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REVIEW

Response of Tomato Root Systems to Environmental Stress under Soilless Culture

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Abstract

We investigated the effects of root-zone environment, humidity around the roots and nutrient solution on the activity and morphology of tomato roots grown in wet-sheet culture (exposed to air) or deep flow technique (submerged in solution). Differences in root external and internal structure between treatment groups could be interpreted as adaptive responses to the root environment. The exposed roots could adapt more readily to extremes of temperature than those in the solution. Those adaptations occurred through short-term physiological responses and long-term additive morphological responses. We also evaluated the facilitating effects of the flow of nutrient solution on root respiration and nutrient uptake rate. Where the root system was split between humid air and nutrient solution, roots in the solution absorbed and supplied nitrogen more efficiently per dry weight than did roots in air. Split root systems between humid air and nutrient solution showed stable growth of tomato plants. Our observations of root plasticity will help the establishment of growing systems that support high yield and stable production.

Discipline: Horticulture
Additional key words: nutrient absorption, root respiration, root structure, root-zone temperature

Introduction

In Japan, the area of vegetables under soilless culture has gradually increased to 1,192 ha (2003)[24], whereas the total area of vegetable cultivation has decreased about 2% yearly[22]. More than 40 types of soilless culture are practiced in Japan[8], but few studies have compared the structure and function of root systems among them, between which close interrelationships should exist. Soilless culture allows reproducible control of the root-zone environment. Nevertheless, even under soilless culture, roots could experience multiple environmental stresses. Especially in systems without solid media, changes in nutrient concentration, pH, temperature, and oxygen concentration would have large impacts on plant growth. Root systems alter their internal structure and external architecture to minimize such impacts and to acquire oxygen, water and nutrients in the most efficient way[12]. We evaluated the structural and functional responses of tomatoes grown in soilless culture to the root-zone environment. We focused on roots in humid air and roots in nutrient solution.

Roots in humid air adapt much better to changes in nutrient concentration, pH and temperature than do those in solution[25]. Root systems of tomatoes grown by capillary hydroponics[21] and in nutrient film[2] develop in both humid air and solution; these two root parts could play complementary roles. Therefore, quantitative evaluation is needed to clarify the responses of both types of root system to the root-zone environment.

External and internal root structures of tomato plants grown hydroponically in humid air or in nutrient solution

We examined the effects of root-zone environment, humid air and nutrient solution on the external and internal structures of tomato roots[17]. Young tomato plants were grown either in wet-sheet culture (WSC), in which all roots develop in humid air, or hydroponically by the deep flow technique (DFT) with or without aeration (Fig. 1). Dissolved oxygen concentration was 45% to 62% of saturation in DFT, and 91% to 96% in DFT+Air.

Growth of tomato plants in DFT+Air and WSC was

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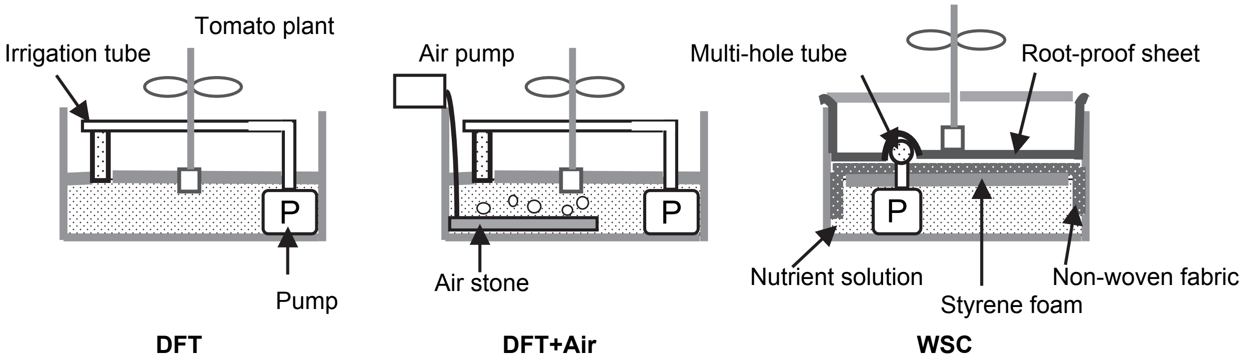

Fig. 1. Schematic diagrams of deep flow technique without aeration (DFT), DFT with aeration (DFT+Air) and wet-sheet culture (WSC) for the cultivation of tomato
Nutrient solution in each container is circulated by a pump.

