Effects of Rooting Volume Restriction on the Growth and Carbohydrate Concentration in Tomato Plants

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ABSTRACT. Tomato plants (*Lycopersicon esculentum* Mill 'Ougata-fukuju' and 'Korokoro') were grown in a soil or a hydroponic culture to study effects of rooting volume restriction on plant growth and carbohydrate concentrations. In soil culture, leaf lengths decreased linearly as container volume decreased, while plant height did not decrease linearly, irrespective of fruiting. The root to shoot ratio decreased in smaller volume containers, irrespective of fruiting, because dry mass accumulation in the stem and leaves was relatively less inhibited than that in the roots. Total plant dry mass did not differ between fruiting and deblossomed plants, irrespective of container volume. In hydroponic culture, plant height in small containers (37 cm³) was similar to that in large containers (2024 or 4818 cm³). The root to shoot ratio of the plants grown in small containers was lower than that of the plants grown in large containers, mainly due to less inhibition of the dry mass accumulation in the stem than in the leaves. When small containers were almost filled with roots (28 days after transplanting), soluble sugar and starch concentrations in leaves became $\approx$ 2-fold higher in the plants grown in small than in those grown in large containers. At the end of experiment (42 days after transplanting), sucrose and starch concentrations in the stem were higher in plants grown in small than in those grown in large containers. However, soluble sugar and starch concentrations in the leaves did not differ between treatments.

Rooting volume restriction leads to the reduction of shoot growth because of several factors; e.g., inhibition of nutrient (Hameed et al., 1987; Reiger and Marra, 1994) and water absorption (Hameed et al., 1987; Tschaplinski and Blake, 1985), limiting oxygen supply (Peterson et al., 1991b), imbalance in growth substances between shoots and roots (Carmi et al., 1983; Liu and Latimer, 1995; Peterson et al., 1991b; Richards and Rowe, 1977), reduction in photosynthesis (Robbins and Pharr, 1988), and changes in carbohydrate mobilization (Reiger and Marra, 1994; Robbins and Pharr, 1988). Rooting volume restriction does not affect root to shoot ratio in peach (*Prunus persica*) (Reiger and Marra, 1994; Richards and Rowe, 1977), soybean (*Glycine max*) (Krizek et al., 1985), or cucumber (*Cucumis sativus*) (Robbins and Pharr, 1988); i.e., suppression of shoot growth is associated with restriction of root growth. Conversely, root to shoot ratio in root-restricted tomato plants is lower than that in unrestricted plants; i.e., the relative amount of assimilates allocated to the shoots is greater in root-restricted than in unrestricted plants (Peterson et al., 1991a). The results of rooting volume restriction of tomato plants indicate that reductions in root to shoot ratio are more pronounced in plants grown in hydroponic than in soil culture (Cooper, 1972; Peterson et al., 1991a; Ruff et al., 1987). Developing tomato fruit are often predominant sink organs for assimilates (Ho, 1979). Although there is a large difference in dry mass, the percentage allocation to tomato fruit is higher in root-restricted than in unrestricted plants (Cooper, 1972) suggesting that fruiting may affect root to shoot ratio in root-restricted tomato plants.

The use of assimilates by roots grown under mechanical impedance is often related to the carbon economy of the whole plant, because the roots are also a predominant sink organ for assimilates (Atwell, 1990). Robbins and Pharr (1988) reported that reduced sink demand by root-restricted cucumber (*Cucumis sativus*) plants

was associated with lower photosynthetic rates. In contrast, rooting volume restriction of tomato plants had little or no effect on net assimilation rate (Ruff et al., 1987). Therefore, tomato plants may have different strategies from other crops for altering carbohydrate accumulation in response to rooting volume restriction. In our study, we determined the interactive effects of fruiting and root restriction on the growth and development of tomato plants grown in soil culture. Moreover, changes in the growth and carbohydrate concentrations in response to rooting volume restriction were determined in plants grown in hydroponic culture.

Materials and Methods

Experiment 1: Effects of rooting volume restriction on growth of fruiting and deblossomed plants grown in soil culture

PLANT MATERIALS AND CULTURAL METHODS. On 21 May 1994, seeds of 'Ougata-fukuju' tomato were sown in 4.5-cm (40-cm³) cells filled with a soilless media (Kureha No.8, Zennoh Co-op, Tokyo, Japan) and grown in a greenhouse. Twelve days after sowing (2 June), seedlings (one seedling per cell) were transplanted to either 0.4-, 1-, 4-, or 7-L containers filled with a mix of 4 sandy soil : 1 vermiculite (by volume). A liquid fertilizer that contained macronutrients (mm) of 3.7 NO₃⁻ N, 1.2 NH₄⁺ N, 1.2 PO₄³⁻ P, 8.8 K⁺, 5.7 Ca²⁺, and 2.9 Mg²⁺, and micronutrients (μ m) of 26 Fe³⁺, 9 Mn²⁺, 46 B³⁺, 0.2 Cu²⁺, 0.3 Zn²⁺, and 0.1 Mo²⁺ (Otsuka Pharmaceutical Inc., Osaka, Japan) were applied daily.

