

Estimation of Root Hydraulic Conductivity on Intact Peach and Citrus Rootstock

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Abstract. Estimates of root hydraulic conductivity (L_p) were obtained on intact peach (*Prunus persica* × *P. davidiana* 'Nemaguard') and sour orange (*Citrus aurantium* L.) rootstock over a broad range of transpiration rates. Within a species, L_p was lower when estimated using the Ohm's law analog than the reciprocal of the slope of the linear regression between transpiration (E) and stem xylem water potential (Ψ). Non-zero y-intercepts in linear regressions of Ψ vs. E resulted in the lack of agreement between L_p estimates. Removal of the root system caused xylem Ψ to rapidly approach zero in both species when $E \approx 0$, suggesting that factors responsible for nonzero y intercepts resided within roots. L_p was 2.2 and 3.5 times lower for sour orange than peach when calculated by the Ohm's law and regression methods, respectively.

Quantification of root hydraulic conductivity (L_p) in fruit tree species is important in developing models of soil water extraction, canopy water relations, growth, and yield of orchard crops. Since L_p is typically less than hydraulic conductivity of other plant organs (Kramer, 1983) and moist soil (Blizzard and Boyer, 1980), this parameter largely determines the water potential (Ψ) of the leaves at a given transpiration rate (E). For example, fruit tree species with high resistance to water transport (low L_p) often experience lower Ψ than species with low resistance in the same environment, despite higher E for the latter (Larsen et al., 1989). Furthermore, L_p has been positively correlated with vegetative vigor of citrus (Syvertsen, 1981) and apple rootstock (Olien and Lakso, 1984).

Estimates of L_p may be obtained from intact plants provided that the water potential gradient across the roots ($\Delta\Psi$) and the steady state rate of water uptake can be measured. Use of intact, transpiring plants allows avoidance of problems associated with the commonly used pressure-chamber method, such as flow through unnatural paths (Koide, 1985) and lack of root-shoot communication (Markhart and Smit, 1990). Also, the transpiration-dependent behavior of L_p can be investigated using intact plants (Camacho-B

et al., 1974; Stoker and Weatherley, 1971). The objectives of this study were to develop a simple method for estimating L_p on intact plants as an alternative to using detopped root systems and to determine whether L_p is transpiration dependent in peach and citrus rootstocks, as reported for herbaceous species (Bunce, 1978; Camacho-B et al., 1974; Stoker and Weatherley, 1971; Tinklin and Weatherley, 1966).

Plant material. Terminal shoots of 'Nemaguard' peach, ≈ 30 cm long, were taken from mature trees in Aug. 1988 and rooted as described by Couvillon and Erez (1980). Following chilling treatment (4 C), cuttings were placed in a greenhouse with $\approx 90\%$ transmission of solar radiation and held at 20-35C day/20-25C night. Twenty uniform plants were grown hydroponically, and the remainder were maintained in commercial soilless medium (Fafard, Springfield, Mass.). The nutrient solution was that described by Jones (1985), except that twice the concentration of Fe (as Fe-EDDHA chelate) was used, since 'Nemaguard' is susceptible to Fe deficiency. Plants were grown hydroponically to facilitate root length and weight determinations, because it was impossible to recover all of the roots from medium with soil-rooted plants due to their highly fibrous structure.

Seed of sour orange was sown in vermiculite in Nov. 1988. After three to four leaves appeared on each seedling, they were transplanted to 12.5-cm-diameter pots in soilless medium and grown in the same greenhouse as the peach plants. Plants were fertilized weekly with a 300-mg N/liter solution from 15 N-15 P₂O₅-15K₂O soluble fertilizer. It was possible to make accurate determinations of root length and weight of soil-rooted citrus plants due to the coarse nature of their roots

and ease with which they separated from the medium. Five plants were root-pruned and grown hydroponically for 2 months to determine the effect of root growth conditions on L_p .

Plants of both species were trained to have one or two lateral shoot(s) with at least 10 fully expanded leaves within 10 cm of the root system. Leaves on this shoot were used to estimate Ψ at the point of attachment of the lateral shoot to the main stem (Powell, 1974).

Experimental procedure. Plants of either species were transferred from the greenhouse to the laboratory at sunrise. The main portion of the canopy was enclosed inside a 42-liter acrylic chamber, while the roots and lateral shoot(s) at the base of the trunk were left outside the chamber. Roots of hydroponically grown plants were suspended in aerated tap water with ≈ 10 mmol Ga³ at room temperature (22-25 C). Soil-rooted plants were thoroughly leached before measurements to minimize the contribution of solutes to soil Ψ . Pots of soil-rooted plants were placed in a container with ≈ 5 mm of standing water so that the soil water content would remain constant as roots extracted water. The Ψ at the outer root surface was considered zero for hydroponically grown and soil-rooted plants.

