Comparative Analysis of Root System Morphology in Tomato Rootstocks

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Additional index words. *Lycopersicum esculentum*, **WinRHIZO, grafted, specific root length, average root diameter, total root length**

Summary. At its most basic, grafting is the replacement of one root system with another containing more desirable traits. Grafting of tomato (*Solanum lycopersicum*) onto disease-resistant rootstocks is an increasingly popular alternative for managing economically damaging soilborne diseases. Although certain rootstocks have demonstrated ancillary benefits in the form of improved tolerance to edaphic abiotic stress, the mechanisms behind the enhanced stress tolerance are not well understood. Specific traits within root system morphology (RSM), in both field crops and vegetables, can improve growth in conditions under abiotic stress. A greenhouse study was conducted to compare the RSM of 17 commercially available tomato rootstocks and one commercial field cultivar (Florida-47). Plants were grown in containers filled with a mixture of clay-based soil conditioner and pool filter sand (2:1 v/v) and harvested at 2, 3, or 4 weeks after emergence. At harvest, roots were cleaned, scanned, and analyzed with an image analysis system. Data collected included total root length (TRL), average root diameter, specific root length (SRL), and relative diameter class. The main effect of cultivar was significant ($P \leq 0.05$) for all response variables and the main effect of harvest date was only significant ($P \leq 0.01$) for TRL. 'RST-106' rootstock had the longest TRL, whereas 'Beaufort' had the shortest. 'BHN-1088' had the thickest average root diameter, which was 32% thicker than the thinnest, observed in 'Beaufort'. SRL in 'Beaufort' was 60% larger than 'BHN-1088'. This study demonstrated that gross differences exist in RSM of tomato rootstocks and that, when grown in a solid porous medium, these differences can be determined using an image analysis system.

The efficacy of herbaceous grafts relies on the replacement of a scion root system with that of a rootstock with known disease resistance. The use of disease-resistant rootstocks in grafted tomato production has proven efficacious in managing numerous economically significant soilborne diseases (Kubota et al., 2008; Kunwar et al., 2015; Lee and Oda, 2002; Louws et al., 2010). In addition, certain rootstocks can improve tolerance to abiotic stress such as cold soils, salinity, drought, and flooding (Albacete et al., 2015; Colla et al., 2006; Djidonou et al., 2013; Estañ et al., 2005; He et al., 2009; Venema et al., 2008; Yetisir et al., 2006). These additional benefits afforded by certain rootstocks can allow a grower to custom tailor the scion–rootstock combination to their local production environment and disease pressure.

Tolerance to edaphic stress has been linked to RSM. Increased TRL has been attributed to improving nutrient uptake, especially phosphorus (P), when availability is low (Hill et al., 2006; Lambers et al., 2006). In drought conditions, increased TRL, particularly in the deeper soil profile, can improve water acquisition (Comas et al., 2013; Ho et al., 2005; Lopes and Reynolds, 2010; Schenk and Jackson, 2005; Wasson et al., 2012). A smaller root diameter may also aid water uptake in dryer conditions by reducing hydraulic resistance (Huang and Eissenstat, 2000; Passioura, 1988; Rieger and Litvin, 1999; Sharp et al., 1988; Steudle and Peterson, 1998). A reduction in root diameter has also been observed in response to low P concentrations (Hill et al., 2006; Zobel et al., 2007) and salinity (Lovelli et al., 2012).

SRL, defined as a proportion of TRL to root dry matter, is a metric used to describe the ratio of the morphological benefit to metabolic cost in root system development (Eissenstat, 1992). An increase in SRL, in relation to a reduction of root diameter, has been observed as a response to low P (Christy and Moorby, 1975; Hill et al., 2006; Lambers et al., 2006; Schroeder and Janos, 2005), drought (Huang and Eissenstat, 2000), and salinity (Lovelli et al., 2012).

