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Linking Hydraulic Conductivity to Anatomy in Plants that Vary in Specific Root Length

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ABSTRACT. **In *Citrus* L. sp., specific root length of whole root systems has been correlated positively with root hydraulic conductivity, but there is little mechanistic understanding of the causes for this association. The hydraulic conductivity of individual roots in relation to root anatomical characteristics in seedlings of three citrus rootstocks [sour orange (SO) (*Citrus aurantium* L.), trifoliate orange (TO) (*Poncirus trifoliate* (L.) Raf.), and Swingle citrumelo (SC) (*C. paradisi* Macf. x *P. trifoliata*)] that vary widely in specific root length (SRL) was measured. Among fibrous roots, first-order and second-order laterals were examined. Relative differences among rootstocks in the overall hydraulic conductivity (L_P) and radial conductivity (L_R) for individual 1-month-old and 6-month-old second- and first-order roots generally were consistent with hydraulic conductivity determined previously for entire root systems. There were no significant differences in axial conductance per unit pressure (K_h) in either first- or second-order roots among the rootstocks. This was consistent with the similarity in number and diameter of xylem vessels. One-month-old second-order roots had no suberized exodermis but varied in cortical radius. Six-month-old second-order roots of TO, however, had more nonsuberized cells (passage cells) in the exodermis than roots of SC and SO, although the cortical radius of SC and SO roots were not different. Compared to 6-month-old second-order roots, 1-month-old second-order roots had much higher L_P and L_R but lower K_h. Differences in overall root hydraulic conductivity among the citrus rootstocks were mainly related to structural differences in the radial pathway for water movement, suggesting that radial hydraulic conductivity was the primary determining factor of water uptake in citrus rootstocks.**

Water flow from the soil to the root xylem is determined by hydraulic conductivities of three components of the root–soil pathway: the soil, the root–soil interface, and the root (reviewed by Passioura, 1988). Under soil drying conditions, the soil rather than the root is a major limiting factor for water uptake (Nobel and Cui, 1992). Rieger and Duemmel (1992) reported that hydraulic conductivities of entire root systems were similar in drying soil in several *Prunus* L. sp., even though they differed in drought resistance. When soil moisture is readily available, however, root hydraulic conductivity can represent two-thirds of the limitations on water movement within the soil–plant system (Nobel and Cui, 1992; Passioura, 1988). Therefore, differences in root hydraulic conductivity in wet soils could result in differences in water transport to shoots that could influence leaf water status, and in turn, plant growth and physiological responses (Passioura, 1988).

Hydraulic conductivity of whole root systems has been reported to be correlated positively with shoot growth rate in several citrus rootstocks (Syvertsen, 1981). Relatively vigorous rootstocks [e.g., rough lemon (*Citrus jambhiri*) and Carrizo citrange] tend to have higher conductivities, stomatal conductance, and transpiration rates than the less vigorous rootstocks [Cleopatra mandarin (*Citrus reshni* Hort. ex Tan) and sour orange (*C. aurantiacum*)] (Syvertsen and Graham, 1985). Root hydraulic conductivity for entire root systems also is higher in citrus rootstock species that have higher specific root lengths (SRLs) (Eissenstat, 1992, 1997; Graham and Syvertsen, 1985). High hydraulic conductivity of roots with large SRL may be attributed to a greater radial hydraulic conductivity of individual roots with smaller diameters. Roots of small diameter may have a shorter radial path for water movement from the root surface into the xylem than large-diameter roots. Variation in root hydraulic conductivity among different citrus rootstocks could also be linked to specific root anatomical features such as suberization and thickness of the secondary wall of the exodermis and endodermis (Huang and Nobel, 1994). Rieger and Litvin (1999) have measured root-system hydraulic conductivity of whole, intact plants, and root anatomical features of two woody and three herbaceous species. They found that root-system hydraulic conductivity is inversely related to root cortical thickness and the presence of a suberized exodermis.

The objectives of this study were to 1) determine overall hydraulic conductivity, radial and axial hydraulic conductivity of different types and ages of fibrous roots for three citrus rootstocks [sour orange (SO), trifoliate orange (TO) (*Poncirus trifoliate* (L.) Raf.), and Swingle citrumelo (SC) (*C. paradisi* Macf. x *P. trifoliata*)] that vary in SRL and root anatomical features; and 2) determine anatomical features that are correlated with radial and axial hydraulic conductivity of individual roots in the three rootstocks. The rootstocks, SO and SC, have similar SRLs and seedling root-system hydraulic conductivity, whereas TO has a much higher SRL and root system hydraulic conductivity (Eissenstat 1997).