All fully expanded leaves on lateral shoots outside the chamber were enclosed in parafilm and aluminum foil to stop E. Expanding leaves were removed to prevent the possibility of growth-induced reduction of Ψ in the lateral shoot (Boyer, 1968). Wrapped leaves typically had Ψ within ± 0.05 MPa of each other after 15 min of equilibration, regardless of their position on the shoot or attachment to shoot vs. trunk. Water potential was measured with a pressure chamber to the nearest 0.025 MPa (PMS Instruments, Corvallis, Ore.). Measurement of the osmotic potential of sap expressed from petioles of wrapped leaves using C-52 psychrometer (Wescor, Logan, Utah) indicated osmotic potentials between 0.0 and -0.1 MPa in preliminary trials. Since psychrometers were inaccurate in this range, this parameter was ignored in subsequent calculations.

Plants were allowed to equilibrate to chamber conditions for 1 to 2 h before commencement of measurements. Light was provided by a 400-W metal halide lamp, giving a photosynthetic photon flux at the top of the canopy of at least 1020 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$. Air temperature was regulated at $\approx 24\text{C}$ ($\pm 0.2\text{C}$) by forcing air through a finned-pipe heat-exchange coil inside the chamber, through which polyethylene glycol was circulated from a temperature-controlled bath. Leaf temperature was generally 0 to 3C above air temperature, depending on position in the canopy, light intensity, and E. Leaf and air temperatures were measured with 24-gauge (0.5-mm diameter) copper-constantan thermocouples and a CR-7 data logger (Campbell Scientific, Logan, Utah).

Vapor pressure deficit (VPD) was controlled by varying the flow rate of moist air from the chamber through a column of silica

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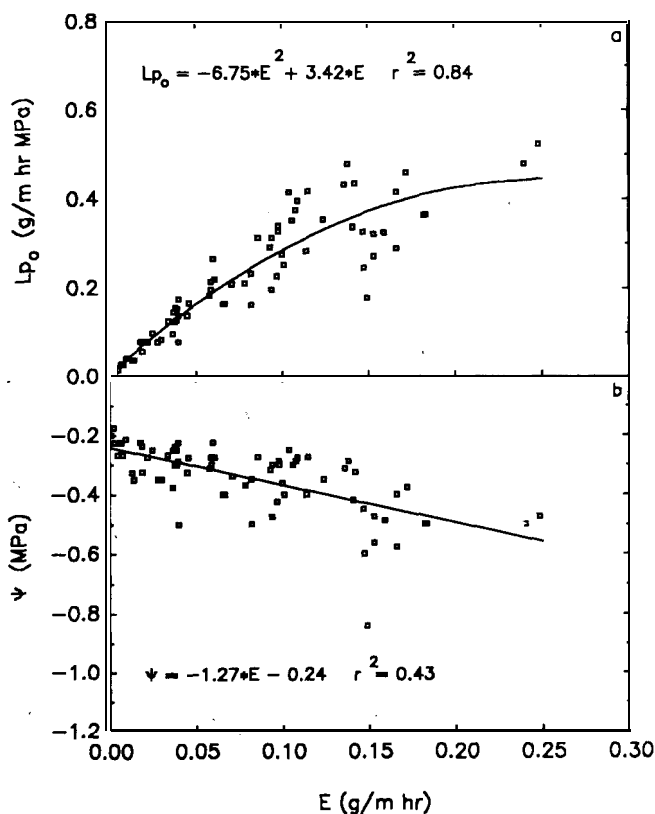


Fig. 1. Relationship between (a) Ohm's law estimates of root hydraulic conductivity (L_{p_0}) and transpiration (E) and (b) "xylem water potential (Ψ) and E for 'Nemaguard' peach. Each point represents a single measurement from one of 10 plants ($n = 73$). All terms included in regression models are significant ($P < 0.05$).

gel desiccant and returning the dry air to the chamber. The airstream reentering the chamber had a VPD of >2.9 kPa. Chamber VPD was maintained within ± 0.03 kPa of the set point, which varied from 0 to 2.1 kPa, depending on the desired level of E . Relative humidity was sensed with an Omega HX-41 capacitance-type humidity probe (Omega Engineering, Stamford, Conn.) and logged continuously with the CR-7 data logger. The humidity probe was calibrated twice during the experimental period using saturated LiCl and NaCl solutions at 20.0C.

