A Model Relating Root Permeability to Flux and Potentials

APPLICATION TO EXISTING DATA FROM SOYBEAN AND OTHER PLANTS

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ABSTRACT

A model that relates hydraulic permeability to water flux and to gradients in pressure potential and solute potential was tested using soybean (Glycine max) plants. Water flux was varied by additions of polyethylene glycol 6,000 around one portion of a divided root system and by changing the light intensity and CO₂ concentration around the plants. The data are compatible with the model only if the hydraulic permeability varies with flux; however, the data were insufficient for rigorous testing. Three sets of published data fit the model only if hydraulic permeability varies. Evidence originally presented as involving constant hydraulic permeability is shown, rather, to require variable hydraulic permeability.

A considerable body of data seemed explainable only if the permeability of plants to water varies with changes in rates of water flux (19, 20, 22). Fiscus (4) proposed a model coupling water and solute fluxes to explain at least some of the data cited. Of that available to him, only the data of Lopushinsky (11) and Mees and Weatherley (12) were adequate for testing; and Fiscus believed his model to be compatible with their data. Dalton et al. (3) independently proposed the same model and also indicated it to be consistent with the data of Mees and Weatherley. Newman (20) used various methods to reject the conclusions of Fiscus and of Dalton et al. Newman also suggested a two-membrane, three-compartment model as more realistic than the single membrane, two-compartment model of Fiscus; nevertheless he concluded that these models predicted essentially the same water flux-pressure gradient relationship.

This manuscript reports the testing of the model of Fiscus (4) and Dalton et al. (3) for applicability to data obtained in my laboratory from soybean divided root systems (10), reexamines the model's applicability to amenable published data, and considers other evidence regarding root permeability to water.

MATERIALS AND METHODS

Experimental. Soybean (Glycine max [L.] Merr. cv Bragg) plants were grown with divided root systems in solution culture as previously (16) except for using half-strength nutrient solution and improved containers. The latter consisted of side by side Plexiglas compartments, each 3 × 3 × 29.5 cm internal dimensions, into which 240 ml of solution was placed (Fig. 1). Improvements were greater sensitivity for measuring liquid absorbed by roots, automation in recording the amounts absorbed, and prevention of mechanical injury to roots. The value of uninjured roots is particularly important in preventing entry of PEG² (9, 16).

To begin treatment, the nutrient solution was drained from one compartment and replaced by nutrient solution plus PEG. To end treatment, the compartment was drained, flushed with distilled H₂O three or four times, and refilled with nutrient solution. Before, during, and after treatment, water absorption rates of both sides of divided root systems were monitored.

The ψ, of the nutrient solution was −0.37 bar. Concentrations required for desired ψ, values of PEG were obtained from published values (17). The PEG content of each slightly diluted solution recovered from treatment of roots was measured gravimetrically (17). Some measurements of the water potentials of leaf discs and of decapitated root exudates were obtained using a Wescor C-51 sample chamber.

Full light from fluorescent and incandescent lamps was 0.3 cal cm⁻² min⁻¹ (Eppley pyrheliometer) or 43,200 lux (Weston illuminometer). Half-light (no incandescents) was 0.12 cal cm⁻² min⁻¹ or 21,600 lux. Temperature mean was 25 °C and vapor pressure was maintained between 10.9 and 12.8 mm Hg. The CO₂ level outside the growth chamber usually was well above 400 μl/l. The chamber was not gas tight; to provide a consistent CO₂ level, supplemental CO₂ was added automatically to maintain 500 μl/l during nonexperimental and some experimental periods. To achieve high transpiration rates, 300 μl/l was used during most of the experimental periods being reported. This was obtainable during light hours partly because of photosynthesis in test and non test plants and partly by absorption of CO₂ into KOH solution in trays on the floor of the chamber.