Though both intrinsic RSM and the changes observed in response to abiotic stress and reduced resources have been well studied, limited research has been conducted to compare tomato root systems. Differences by cultivar have been observed in the RSM of processing tomato (Portas and Dordio, 1979; Zobel, 1975). For tomato rootstock root systems, one hydroponic study comparing two commercial rootstocks ('Beaufort' and 'Heman') indicated differences in root density but not of average root diameter (Oztekin et al., 2009). The physical aspects of solid substrates can greatly affect root systems grown in soil compared with those in hydroponics (Chapman et al., 2012). The spatial heterogeneity of nutrient and water content within solid substrates affects both root morphology and architecture (Desnos, 2008; Forde and Lorenzo, 2001; Lopez-Bucio et al., 2003). Hydroponic systems are designed to optimize growth by supplying roots with homogenous root zone resources. Consequently, translation of results from hydroponic

Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
29.5735	fl oz	mL	0.0338
3.7854	gal	L	0.2642
2.54	inch(es)	cm	0.3937
25.4	inch(es)	mm	0.0394
0.0896	inch(es)/oz	$cm \cdot g^{-1}$	11.1612
6.4516	$inch^2$	cm^2	0.1550
1	ppm	$mg \cdot L^{-1}$	1
(°F – 32) ÷ 1.8	°F	°C	(°C × 1.8) + 32

This material is based on work that is supported by the National Institute of Food and Agriculture, U.S Department of Agriculture, under award number 2011-01397.

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doi: 10.21273/HORTTECH03654-17

studies, especially solution-based systems, to plants grown in the field or solid substrate should be done so with caution. To date, no research has been conducted comparing commercial tomato rootstock RSM in substrate-grown plants.

The goal of this study was to assess tomato rootstock RSM and development in solid substrates. This information may help characterize rootstocks for their potential increase in abiotic stress tolerance observed and aid in screening and/or breeding for stress tolerance in tomato rootstocks. The specific objectives of this study were to 1) compare RSM of 17 commercially available rootstocks and one commonly used tomato cultivar grown in a porous, solid substrate, at the seedling stage and 2) determine how RSM in these cultivars changes over time.

Materials and methods

This experiment was conducted in the Marye Anne Fox Science Teaching Laboratory Greenhouses on North Carolina State University Campus, Raleigh, NC, between 15 Oct. 2015 and 21 Nov. 2015. The second trial of the study was conducted between 23 Nov. 2015 and 3 Jan. 2016. Seventeen commercially available tomato rootstocks and one common determinate tomato cultivar (Florida 47; Seminis Vegetable Seeds, St. Louis, MO) were used (Table 1).

Three seeds of each cultivar were planted 2 mm deep in 2.8-L black polyethylene pots with dimensions of 6 inches top diameter × 7 inches height × 5 inches bottom diameter (Poly-Tainer #1; Hummert International, Earth City, MO). On emergence, seedlings were thinned to one plant per pot. Pots were lined with woven 20 × 20 mesh of 0.02-cm-diameter thread [about 0.016-cm^2 opening size (Clear Advantage Charcoal Fiber Glass Insect Screen; New York Wire, Hanover, PA)] and filled with a 2:1 (v/v) mixture of clay-based soil conditioner (Turface MVP; Profile Products, Buffalo Grove, IL) and sand (#20 Pool Filter Sand; Aquabrite®, Pleasanton, CA). This mixture was chosen as it provides a rooting medium more similar to that of the field while still allowing for easy separation and cleaning of the medium from roots (Manavalan et al., 2010). The mesh liner was used to prevent the medium from falling through the large drainage holes in the container as well as to aid in root harvest.

Plants were destructively harvested based on chronological age at 2, 3, or 4 weeks after emergence, which corresponded to the appearance of the first set of true leaves, the full expansion of the first two true leaves and the appearance of the second set of true leaves, and the full expansion of the second set of true leaves, respectively. This resulted in 54 unique treatments (18 cultivars × 3 harvest dates). The experiment followed a randomized complete block design with four blocks each containing all 54 unique treatments. Each block was arranged north to south on a greenhouse bench to take into account potential variation due to sunlight gradients. Since rootstocks differed in date to emergence, the date of emergence from the soil was noted and harvest date was calculated accordingly. Greenhouse temperatures during the day were maintained at 26.7 ± 4 °C and 18.3 ± 3 °C at night. Watering occurred every 3 d with fertilizing applied via irrigation [200 $mg \cdot L^{-1}$ concentration of 20N–4.4P–16.6K (Peters Professional; JR Peters, Allentown, PA)] once per week.