The CO_2 concentration was maintained by injecting air with 950 to 1100 μl CO_2 /liter into the chamber at a rate that offset CO_2 uptake by photosynthesis. The CO_2 concentration was generally maintained at 330 ± 10 μl -liter $^{-1}$, but occasionally was lowered to 100 or 200 μl -liter $^{-1}$ or raised to >1000 μl -liter $^{-1}$ to increase or decrease, respectively, leaf conductance and, consequently, E . Air from the chamber was intermittently pumped through a closed loop with a LI-6200 infrared gas analyzer (LI-COR, Lincoln, Neb.) to monitor CO_2 concentration.

Canopy E was measured by cycling air from the chamber through a pre-weighed tube of silica gel desiccant for a given length of time sufficient to collect ≈ 1 g of water, typically 5 to 30 min. The weight of the tube was determined to the nearest 0.01 g, and E was calculated as the weight change of the tube divided by the water collection period. During water collection, air temperature and

relative humidity were maintained at $\pm 0.1C$ and $\pm 1\%$, respectively, by varying the rate of air flow through the desiccant. The displacement of moist air by the dry, CO_2 -enriched air was also considered in the calculation of E by multiplying the flow rate of CO_2 -enriched air by the water vapor density of the air in the chamber.

In initial experiments, similar values of Ψ were obtained under different environmental conditions as long as E was about the same between conditions, suggesting that Ψ and E changed together. For example, reducing CO_2 to ≈ 100 μl -liter $^{-1}$ when plants were shaded increased E to levels obtained with 330 μl -liter $^{-1}$ CO_2 and full light exposure, and Ψ values were about ± 0.1 MPa between these sets of conditions. A range of E and corresponding Ψ values were obtained on 10 plants of each species by altering environmental conditions at random in subsequent experiments. Generally, high VPD (>1.5 kPa), low CO_2 (100 μl -liter $^{-1}$), and high light intensity (> 1000 μmol - s^{-1} - m^{-2}) yielded maximal E ; the opposite conditions yielded low E . Temperature was not varied by more than 2C among different environmental conditions. Steady-state E was assumed if the difference between consecutive measurements at 15- to 30-min intervals was $< 10\%$. This state was attained within 1 h in most cases, but at least 1 h was allowed to pass between an environmental perturbation and the measurement of the new E .

The $\Delta\Psi$ across the roots was given by the

balance pressure of wrapped leaves, since the water surrounding the roots had $\Psi \approx 0$ and the wrapped leaves gave an estimate of Ψ in the xylem just above the root system. Steady-state Ψ was assumed if sequential measurements at a 30-min interval differed by < 0.05 MPa. Similar to E , Ψ generally reached steady-state 1 h after an environmental perturbation.

Estimates of L_p were calculated using two methods: 1) the Ohm's law analog (Elfving et al., 1972), where $L_p = E/\Delta\Psi$ at steady state (L_{p_0}), and 2) the reciprocal of the slope of the linear regression between wrapped leaf Ψ (ordinate) and E (abscissa) (L_p) for each plant. In both methods, E was expressed on a root-length basis, yielding units of grams per meter per hour per megaPascal for L_p . Root length was determined by the line intersect method of Tennant (1975), using a 3×3 -cm grid. Use of the Ohm's law analog yielded multiple L_p values for each plant, from which a mean was calculated, whereas the regression method yielded only one value per plant.

Data were analyzed by t test for differences between methods of L_p estimation within species and also for estimates made by the same method between species. Linear, quadratic, and cubic regression models of Ψ vs. E and L_{p_0} vs. E were tested for each plant individually and all plants of one species collectively to determine the transpiration-dependent behavior of L_p (General Linear Models procedure; SAS Inst., 1985).

Mean values of L_{p_0} were consistently lower than L_p values for peach and sour orange, whether evaluated on an individual plant basis or collectively (Table 1). However, L_{p_0} and L_p values were correlated ($P < 0.05$) within each species. Values of L_{p_0} and L_p were 3.5- and 2.2-fold higher, respectively, for peach than sour orange, indicating a greater capacity for water absorption per unit root length in peach. This difference was not entirely due to root growth conditions, as hydroponically grown sour orange still had lower values of L_{p_0} and L_p than peach (data not shown). Values of L_{p_0} for peach were similar to those reported previously using the pressure-chamber method (Rieger and Scalabrelli, 1990), a result that supports earlier findings that L_{p_0} estimates were similar for 'Nemaguard' whether intact or detopped plants were used (Rieger, 1989). However, L_{p_0} estimates for sour orange were ≈ 6 -fold higher than previously reported for this species using a pressure-chamber method (Syvertsen and Graham, 1985).