At harvest, the top was severed at the hypocotyl and weighed. After exudation measurements, using a pipette attached with rubber tubing to the decorticated stump, divided root systems were blotted between paper towels and weighed. Based on growth rate measurements, weights at the start of the experimental period were estimated; and, using straight line interpolation, intermediate values were calculated to permit computation of best estimates of rates. Treated roots were assumed not to grow during exposure to PEG but to enlarge normally at all other times.

To permit expression of Jᵣ as water flux, estimates of root surface areas were needed. By assuming a density of 1 and an average diameter of 0.5 mm, multiplication by 80 cm² g⁻¹ con-

² Abbreviations: PEG: polyethylene glycol 6,000; Jᵣ: volume flow, equivalent to water flux; L: hydraulic permeability; ψᵣ: water potential; ψₛ: pressure potential; ψᵣ: solute or osmotic potential; nᵣ: reflection coefficient; Jₛ: solute flux; n: effective number of ions per mol of solute (2.3 for Hoagland No. 2 nutrient solution based on −nRTC = ψₛ = −0.74 bar); R: gas constant; T: Kelvin temperature; C: mol cm⁻² of solute; k: coefficient of active solute absorption; w: coefficient of solute permeability at Jₛ = 0; S: selectivity; subscript 1: ambient; subscript 2: within xylem; superscript u: untreated; superscript t: treated; r: correlation coefficient.

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Fig. 1. Schematic diagram (not to scale) of an apparatus for testing plants with divided root systems. Only parts for one compartment of one container are shown. The large circle in the root compartment represents a cavity in the base protected from root entry by a 100 mesh stainless steel screen thimble. The small circle is a cavity accepting a tube to complete an air-lift water pump for aeration and circulation of compartment liquid. The dashed lines represent the growth chamber walls. An aquarium pump pushes growth chamber air for 24 compartments through a Y-tube into two wide-mouth, pint jars for distribution through a set of 12 capillary tubes in each jar. Numbers 1, 2, and 3 are solenoid values. The drain line is clamped during filling. Solenoid 3 usually is actuated by the controller for a preset time period when the liquid level drops below the thermistor, permitting the thermistor to self-heat. Each event is recorded. The thermistor is located in a small column attached near the top front of each compartment. The column provides an accessible location free of roots and surface disturbance.

Verted fresh weights to approximate areas. An error in average diameter, though modifying absolute values, would not change general relationships or introduce errors in determining model applicability.

Analysis. Although Fiscus (4) and Dalton et al. (3) used osmotic pressure notation, and Newman (20) continued this usage, \( \psi \) notation is preferred and will be used here. Basic equations are

\[
J_r = -L(\Delta\psi_r + \sigma\Delta\psi_t) \quad (1)
\]

\[
J_r = -\psi_{at} J_r / nRT = k + \omega \Delta\psi_r - (1 - \sigma)(\psi_{at} + \psi_{at} J_r / 2nRT) \quad (2)
\]

\[
\Delta\psi_r = \psi_{at} - \psi_{at} \quad \text{and} \quad \Delta\psi_t = \psi_{at} - \psi_{at} \quad (3)
\]

To permit equation 1 to be used without knowledge of \( \psi_{at} \) and, therefore, \( \Delta\psi_t \), equation 2 was solved for \( \psi_{at} \) and this value substituted in the right hand equation 3. Simplification showed \( \Delta\psi_r = -S\psi_{at1} \), where

\[
S = (\sigma + nRTk/\psi_{at} J_r) / (1/\psi_{at} + \sigma/2 + nRT\omega / J_r) \quad (4)
\]

Dalton et al. (3), by using \( \psi_{at} \) rather than \( \psi_{at} + \psi_{at} / 2 \), obtained slightly different forms for equations 2 and 4.

Because \( \sigma, k, \) and \( \omega \) were not measured, reasonable estimates were selected for evaluation. The value of \( \sigma \) for nutrient solution ions is likely to be within 0.7 to 1.0 (5, 13); and, because the effect on the model within this range is small (Fig. 2), the midpoint value of 0.85 was utilized in most places.