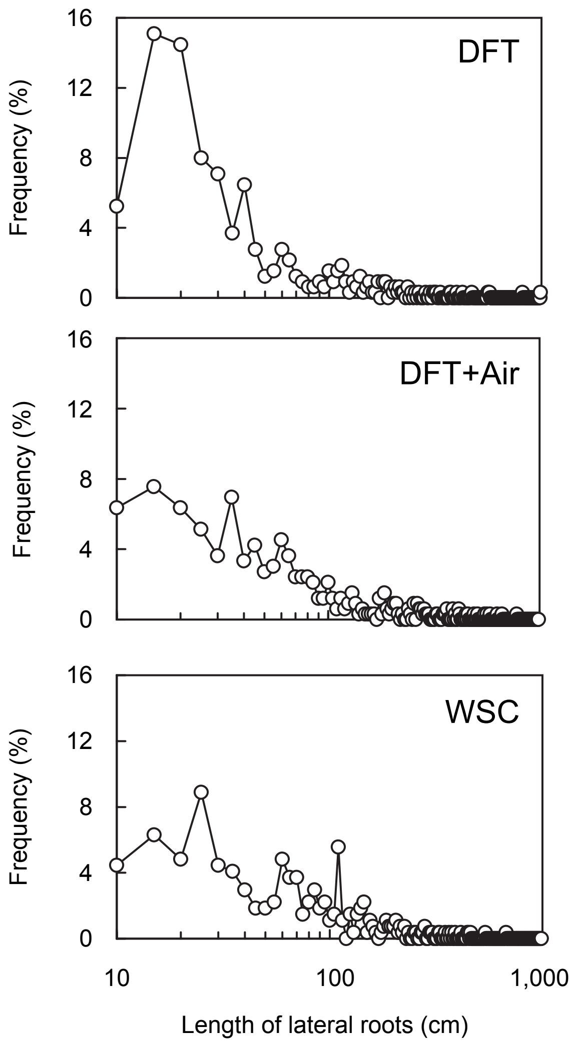

Fig. 2. Frequency distribution of total length of individual lateral roots of tomato seedlings grown in different hydroponic systems
Lateral roots are first-order laterals including higher-order laterals. Details of treatments are described in Fig. 1.

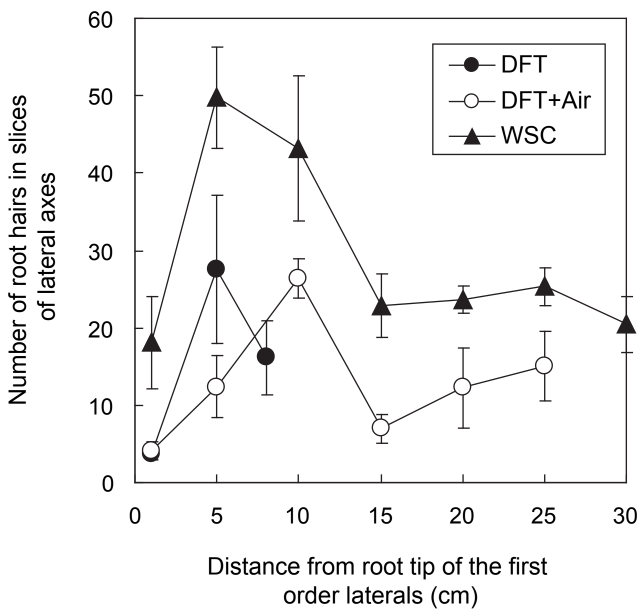

Fig. 4. Numbers of root hairs on 250-µm lengths of lateral roots of tomato seedlings grown in different hydroponic systems
Vertical lines indicate SD (n = 3).

more vigorous than that in DFT (Table 1). The shoot-to-root ratio decreased in the order DFT+Air > WSC > DFT, but computerized image analysis of the root systems with image-processing software (NIH-Image) revealed no differences in the total root lengths or root surface areas among the three treatments. DFT had a larger proportion of shorter lateral roots than DFT+Air and WSC (Fig. 2), suggesting that oxygen deficit in DFT inhibited root elongation. Aerenchyma, considered to be an adaptation to anaerobic conditions[9], was present in the stele only in

