Effects of Nutrient Stress by Split–Root System on the Growth and K, Ca, and Mg Contents at Different Stages of Hydroponically–Grown Tomato Seedlings

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Summary

Effects of nutrient stress by the split root system on the growth and major cation (K, Ca and Mg) contents were investigated at three stages of hydroponically grown tomato (*Lycopersicon esculentum* Mill. cv. House Momotaro) in spring and autumn. Nutrient stress was applied to tomato plant seedlings by halving their roots; one part was cultured in 1/2 strength Enshi standard nutrient solution (ESNS), whereas the other was immersed in tap water. Seedlings with intact roots, cultured in 1/2 strength ESNS, were used as non–stressed control. No significant difference was observed in major growth parameters between the stressed and non–stressed plants at three stages.

Nutrient stress significantly increased the percentage of dry weight of the split roots cultured in 1/2 strength ESNS at three stages, and that of the shoot 10 days after treatment. The dry weight of the split roots, immersed in tap water, was significantly reduced at three stages. Nutrient stress significantly reduced K contents in leaves and roots at three stages, and also in stems except 20 days after the treatment. Nutrient stress significantly increased Ca content of the split roots, cultured in 1/2 strength ESNS, 10 and 20 days after treatment. A significantly high Mg content was found in the split roots, immersed in tap water, at three stages. Under nutrient stress, leaf and stem Mg contents were increased at three stages. Nutrient stress significantly decreased the EC value of the nutrient solution, and significantly increased the total amount of water absorbed.

Key Words: cation content, nutrient stress, split–root hydroponics, tomato.

Introduction

The split–root technique has been used in horticulture for various purposes. Matsuda et al. (1979) reported that when the root system of tea plants was split into two parts, one which was cultured in nutrient solution containing Al, and the other cultured without Al, Al was translocated from the split roots which received Al to the split roots not administered Al. In cowpea seedlings, Zn was translocated from the split roots which received Zn to the split roots not receiving Zn (Marsh et al., 1985). Taylor and Fenn (1985) reported that water moves from pecan, grape, and tomato split roots growing in a moist soil medium, across stem or crown to the split roots growing in a dry soil medium; it is exuded during periods of high transpiration. The above reports demonstrate that in a split–root system nutrients and water can move from one part to the other.

In tomato, numerous studies on their nutritional aspects with respect to environmental stresses, such as low and high temperatures, and salinity have been reported but only a few reports on the effects of nutrient stress. Sonneveld and Voogt (1991) reported the effects of calcium–stress on blossom–end rot (BER) and magne-

sium–deficiency in rockwool–grown tomato. They found that two weeks after the beginning of the stress period, the top leaves and young fruits showed symptoms of Ca–deficiency (BER), and Ca–stress alleviated Mg–deficiency. Goldstein et al. (1988a, 1988b, and 1989) reported that phosphate starvation induced the excretion of acid phosphatase by tomato plants and suspension–cultured cells. Sanders et al. (1996) who studied the vascularization response of three tomato cultivars to soil type, nutrient stress, and water stress, found that plants subjected to nutrient stress had the most veins.

Although the split–root technique has been widely applied to horticultural researches, little is known about the physiological responses of tomato plants to the nutrient stress using this treatment. This study explores the effects of nutrient stress by split–root system on the growth and K, Ca, and Mg uptake at different stages of hydroponically–grown tomato seedlings.

Materials and Methods

Plant material

Tomato seedlings (*Lycopersicon esculentum* Mill. cv. House Momotaro, Takii & Co., Ltd., Japan) were hydroponically cultured in the greenhouse of Chiba

University.