Relationships expressed by the model for certain special cases proved useful in selecting appropriate values for \( k \) and \( \omega \). When \( \psi_{at2} = \psi_{at1} \), equation 2 simplifies to \( J_r = -k nRT / \psi_{at1} \). With \( \psi_a = -nRTC, nRT = 5.7 \times 10^4 \text{ bar cm}^2 \text{ mol}^{-1} \) for the nutrient solution used; and \( J_r \) becomes (15.4 \times 10^4 \text{ kJ} / \text{mol}) / (\sigma/\omega). That \( k \) could be greater than \( 1 \times 10^{-11} \text{ mol cm}^{-2} \text{ sec}^{-1} \) seems unlikely because any value above this requires \( \psi_{at2} \) to be equal to \( \psi_{at1} \) at rates of water flux that are much too high (8, 18). This value of \( k \) is within the ranges used by Fiscus (4), Dalton et al. (3), and Newman (20).

Maximum developable root pressure is \( \psi_{at} \) at \( J_r = 0 \). On the untreated side of the divided root system, \( \psi_{at} \) was always 0; therefore \( \psi_{at2} = \Delta\psi_{at} \) (equation 3) and, at \( J_r = 0, \Delta\psi_{at} = \sigma k / \omega \) (reduced equations 1 and 2). Setting maximum root pressure to range between 0.2 and 5 bars and \( k \), between 0.1 \times 10^{-11} \text{ and } 1.0 \times 10^{-11} \text{ mol cm}^{-2} \text{ sec}^{-1} \), the above equation set corresponding values for \( \sigma \). All of these were used, in equation 4 with and with the relationship of \( S \) to \( \psi_{at1} \), to relate \( \sigma \Delta\psi_{at} \) to \( J_r \) for four limiting combinations of \( k \) and maximum root pressure, within which any actual combinations should fall (Fig. 2).

Because PEG does not penetrate cell walls (14), its \( \psi_{at} \) should be equivalent to the \( \psi_{at} \) of roots immersed in unpressurized solutions. Rewriting equation 1 as

\[
J_r = -L(\psi_{at} - \psi_{at} + \sigma\Delta\psi_t) \quad (5)
\]

and adding increasing concentrations of PEG to a treated side until \( J_r \) approached 0, should have brought \( \psi_{at2} \) to near 0 also, regardless of the magnitude of \( L \). Using \( \psi_{at} \) of the PEG to predict \( \psi_{at} \) and Figure 2 to predict \( \sigma \Delta\psi_{at} \), close approximations of \( \psi_{at2} \) could be reached. Considering \( \psi_{at2} = \psi_{at} \), remembering that \( \phi_{at} = 0 \), and obtaining \( \sigma \Delta\psi_{at} \) from Figure 2, values for \( L \) at that particular \( J_r \) were calculated. These values were then used to test experimental data against those predicted by the model.

After finding that the experimental data were incompatible with the model when \( L \) was constant, several procedures were used to predict possible values for variable \( L \). Because untreated plants exposed to constant conditions exhibited a predictable rhythm of \( J_r \) throughout a day and because root \( L \) has been reported to fluctuate diurnally (21, 22), \( L \) was considered as possibly varying in direct proportion to the \( J_r \) of a typical, untreated plant. It might also be possible for \( L \) to vary in a circadian rhythm not related on a one to one basis to the \( J_r \), so exaggerated circadian patterns of variation also were considered. Finally, the possibility that \( L \), without regard to a rhythm pattern, might be a function of any temporary \( J_r \) was investigated. For the latter, all data were grouped in simultaneous
pairs, treated side during one measurement period versus untreated side during the same period. A value of \( L^* \), when \( J^* \) was near 0, was observed as outlined above. For other values of \( J^* \) and \( J^* \), arbitrarily selected values of \( L^* \) were substituted in simultaneous equations (equation 5) to find matching values for \( L^* \). These paired values for \( L^* \) and \( L^* \) were plotted versus \( J. \) Iteration permitted best values to be picked.