A completely randomized block design was used with five single-plant replications per treatment. Half of the plants in each volume of containers was allowed to fruit from primary to tertiary trusses (three fruits per truss) by spraying a 90 mM *p*-chlorophenoxyacetic acid solution to the trusses. On the other hand, all trusses of remaining plants were removed when they emerged. All plants were kept to a single stem by removing lateral shoots as they emerged. Leaves were designated as L1, L2, L3,... from the proximal end. On 6 Aug. [65 d after transplanting (DAT)], leaf lengths were measured individually and plants were harvested, and separated into root, stem, leaf, and fruit fractions, dried in convection oven at 85 °C and weighed.

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Table 1. Influence of restricted root zone volume on plant height 65 d after transplanting in fruiting (F) and deblossomed (D) 'Ougata-fukuju' tomato plants grown in soil culture (Expt. 1).

Container vol (L)	Plant ht (cm)	
	Plants	
	F	D
7	93.6 a ²	97.1 a
4	91.5 a	87.4 a
1	73.1 b	75.9 b
0.4	55.0 c	61.0 c
Significance		
Linear	NS	NS
Quadratic	NS	NS
F vs. D	NS	

²Mean separation within columns by Duncan's multiple range test at $P \leq 0.05$.

^{NS}Nonsignificant.

Experiment 2: Effects of rooting volume restriction on growth and carbohydrate concentrations of deblossomed plants grown in hydroponic culture

PLANT MATERIALS AND CULTURAL METHODS. On 21 May 1994, seeds of 'Ougata-fukuju' tomato were sown in an urethane foam. Ten days after sowing (31 May), seedlings (one seedling per cell) were transplanted to either large (11.5 cm diameter $\times$ 19.5 cm depth, 2024 cm³, unrestricted control) or small (2.5 cm diameter $\times$ 7.5 cm depth, 37 cm³, rooting volume restriction) culture containers and grown in a greenhouse. Two polyethylene pipes were inserted in the middle of each container to supply of nutrient solution and air, respectively. Total volume of the pipes inserted in the containers was 6 mL for unrestricted controls and 2 mL for the root-restricted plants. Therefore, net volumes of large and small containers were 2018 and 35 cm³, respectively. A liquid fertilizer as shown in Expt. 1 was circulated for 1 min at 12- to 14-min intervals at 1 L·min⁻¹ for large and 0.5 L·min⁻¹ for small containers. Air was supplied throughout the experimental period at 1 L·min⁻¹ for large and 0.5 L·min⁻¹ for small containers. All flower trusses and lateral shoots were removed as they emerged. On 31 May, four plants were harvested, and four plants from each container were harvested at 9, 16, 23, 30, and 37 DAT, separated into root, stem, and leaf fractions, dried at 85 °C, and weighed.

Seeds of 'Korokoro' tomato also were sown on 13 Aug. 1994. On 27 Aug. (14 d after sowing), seedlings were transplanted to either

large or small containers and grown in a greenhouse as described above. On 28 DAT, unrestricted control plants were transplanted again to 4818-cm³ (9.5 cm diameter $\times$ 17 cm depth) containers. The nutrient solution was circulated for 1 min at 3- to 14-min intervals. On 27 Aug. (0 DAT), four plants were harvested, and four plants from each container were harvested at 14, 28, and 42 DAT. All plants were harvested at 0900 HR and then immediately separated into root, stem and leaf fractions. The roots and stem were lyophilized at -50 °C. Three to four leaf disks from each leaf were punched out by using a leaf punch (1.13 cm²/disk), and lyophilized at -50 °C. The remaining leaves were dried at 85 °C and used for measuring leaf dry mass.