Table 1. List of seed companies, their locations, and tomato cultivars used in this experiment.

Company	City, state	Cultivar
Sakata	Morgan Hill, CA	FTM2492
Rijjk Zwaan	Salinas, CA	Emperador
		Kaiser
		Shield RZ
DP Seeds	Yuma, AZ	RST-04-106-T
		RST-04-105-T
De Ruiter	St. Louis, MO	Shincheong gang
		Cheong gang
		Beaufort
		Multifort
BHN Seed	Immokalee, FL	BHN 1087
		BHN 1088
American Takii	Salinas, CA	Armada
		B.B.
		Camel
		TD-1
		TD-2
Seminis Vegetable Seeds	St. Louis, MO	Florida 47

At the time of harvest, plants and medium were pulled from the container with the aid of the mesh liner. Plants were gently excavated by hand from the medium. Once the root system was freed, the medium was thoroughly examined for any roots that may have broken off during the processing. All roots were water-rinsed of any remaining medium and placed in a container filled with 10 mL of 0.5 $g \cdot L^{-1}$ neutral red stain (Sigma Aldrich, St. Louis, MO) and stored for 24 h at 6.7 °C. The staining process was imposed to improve contrast and overall resolution during the scanning process as recommended by Bouma et al. (2000).

Following the staining process, roots were thoroughly rinsed for 3 min in deionized (DI) water before scanning. A 30 × 42-cm acrylic tray was placed on top of a flatbed scanner (Expression® 10000XL; Epson America, Long Beach, CA) and filled with about 2 cm of DI water. Roots were placed in the tray and gently positioned with no overlapping roots to allow for more uniform scanning. Scans were done in gray scale at 800 dots per inch to increase resolution of fine roots. Each image was analyzed using an image analysis system (WinRHIZO™ version 2012b; Regent Instruments, Quebec, QC, Canada). Image analysis data collected included TRL, average root diameter, and length per diameter class (diameter classes were in increments of 0.5 mm). Length per diameter class data were normalized by dividing by

Table 2. Results from a two-way ANOVA for a fully factorial arrangement (18 tomato cultivars × 3 harvest dates) of treatments for the combined experimental replicates.

Effect	df	Total root length	Avg diam[z]	Diam class 1[y]	Diam class 2[x]	Specific root length[w]
Cultivar	17	*	***	***	***	***
Harvest date	2	**	NS	NS	NS	NS
Interaction	34	NS	NS	NS	NS	NS

ANOVA = analysis of variance.

[z] Average root diameter for an entire root system.

[y] Relative diameter class calculated as total length of roots of diameter <0.5 mm as a proportion of total root length; 1 mm = 0.0394 inch.

[x] Relative diameter class calculated as total length of roots of diameter between 0.5 and 1.0 mm as a proportion of total root length.

[w] Total root length divided by root dry weight.

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

TRL, resulting in a ratio of diameter class root length per TRL (relative diameter class). Following scanning, roots were dried at 70 °C for 24 h (Thelco 130D Laboratory Oven; Precision Scientific Co., Winchester, VA) and dry weights of the total root system were taken (AE100 Digital Analytical Scale; Mettler-Toledo, Columbus, OH). Dry weight measurements were used to calculate SRL (TRL/total dry weight).

Data from both trials were combined and analyzed with PROC MIXED in SAS (version 9.4; SAS Institute, Cary, NC). The model used to analyze all data contained cultivar, harvest date, and their interaction as fixed effects with trial and block nested in trial as random effects. Residual plots were studied for any violation of the assumptions in analysis of variance such as heterogeneity and outliers. No outliers were observed; however, residual plots for TRL and relative diameter class showed strong heteroscedasticity. An arcsin and log conversion was imposed on relative diameter class and TRL data, respectively, to homogenize residual variance. For reporting, data were back-transformed. When appropriate, Tukey's honest significant difference was used as a post hoc mean separation test.