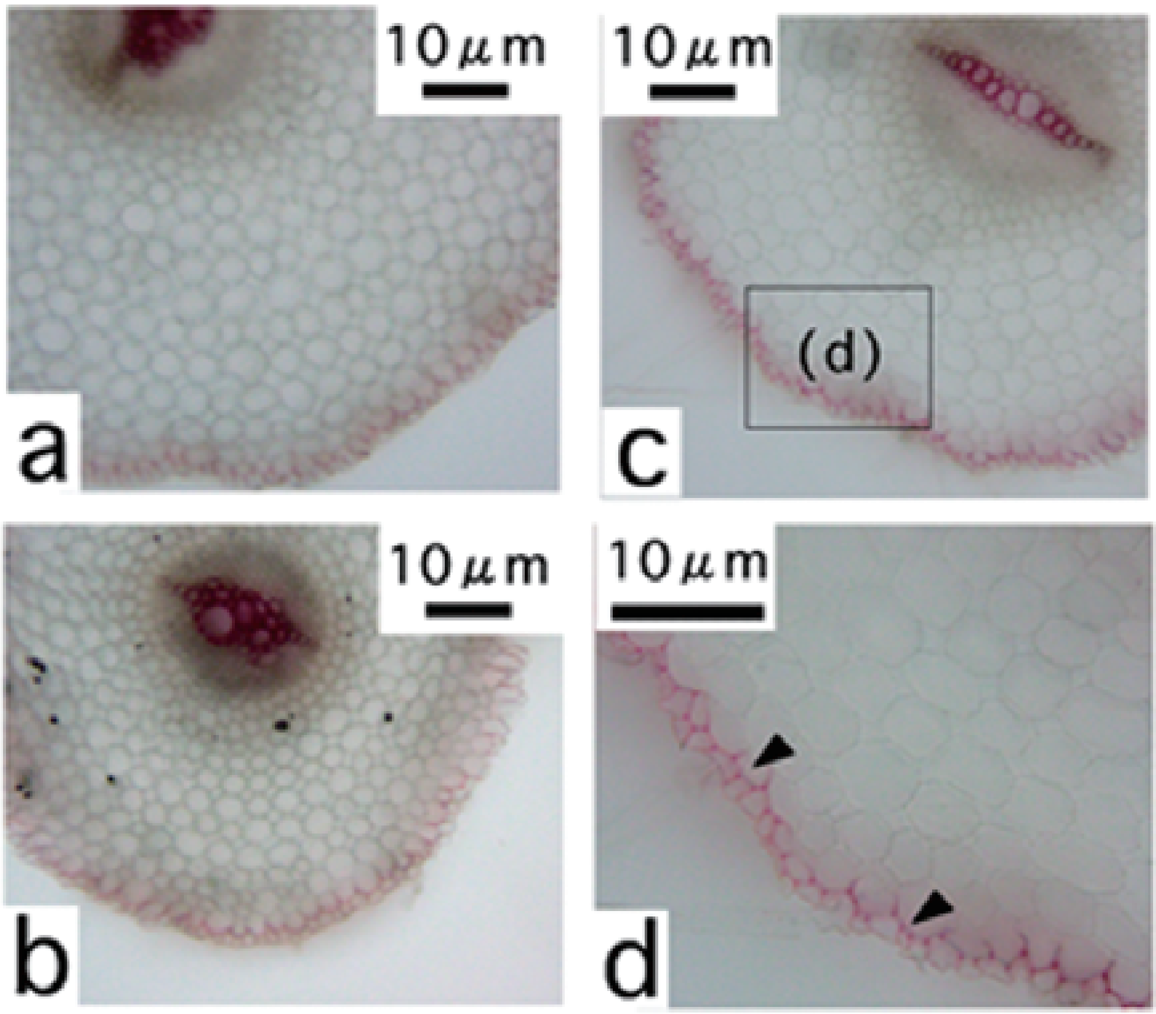

Fig. 3. Transection of tomato roots with phloroglucinol staining of lignin lamellae (arrowheads) within exodermal walls
Samples were prepared from first-order lateral roots developed in each hydroponic system. a: Deep flow technique without aeration (×200), b: Deep flow technique with aeration (×200), c: Wet-sheet culture (×200), d: Wet-sheet culture (×400). Rectangle marked (d) in c is the image in d.

DFT. Roots in WSC had larger cortical cells, metaxylem and stele, more deposits of lignin lamellae in the exodermis, and more root hairs than roots in DFT (Figs. 3 & 4). Enlarged cortical cells and increased deposits of lignin are also found under drought stress[4,26]. Water deficit promotes the development of root hairs[13], which play an important role in uptake of minerals and water. Accordingly, the greater allocation of photosynthates, namely dry matter, to the roots in WSC than in DFT (Table 1) could be a response to the drier conditions in WSC. These changes in external and internal structures of the roots could be interpreted as adaptive responses to the root environment, that is, anoxia in DFT and water deficit in WSC.

Table 1. Effects of root-zone environment on the growth of tomato seedlings[z]

Hydroponic system[y]	Dry weight ($g \cdot plant^{-1}$)[w]		S/R[x,w]
	Shoot	Root	
DFT	1.29 b	0.25 b	5.0 c
DFT+Air	1.79 a	0.28 ab	6.3 a
WSC	1.73 a	0.30 a	5.6 b

[z] Data are shown as the mean of 20–21 samples at 8 days from transplanting.
[y] DFT: Deep flow technique without aeration, DFT+Air: Deep flow technique with aeration, WSC: Wet-sheet culture.
[x] Shoot dry weight/root dry weight.
[w] Values followed by the same letter within a column are not significantly different at $P = 0.05$.