NONSTRUCTURAL CARBOHYDRATE DETERMINATION. Carbohydrate concentrations were determined only from the plants harvested on 14, 28, and 42 DAT because dried samples obtained from the plants harvested on 0 DAT were too small to use for analysis. Lyophilized samples were ground in a mill, and 150 to 200 mg of each were extracted three times in boiling 80% ethanol. The homogenates were centrifuged at 2400 g, after each extraction. The pellets were saved for starch determination. The ethanolic extracts were evaporated to dryness and resolubilized in 10 mL distilled water. A sample of 100 μ L of the supernatant was analyzed by a spectrophotometer (model UV-1200; Shimadzu, Kyoto, Japan) for glucose, fructose and sucrose concentrations as described previously (Nishizawa and Shishido, 1998). Insoluble starch grains in the pellet were dehydrated by amyloglucosidase (EC3.2.1.3, 2.0 unit per mL; Wako Pure Chemical, Osaka, Japan), and starch concentrations were determined by the above-mentioned spectrophotometer. The data were expressed as milligrams of glucose per gram of dry mass (Nishizawa and Shishido, 1998).

STATISTICAL ANALYSIS. Regression analysis was performed by using SAS (Cary, N.C.) to determine the effect of container volumes. Means $\pm$ standard errors are shown in all figures.

Results

EXPERIMENT 1. Although plants grown in the smallest (0.4-L) containers were $\approx$ 60% as tall as those grown in the largest (7-L) containers at 65 DAT and it was significant difference in a mean separation test, no linear or quadratic relationship was detected in plant height, irrespective of fruiting (Table 1).

The length of leaves below L6 was not inhibited by root restriction (data not shown), while leaves at the seventh node and above (L7 to L15) showed gradual decreases in length with progressively smaller volume containers, irrespective of leaf posi-

Table 2. Influence of restricted root zone volume on leaf length 65 d after transplanting in fruiting (F) and deblossomed (D) 'Ougata-fukuju' tomato plants grown in soil culture (Expt. 1).

Container vol (L)		Leaf position ²																	
		L7		L8		L9		L10		L11		L12		L13		L14		L15	
		Leaf length (cm)																	
		F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D
7	44.4	44.6	43.6	43.7	42.5	43.9	43.5	42.6	40.4	42.4	41.6	42.5	39.6	40.7	37.0	39.7	33.3	36.6	
4	36.9	36.3	36.8	37.0	34.1	36.8	31.4	35.5	35.0	37.8	33.3	37.6	32.1	35.1	30.9	36.6	29.0	33.9	
1	30.0	28.9	29.1	29.6	31.1	30.3	29.1	31.6	32.0	32.0	26.9	28.4	23.4	27.1	22.1	27.5	21.6	25.6	
0.4	27.0	27.3	28.8	29.9	24.9	28.6	22.8	28.4	21.6	28.0	17.6	24.4	14.6	23.5	12.7	19.1	12.1	20.1	
Significance																			
Linear	**	***	**	**	*	***	*	**	*	*	*	*	*	**	*	*	*	*	
Quadratic	NS	**	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	
F vs. D	NS		NS		NS		NS		*		*		*		**		**		

²Leaves were designated as L1, L2, L3... from the proximal end.

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 3. Influence of restricted root zone volume on dry mass of each plant part and root to shoot ratio 65 d after transplanting in fruiting (F) and deblossomed (D) 'Ougata-fukuju' tomato plants grown in soil culture (Expt. 1).

Container vol (L)	Dry mass (g)										Root to shoot ratio	
	Roots		Leaves		Stems		Fruit		Total plant		ratio	
	F	D	F	D	F	D	F	D	F	D		
7	31.9	49.0	66.6	79.4	26.6	30.3	58.0	---	183.1	158.7	0.21	0.45
4	19.0	23.1	35.8	53.4	17.1	21.5	43.9	---	115.8	98.0	0.20	0.31
1	8.6	5.1	10.6	21.0	4.7	7.9	10.5	---	29.0	34.0	0.12	0.18
0.4	3.2	5.1	10.6	21.0	4.7	7.9	10.5	---	29.0	34.0	0.12	0.18
Significance												
Linear	**	**	**	***	**	**	*	---	**	***	*	**
Quadratic	NS	**	NS	*	NS	**	*	---	NS	***	NS	NS
F vs. D		*		***		**		---		NS		*

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

tion or fruiting (Table 2). The length of leaves above L11 was shorter in fruiting than in deblossomed plants.

The dry mass in individual plant fractions decreased in smaller volume containers and the values were smaller in fruiting than in deblossomed plants (Table 3). However, total plant dry mass did not differ significantly between fruiting and deblossomed plants. The root to shoot ratio also decreased in smaller volume containers.