Experimental procedure

Experiment 1. On February 20, 1998, seeds were sown in rice husk charcoal. On March 3, seedlings with fully expanded cotyledons were transplanted to polyurethane substrates ($2.4 \times 2.4 \times 2.8$ cm) and inserted into plastic cell trays (128 cells per tray, leaving one cell apart between two adjacent seedlings, distance between seedlings was 7 cm). These trays were immersed into a plastic tank ($90 \times 60 \times 20$ cm) containing 1/8 strength ($EC=0.73 \text{ dS} \cdot \text{m}^{-1}$) ESNS (major nutrients, as $\text{meq} \cdot \text{l}^{-1}$, 16NO_3 , 1.3NH_4 , 4P, 8K, 8Ca, 4Mg, 4S, and micronutrients, as ppm, 3Fe, 0.5B, 0.5Mn, 0.05Zn, 0.02Cu, and 0.01Mo). Nutrients were absorbed by the seedlings through the bottom of the tray. The nutrient solution in the tank was renewed every three days. On March 24, seedlings with four expanded leaves were transplanted into individual Wagner pots and aerated. Two treatments were as follows. 1) All roots of the seedling were cultured in one pot containing 10 liters of 1/2 strength ($EC=1.46 \text{ dS} \cdot \text{m}^{-1}$) ESNS. 2) Seedling roots were evenly split into two parts; half was cultured in a black plastic bag containing 5 liters of 1/2 strength ESNS; and the other half was immersed in a similar bag holding 5 liters of tap water ($EC=0.36 \text{ dS} \cdot \text{m}^{-1}$, mineral contents, as $\text{meq} \cdot \text{l}^{-1}$, NO_3^- 1.08, NH_4^+ 0, PO_4^{3-} 0, K^+ 0.06, Ca^{2+} 1.74, and Mg^{2+} 1.25), to impose nutrient stress. A Wagner pot was separated into two by inserting a thin wooden plate vertically at its diameter. There were 15 plants per treatment. The nutrient solution and tap water in the pots were renewed weekly. As the plants grew, all lateral shoots were removed. Ten, 20, and 30 days after treatment, the growth parameters of the plants, including plant height, stem diameter, number of expanded leaves, and relative chlorophyll content were measured. The relative chlorophyll content at seven locations on the fifth leaf from the top of plant was measured with a chlorophyll meter (SPAD-502, Minolta Co., Ltd., Japan). At each sampling date, 5 plants were harvested,

and the fresh weight of shoots and roots determined.

Experiment 2, a replicate of Exp. 1 was carried out in the autumn of 1998. Seeds were sown on August 27 and seedlings transferred into polyurethane substrates on September 3. On September 21, seedlings with four expanded leaves were transplanted into 2000 Wagner's pots for treatment. The control and split-root plants were harvested 10, 20, and 30 days after treatment and analyzed as in Exp. 1.

The daily maximum and minimum air temperatures were recorded constantly, whereas the solution temperature was recorded at 9:00 a.m. throughout this experiment.

Sampling and cation analysis

Harvested plants were divided into root, stem, and leaf and the parts weighed and then dried in an oven at 65°C for one week. Upon weighting the shoots and roots, the percentages of dry matter were calculated. The dried samples were milled and digested with H_2SO_4 -salicylic acid- H_2O_2 in flasks (Walinga et al., 1995) for cation (K, Ca, and Mg) analysis. Cation contents were determined by atomic absorption spectrophotometer. Data were subjected to analysis of variance and the means were separated at $P<0.05$ by Duncan's new multiple range test.

Results

Maximum and minimum air and solution temperatures

During spring cultivation, the daily maximum and minimum air temperatures ranged from 17 to 33°C and 10 to 18°C respectively, and solution temperature varied from 12 to 24°C . During autumn cultivation, the daily maximum and minimum air temperatures ranged from 22 to 35°C and 15 to 24°C respectively, and solution temperature fluctuated between 18 and 26°C . The mean temperatures during the spring were lower than those in autumn.

Table 1. Effects of nutrient stress on the plant height and stem diameter at different stages of hydroponically-grown tomato seedlings.

Treatment	Plant height (cm)			Stem diameter (mm)		
	10d ^z	20d	30d	10d	20d	30d
Spring						
1/2 ESNS ^y	23.8a ^x	37.4a	59.8a	7.4a	8.9a	10.2a
1/2 ESNS + water	23.6a	37.2a	63.0a	7.2a	8.8a	10.8a
Autumn						
1/2 ESNS	37.2a ^x	63.4a	94.0a	8.0a	9.3a	11.9a
1/2 ESNS + water	37.2a	62.8a	94.2a	8.0a	9.7a	12.4a

^z Samples were taken 10, 20, and 30 days after treatments were begun.