Results

Initial analysis was conducted by experiment; however, there was no significant experiment × treatment interaction. Consequently, data from both experiments were combined. No significant cultivar × harvest date interactions were found for any of the response variables (Table 2). The main effect of harvest date was significant only for TRL ($P \leq 0.01$), which increased with harvest date (Fig. 1). TRL was also significantly affected ($P \leq 0.05$) by rootstock. 'RST-106' had the longest TRL with 'Beaufort' having the shortest (Fig. 2). These two rootstocks represent the extremes in TRL with the remaining 16 cultivars falling in between as intermediate in their TRL. For all other response variables, the main effect of cultivar was significant at $P \leq 0.001$ (Table 2). Average root diameter was narrowest in 'Beaufort' (0.28 mm), 'TD-1' (0.29 mm), 'Kaiser' (0.29 mm), 'RST-105' (0.29 mm), 'Multifort' (0.30 mm), and 'Emperador' (0.30 mm) (Fig. 3). 'BHN-1088' had the widest average root diameter (0.37 mm) compared with all other cultivars. All remaining 11 cultivars were intermediate in the average root diameter compared with those found in the extremes.

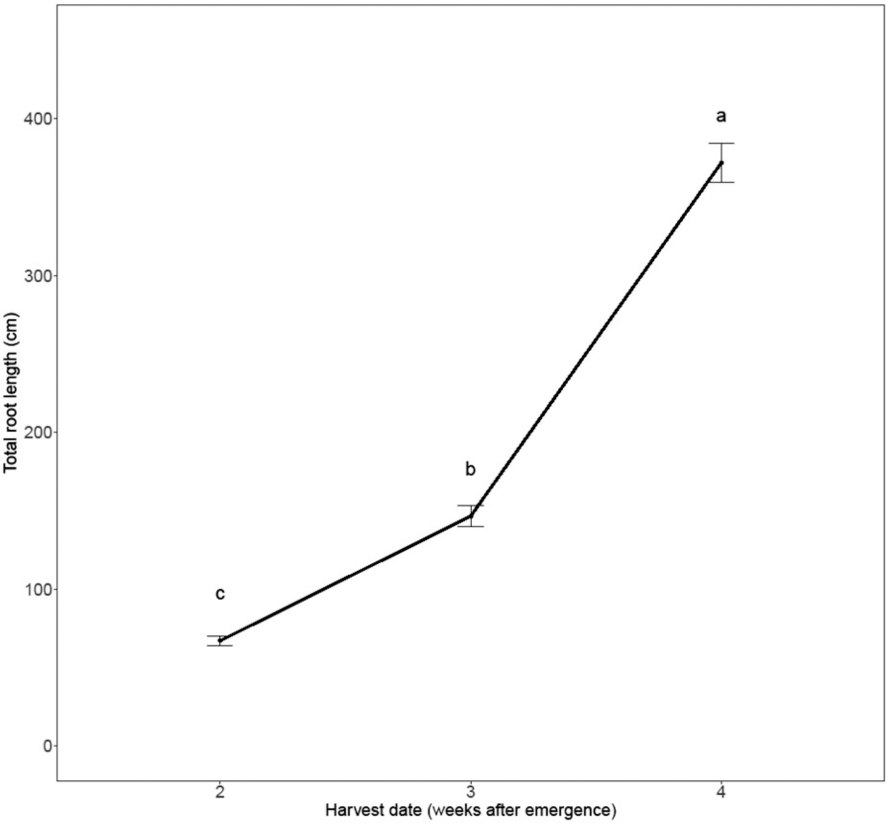

Fig. 1. Main effect of harvest in tomato rootstock total root length ± SE over time. Means with common letters are not different (Tukey's honest significant difference at α = 0.05) and represent the mean of four replicate samples, 18 cultivars, and two repeated experiments (n = 144 data points for each mean); 1 cm = 0.3937 inch.

SRL was largest in 'Beaufort' (40,124 $cm \cdot g^{-1}$), 'TD-1' (40,056 $cm \cdot g^{-1}$), 'Multifort' (39,333 $cm \cdot g^{-1}$), and 'Kaiser' (37,967 $cm \cdot g^{-1}$) (Fig. 4). BHN-1088 (25,147 $cm \cdot g^{-1}$), Camel (26,147 $cm \cdot g^{-1}$), and Cheong Gang (26,996 $cm \cdot g^{-1}$) were among the cultivars that had the lowest SRL.