Materials and Methods

PLANT MATERIALS AND GROWTH CONDITIONS. Rootstocks were grown in sand in 2-L pots for 6 months after seedling emergence in a growth chamber with average day/night temperatures of 30/25 °C, a photosynthetic photon flux (PPF) of 600 $\mu mol\cdot m^{-2}\cdot s^{-1}$ at

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the canopy level, and a 12 h photoperiod provided by flourescent lamps and incandescent bulbs. Plants were fertilized weekly with full-strength Hoagland's solution (Hoagland and Arnon, 1950) and watered every other day with deionized water.

Hydraulic conductivity measurements. Overall root hydraulic conductivity (L_p), radial conductivity (L_R), and axial conductance per unit pressure gradient (K_h) were determined on three types of individual fibrous roots in each rootstock: a) distal 5-cm root segments from 1-month-old second-order lateral roots (roots bearing first-order lateral roots) of various diameters; b) basal 5-cm root segments from 6-month-old second-order lateral roots of similar diameters; and c) entire first-order lateral roots (roots having a root tip) of various diameters associated with the 6-month-old second-order roots. Root age was estimated by tagging roots with different color strings when roots were ≈1 cm long. After tagging, roots were returned to their original position in the soil and allowed to grow for 1 to 6 months before the measurements.

Hydraulic conductivities of three types of individual fibrous roots (L_p) as described above were measured with the tension-induced flow technique, in which water flow is induced through excised roots by application of negative pressures (Huang and Nobel, 1992; Nobel and Sanderson, 1984). About 5 mm of the stele at the proximal end of the root was exposed by dissecting away cortical tissue. The exposed stele was trimmed under water and inserted through Tygon tubing (10 mm in length, internal diameter of 1 mm) and into an attached glass capillary (100 mm in length, internal diameter of 0.5 mm) that was half-filled with distilled water. The tubing was gently compressed around the stele using brass and silicone washers inside a compression fitting (Lopez and Nobel, 1991).

For L_P measurements of second-order lateral roots, an entire root or root segment was suspended in aerated 0.1 strength Hoagland's solution (Hoagland and Arnon, 1950). Water flow through the root was induced by applying a partial vacuum, whose pressure was measured with a pressure transducer (Kane-May Ltd., Welwyn Garden City, U.K.) connected to the open end of the capillary tube. To measure L_P of first-order lateral roots attached to second-order lateral roots, the proximal end of the second-order root was inserted into the capillary where a 20 to 40 kPa vacuum pressure was applied, with the entire first-order lateral root submerged in nutrient solution. The flow rate was determined by monitoring the progress of the meniscus in the capillary with a traveling microscope capable of resolving 0.01 mm. When the volumetric flow rate (Q_v, $m^3 \cdot s^{-1}$) became constant at a given pressure (P, MPa), L_P was calculated as follows (Nobel et al., 1990):

$$L_P = (\Delta Q_v/\Delta P)\,(1/A) \qquad [1]$$

where A is the root surface area (m^2).

To measure K_h, the distal end of the segment was recut under distilled water and ≈1 mm at the distal end was immersed in 10 $mol \cdot m^{-3}$ oxalic acid in filtered, degassed, distilled water (to reduce blockage of the vessels; Sperry et al., 1988). After applying a partial vacuum to the capillary tube on the proximal end, Q_v was measured as for L_P and used to calculate K_h:

$$K_h = Q_v/(\Delta P/l) \qquad [2]$$

where l is the length (m) of the root across which ΔP was applied.

After L_P and K_h were determined, L_R ($m^3 \cdot m^{-2} \cdot s^{-1} \cdot MPa^{-1}$), averaged over the root, was calculated by incorporating L_P, K_h, the length, and the radius (r_{root}) of root segments into the model of Landsberg and Fowkes (1978): $L_R = (L_p \alpha\, l\,)/(\tanh \alpha\, l\,)$, where α equals $(2\pi\, r_{root}\, L_R/K_h)^{1/2}$

Morphological and anatomical features. Root diameter of individual roots was measured with a micrometer on a light microscope. Freehand sections were cut with a razor blade at the midlength of the root segments after measurements of L_P, L_R, and K_h. The sections were stained with toluidine blue O for determination of cortical thickness and number and diameter of xylem vessels or with Sudan III and IV for identifying suberization of the exodermis.