^y ESNS stands for Enshi standard nutrient solution.

^x Different letters within short columns show significant difference by Duncan's new multiple range test at 5% level.

Table 2. Effects of nutrient stress on the number of expanded leaves and relative chlorophyll content at different stages of hydroponically - grown tomato seedlings.

Treatment	No. of expanded leaves			Relative chlorophyll content ^w		
	10d ^z	20d	30d	10d	20d	30d
Spring						
1/2 ESNS ^y	8.6a ^x	11.2a	15.8a	35.4a	42.6a	47.5a
1/2 ESNS + water	8.8a	11.4a	15.4a	39.0a	42.4a	49.2a
Autumn						
1/2 ESNS	8.0a ^x	14.0a	17.6a	37.5a	38.3a	41.8a
1/2 ESNS + water	8.4a	14.0a	17.8a	38.0a	38.8a	45.0a

^{z, y, x} See Table 1.^w Values obtained with a chlorophyll meter (SPAD - 502, Minolta Co., Ltd., Japan).**Table 3.** Effects of nutrient stress on the shoot dry weight and its dry weight percentage at different stages of hydroponically - grown tomato seedlings.

Treatment	Shoot dry weight (g)			Percentage of shoot dry weight (%)		
	10d ^z	20d	30d	10d	20d	30d
Spring						
1/2 ESNS ^y	1.90a ^x	6.76a	21.52a	8.4b	7.8a	8.3a
1/2 ESNS + water	1.83a	6.01a	22.05a	10.1a	8.1a	8.4a
Autumn						
1/2 ESNS	3.11a ^x	12.82a	41.44a	5.5b	7.3a	7.9b
1/2 ESNS + water	2.63a	13.02a	38.40a	5.9a	7.5a	8.8a

^{z, y, x} See Table 1.

Seedling growth

The data on nutrient stress 10, 20, and 30 days of treatment of hydroponically - grown tomato seedlings reveal that in Exp. 1 and 2, the stress had no significant effects on plant height, stem diameter, number of expanded leaves nor relative chlorophyll content (Tables 1 and 2). In the spring and autumn trials, nutrient stress did not significantly influence the shoot dry weight at three sampling dates (Table 3). Nutrient stress significantly increased the percentage of shoot dry weight 10 days after treatment in both trials and 30 days after treatment in the autumn trial. Among three stages, in the spring trial the highest percentage of shoot dry weight was observed 10 days after treatment, whereas, in the autumn trial this was found 30 days after treatment. Under both spring and autumn conditions, dry weight of the split roots immersed in tap water had significantly decreased compared with that cultured in 1/2 strength ESNS except 10 days after treatment in the spring trial (Table 4). A significantly high dry weight was accumulated by roots in the split roots which were cultured in 1/2 strength ESNS in Exp. 1 and 2. As the seedlings grew, the percentage root dry weight increased gradually, especially in the autumn trial.

Major cation contents

In both spring and autumn trials, nutrient stress significantly reduced potassium contents in leaves at three growing stages (Table 5). Among three sampling dates, in the spring trial, the leaf K content increased gradually as seedlings grew; whereas, in the autumn trial the highest leaf K content was found 20 days after treatment was begun.

Nutrient stress significantly reduced stem K contents 10 and 30 days after treatment, but not at 20 days. Among three growth stages in the autumn trial, the stem K content declined as the seedlings grew, but not in the spring trial.

Root K contents were significantly high in the spring and autumn in the non-split root control; they were significantly low in the split roots immersed in tap water. In the spring trial root K contents remained constant; whereas, in the autumn trial root K contents tended to increase, peaking 20 days after treatment and then declined.

In both spring and autumn trials, nutrient stress did not affect significantly the leaf and stem Ca contents at three stages (Table 6). Among three stages, no obvious changes in leaf and stem Ca contents were found in both trials. In roots, however, 10 and 20 days after treatment significantly high values of Ca contents were found in

Table 4. Effects of nutrient stress on the root dry weight and its dry weight percentage at different stages of hydroponically – grown tomato seedlings.