Lack of agreement between L_{p_0} and L_p was caused by the invariable occurrence of nonzero y-intercepts in linear regression analyses of Ψ vs. E (Figs. 1b and 2b). Mathematically, a linear or curvilinear relationship between L_{p_0} and E must occur if the linear relationship between Ψ and E does not pass through the origin, since L_{p_0} is the ratio E/W . Furthermore, as the absolute value of the y-intercept in plots of Ψ vs. E increases, the curvature of the plot of L_{p_0} vs. E decreases and the range of L_{p_0} values decreases. This relationship is exemplified by

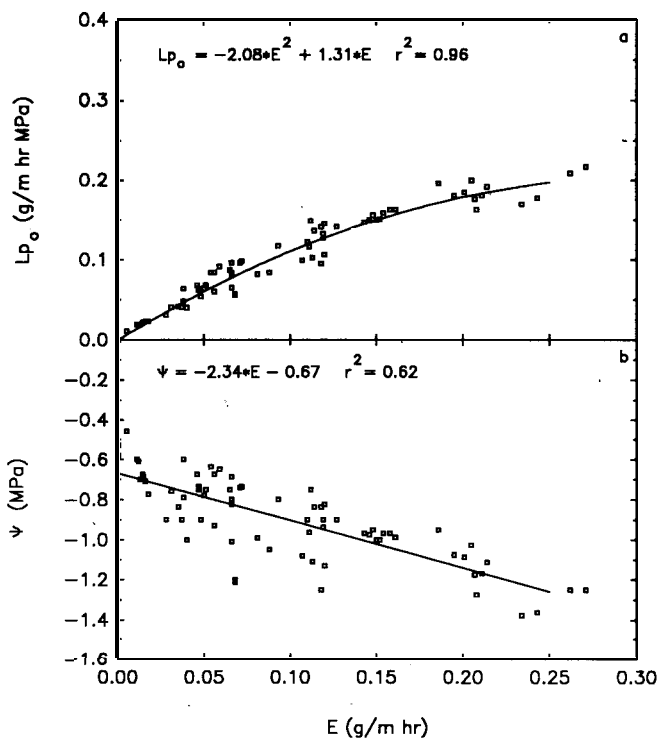


Fig. 2. Relationship between (a) Ohm's law estimates of root hydraulic conductivity (L_{p_o}) and transpiration (E) and (b) xylem water potential (Ψ) and E for sour orange. Each point represents a single measurement from one of 10 plants ($n = 73$). All terms included in regression models are significant ($P < 0.05$).

Table 1. Estimates of root hydraulic conductivity of peach and sour orange plants obtained by the Ohm's law analog (L_{p_o}) or the reciprocal of the slope of the linear regression between xylem water potential and transpiration (L_{p_i}), and correlation (r) between estimates.

Species ^{2,3}	L_{p_o} ($g \cdot MPa^{-1} \cdot h^{-1} \cdot m^{-1}$)		L_{p_i} ($g \cdot MPa^{-1} \cdot h^{-1} \cdot m^{-1}$)		r^4
	Mean	Range	Mean	Range	
Peach	0.22 b	0.01-0.52	0.96 a	0.22-1.64	0.66
Sour orange	0.10 b	0.00-0.22	0.27 a	0.10-0.42	0.91

¹Means followed by same lowercase letter within a species are not significantly different (t test, $P < 0.05$). L_{p_o} and L_{p_i} estimates for peach are significantly higher (t test, $P < 0.05$) than for sour orange. ² $n = 10$ for each species.

³Correlation coefficients significant ($P < 0.05$) for both species.

the greater range of L_{p_o} values (Table 1) and lower magnitude of the y -intercept (Figs. 1 and 2) for peach than sour orange. Thus, L_{p_o} values obtained by the Ohm's law analog are strongly dependent on E due to failure of Ψ to approach 0 when $E \approx 0$.

The y -intercept in linear regressions between Ψ and E has been proposed as representing Ψ of the outer root surface (Newman, 1976). However, root systems of both species were in contact with water with negligible osmotic and/or matric potentials, and even when $E \approx 0$, steady state Ψ was less than -0.25 MPa in peach and less than -0.50 MPa in sour orange. When the root system was severed and the stem placed in water, Ψ increased to 0.0 to -0.05 MPa within 15 to 20 min. Thus, factors that prevented Ψ from reaching 0 when $E \approx 0$ resided within the roots. This result suggests that L_p approached 0 at low E , inhibiting equilibration of xylem Ψ with the surrounding medium. This behavior has been documented previously with mature citrus trees under field conditions (Elfving et al., 1972).

