Comparative Analysis of Root System Morphology in Tomato Rootstocks

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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 ≤ 0.05) for all response variables and the main effect of harvest date was only significant (P ≤ 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.

ADVANCED INDEX WORDS. Lycopersicum esculentum, WinRHIZO, grafted, specific root length, average root diameter, total root length

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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-cm² 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; Aquabrute®, 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 at 200 mg L⁻¹ concentration of 20N–4.4P–16.6K (Peters Professional; JR Peters, Allentown, PA) once per week.

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 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® 1000XL; 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 1. List of seed companies, their locations, and tomato cultivars used in this experiment.

| Company          | City, state | Cultivar          |
|------------------|-------------|-------------------|
| Sakata           | Morgan Hill, CA | FTM2492          |
| De Ruiter        | St. Louis, MO | Kaiser            |
| De Ruiter        | St. Louis, MO | Shield RZ         |
| BHN Seed         | Immokalee, FL | RST-04-105-T      |
| BHN Seed         | Immokalee, FL | RST-04-106-T      |
| American Takii   | Salinas, CA  | Shincheong gang   |
| American Takii   | Salinas, CA  | Cheong gang       |
| American Takii   | Salinas, CA  | Beaufort          |
| American Takii   | Salinas, CA  | Multifort         |
| BHN Seed         | Immokalee, FL | BHN 1087          |
| BHN Seed         | Immokalee, FL | BHN 1088          |
| Teon Seeds       | St. Louis, MO | Florida 47        |
| Teon Seeds       | St. Louis, MO | Florida 47        |
| Multifort        |              |                   |
| Kaiser           |              |                   |
| Multifort        |              |                   |
| BHN 1087         |              |                   |
| BHN 1088         |              |                   |
| Florida 47       |              |                   |
| Florida 47       |              |                   |

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 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

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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 ≤ 0.01), which increased with harvest date (Fig. 1). TRL was also significantly affected (P ≤ 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 ≤ 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.

SRL was largest in ‘Beaufort’ (40,124 cm g⁻¹), ‘TD-1’ (40,056 cm g⁻¹), ‘Multifort’ (39,333 cm g⁻¹), and ‘Kaiser’ (37,967 cm g⁻¹) (Fig. 4). BHN-1088 (25,147 cm g⁻¹), Camel (26,147 cm g⁻¹), and Cheong Gang (26,996 cm 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).
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 conductivity 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).
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.

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

| Cultivar            | Diam class 1 (<0.5 mm) | 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                     |

*Means followed by the same letter within a diameter class are not significantly 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.

| 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 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·g⁻¹ = 11.1612 inches/oz. |
|---|---|

| Rootstock | 50000 | 40000 | 30000 | 20000 | 10000 |
|-----------|-------|-------|-------|-------|-------|
| Armada    | a     | a     | a     | a     | a     |
| B.B.      | abc   | abc   | abc   | abc   | abc   |
| BHN1087   | abc   | abc   | abc   | abc   | abc   |
| Camellia  | ab    | ab    | ab    | ab    | ab    |
| Emperador | ab    | ab    | ab    | ab    | ab    |
| FTM2492   | a     | a     | a     | a     | a     |
| Florida 47| a     | a     | a     | a     | a     |
| Kaiser    | a     | a     | a     | a     | a     |
| Multifort | a     | a     | a     | a     | a     |
| RST-106   | a     | a     | a     | a     | a     |
| RST-105   | a     | a     | a     | a     | a     |
| RST-108   | a     | a     | a     | a     | a     |
| Shincheong Gang | a | a | a | a | a |
| T-1       | a     | a     | a     | a     | a     |
| T-2       | a     | a     | a     | a     | a     |

*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·g⁻¹ = 11.1612 inches/oz.

### Literature cited

Albacete, A., C. Andujar, I. Dodd, F. Giuffrida, I. Hichri, S. Lutts, A. Thompson, and M. Asins. 2015. Rootstock-mediated variation in tomato vegetative growth under drought, salinity and soil impedance stresses. Acta Hort. 1086:141–146.