Treatment	Sampled part ^v	Root dry weight (g)			Percentage of root dry weight (%)		
		10d ^z	20d	30d	10d	20d	30d
Spring							
1/2 ESNS ^y	N	0.51a ^x	1.64a	4.52a	6.2b	6.0b	7.1c
1/2 ESNS + water	Total	0.48a	1.55a	4.57a			
	N	0.33+ ^u	1.09+	3.44+	7.4a	7.3a	8.2a
	W	0.15	0.46	1.13	6.0b	6.3b	7.5b
Autumn							
1/2 ESNS	N	0.40a ^x	1.56a	6.08a	5.4b	6.0b	6.2b
1/2 ESNS + water	Total	0.35a	1.56a	5.81a			
	N	0.28+ ^u	1.23+	3.91+	5.9a	6.8a	8.0a
	W	0.07	0.33	1.90	5.1c	6.3ab	6.7b

^{z,y,x} See Table 1.^v For the treatment of 1/2 ESNS + water, there are two root samples, one of which is from nutrient solution (N), the other from tap water (W).^u Symbol “+” represents significant difference by Duncan’s new multiple range test at 5% level between root samples from nutrient solution (N) and from tap water (W).**Table 5.** Effects of nutrient stress on the potassium contents (mg · g⁻¹DW) in the leaves, stems and roots at different stages of hydroponically – grown tomato seedlings.

Treatment	Sampled part ^v	Leaf			Stem			Root		
		10d ^z	20d	30d	10d	20d	30d	10d	20d	30d
Spring										
1/2 ESNS ^y	N	45.7a ^x	59.5a	67.6a	107.1a	96.3a	92.1a	69.8a	69.3a	70.7a
1/2 ESNS + water	N	37.8a	50.4b	60.6b	86.9b	93.8a	83.6b	58.6b	61.1b	64.0b
	W							39.5c	40.7c	38.0c
Autumn										
1/2 ESNS	N	64.9a ^x	70.8a	59.5a	161.3a	112.1a	77.8a	65.9a	75.5a	71.6a
1/2 ESNS + water	N	60.0b	64.2b	46.8b	143.9b	105.7a	61.2b	57.8b	64.4b	38.1b
	W							40.8c	47.8c	28.1c

^{z,y,x} See Table 1.^v See Table 4.**Table 6.** Effects of nutrient stress on the calcium contents (mg · g⁻¹ DW) in the leaves, stems and roots at different stages of hydroponically – grown tomato seedlings.

Treatment	Sampled part ^v	Leaf			Stem			Root		
		10d ^z	20d	30d	10d	20d	30d	10d	20d	30d
Spring										
1/2 ESNS ^y	N	25.8a ^x	24.4a	26.0a	13.9a	13.0a	11.9a	6.7b	6.8b	6.3a
1/2 ESNS + water	N	26.3a	24.9a	26.9a	12.0a	12.9a	12.6a	10.5a	8.8a	6.3a
	W							4.4c	4.2c	4.3b
Autumn										
1/2 ESNS	N	18.1a ^x	18.4a	22.8a	10.3a	10.3a	11.4a	16.5b	9.3b	10.6a
1/2 ESNS + water	N	20.2a	19.5a	21.1a	11.8a	11.9a	11.0a	23.3a	11.0a	10.5a
	W							4.0c	5.3c	6.8b

^{z,y,x} See Table 1.^v See Table 4.

the split roots which were cultured in 1/2 strength ESNS, and significantly low values were found in the split roots in tap water. In the spring trial among three stages no obvious changes in root Ca contents were observed in the non-split roots cultured in 1/2 strength ESNS and in the split roots immersed in tap water. In the split roots cultured in 1/2 strength ESNS, however, the highest root Ca content was observed 10 days after treatment; it decreased gradually as seedlings grew. In the autumn trial among three stages, for both non-split and split roots which were cultured in 1/2 strength ESNS, the highest root Ca content was found 10 days after treatment. However, for the split roots immersed in tap water, as seedlings grew, root Ca content increased gradually.