Satistical analysis. Data were collected from five plants of each rootstock and analyzed using analysis of variance procedures of the SAS (SAS Institute Inc., Cary, N.C.). Differences among rootstock means were separated least significance difference (LSD) procedures at $P < 0.05$.

Results

For individual first-order lateral roots, both overall hydraulic conductivity (L_p) and radial conductivity (L_R) of TO were signifi-

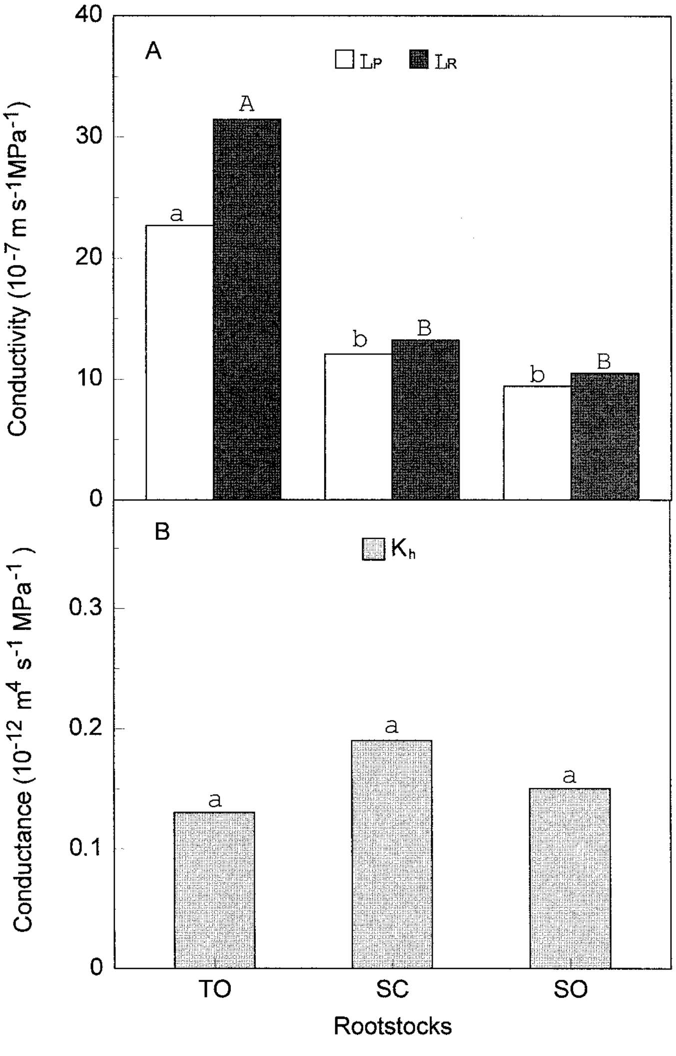

Fig. 1. (**A**) Hydraulic conductivity (L_P)and radial conductivity (L_R), and (**B**) axial conductance per unit pressure gradient (K_h) of first-order lateral roots in three citrus rootstocks, trifoliate orange (TO), Swingle citrumelo (SC), and sour orange (SO). Data were means of five individual roots from each of five plants in each rootstock. Columns marked with the same lowercase or uppercase letters are not significantly different based on an LSD test ($P = 0.05$).

Table 1. Anatomical features of first-order lateral roots of three citrus rootstocks, trifoliate orange (TO), Swingle citrumelo (SC), and sour orange (SO), measured on cross sections at the midlength of individual roots. Data are means of five individual roots from each of five plants in each rootstock.