By having set limits for \( \sigma, k, \omega, \) and \( \Delta \psi \), at \( J^* = 0 \), so that \( \sigma \Delta \psi \) became some function of \( J^* \) (Fig. 2), extremes of exudation rates of decapitated roots became predictable (with \( \Delta \psi = 0, J^* = -\Delta \psi \), where \( L \) may be constant or a function of \( J^* \)). In addition, extremes of \( \Delta \psi \) for exudates became predictable.

**RESULTS**

The lag time from a change in conditions, even from darkness to bright light and the reverse, was no more than 15 min (Fig. 3, upper). Summing the number of additions by 15-min periods produced totals not varying by more than two, except for very long periods where circadian rhythms were responsible (Fig. 3, lower). Such results permitted treatment periods to be kept short without destroying confidence in the values found and made possible several successive treatments during a portion of the day when absorption rates were normally high. Untreated plants typically showed a steady increase in absorption from a relative value of about 0.77 at 1 hr after lights on to 1.00 at about 5 to 6 hr after lights on followed by a gradually steepening rate of decrease to about 0.64 at 13 hr after lights on (10).

Progressively increased concentrations of PEG slowed and eventually nearly stopped water absorption from the treated side (Fig. 4). In the example shown, the treated side had originally supplied more than half of the water. Marked reduction on the treated side resulted in slight reduction of the total absorbed (Table I), but no symptoms of plant stress ever were evident.

Values for \( J^* \) and \( J^* \) (Table I) were calculated from absorption rates and the data of Table II as described under "Materials and Methods."

When \( J^* = 1.3 \times 10^{-7} \text{ cm sec}^{-1} \), \( \Delta \psi \) is a result of treatments (equation 5) should have been close enough to 0 to permit accurate assessment of \( L^* \) ("Materials and Methods"). The first two and fourth limiting combinations (Fig. 2) gave \( L = 10 \times 10^{-7} \text{ cm sec}^{-1} \text{ bar}^{-1} \). Because these three combinations also gave significantly different calculated values for \( \psi_{\text{PEG}} \), only data from the first will be presented. The third combination gave \( L = 13.8 \times 10^{-7} \text{ cm sec}^{-1} \text{ bar}^{-1} \). To make \( \psi_{\text{PEG}} \approx \psi_{\text{PEG}} \) in the absence of PEG, corresponding values for \( L^* \) were 12.9 \( \times 10^{-7} \) and 17.8 \( \times 10^{-7} \text{ cm sec}^{-1} \text{ bar}^{-1} \). These values for \( L \) were then used for each set of conditions (Table I) to calculate paired values for \( \psi_{\text{PEG}} \) and \( \psi_{\text{PEG}} \) (Fig. 4). Because of the manner of determining \( L \) in the absence of PEG, \( \psi_{\text{PEG}} \) closely matched \( \psi_{\text{PEG}} \), so most such matched pairs (Table I) were omitted from Figure 4.

Two types of results cast serious doubt that \( L \) could be constant within the context of the model. First, although \( L \) values were obtained by methods that caused \( \psi_{\text{PEG}} \) to match \( \psi_{\text{PEG}} \) both before treatment and at the highest PEG concentration, large discrepancies exist between predicted values for \( \psi_{\text{PEG}} \) and \( \psi_{\text{PEG}} \) at intermediate PEG concentrations. Second, predicted \( \psi_{\text{PEG}} \) values at moderate to low \( J^* \) appear to be too high. Leaf \( \psi \) measurements from comparable, untreated plants ranged from −7.2 to −9.3 bars (unpublished). If 75% of the resistance in soybeans is across the roots (1), \( \psi_{\text{PEG}} \) values would be expected in the range of −5 to −6.5 bars. Direct measurement of untreated soybean hypocotyl \( \psi \) (unpublished) showed values within this range. The calculated values (Fig. 4, L constant) were much closer to 0.