In both spring and autumn trials, on the whole, the leaf and stem Mg contents of the stressed seedlings were higher than those of the non-stressed seedlings (Table 7). In leaves, nutrient stress significantly increased Mg contents 20 days after treatment in both spring and autumn trials and 10 days after treatment in the autumn trial. Among three stages, leaf Mg contents did not change dramatically.

In stems, nutrient stress significantly increased Mg contents 20 and 30 days after treatment in the spring trial, and 10 and 20 days after treatment in the autumn trial. Among three stages, the highest stem Mg content occurred 10 days after treatment. It declined as seedlings grew.

In roots, significantly high Mg contents were found in the split roots immersed in tap water at three stages in both spring and autumn trials. In general, even if the roots were cultured at the same concentration of the nutrient solution, i.e., 1/2 strength ESNS, the magnesium content of the split roots tended to be higher than that of the intact ones. In the spring trial, among three stages for split and control roots which were cultured in 1/2 strength ESNS, the highest Mg content was observed 10 days after treatment. However, for the split roots

immersed in tap water, Mg content increased gradually as seedlings grew. In the autumn trial, among three stages, for both split and non-split roots cultured in 1/2 strength ESNS, root Mg content reached the highest value 30 days after treatment. For the split roots immersed in tap water, root Mg content peaked 20 days after treatment, then decreased.

EC values and water absorption

Nutrient stress significantly decreased the EC value of 1/2 strength ESNS in which the split roots were cultured (Table 8); it significantly increased the total amount of water absorbed.

Discussion

Our data showed that nutrient stress did not significantly inhibit shoot growth compared with the non-stressed control (Tables 1, 2 and 3). Under nutrient stress, only half of the split root system was cultured in the nutrient solution but to meet the nutrient demand for shoot growth, the mineral uptake rate by this part of roots exceeded that of the control. Cogliatti and Clarkson (1983) reported that when the root system of potato plants was split into two parts, one of which was cultured in nutrient solution containing P, and the other cultured without P, P uptake by the split roots receiving P was 3 to 4-fold greater than that of the intact roots. This phenomenon may be attributed to the compensatory function of split roots under different stress conditions (Ruter and Ingram, 1990; Ozawa et al., 1989). Under nutrient stress, the percentage of root dry weight of the split roots cultured in 1/2 strength ESNS was greater than that of the control roots (Table 4), indicating that the pattern of water absorption and assimilate accumulation of the split roots cultured in 1/2 strength ESNS is different from that of the control roots.

Ten and 20 days after treatment, Ca contents in the split roots cultured in 1/2 strength ESNS were significantly higher than those in the control roots, then

Table 7. Effects of nutrient stress on the magnesium contents ($\text{mg} \cdot \text{g}^{-1} \text{DW}$) in the leaves, stems and roots at different stages of hydroponically-grown tomato seedlings.

Treatment	Sampled part ^v	Leaf			Stem			Root		
		10d ^z	20d	30d	10d	20d	30d	10d	20d	30d
Spring										
1/2 ESNS ^y	N	9.2a ^x	8.2b	9.9a	7.4a	5.6b	5.6b	7.1c	6.6b	7.0c
1/2 ESNS + water	N	9.5a	10.4a	10.8a	8.3a	7.5a	6.2a	9.5b	7.9b	8.5b
	W							11.1a	14.8a	14.9a
Autumn										
1/2 ESNS	N	8.5b ^x	7.3b	8.8a	6.0b	5.2b	5.0a	6.4b	7.1b	8.1b
1/2 ESNS + water	N	9.7a	8.8a	8.9a	7.6a	6.9a	5.2a	7.7b	7.8b	8.2b
	W							11.3a	13.4a	12.9a

^{z,y,x} See Table 1.

^v See Table 4.

Table 8. Influences of nutrient stress on the EC values of nutrient solution and tap water and on water absorption of hydroponically - grown tomato seedlings in 1998 spring cultivation[†].