Bouma, T.J., K.L. Nielsen, and B.A.S. Koutstaal. 2000. Sample preparation and scanning protocol for computerised analysis of root length and diameter. Plant Soil 218:185–196.

Chapman, N., A.J. Miller, K. Lindsey, and W.R. Whalley. 2012. Roots, water, and...
nutrient acquisition: Let’s get physical. Trends Plant Sci. 17:701–710.

Christy, E.K. and J. Moorby. 1975. Physiological responses of semi-arid grasses I. The influence of phosphorus supply on growth and phosphorus absorption. Austral. J. Agr. Res. 26:423–436.

Colla, G., Y. Roupahel, M. Cardarelli, and E. Rea. 2006. Effect of salinity on yield, fruit quality, leaf gas exchange, and mineral composition of grafted watermelon plants. HortScience 41:622–627.

Comas, L.H., S.R. Becker, V.C. Von Mark, P.F. Byrne, and D.A. Dierig. 2013. Root comas, L.H., S.R. Becker, V.C. Von Mark, P.F. Byrne, and D.A. Dierig. 2013. Root traits contributing to plant productivity under drought. Front. Plant Sci. 4:442.

Desnos, T. 2008. Root branching responses to phosphate and nitrate. Curr. Opin. Plant Biol. 11:82–87.

Djidonou, D., X. Zhao, E.H. Simonne, K.E. Koch, and J.E. Erickson. 2013. Yield, water-, and nitrogen-use efficiency in fieldgrown, grafted tomatoes. HortScience 48:485–492.

Eissenstat, D.M. 1992. Costs and benefits of constructing roots of small diameter. J. Plant Nutr. 15:763–782.

Estañ, M.T., M.M. Martinez-Rodriguez, F. Perez-Allocca, T.J. Flowers, and M.C. Bolarin. 2005. Grafting raises the salt tolerance of tomato through limiting the transport of sodium and chloride to the shoot. J. Exp. Bot. 56:703–712.

Forde, B. and H. Lorenzo. 2001. The nutritional control of root development. Plant Soil 232:51–68.

He, Y., Z. Zhu, J. Yang, X. Ni, and B. Zhu. 2009. Grafting increases the salt tolerance of tomato by improvement of photosynthesis and enhancement of antioxidant enzymes activity. Environ. Expt. Bot. 66:270–278.

Hill, J.O., R.J. Simpson, A.D. Moore, and D.F. Chapman. 2006. Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. Plant Soil 286:7–19.

Ho, M.D., J.C. Rosas, K.M. Brown, and J.P. Lynch. 2005. Root architectural tradeoffs for water and phosphorus acquisition. Funct. Plant Biol. 32:737–748.

Huang, B. and D.M. Eissenstat. 2000. Linking hydraulic conductivity to anatomy in plants that vary in specific root length. J. Amer. Soc. Hort. Sci. 125:260–264.

Kubota, G., M.A. McClure, N. Kokalis-Burelle, M.G. Bausher, and E.N. Rosskopf. 2008. 1240 Vegetable grafting: History, use, and current technology status in North America. HortScience 43:1664–1669.

Kunwar, S., M.L. Paret, S.M. Olsen, L. Ritchie, J.R. Rich, J. Freeman, and T. McAvoy. 2015. Grafting using rootstocks with resistance to Ralstonia solanacearum against Meloidogyne incognita in tomato production. Plant Dis. 99:119–124.

Lambers, H., M.W. Shane, M.D. Cramer, S.J. Pearse, and E.J. Veneklaas. 2006. Root structure and functioning for efficient acquisition of phosphorus: Matching morphological and physiological traits. Ann. Bot. (Lond.) 98:693–713.

Lee, J. and M. Oda. 2002. Grafting of herbaceous vegetable and ornamental crops. Hort. Rev. 28:61–124.

Leonardi, C. and F. Giuffrida. 2006. Variation of plant growth and macronutrient uptake in grafted tomatoes and eggplants on three different rootstocks. Eur. J. Hort. Sci. 71:97–101.

Lopes, M.S. and M.P. Reynolds. 2010. Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. Funct. Plant Biol. 37:147–156.