EXPERIMENT 2. Small containers of 'Ougata-fukuju' tomato were approximately half filled with roots by 16 DAT and almost filled by 23 DAT (Fig. 1). Small containers of 'Korokoro' tomato were almost filled with roots by 28 DAT (data not shown). The increase in plant height of root-restricted 'Ougata-fukuju' was inhibited at 30 DAT, and was 73% (71 cm) of unrestricted controls (97 cm) on 37 DAT (Fig. 2). However, height of root-restricted 'Korokoro' plants was greater than that of unrestricted controls beginning at 10 DAT; by 42 DAT the plants were 27% taller than those of unrestricted controls (119 vs. 94 cm).

The total leaf area in unrestricted controls increased rapidly after 9 to 14 DAT, while that in root-restricted plants increased only slightly, irrespective of cultivars (Fig. 3). By the end of the experimental period (37 or 42 DAT), leaf area was 36% as great in the cultivar 'Ougata-fukuju' (32 vs. 90 dm²) and 32% in the cultivar 'Korokoro' (24 vs. 75 dm²).

Dry mass accumulation differed between unrestricted controls and root-restricted plants, starting on or after 14 to 16 DAT, irrespective of cultivars and plant parts (Fig. 4). Inhibition of dry mass accumulation in root-restricted plants was less in the stem than in the leaves; i.e., at the end of the experimental period (37 or 42 DAT), leaf dry masses in root-restricted plants were only 29% to 35% of those in unrestricted controls (14.2 vs. 41.0 g for 'Ougata-fukuju' and 9.6 vs. 32.8 g for 'Korokoro'). Root restriction had a similar effect on biomass production in the stems. At 37 d, stem dry mass of root-restricted 'Ougata-fukuju' plants were 51%

Fig. 1. Root systems of 'Ougata-fukuju' tomato plants grown in hydroponic culture for (A) 16 and (B) 23 d after transplanting in large (2024 or 4818 cm³, unrestricted) or small (37 cm³, restricted) containers (Expt. 2).

Fig. 2. Plant height of (A) 'Ougata-fukuju' and (B) 'Korokoro' tomato plants grown in large (2024 or 4818 cm³, unrestricted control) or small (37 cm³, restricted) containers for 36 to 48 d after transplanting. Each point represents the mean of four replications $\pm$ SE; SE bars present only when larger than symbol (Expt. 2).

of those in unrestricted controls (7.2 vs. 14.0 g) while those of 'Korokoro' were 69% as great (9.5 vs. 13.7 g). Although, root to shoot ratio in both treatments decreased almost steadily during the experi-

Fig. 3. Leaf area of (A) 'Ougata-fukuju' and (B) 'Korokoro' tomato plants grown in large (2024 or 4818 cm³, unrestricted control) or small (37 cm³, restricted) containers for 37 to 42 d after transplanting. Each point represents the mean of four replications $\pm$ SE; SE bars present only when larger than symbol (Expt. II).

Fig. 4. Dry mass of (A) 'Ougata-fukuju' and (B) 'Korokoro' tomato plants grown in large (2024 or 4818 cm³, unrestricted control) or small (37 cm³, restricted) containers for 37 to 42 d after transplanting. Each point represents the mean of four replications $\pm$ SE; SE bars present only when larger than symbol (Expt. 2).

mental period, the decline in root-restricted plants was greater than that in unrestricted controls, irrespective of cultivars (Fig. 5).

The nonstructural carbohydrate concentrations in the roots were lower than in the other plant parts during the experimental period, and the concentrations did not differ between treatments (Fig. 6). The highest nonstructural carbohydrate concentrations in all parts of the plant were detected in the stems of root-restricted plants. By the end of the experimental period (42 DAT), sucrose

Fig. 5. Root to shoot ratio of (A) 'Ougata-fukuju' and (B) 'Korokoro' tomato plants grown in large (2024 or 4818 cm³, unrestricted control) or small (37 cm³, restricted) containers for 37 to 42 d after transplanting. Each point represents the mean of four replications $\pm$ SE (Expt. 2).

Fig. 6. Carbohydrate concentrations (mg g⁻¹ dry mass) of 'Korokoro' tomato plants grown in large (2024 or 4818 cm³, unrestricted control) or small (37 cm³, restricted) containers for 42 d after transplanting. Each point represents the mean of four replications $\pm$ SE; SE bars present only when larger than symbol (Expt. 2).

and starch concentrations in the stems of root-restricted plants (96 and 40 mg·g⁻¹ dry mass, respectively) were ≈2- to 5-fold greater than those in the stems of unrestricted controls (52 and 8 mg·g⁻¹ dry mass, respectively), while reducing sugar (glucose + fructose) concentrations were similar between treatments. At 28 DAT, reducing sugar, sucrose and starch concentrations in the leaves of root-restricted plants (25, 21, and 26 mg·g⁻¹ dry mass, respectively) were ≈2-fold greater than those in the leaves of unrestricted controls (11, 10, and 12 mg·g⁻¹ dry mass, respectively), but there was no difference between treatments 42 DAT.