Treatment	EC value (ds · m ⁻¹)	Amount of water absorbed (liter · plant ⁻¹ · week ⁻¹)	
		Mean of sector	Mean of treatment
1/2 ESNS ^y	1.39a ^x	3.38	3.38b
1/2 ESNS +	1.18b	2.33	3.88a
water	0.34c	1.55	

^{y, x} See Table 1.[†] Nutrient solution was renewed weekly. At the end of the fourth week, EC values were measured with a portable EC meter (ES-12, KITZ Corporation, Japan), and amount of water absorbed during the fourth week was measured by slowly adding water into the Wagner pots until reaching the original level of nutrient solution/tap water with a water volume meter (LD5, STEC Inc., Japan).

declined 30 days after treatment (Table 6). The elevation of Ca content might initiate the transduction of nutrient stress signal because Ca²⁺ is regarded as an important intracellular secondary messenger (Poovaiah and Reddy, 1993). Various studies have provided strong evidence implicating the regulation of various cell functions by cytosolic Ca²⁺ concentration. Our data indicate that Ca²⁺ may be a messenger in transducing external stimuli in plants.

Twenty days after treatment, nutrient stress significantly increased Mg contents in leaves and stems (Table 7). While split roots immersed in tap water were subjected to a severe nutrient stress, they significantly increased root Mg content at three stages (Table 7). Many enzymes, e.g., succinate dehydrogenase, H⁺-pyrophosphatase, and H⁺-ATPase (Casolo et al., 1998), require Mg²⁺ for activity as they require Mg-ATP as substrate. Hence, we postulate that the increased Mg contents in roots, leaves, and stems are related to the increased activity of some enzymes.

Nutrient stress significantly reduced K contents in leaves, stems, and roots (Table 5). Ilan et al. (1995) reported that an increase of external and cytosolic Ca²⁺ concentration inhibited inward K channels in plasma membrane and resulted in the reduction of K uptake. In addition, there are interference and competition with K uptake by other major cations under stress conditions (Gadallah, 1996; Okubo and Utsunomiya, 1996). These factors might result in the reduction of K content in tomato seedlings under nutrient stress.

Based on the above discussion, it is reasonable to conclude that in the present split-root hydroponic system, tomato plants suffered from a nutrient stress which induced changes in mineral contents of the plants. K contents in leaves and roots decreased significantly at three stages while Ca contents in leaves and stems were unaffected. But a significantly high Ca content was found in the split roots cultured in 1/2 strength ESNS 10 and 20 days after treatment. Mg contents in leaves and stems increased 20 days after treatment; a significantly high Mg content was found in the split roots immersed in tap water.

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根分け法による養分ストレスが異なる生長期における水耕トマト苗の生長と主要カチオン含有率に及ぼす影響

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摘 要

根分け法による養分ストレス条件で、異なる生長期における水耕トマト (*Lycopersicon esculentum* Mill. 'ハウス桃太郎') 苗の生長と主要カチオン (K, Ca および Mg) 含有率を、1998年の春作と秋作で調査した。トマト苗の根を二つに分け、一つは園試処方 of 1/2 単位濃度で水耕し、もう一つは水道水に浸漬した。これにより、養分ストレスをトマト苗に与えた。対照区として、トマト苗を園試処方 of 1/2 単位濃度で水耕した。養分ストレスはトマト苗の生長には影響を与えなかった。養分ストレスは、園試処方 of 1/2 単位濃度で水耕した根の乾物率と、処理後 10 日の地上部乾物率を、有意に増加させ

た。水に浸漬した根の生体重と乾物重は、有意に低かった。養分ストレスは葉と根の K 含有率を低下させ、処理後 20 日を除いた時期には茎の K 含有率も低下させた。養分ストレスは、処理後 10 日と 20 日には園試処方 of 1/2 単位濃度で水耕した根の Ca 含有率を増加させた。水に浸漬した根では有意に高い Mg 含有率がみられた。養分ストレスは葉と茎の Mg 含有率も増加させた。養分ストレスは園試処方 of 1/2 単位濃度の培養液の EC 値を著しく低減させ、トマト苗の水吸収量を有意に増加させた。