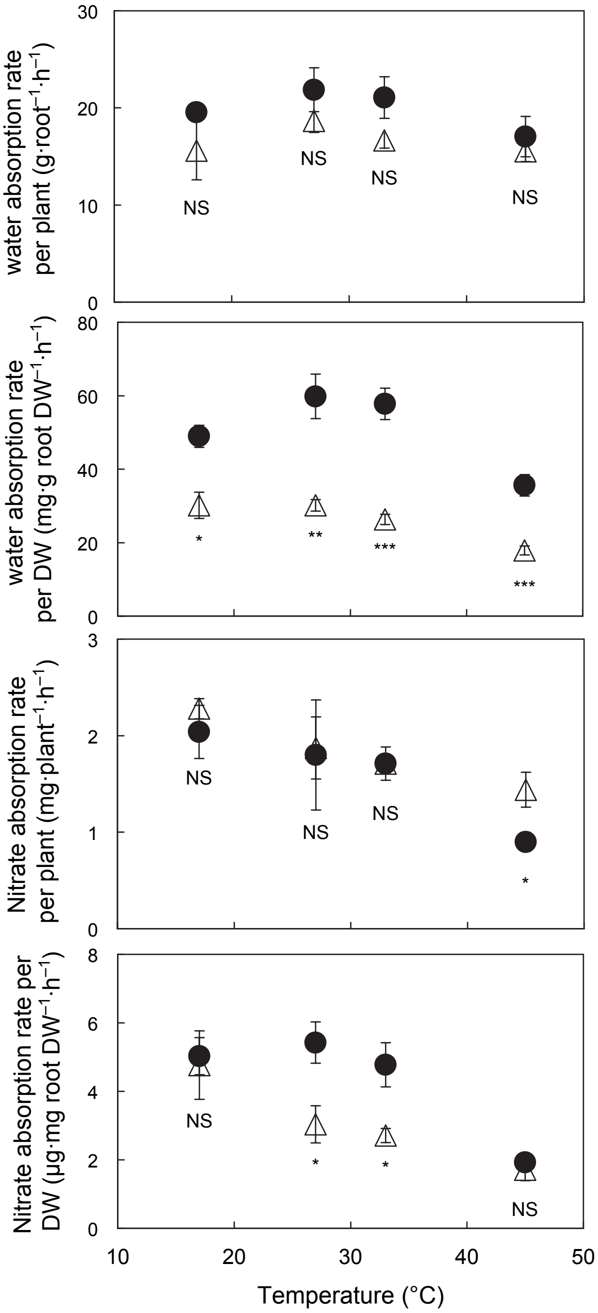

Fig. 5. Effects of root zone temperature on water and nitrate absorption rates of tomato seedlings in two hydroponic systems

●: Deep flow technique, △: Wet-sheet culture.
Data are means of 3 or 5 samples. Water and nitrate absorption rates were measured during the period 10:00 to 14:30.
*, **, and *** indicate significant difference at $P = 0.05$, 0.01 and 0.001, respectively with Fisher's PLSD test. DW: Dry weight.

Influence of growing temperature on activity and structure of roots in humid air and in nutrient solution

The root-zone temperature directly affects nutrient absorption[1] and respiration[11] and indirectly affects root development[5] and allocation of photosynthates[3,7]. We studied the short-term and long-term effects of root-zone temperature on root physiology[15,18].

1. Short-term influence of growing temperature

We compared short-term differences in water and nitrate absorption between tomato roots in humid air (WSC) and roots in nutrient solution (DFT) at four root temperatures, 17, 27, 33, and 45ºC[18]. Tomato seedlings were transplanted into acryl growing containers with DFT or WSC in growth chambers set to a 35ºC (day) / 22.5ºC (night) temperature cycle. At 9 to 11 days after transplanting, each growing container was immersed in a water bath with temperature controlled at 17, 27, 33, or 45ºC. Rates of water and oxygen absorption by tomato roots were monitored by using an electronic balance and oxygen sensor during daytime.

Water absorption rates per plant were almost equal in both systems at all temperatures (Fig. 5). On the other hand, nitrate absorption rate per plant was greater in WSC than in DFT at 45ºC, although no significant differences were found at other temperatures. Root respiration in DFT increased as the root temperature increased from 17 to 33ºC, but decreased at 45ºC, while water absorption per root respiration decreased with increasing temperature (Fig. 6). These results suggest that roots in the humid air