Discussion

Peterson et al. (1991a) reported that leaf area on the main stem of root-restricted 'Better Bush' tomato plants grown in hydroponic culture was only 35% of that on the main stem of an unrestricted controls, while the stem length was 85% as great. Our experiment also showed that the leaf area of root-restricted tomato plants grown in hydroponic culture was only 32% to 36% of that of unrestricted controls at the end of the experiment (Fig. 3), while the plant height of root-restricted plants was similar to that of unrestricted controls (Fig. 2). Thus, the inhibition of stem elongation in tomato plants grown under root restriction is less than that of leaf expansion. In contrast to the results obtained in hydroponic culture, the height of plants grown in 0.4-L containers of soil was only ≈60% of that of the plants grown in 7-L containers, irrespective of fruiting (Table 1). Ruff et al. (1987) also reported that the plant height of root-restricted 'Better Bush' tomato plants grown in soil culture was only 60% of that of unrestricted controls. In soil culture, the roots are always stimulated by soil contact, and such a stimulation can enhance ABA and ethylene levels in the shoots (Liu and Latimer, 1995; Peterson et al., 1991b), while translocation of gibberellins and cytokinins from the roots to shoots is inhibited (Carmi and Heuer, 1981). Therefore, in Expt. 1, the stimulation by soil contact might accelerate an imbalance of these hormones and inhibit the stem elongation, even if the plants were grown in large (7-L) containers.

Leaf expansion in fruiting tomato plants is often inhibited compared to that in deblossomed plants, because the fruits enhance sink capacity as they enlarge (Cooper, 1972). In Expt. 1, leaf length in fruiting plants was less than that in deblossomed plants in the leaves above L11 (Table 2). Leaf dry mass was also smaller in fruiting than in deblossomed plants (Table 3). These larger inhibitions of leaf growth observed in fruiting than in deblossomed plants may be attributed to the enhanced sink demand by fruits. Although leaf expansion was inhibited by fruiting, total plant dry mass did not differ between fruiting and deblossomed plants, irrespective of container volume (Table 3) as reported in fruiting and deblossomed strawberry plants (Nishizawa and Shishido, 1998).

Lower root to shoot ratio of 'Ougata-fukuju' tomato plants grown in small volume containers in soil culture was due to relatively less growth inhibition in the stem and leaves compared to that in the roots (Table 3). Ruff et al. (1987) also reported that dry mass of the leaves and stems in 'Better Bush' tomato plants grown in 0.45-L containers in soil culture was only 29% and 34% of the plants grown in 13.5-L containers, respectively, when measured 12 weeks after transplanting. In Expt. 2, however, the lower root to shoot ratio in small rather than in large containers was mainly attributed to less inhibition of dry mass accumulation in the stem than in the leaves (Figs. 4 and 5). Peterson et al. (1991a) also detected a similar result among 'Better Bush' tomato plants in hydroponic culture. The different results obtained in soil and hydroponic cultures suggests that mechanical impedance of the roots by soil contact, even if it is slight stimulation, may greatly inhibit stem growth.

Root volume restriction often promotes an accumulation of nonstructural carbohydrates in the leaves in response to the lack of active sinks. Robbins and Pharr (1988) reported that reduced sink demand of root-restricted cucumber plants was associated with an increase in nonstructural carbohydrate concentrations in the source leaves. Thus, accumulation of nonstructural carbohydrates in the leaves in response to root restriction could have provided a feedback mechanism that reduced carbon metabolism. In our study, nonstructural carbohydrate concentrations in the leaves of root-restricted 'Korokoro' tomato plants were higher than those in the leaves of unrestricted controls when the containers were almost filled with roots (28 DAT) (Fig. 6). At 42 DAT, however, higher carbohydrate concentrations in root-restricted plants than in unrestricted controls were observed only in the stem (Fig. 6). These results suggest that the role of the stem as a sink organ may increase when root growth is extremely limited by root restriction, and relatively larger amount of carbohydrates may accumulate in the stem than in other sink organs. Thereby, a new shoot to root equilibrium may be established for increased function in the stem and for diminished function in the roots.

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