Lopez-Bucio, J., A. Cruz-Ramirez, and L. Herrera-Estrella. 2003. The role of nutrient availability in regulating root architecture. Curr. Opin. Plant Biol. 6:280–287.

Louws, F.J., C.L. Rivard, and C. Kubota. 2010. Grafting fruiting vegetables to manage soilborne pathogens, foliar pathogens, arthropods and weeds. Sci. Hort. 127:127–146.

Lovelli, S., M. Perniola, T. Di Tommaso, R. Bochichio, and M. Amato. 2012. Specific root length and diameter of hydroponically-grown tomato plants under salinity. J. Agron. 11:101–106.

Manavalan, L.P., S.K. Guttikonda, V.T. Nguyen, J.G. Shannon, and H.T. Nguyen. 2010. Evaluation of diverse soybean germplasm for root growth and architecture. Plant Soil 330:503–514.

Oztekin, G.B., F. Giuffrida, Y. Tuzel, and C. Leonardi. 2012. Grafting tomato (Solanum lycopersicum) onto the rootstock of a high-altitude accession of Solanum habrochaites improves suboptimal-temperature tolerance. Environ. Expt. Bot. 63:359–367.

Passioura, J.B. 1988. Water transport in and to roots. Annu. Rev. Plant Physiol. 49:223–251.

Portas, C.A.M. and J.J.F.B. Dordio. 1979. Tomato root systems. A short review with reference on tomatoes for processing. Acta Hort. 100:113–124.

Rieger, M. and P. Litvin. 1999. Root system hydraulic conductivity in species with contrasting root anatomy. J. Expt. Bot. 50:201–209.

Savvas, D., A. Savva, G. Ntatsi, A. Ropokis, I. Karapanos, A. Krumbein, and C. Olympios. 2011. Effects of three commercial rootstocks on mineral nutrition, fruit yield, and quality of salinized tomato. J. Plant Nutr. Soil Sci. 174:154–162.

Schenk, H.J. and R.B. Jackson. 2005. Mapping the global distribution of deep roots in relation to climate and soil characteristics. Geoderma 126:129–140.

Schnerr, M.S. and D.P. Janos. 2005. Plant growth, phosphorus nutrition, and root morphological responses to arbuscular mycorrhizas, phosphorus fertilization, and intraspecific density. Mycorrhiza 15:203–216.

Sharp, R.E., W.K. Silk, and T.C. Hsiao. 1988. Growth of the maize primary root at low water potentials I. Spatial distribution of expansive growth. Plant Physiol. 87:50–57.

Spiegelman, Z., H. Byung-Kook, Z. Zhao-liang, T. Toal, S. Brady, Y. Zheng, Z. Fei, W. J. Lucas, and S. Wolf. 2015. A tomato phloem-mobile protein regulates the shoot-to-root ratio by mediating the auxin response in distant organs. Plant J. 83:853–863.

Steudle, E. and C.A. Peterson. 1998. How does water get through roots? J. Expt. Bot. 49:775–788.

Venema, J.H., B.E. Dijk, J.M. Bax, P.R. van Hasselt, and J.T.M. Elzenga. 2008. Grafting tomato (Solanum lycopersicum) onto the rootstock of a high-altitude accession of Solanum habrochaites improves suboptimal-temperature tolerance. Environ. Expt. Bot. 63:359–367.

Wasson, A.P., R.A. Richards, R. Chatrath, S.C. Misra, S.V. Prasad, and G.J. Rebetzke. 2012. Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. J. Expt. Bot. 63:3485–3498.

Yetisir, H., M.E. Çalışkan, S. Soylu, and M. Sakar. 2006. Some physiological and growth responses of watermelon [Citrullus lanatus (thunb.) Matsum. & Nakai] grafted onto Lagenaria siceraria to flooding. Environ. Expt. Bot. 58:1–8.

Zobel, R.W. 1975. Genetics of root development, p. 261–275. In: J.G. Torrey and D.F. Clarkson (eds.). The development and function of roots. Academic Press, London, UK.

Zobel, R.W., V.C. Baligar, and T.B. Kinraid. 2007. Fine root diameters can change in response to changes in nutrient concentrations. Plant Soil 297:243–254.