				Xylem vessels	
Rootstock	Root diam (µm)	Cortical thickness (µm)	Nonsuberized exodermal cells (%)	No.	Diam (µm)
TO	344 b^z	84 b	12.4 a	9 ab	4.6 a
SC	411 a	115 a	7.4 b	11 a	6.0 a
SO	445 a	120 a	8.6 b	7 b	5.2 a

^{z}Mean separation within columns by LSD at $P \le 0.05$.

cantly higher than those for SC and SO (Fig. 1A), but axial conductivity (K_h) of the three rootstocks, however, were not significantly different (Fig. 1B). The larger L_P and L_R for TO than SC and SO, was related to the shorter radial pathway and greater percentage of nonsuberized cells (passage cells) in the exodermis in TO (Table 1). First-order lateral roots of TO were significantly thinner than those of SC and SO (Table 1). First-order lateral roots of TO also had a thinner cortical tissue and a significantly higher proportion of nonsuberized cells in the exodermis in roots of TO than those of SC and SO . Axial hydraulic conductance (K_h) was quite similar among rootstocks (Fig 1.), which probably reflects the similarity in xylem vessel diameter (Table 1).

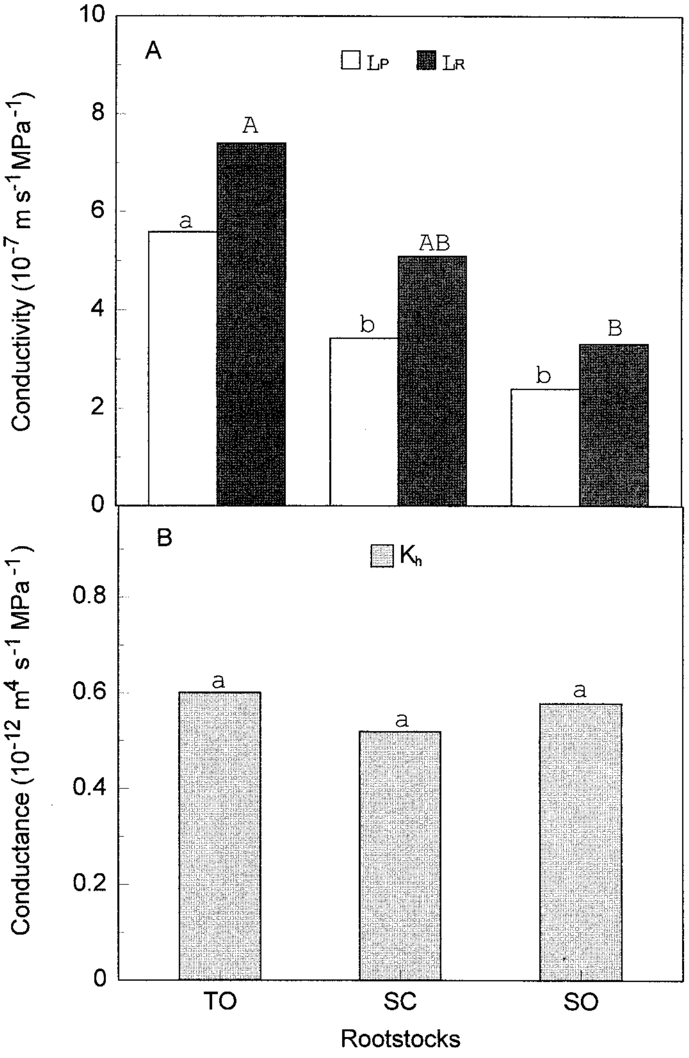

Fig. 2. (**A**) Hydraulic conductivity (L_p), radial conductivity (L_R), and (**B**) axial conductance per unit pressure gradient (K_h) of 1-month-old second-order lateral roots in three citrus rootstocks, trifoliate orange (TO), Swingle citrumelo (SC), sour orange (SO). Data were means of five individual roots from each of five plants in each rootstock. Columns marked with the same lowercase or uppercase letters were not significantly different based on an LSD test ($P = 0.05$).

For 1-month-old second-order lateral roots, L_p values for SC and SO were similar, but both had significantly lower L_P than that of TO (Fig. 2A). L_R was highest for TO, intermediate for SC, and lowest for SO. The rootstock difference in L_R of 1-month-old second-order lateral roots were reflected in the variation in root diameter and cortical radius. Roots were thinnest for TO, intermediate for SC, and thickest for SO (Table 2). TO also had a smaller cortical radius than SC and SO. Similar to first-order roots, K_h of the 1-month-old second-order lateral roots was not significantly different among rootstocks (Fig. 2B). Similarly, there were no differences in number and diameter of xylem vessels between rootstocks (Table 2).