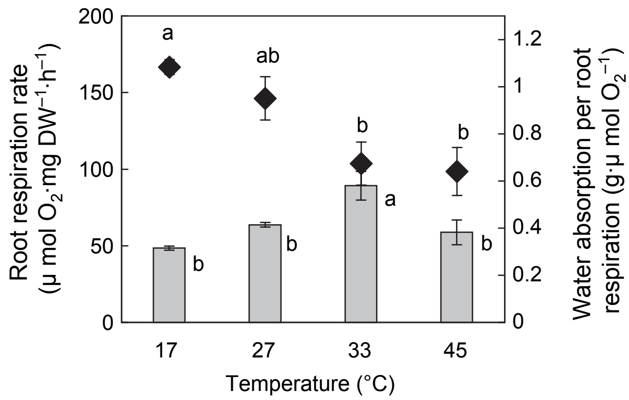

Fig. 6. Effects of root zone temperature on root respiration rate and water absorption per unit of respiration in deep flow technique (DFT)

□: Root respiration, ◆: Water absorption per root.
Values are means of 3 or 4 measurements ± SD.
Different letters represent significant differences at $P = 0.05$.

would be more tolerant of supraoptimal temperature than those in the solution.

2. Long-term influence of growing temperature

We also analyzed the long-term effects of root-zone temperature on root development[15]. Tomato seedlings growing in WSC or DFT were raised in growth chambers kept at a constant 15, 25 or 35ºC for 6 to 12 days until the five-leaf stage. We evaluated the adaptability of the root systems to high or low temperature by comparing the root activity and structure between the systems (Fig. 7). At all temperatures, WSC tomato plants grew larger than DFT plants. The bleeding rate of xylem sap per whole root system was higher in WSC than in DFT at 15 and 35ºC, and the root respiration rate per dry weight was higher in DFT than in WSC at all temperatures (Table 2). The root respiration rate measured in DFT showed different trends from the growth and bleeding rates of xylem sap, so we used it in further examination as an index of physiological activity.

The root systems in WSC had more first-order laterals and greater projected areas than those in DFT at 15 and 35ºC, but were similar to those in DFT at 25ºC (Table 3). The fractal dimension of the root systems, characterizing their complexity[23], was higher in WSC than in DFT at 15ºC, but lower at 35ºC. The higher root density and the shorter or equivalent mean length in DFT than in WSC at all temperatures (Table 3) means that root elongation was inhibited by high temperature. There was a high correlation between total root length, projected area and the fractal dimensions at 25 and 35ºC.

These results indicate that roots in humid air would adapt more readily to high or low temperature than those in solution. This agrees well with the observation by Yamazaki (1986)[25].

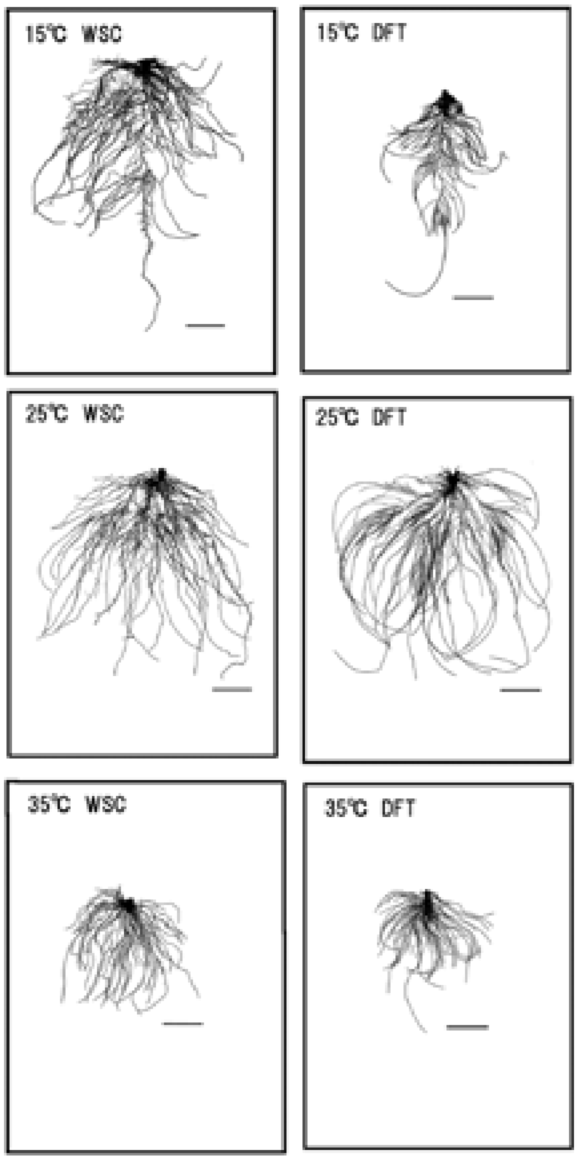

Fig. 7. Digitized images of tomato root systems grown at 15, 25 and 35ºC in the two hydroponic systems
WSC: Wet-sheet culture, DFT: Deep flow technique. Each bar indicates 5 cm.