Significant quadratic and cubic regression models for Ψ vs. E data occurred in one and three plants, respectively, of each species. However, in only one case (peach) was there a large improvement in r^2 of the cubic ($r^2 = 0.92$) over the linear model ($r^2 = 0.62$). The occurrence of a curvilinear response of Ψ vs. E was not correlated to any morphological characteristics on the few plants that exhibited these relationships or to the environmental conditions to which they were exposed, but has been reported previously for citrus (Camacho-B et al., 1974; Elfving et al., 1972) and herbaceous plants (Black, 1979; Stoker and Weatherley, 1971; Tinklin and Weatherley, 1966). The predominant response of Ψ vs. E was taken as linear with a significant y -intercept, since data for every plant showed this characteristic.

Several explanations have been proposed that could account for nonzero Ψ at zero E without invoking variable L_p . Koide (1985) proposed that nonzero Ψ at zero E in sunflower was caused by growth-induced Ψ

depression (Boyer, 1968), but preliminary studies with peach and sour orange showed no change in Ψ due to removal of expanding shoot tips and leaves. Apparent nonlinearity in the relationship between flux through roots and driving force has been explained by models that account for an osmotic potential gradient as part of the driving force for water uptake (Fiscus, 1975). It is unlikely that these models explain the nonzero y -intercepts for two reasons. First, the solute concentration of the water bathing the roots and the L_p values in this experiment were both about three orders of magnitude lower than values that produce a pronounced curvilinear response. Second, use of relatively pure water would tend to minimize the likelihood of a build-up of solutes at the root membranes (due to high reflection coefficients), possibly explaining the nonzero Ψ at zero E . Lack of consideration of osmotic potential in xylem sap probably resulted in underestimation of the magnitude of $\Delta\Psi$ across the root membranes; however, accounting for osmotic potential would only serve to strengthen the conclusion that L_p decreases at low E , since a slightly larger Ψ gradient existed across the roots than that estimated by Ψ of wrapped leaves.

Data from several studies show nonzero y -intercepts on Ψ vs. E plots, but few have offered an explanation as to why the y -intercept is often less than Ψ at the root surface (Black, 1979; Bunce, 1978; Camacho-B et al., 1974; Elfving et al., 1972; Hailey et al., 1973). Results similar to those reported here were obtained by Passioura and Munns (1984) using intact wheat plants. They suggested that root resistance (inverse of L_p) consisted of two components: 1) a "true" hydraulic resistance, given by the slope of the relationship between Ψ and E , and 2) an "offset", representing the water potential gradient that must be overcome before flow through roots can occur. The magnitude of the latter is given by the y -intercept. Our data show that sour orange has lower "true" L_p , as well as a lower offset than peach. It may be important, therefore, to consider both values, since they are probably genetically determined and one or both may change with environmental stress or other factors.

The biological interpretation of the offset is unclear, but it may represent the pressure difference required to force obstructions out of the lumen of the plasmodesmata of endodermal cells, thereby permitting flow of water through the symplasm of the endodermis to the stele (Passioura and Munns, 1984). However, even unobstructed plasmodesmata may not offer a suitable pathway for water flow across the endodermis (Weatherley, 1982). Alternatively, the pores in the plasma membrane of the endodermis may act in this way, requiring a minimum pressure gradient to force obstructions from them and permit water flow (Hylmo, 1955). The hypothesis proposed by Powell (1978) explains variable L_p in terms of turgor-pressure dependency of plasma membrane hydraulic conductivity of endodermal cells and also is in general agreement with this con-

cept. Tinklin and Weatherley (1966) compared the transpiration-dependent behavior of L_p to the operation of a rotometer, a device that requires a minimum pressure gradient to permit flow and thereafter allows an increase in flow rate without an increase in driving force. AH of these hypotheses suggest L_p can be transpiration dependent and are compatible with our results.

This study provides evidence for the existence of variable L_p , or at least the requirement for a finite $\Delta\Psi$ across roots to allow flow in two rootstock species. The transpiration-dependent behavior of L_p depends heavily on the method of data presentation—use of the Ohm's law analog suggests a more complex relationship between L_p and E than the regression method. The latter indicates that L_p is constant over a large range of E , but approaches zero at low E . Calculation of L_p by the Ohm's law analog will lead to the conclusion that L_p increases with E , provided that the extrapolated value of Ψ at zero flow does not pass through the origin. Models that imply constant L_p (Fiscus, 1975) may be inadequate to explain entirely the mechanism of root water uptake in light of these data and other similar results (Passioura and Munns, 1984).

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