For 6-month-old second-order lateral roots, both L_p and L_R of TO were significantly higher than those for SC and SO (Fig. 3A). Root diameter and cortical radius were not significantly different among rootstocks (Table 3). TO had more passage cells in the exodermis than either SC or SO. These results indicated that the difference in L_p and L_R of 6-month-old second-order lateral roots among the three rootstocks was related mainly to the greater percent of passage cells. Although the diameters of xylem vessels were not different among rootstocks, K_h was highest in TO, intermediate in SO and lowest in SC, which was consistent with the results for the number of xylem vessels (Fig. 3B, Table 3).

For all the three rootstocks, L_p and L_R of 1-month-old second-order lateral roots (Fig. 2A) were significantly larger than those of 6-month-old roots (Fig. 3A). However, K_h of 1-month-old second-order lateral roots (Fig. 2B) was much lower than that of 6-month-old roots (Fig. 3B).

Table 2. Anatomical features of 1-month-old second-order lateral roots of three citrus rootstocks, trifoliate orange (TO), swingle citrumelo (SC), sour orange (SO), measured on cross sections at the midlength of individual roots. Data are means of five individual roots from each of five plants in each rootstock.

			Xylem vessels	
Rootstock	Root diam (µm)	Cortical thickness (µm)	No.	Diam (µm)
TO	620 c^z	227 b	15 a	9.4 a
SC	754 b	301 a	13 a	8.2 a
SO	871 a	348 a	16 a	10.1 a

^{z}Mean separation within columns by LSD at $P \le 0.05$.

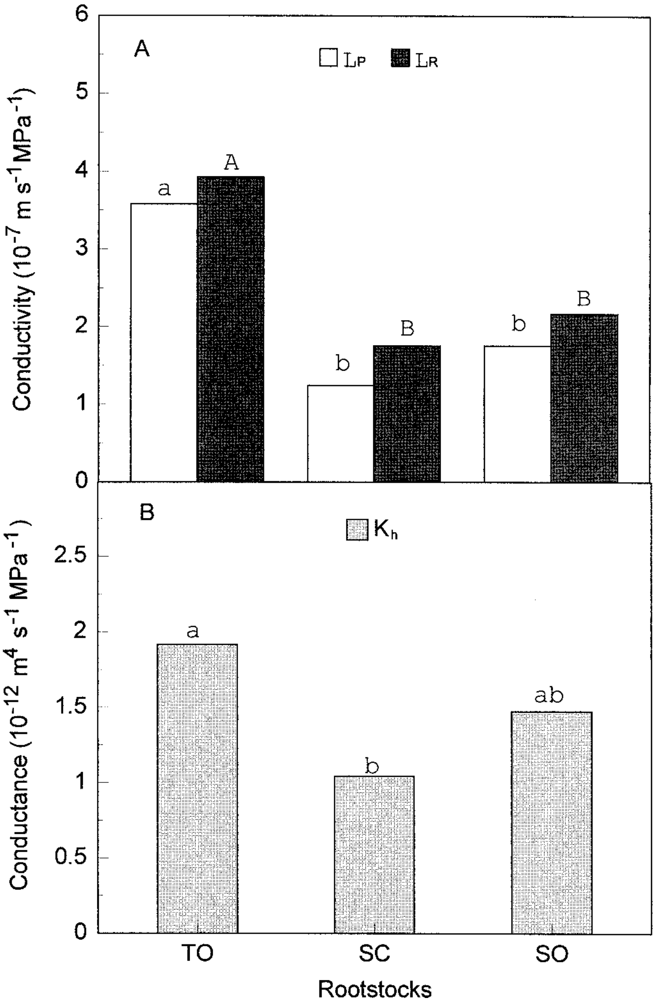

Fig. 3. (**A**) Hydraulic conductivity (L_P) and radial conductivity (L_R), and (**B**) axial conductance per unit pressure gradient (K_h) of 6-month-old second-order lateral roots in three citrus rootstocks, trifoliate orange (TO), Swingle citrumelo (SC), sour orange (SO). Data were means of five individual roots from each of five plants in each rootstock. Columns marked with the same lowercase or uppercase letters were not significantly different based on an LSD test ($P = 0.05$).

