuis, F.J.M. and Sanders, D. (1999). Plasma membrane transport in context – making sense out of complexity. Current Opinion in Plant Biology 2: 236-243.

Markhart, A.H. III, Peet, M.M., Sionit, N. and Kramer, P.J. (1980). Low temperature acclimation of root fatty acid composition, leaf water potential, gas exchange and growth of soybean seedlings. Plant Cell and Environment 3: 345-441.

Marschner, H. (1995). Mineral nutrition of higher plants. San Diego: Academic Press.680 p.

McMichael, B.L. and Burke, J.J. (1996). Temperature effects on root growth. In : Waisel Y, Eshel A, Kafkafi U, eds. Plant Roots : The Hidden Half. New York: Marcel Dekker, p 383 – 394.

Morales, D., Rodriguez, P., Dell`Amico, J., Nicolas, A., Torrecillas, A. and Sanchez-Blanco, M.J. (2003). High-temperature preconditioning and thermal shock imposition affects water relations, gas exchange and root hydraulic conductance in tomato. Biology Plantarum 47: 203-208.

Nielsen, K.F. (1974). Roots and root temperature. In : EW Carson ed. The plant roots and its environment. Charlottesvile: Univ Press Virginia, p 293-333.

Nissen, P. (1996). Uptake mechanisms. In : Waisel Y, Eshel A, Kafkafi U, eds. Plant Roots : The Hidden Half. New York : Marcel Dekker , p 511 – 524.

Nobel, P.S. (1999). Physicochemical and environmental plant physiology. San Diego: Academic Press. 635 p.

Oosterhuis, D.M. (1983). Resistance to water flow through the soil-plant system. South Africa Journal of Science 79: 459-465.

Schurr, U. (1998). Xylem sap sampling- new approaches to an old topic. Trends in Plant Science 3: 293-298.

Shaul, O. (2002). Magnesium transport and function in plants: the tip of the Iceberg. Biometals 15: 309-323.

SPSS Ver 10.05. 1999. SPSS., Inc. Chicago.

Wells, C.E. and Eissenstat, D.M. (2003). Beyond the roots young seedlings: the influence of the age and order on fine root physiology. Journal Plant Growth Regulation 21: 324-334.

White, P.J. (2001). The Pathways of calcium movement to the xylem. Journal of Experimental Botany 52: 891-899.

Yasutake, D., Affan, M.F.F., Wajima, T., Hidaka, K., Kitano, M. and Maki, T. (2005). System for evaluating root uptake capacity in relation to phytoremediation. Journal of Agricultural Meteorology 60(5): 829 - 832.

(Received 17 October 2009; accepted 5 May 2010)