![Fig. 3. Upper: record of replacement of absorbed liquid by both sides of a soybean divided root system. Photographs of the event recorder paper were cut and assembled in hourly segments, appropriate hr of day being indicated at each end. Upper record in each pair is from treated side (each event = 0.44 ml). Lower record from untreated side (each event = 0.49 ml). Treated side was drained and refilled starting at 1030, 1200, 1345, and 1530 to produce \( \psi_{\text{PEG}} \) lowering from PEG of 1.8, 3.8, 5.6, and 7.4 bars, respectively. After draining at 1715, treated side was washed four times before refilling with nutrient solution. Light came on a few minutes after 0800 and went off at 2200. Lower: Fifteen-min totals of water increment additions to both sides of the soybean divided root system. Increment counts are from record in upper portion of figure.](www.plantphysiol.org)
Moreover, predicted $\psi_{p2}$ night values were about −0.5 and 0.5 bar (Fig. 4). Corresponding $\psi$ values would be about −0.7 and −0.3 bar. Highest soybean stem and leaf $\psi$ measured at night (15 and unpublished) have been near −2 bars.

Because constant $L$ has the model predicting widely different simultaneous values for $\psi_{p2}$ and $\psi_{p2}$ and values for $\psi_{p2}$ that are too high at moderate to low $J_s$, curves for variable $L$ were obtained by procedures outlined under “Methods.”

Considering $L$ to vary in direct proportion to the circadian rhythm of $J_s$ for a typical, untreated plant reduced slightly some of the discrepancies cited above but increased others. Exaggerating the rhythmic variations of $L$ had a similar effect. Neither constant $L$ nor any circadian pattern of variation of $L$ seemed to permit the model to account for the results obtained.

Following procedures outlined in “Methods” for combination 1 (Fig. 2), the 13 pairs of $J_s$ during light hours (Table I) yielded this straight line relationship between $L$ and $J_s$: $L = 0.118 J_s + 1.70 \times 10^{-7}$ (Fig. 5). Regression analysis modified this to $L = (0.121 \pm 0.004) J_s + (1.60 \pm 0.16) \times 10^{-7}$, $r^2 = 0.973$, which is insignificantly different from the original. In all instances but two, predicted values for $\psi_{p2}$ and $\psi_{p2}$ are within 0.7 bar of each other (Fig. 4). In one of the exceptions, 1st day and −7.4 bars PEG, a reduction in $J_s$ by $0.6 \times 10^{-7}$ cm sec$^{-1}$ would have brought $\psi_{p2}$ into line. With the rate of absorption so near 0, a measurement error of this magnitude could have occurred easily. The second exception, 2nd day and −3.5 bars PEG, would have required a measuring error much greater than was likely.

Results for combinations 2 and 4 were sufficiently comparable with those for combination 1 to warrant omission here.

Combination 3 yielded this relationship, $L = 0.138 J_s + (4.10 \times 10^{-7})$, and predicted values for $\psi_{p2}$ and $\psi_{p2}$ shown in Figure 4. Fit was nearly as good as for combination 1, but predicted values for $\psi_{p2}$ at low $J_s$ appear to be too high.

In general, a linear relationship between $L$ and $J_s$ occurs much closer to matching predicted values of $\psi_{p2}$ and $\psi_{p2}$ than either constant $L$ or $L$ varying in circadian rhythm.

The exudation rate of the example used (Table II) was among the lowest for 28 plants measured, for which the range was $0.25 \times 10^{-7}$ to $1.27 \times 10^{-7}$ and the mean was $0.64 \times 10^{-7}$ cm sec$^{-1}$. Combinations 1 and 2, with constant $L$, and combinations 1, 2, and 4, with variable $L$, predicted values within this range (Table III). A value of $k$ closer to $0.1 \times 10^{-11}$ than to $1.0 \times 10^{-11}$ mol cm$^{-2}$ sec$^{-1}$ appears to be favored by such results.

Ten comparisons of the $\psi_{ex}$ values of exudates from decapitated roots in full strength nutrient solution ranged from 0.5 bar greater to 0.5 bar less than $\psi_{p2}$, with a mean of nearly 0.2 bar more negative. Only combination 3 with variable $L$ (Table III) is excluded from this range. The data are not adequate to help with a decision; however more precise data of this type would be quite useful.