Table 2. Effects of growing temperature on the bleeding rate of xylem sap and root respiration of young tomato seedlings in the two types of hydroponic system[z]

Hydroponic system[y]	Bleeding rate[x, w]						Root respiration rate[w]					
	mg·plant^{-1}·h^{-1}			mg·root length (m)$^{-1}$·h^{-1}			µ mol O_2.root^{-1}·h^{-1}			µ mol O_2.mg DW^{-1}·h^{-1}		
	15ºC	25ºC	35ºC	15ºC	25ºC	35ºC	15ºC	25ºC	35ºC	15ºC	25ºC	35ºC
WSC	460	414	140	15.3	12.9	7.3	22.9	13.5	14.4	0.093	0.102	0.164
DFT	191	339	69	12.8	9.6	5.2	19.8	26.2	12.4	0.156	0.266	0.221
	***	NS	***	NS	*	NS	NS	**	NS	***	***	*

[z] Data are shown as the mean of 5 or 6 samples.
[y] WSC: Wet-sheet culture, DFT: Deep flow technique.
[x] Average of the bleeding rate measured during the period from 7:30 to 12:00.
[w] NS, *, **, and *** indicate no significant difference or significant difference at P = 0.05, 0.01 and 0.001, respectively with Fisher's PLSD test.

Table 3. Effects of growing temperature on the number of first order lateral roots, total projected root area, average root diameter, and fractal dimension in tomato root in the two types of hydroponic system[z]

Hydroponic system[y]	First order lateral roots[w]									Average root diameter (mm)[w]			Total projected root area (cm^2)[w]			Fractal dimension[x,w]		
	No. (No.·plant^{-1})			Mean length (cm)			Density (No.·cm tap root axis^{-1})											
	15ºC	25ºC	35ºC	15ºC	25ºC	35ºC	15ºC	25ºC	35ºC	15ºC	25ºC	35ºC	15ºC	25ºC	35ºC	15ºC	25ºC	35ºC
WSC	108	112	89	6.0	5.5	6.5	4.0	4.7	5.7	0.58	0.43	0.43	179.7	123.1	76.7	1.74	1.66	1.59
DFT	80	107	111	4.6	6.1	4.6	4.5	5.2	21.3	0.58	0.43	0.44	79.4	142.3	53.1	1.68	1.63	1.64
	*	NS	*	*	NS	***	NS	NS	***	NS	NS	NS	***	NS	**	*	NS	*

[z] Data are shown as the mean of 5 or 6 samples.
[y] WSC: wet-sheet culture; DFT: deep flow technique.
[x] The fractal dimension was determined using the average of the local fractal by mass-radius method (Ketipearachchi & Tatsumi, 2000)[10].
[w] NS, *, **, and *** indicate no significant difference or significant difference at P = 0.05, 0.01 and 0.001, respectively with Fisher's PLSD test.

Effects of flow rate of hydroponic nutrient solution on growth and ion uptake by tomato seedlings

In many hydroponic systems, nutrient solution is circulated for aeration. Even apart from the effects of aeration, circulation itself has an effect on plant growth, but no quantitative analysis had been done. We determined the effects of stirring of nutrient solution on respiration and ion uptake by tomato roots, and the effects of increased flow rate of nutrient solution on growth of tomato seedlings cultivated by DFT[14].

We used stirrers in buffer with a manometer at 500, 700, 900, and 1,200 rpm to measure the respiration rate of detached roots cultured in DFT. The respiration rate increased with the stirring rate. Even though the level of dissolved oxygen (DO) dropped rapidly, the root respiration rate stayed constant.

Tomato seedlings were transferred into containers with nutrient solution containing ^{15}N-labeled nitrate in a growth chamber. Absorption of water and ^{15}N also tended to increase with increased stirring rate, and this increase was also independent of DO.

We determined the effects of the flow rate of the nutrient solution (0.35, 1.5 and 3.6 L·min^{-1}) in DFT on seedling growth. Higher flow rates stimulated shoot and root growth (Fig. 8). DO values in the nutrient solution for flow rates of 0.35, 1.5 and 3.6 L·min^{-1} were 1.1–3.4 ppm, 1.8–4.4 ppm and 2.6–5.8 ppm, respectively. Changes in the flow rate of the solution may affect plant growth through changes in the level of DO in the solution and in the rate of transfer of oxygen and ions close to the root surfaces, where the diffusion process is dominant. These results support the hypothesis that a boundary layer exists on the root surface and gets thinner as the flow of nutrient solution increases[19].