The majority of the TRL for all cultivars fell into diameter class 1 [≤0.5 mm (Table 3)]. Within this relative diameter class, 'Beaufort' had the highest proportion (0.9625)

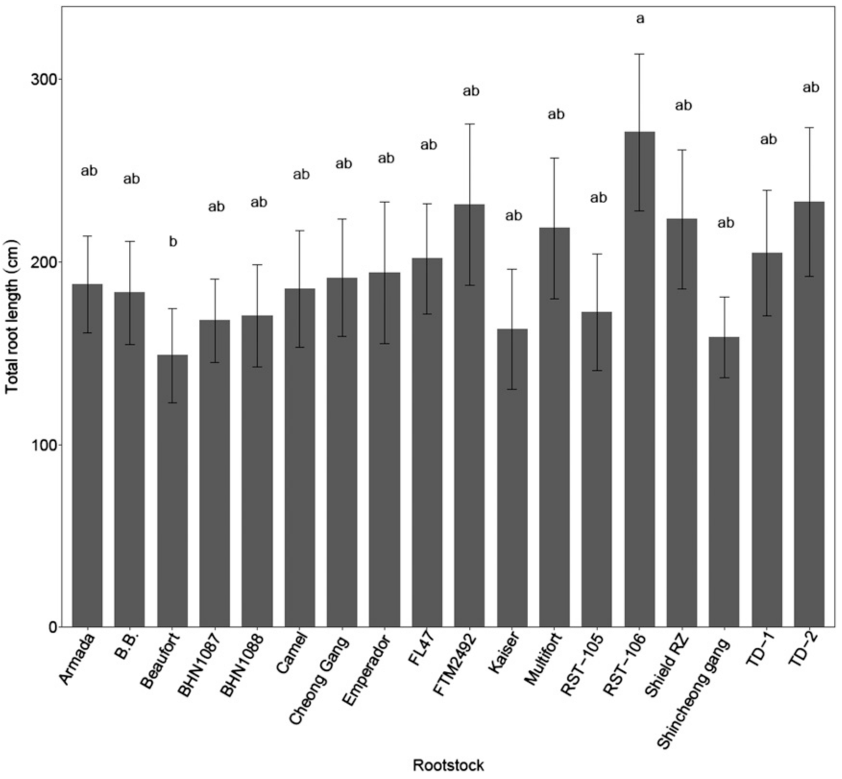

Fig. 2. Main effect of tomato rootstock on total root length ± SE. Means with common letters are not different (Tukey's honest significant difference at α = 0.05) and represent the average of four replicate samples, three harvest dates, and two repeated experiments (n = 24 data points for each mean); 1 cm = 0.3937 inch.