**DISCUSSION**

The results indicate that if the model demands $L$ to be a constant, the model fails to predict reasonable values of internal water potential. A linear relationship between $J_s$ and $L$ provided, with one major exception, a fit between measured and model-predicted values considered to be within experimental error. The poor data available regarding exudation rates and $\psi$, measurements of exudate were compatible with but not really definitively supportive of variable $L$ within the model. Not only better exudation data but also $\psi$ measurements in the lower stem and $\psi_{ex}$ measurements other than of exudates are needed if the feasibility of the model is to be proved.

Even though $J_s$ and $L$ values obtained can only be considered relative, because average root diameter was only estimated, the range obtained for exudation $J_s$ values and $L$ values at exudation are within the range found or cited by others (8, 18).

Newman (20), considering the model to require constant $L$, showed that the data from decapitated tomato root systems of Mees and Weatherley (12) were incompatible with the model. Calculated $L$ values from three experiments reported by Mees
and Weatherley, referred to but not given by Newman (20) (though values for one had been reported by him earlier [19]) are related to \( J_r \) expressed in arbitrary units in Figure 6. Because Mees and Weatherley reported \( J_r \) as rates of rise in different sized capillary tubes and without relation to root system size, direct comparison among experiments was impossible; therefore, the \( J_r \) values were normalized in relation to \( \Delta \psi_p \) in the 1.39 to 1.60 bars range. Although all but one of the \( \Delta \psi_p \) values are in sequence, there are obvious discrepancies in relative distancing. No vertical normalization of \( L \) was attempted, so values are relative only within each curve and not among curves. Regardless, Figure 6 does indicate that \( L \) was approximately linearly related to \( J_r \); at \( \Delta \psi_p \) below about 1.5 bars, but \( L \) became nearly constant at higher values of \( \Delta \psi_p \). Such results contrast sharply with those for soybean (Fig. 5) in a linear relationship extended to \( \Delta \psi_p > 7 \) bars. Nevertheless, within the context of variable \( L \), the model appears applicable to both the tomato data of Mees and Weatherley (12) and the soybean data of this paper.

Lopushinsky's data for decapitated tomato roots (Fig. 6 in ref. 11) supply values for all terms of equation 1 but \( L \) and \( \sigma \). They can be compared directly with the similar data of Mees and Weatherley (12). Lopushinsky used full strength Hoagland solution without citing a reference or assigning a \( \psi \). Mees and Weatherley used Hoagland No. 2 nutrient solution and indicated \( \psi = -0.88 \) atm. I used the latter solution but measured \( \psi \) to be \(-0.74 \) bar. Newman (20) used \(-0.4 \) bar as \( \psi \) of Lopushinsky's external medium when showing his "tangent test" to reject Fiscus' model for Lopushinsky's results. The model would not be rejected if \( \psi \) were more negative than \(-0.7 \) bar, which it must have been. To make the best possible comparison with the results of Mees and Weatherley, these values were assigned: \( \psi_1 = -0.89 \) bar and \( \sigma = 0.76 \) (19). The results (Fig. 6), normalized with the data of Mees and Weatherley for \( J_r \) and \( \Delta \psi_p \), essentially corroborate those of the latter in showing \( L \) to vary nearly linearly with \( J_r \) in a lower range before becoming almost constant in a higher range. Lopushinsky's data are compatible with Fiscus' model only with \( L \) variable.