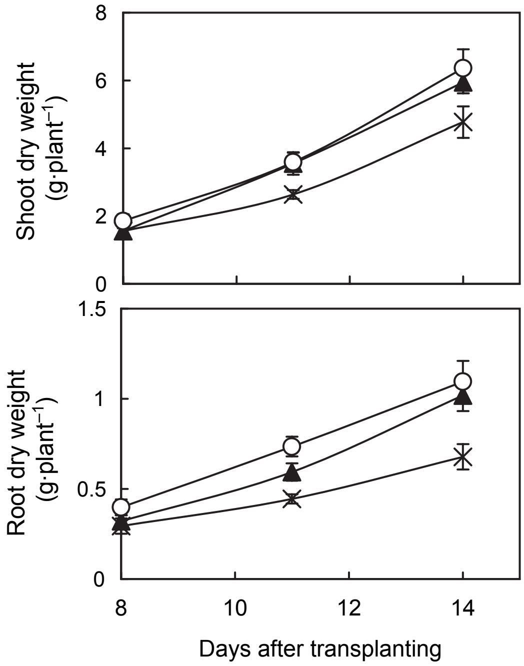

Fig. 8. Effect of flow rate of nutrient solution on growth of tomato seedlings
×: 0.35 L·min^{-1}, ▲: 1.5 L·min^{-1}, ○: 3.6 L·min^{-1}.

Effects of a combination of roots in humid air and roots in nutrient solution

As discussed above, tomato roots in the humid air and in the nutrient solution differed in their morphology and physiology. To allow plants to cope with root-zone stresses, we propose a soilless culture system that develops both types of root.

1. Absorption and distribution of ^{15}N by tomato roots divided between humid air and nutrient solution

We divided the root systems of plants between humid air and nutrient solution and analyzed the absorption and distribution of ^{15}N by the different parts[16]. Equal concentrations of $K^{15}NO_3$ solution were administered simultaneously to the nutrient solution by a nutrient tube, and the humid air through non-woven fabric and a nutrient tube. At the end of 72-h exposure to ^{15}N, we analyzed the roots and shoots.

Dry weight and percentage dry matter were significantly higher in roots in the humid air than in the nutrient solution. Percentage nitrogen contents of roots in the humid air and in the nutrient solution were 1.52% and 0.38%, respectively. Respiration rate was higher in roots in the nutrient solution than those in the humid air, by 2 times on a whole-root dry weight basis and by 3 times on a dry-weight basis. Roots in the humid air exported less ^{15}N to other parts of the plant than did roots in the solution; the former retained 5 times as much ^{15}N that they absorbed than the latter and imported more ^{15}N than the latter did (Fig. 9).

Roots in the solution absorbed and supplied nitrogen more efficiently per dry weight than did roots in the humid air. The large accumulation of dry matter by roots in the humid air may increase nitrogen absorption, even though the efficiency is low.

2. Influence of percentage of air and solution spaces in the root-zone on vegetative growth and fruit yield of tomato grown in wet-sheet culture

Some soilless culture systems have humid air and solution spaces in the root-zone. Although those systems are suitable for growing vegetables, the appropriate ratio of spaces and their physiological roles were unknown. So we investigated the effects of percentages of humid air and solution spaces in the root-zone on vegetative growth and fruit yield of tomato[20]. Percentages of air space in the root-zone were 0 (all roots were submerged in nutrient solution), 25, 50, 75, and 100% (the entire root system was developed on the wet sheet and exposed to the humid air).

Enlarging the air space in the root-zone up to 50% increased the dry weight of shoots and roots. Leaf expansion was suppressed at both 0% and 100% air space. Fruit yield and weight were heavier when the air space exceeded 50% (Fig. 10), but the percentages of dry matter and soluble solids were lower (5.1–5.3%) than at 25% (6.0%) and at 0% (7.1%). The photosynthetic rate of leaves was significantly lower at 0% air space. Respiration rates of roots near the base were almost equal in all treatments, whereas those of roots from middle to tip were higher at 50% and 75% air space than at other proportions (Fig. 11). Total root respiration increased as the air space increased to 75%.

Partial exposure of roots to humid air promoted the physiological activity of the whole root system and increased yield. Hence, for stable growth of tomato plants in soilless culture, the roots need exposure to both environments identically in soil culture.

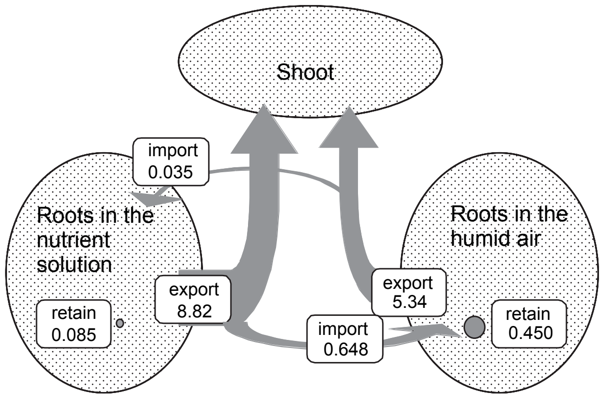

Fig. 9. Schematic diagram of nitrogen flow from roots in the nutrient solution and in the humid air (µg·g DW^{-1}·h^{-1})