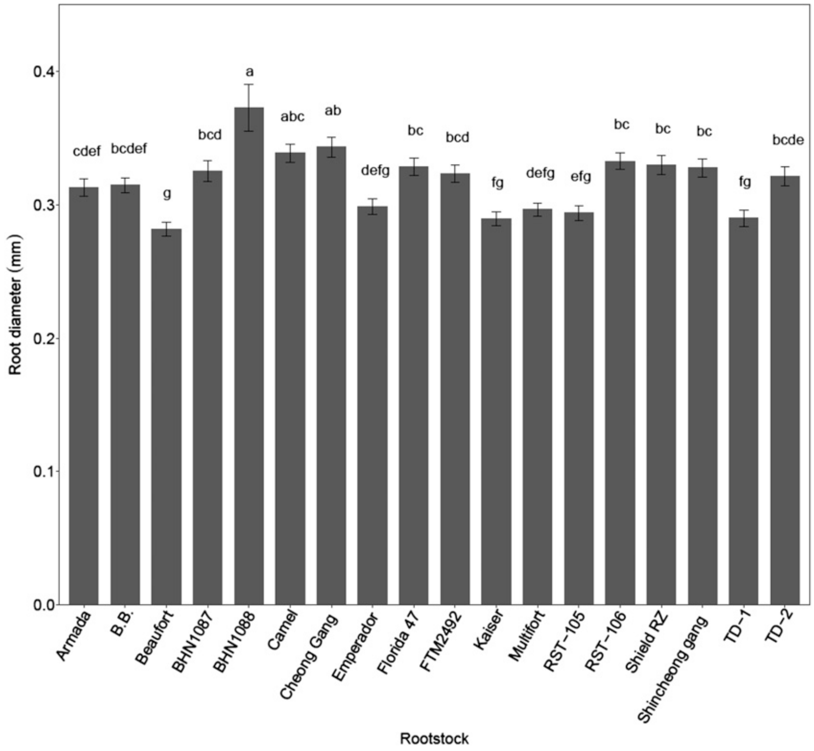

Fig. 3. Main effect of tomato rootstock on average root diameter ± SE by cultivar. Means with common letters are not different (Tukey's honest significant difference at α = 0.05) and represent the average of four replicate samples, three harvest dates, and two repeated experiments (n = 24 data points for each mean); 1 mm = 0.0394 inch.

followed by 'RST-105' (0.9524), 'Multifort' (0.9488), and 'Kaiser' (0.9458). 'BHN-1088' had the lowest proportion (0.8661) of TRL in this relative diameter class. Results for relative diameter class 2 (0.5 to 1.0 mm) were opposite to that of relative diameter class 1—'BHN-1088' had the highest proportion (0.1266) of TRL with 'Beaufort' (0.0361), 'RST-105' (0.0459), 'Multifort' (0.0498), and 'Kaiser' (0.0514) having the lowest proportion in relative diameter class 2.

Discussion

This research indicates that quantifiable morphological differences exist between tomato rootstock root systems. Some of the differences observed may explain the improved stress tolerance provided by specific tomato rootstocks. When used as rootstocks for grafted 'Florida 47', both 'Multifort' and 'Beaufort' improved water use efficiency compared with nongrafted 'Florida 47' (Djidonou et al., 2013). The authors suggested that this improved water use efficiency may be due to root morphology. Our results with these cultivars show that SRL in Beaufort and Multifort were 41% and 38% greater than Florida 47, respectively (Fig. 4). This difference is due to both 'Beaufort' and 'Multifort' having significantly thinner average root diameters than 'Florida 47'. High SRL has been shown to increase hydraulic conductance in a trifoliate orange (*Poncirus trifoliata*) rootstock (Huang and Eissenstat, 2000). The authors attributed this increased hydraulic conductivity to the increased radial conductivity of the thinner rooted trifoliate orange. The increase in water use efficiency observed by Djidonou et al. (2013) may be due to the increased radial conductivity of thinner rooted 'Beaufort' and 'Multifort' rootstocks, allowing for increased hydraulic conductivity even with reduced irrigation.

At low levels of salinity (22 mM sodium chloride), grafting of the tomato cultivar Belladona onto Beaufort improved yields compared with nongrafted controls (Savvas et al., 2011). Reduction of average root diameter and consequent increase in SRL has been demonstrated to be a response in tomato to increasing levels of salinity (Lovelli et al., 2012).