Discussion

Root L_p and L_R decreased while K_h increased with root age in all three rootstocks. These results were consistent with observations in other species (Huang and Nobel, 1992, 1993; Jones et al., 1988; North and Nobel, 1991; Radin and Eidenbock, 1984; Sanderson, 1983). Such changes often correspond to developmental changes in suberization of cell layers along the radial pathway and to the maturation of xylem vessels (Drew, 1979, 1987; Huang and Nobel, 1992, 1993; Moreshetet al., 1996). Increases in K_h as roots age in *Agave deserti* Engelm., coincides with increases in the number of xylem vessels that are functional in water uptake and transport, since cross walls of xylem vessels disappear as roots become mature(Huang and Nobel, 1992).

As water from the surrounding soil enters a root, it moves radially through the exodermis and cortical tissues external to the stele before reaching the xylem vessels. Exodermis and cortical tissues can impose considerable resistance to water movement in the radial pathway (Moreshet et al., 1996). The exodermis can become suberized as roots age or under environmental stresses such as drought stress which reduces permeability to water (Huang and Nobel, 1994; Peterson and Lefcourt, 1990; Peterson et al., 1993). Therefore, roots with a large cortical radius and well-suberized exodermis could have a low L_R. Rieger and Litivin (1999)reported that the low hydraulic conductivity of intact root systems is related to thick root cortex and the presence of a suberized exodermis.

Previous research (reviewed by Eissenstat, 1997) of detopped seedlings indicates that SO and SC have quite similar whole-root-system hydraulic conductivity of ≈5 to 7 $\mu g \cdot m^{-1} \cdot s^{-1} \cdot MPa^{-1}$ whereas TO has a hydraulic conductivity 3 to 4 times higher (≈20 $\mu g \cdot m^{-1} \cdot s^{-1} \cdot MPa^{-1}$). Results from hydraulic conductivity of individual roots in this study are consistent with differences in whole-root-system conductivity among rootstocks. All three rootstocks had similar K_h and diameters of xylem vessels. Results of the present study indicated that the primary cause for the differences in L_p was due largely to differences in L_R and only to a minor extent in K_h. The morphological and anatomical characteristics correlated to these differences in hydraulic conductivity are thinner roots with a shorter radial path length (Rieger and Litvin, 1999), thinner outer tangential exodermal walls (Eissenstat and Achor, 1999), and more passage cells in the exodermis (this study).

The relative importance of the two components of L_P, L_R, and K_h, varies with plant species and with the developmental stage of the root (Huang and Nobel, 1994). For both first and second-order lateral roots of citrus rootstocks, changes in L_P were consistent with that in L_R, which indicated that L_R was mainly responsible for changes in L_P in citrus. Radial conductivity is the major limitation for water uptake in cotton (*Gossypium hirsutum* L.) (Taylor and Klepper, 1975) and corn (*Zea mays* L.), except at the root tip (Frensch and Steudle, 1989; Huang and Nobel, 1992). In contrast, K_h has been found to limit water movement in seminal roots of wheat (*Triticum aestivum* L.) (Passioura, 1980), especially at a distance >1 m from the base. These K_h limitations may not be crucial for dicotyledonous crops with secondary xylem vessels (Rendig and Taylor, 1989) but K_h may be important distally in the fully mature xylem (Oosterhuis and Wullschleger, 1987; North and Nobel, 1992).

Table 3. Anatomical features of 6-month-old second-order lateral roots of three citrus rootstocks, trifoliate orange (TO), swingle citrumelo (SC), and sour orange (SO) measured on cross sections at the midlength of individual roots. Data are means of five individual roots from each of five plants in each rootstock.

Rootstock	Root diam (µm)	Cortical thickness (µm)	Nonsuberized exodermal cells (%)	Xylem vessels	
				No.	Diam (µm)
TO	585 a[z]	180 a	9.3 a	35 a	11.2 a
SC	592 a	184 a	4.1 b	28 b	12.0 a
SO	605 a	192 a	3.2 b	33 ab	12.5 a

[z] Mean separation within columns by LSD at $P \leq 0.05$.

In summary, the fineness of individual roots was related positively to radial hydraulic conductivity, supporting previous work on whole root systems. Variations in hydraulic conductivity of individual roots among citrus rootstocks were due mainly to differences in radial hydraulic conductivity. Higher L_p and L_R for citrus rootstocks with higher SRL and smaller root diameter were associated with a less prominent exodermis (thinner secondary walls, greater percentage of passage cells), and a short radial pathway.

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