Brouwer (2) reported \( L \) to vary both with distance from the root tip and with \( \Delta \psi_p \). The \textit{Vicia faba} roots used were uniformly near 1 mm diameter, so points plotted by Brouwer (Fig. 2 in ref. 2) could be converted to units used here. Values for his four zones covering a total root length of 10 cm were averaged to provide better comparison with the soybean data for large portions of root systems. Although of a similar magnitude, Brouwer's values for \( L \) were larger, changed over a 2-fold rather than the 3.4-fold range predicted for soybean, and formed a curvilinear relationship with \( J_r \) ( \( L \) increasing but little at higher \( J_r \) values reminiscent of tomato [11, 12]) (Table IV) rather than the linear one fitting soybean data (Fig. 5). Brouwer's results also show \( \Delta \psi_p \) in darkness (Table IV, first row) to be \(-1.6 \) bars, which is close to that suggested earlier in this paper for soybean.

Some authors have assumed that a straight line relationship between \( \Delta \psi_p \) or \( \Delta \psi_p \) and \( J_r \), indicated constancy of \( L \) (6, 7), and/or that the slope of the line is \( L \) (4, 6). The model of Ficus (4) and Dalton et al. (3) does predict a straight line with slope \( L \) at sufficiently negative values of \( \Delta \psi_p \), however, not just any straight line. The \( \Delta \psi_p \) intercept must be less negative than \( \psi_1 \) (20), but also cannot be greater than 0 (equation 1).

Consider the frequently cited results of Jensen et al. (7). Although straight lines fit well their \( J_r \) versus \( \Delta \psi_p \) data, extrapolated intercepts range from slightly below \(-0.1 \) to slightly above \(-0.05 \) bar. Two things show that such intercepts do not permit using the slopes of the lines, as they did, to be measures of permeabilities. First, with \( \Delta \psi_p \) values ranging only from \(-0.2 \) to \(-0.6 \) bar, the above intercepts are significant departures from 0, the value of \( \psi_1 \). Second, because insignificantly different values were found with flux in the normal and reverse directions, any effect of \( \sigma \Delta \psi_p \) must have been insignificant, with equation 1 reducing to \( J_r = -L \Delta \psi_p \); and the \( \Delta \psi_p \) intercept should have been 0 for \( J_r / \Delta \psi_p \) to equal \(-L \). Calculation from individual values of \( J_r \) and \( \Delta \psi_p \) for minimum and maximum differences of the latter show \( L \) for stem, stem plus leaves, stem plus roots, and whole plants of sunflower increasing by 21, 14, 22, and 15%, respectively, with \( \Delta \psi_p \) change of only \(-0.4 \) bar. Of particular interest is the implication of departure from Darcy's law (constant \( L \)) not only in roots but also in stem and leaf vascular tissue as well. Incidentally, use of extrapolation to calculate \( L \) values at one value of \( J_r \) greatly improved the comparison of whole plant \( L \) with that combined from separate parts made by the authors (7).

Consider, also, the data presented by Hailey et al. (6). None of the straight lines drawn in the range of large negative values of \( \Delta \psi_p \) extrapolates to within \( \Delta \psi_p = 0 \) to \( \psi_1 \). Thus, the model of Ficus (4) and Dalton et al. (3) must be rejected and the slope, \( J_r / \Delta \psi_p \), cannot equal \(-L \). Of interest and contrary to other results cited, experiments 2, 3, and 4 of Hailey et al. (6) showed \( L \) decreasing rather than increasing as \( \Delta \psi_p \) became more negative.

The overwhelming weight of evidence favors variable root permeability to water. If \( L \) varies, then so may some of the other "constants" of the model; and the question of valid use of the model when \( L \) is permitted to vary must be raised. Satisfactory knowledge of these relationships for any species and possible utility of the model as defined by equations 1 through 3 must await more nearly complete data.

Table IV. Average values of \( L_n, \Delta \psi_p \), and \( J_r \) for the Apical 10 cm of \textit{Vicia faba} roots from Brouwer (Fig. 2 in ref. 2) and soybean L's at these \( J_r \) values 

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Fig. 6. Hydraulic permeability coefficient versus water flux for decapitated tomato roots from Mees and Weatherley (12) and Lopushinsky (11). Abscissa was normalized according to \( \Delta \psi_p \) in the range of 1.38 to 1.60 bars. Ordinates were normalized in which the linear relationship

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LITERATURE CITED


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