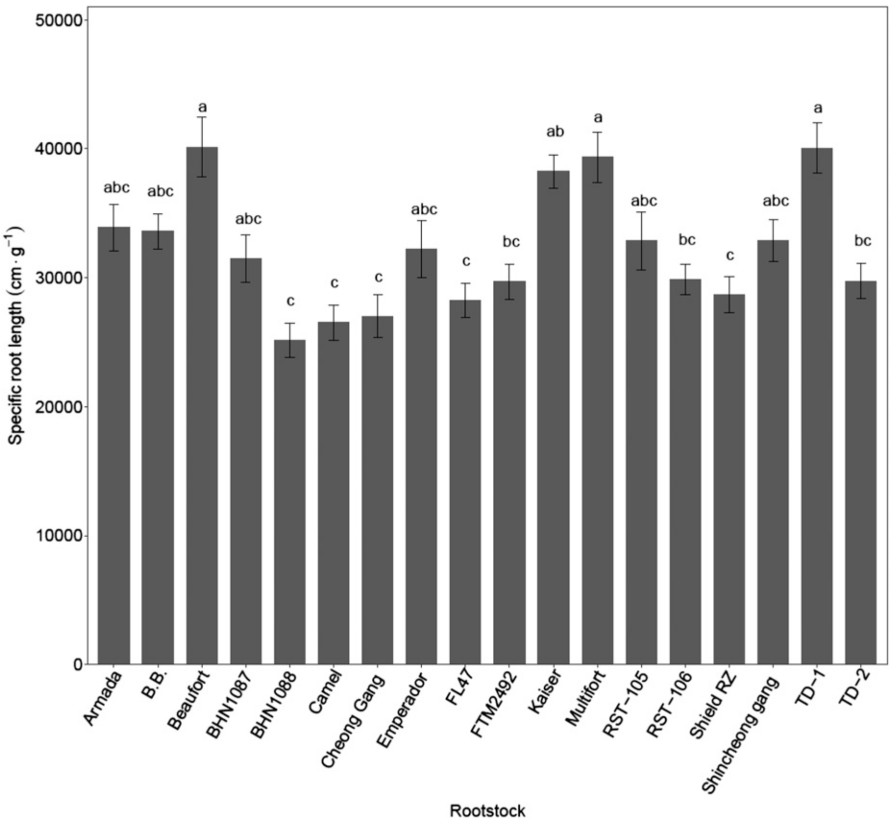

Fig. 4. Main effect of tomato rootstock on specific root length ± SE by cultivar. Means with common letters are not different (Tukey's honest significant difference at $\alpha = 0.05$) and represent the average of four replicate samples, three harvest dates, and two repeated experiments (n = 24 data points for each mean); 1 cm·g^{-1} = 11.1612 inches/oz.

Table 3. Main effect of tomato rootstock on proportional distribution of root diameter class.

Cultivar	Diam class 1 (<0.5 mm)[z]	Diam class 2 (0.5 to 1.0 mm)
Beaufort	0.9625 a	0.0361 e
RST-105	0.9524 ab	0.0459 de
Multifort	0.9488 abc	0.0498 cde
Kaiser	0.9458 abcd	0.0514 cde
Emperador	0.9417 abcd	0.0564 bcde
TD-1	0.9416 abcd	0.0568 bcde
B.B.	0.9148 bcde	0.0814 abcd
Shincheong Gang	0.9142 bcde	0.0817 abcd
Armada	0.9124 bcde	0.0844 abcd
BHN1087	0.9108 bcde	0.0853 abcd
TD-2	0.9043 cde	0.0901 abcd
FTM2492	0.9026 de	0.0924 abc
RST-106	0.8957 e	0.0994 ab
Florida 47	0.8925 e	0.1032 a
Shield RZ	0.8869 e	0.1076 a
Camel	0.8794 e	0.1133 a
Cheong Gang	0.8719 e	0.1206 a
BHN1088	0.8661 e	0.1266 a

[z] Means followed by the same letter within a diameter class are not significantly different (Tukey's honest significant difference at $\alpha = 0.05$) and represent the average of four replicate samples, three harvest dates, and two repeated experiments (n = 24 data points for each mean); 1 mm = 0.0394 inch.

The authors hypothesized that the increased SRL allows for osmotic adjustment without a large investment in carbon partitioned to the roots. Moreover, they concluded that the increase in SRL may be an adaption to increase overall root surface area, aiding in water, and nutrient uptake in saline conditions. The improved yield in tomato with 'Beaufort' rootstock at low levels of salinity also coincided with an increase in leaf calcium concentrations (Savvas et al., 2011). A separate study found that 'Beaufort' rootstock improved uptake of nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur compared with self-grafted controls (Leonardi and Giuffrida, 2006). The high SRL observed in 'Beaufort' in our study may aid in improving nutrient uptake due to increased surface area.

Recent evidence suggests that shoot-derived compounds can alter root morphology (Spiegelman et al., 2015). Our study analyzed root systems from nongrafted plants. Future work is warranted to determine if scion selection alters rootstock RSM. Furthermore, studies are needed to elucidate whether the morphological traits observed in this study are static or plastic with changing edaphic environments and what the relative role RSM plays compared with physiological mechanisms in stress.

Tomato rootstocks offer growers the ability to manage soilborne diseases and ameliorate the negative effects of edaphic stress. This study demonstrates that RSM in tomato rootstocks differs by cultivar and remains similar over time, other than TRL. These differences may help explain the improved growth and production associated with specific rootstocks and could be used to classify cultivars for their suitability for use in specific growing conditions. Furthermore, the use of a porous medium coupled with scanning and analysis using an image analysis system allows for a detailed analysis of roots for plants grown in a solid substrate.

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