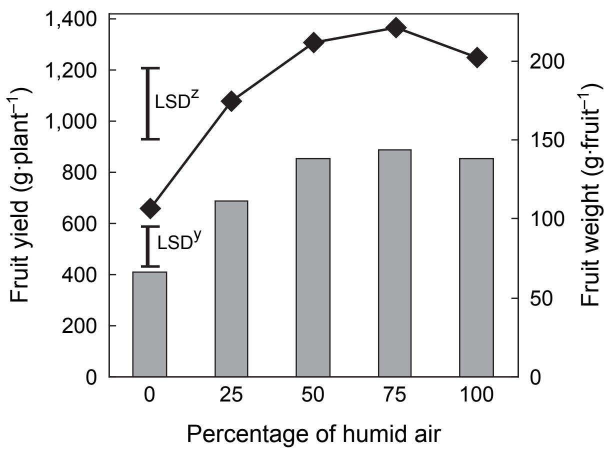

Fig. 10. Effects of percentage of humid air space in the root-zone on fruit yield and weight of single-truss tomato

□: Fruit yield, ◆: Fruit weight.
Vertical bars represent LSD at $P = 0.05$. [z]LSD on fruit weight. [y]LSD on fruit yield.

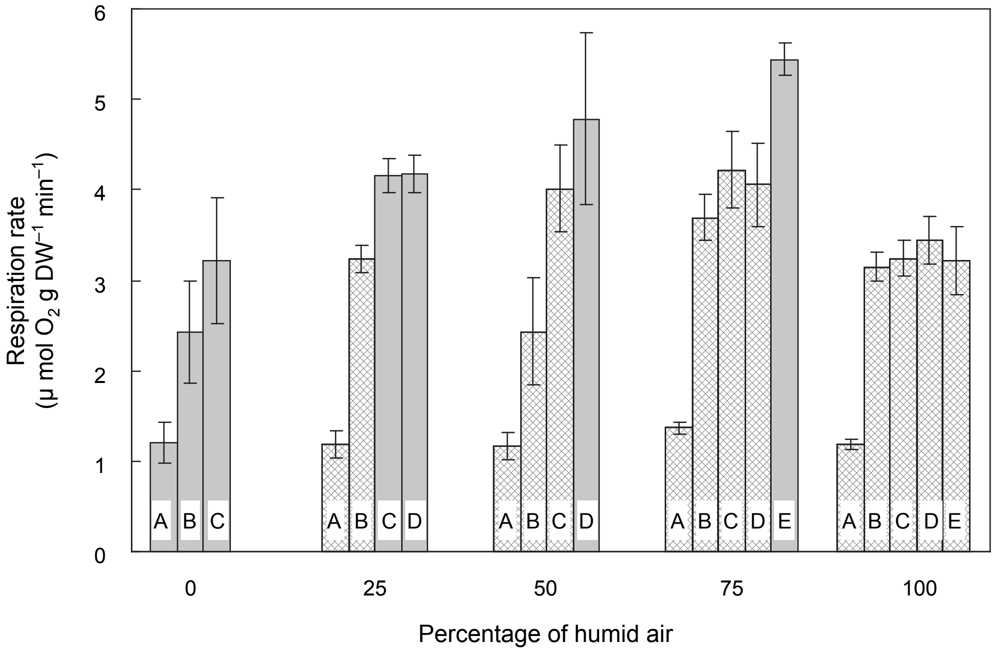

Fig. 11. Effects of percentage of humid air spaces in the root-zone on respiratory rate of tomato root segments
: Roots in the nutrient solution, : Roots in the humid air.
Measurement was carried out at flowering stage. Roots were divided at 6-cm intervals from the basal part of the stem. A: 0–6 cm, B: 6–12 cm, C: 12–18 cm, D: 18–24 cm, E: >24 cm. Values are means of 3 to 5 measurements ± SD.

Responses of root system to environment and stress adaptability

We undertook a series of experiments to test the plasticity of roots in response to variations in the root-zone environment. In humid air, roots adapt to mild water stress by changing their morphology and function, resulting in a large and well branched root system. On the other hand, roots in nutrient solution have few branches and root hairs. Roots in humid air have lower respiration and nutrient absorption than roots in nutrient solution on a dry weight basis, but almost the same on a root system basis. The adaptations in roots in the humid air allowed plants to withstand temperature stress. Where there is little likelihood of stress, as in a highly regulated nutrient solution with plenty of resources, the 'optimum' root system will be small. The balance between root development (costs) and water and nutrient availability (benefits) will reflect the stress adaptability of roots[6]. When several stresses overlap coincidentally, various responses would interact with each other and, hence, total ability of roots would be defined. Minimizing the risk of stresses should be a basic strategy, but our observations of root plasticity will help the establishment of growing systems that support high yield and stable production.

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