Relationships between Root System Water Transport Properties and Plant Size in Phaseolus

EDWIN L. FISCUS
Crops Research Laboratory, United States Department of Agriculture, Science and Education Administration, Agricultural Research, Colorado State University, Fort Collins, Colorado 80523

ALBERT H. MARKHART III
Department of Botany, Duke University, Durham, North Carolina 27706

Received for publication January 30, 1979 and in revised form June 4, 1979

ABSTRACT

Root system hydraulic conductivity (Lp) was measured on Phaseolus plants of different ages and sizes. Data analysis showed that Lp changed in a complex manner depending on plant size. As the plants increased in size, Lp increased initially then gradually decreased followed by a final modest increase. Values for Lp ranged between 0.8 x 10^-4 and 6.1 x 10^-4 centimeter per second per bar. Relationships between the root flow per unit leaf area at a pressure differential of 3 bars (QPLm), as well as the total root system conductance (Lam), and plant size were also examined. Values for QPLm varied with plant size, somewhat like Lp. Lm values continuously increased with plant size at rates which depended on the growth rate of the root surface area as well as Lp. Comparison of our data with the root conductivity constant (k) of Taylor and Klepper (1975 Soil Sci, 120: 57-67) showed good agreement. The observations on Phaseolus were also confirmed for Glycine. Values for Lp and k, of both species were within the same range.

MODELING WATER UPTAKE

Modeling water uptake and loss by plants is a complicated endeavor. Any such attempt requires careful measurement of the environmental factors impinging upon the plant, as well as an accurate assessment of the plant's ability to respond to environmental demands. Calculating rates of soil water uptake by root systems requires not only that we know what demands are placed on the root system by the shoot, as well as the magnitude of the soil water source term, but also that we accurately know the water transfer function of the root system.

In general, the root system water transfer function may be written as

$$J_v = L_p \left( \Delta P - \sigma \Delta \Pi \right)$$

(1)

where the flow of volume, Jv, is in cm³ cm⁻² s⁻¹; the hydrostatic pressure difference ∆P, is in bars, as is the osmotic pressure difference ∆Π; σ is the dimensionless reflection coefficient or osmotic efficiency factor; and Lp is the hydraulic conductivity coefficient in cm² cm⁻² s⁻¹ bar⁻¹.

Taking into account the fact that the osmotic pressure difference is a function of the total volume flow, Jv, as well as the solute flux, Jm, in mol cm⁻² s⁻¹, Fiscus (2) arrived at an expression for the apparent or differential resistance to pressure-induced water flow. This apparent or differential resistance is given as the slope of the force-flux curve when the force is taken as the dependent variable. The apparent resistance to pressure-induced flow, R*, is of the form

$$R^* = \frac{dJ_v}{d\Delta P} = \frac{1}{L_p} + \frac{k}{(m + J_v)^2}$$

(2)

where k and a contain several constants relating to solute diffusion, active solute uptake, and osmotic efficiency. It is evident from equation 2 that the second term on the right decreases as Jv increases and that at high flow rates R* approximates 1/Lp. This relationship at high flow rates provides a convenient method for estimating an average Lp value either for an entire root system or for any particular segment of a system.

Values of Lp² determined either by this method (3) or by osmotic means (6-8, 13, 14), are relatively scarce and mostly confined to small systems and terminal root segments, which cannot be expected to reflect average conditions for the whole system. We know of no attempt to determine the relationship between the average Lp and the root system size or shoot leaf area. Our purpose here is to establish the broad outline of this relationship in bean plants and to compare the magnitude of our data with field data obtained by others.

MATERIALS AND METHODS

Phaseolus vulgaris L. (cv. Ouray) seeds were germinated on paper towels for 4 days then transferred to 25-cm plastic pots filled with half-strength modified Hoagland solution. The date of transfer is taken as day 0. The nutrient solution was a commercial mix available from Robert B. Peters Co., 2833 Pennsylvania St., Allentown, Pa. 18104. The solutions were continuously aerated and the plants maintained in a controlled temperature greenhouse (27 ± 1.5 C). Supplemental sodium vapor lamps were used resulting in a mean midday flux density over the growth period of 425 μE m⁻² s⁻¹. Additional plants were grown without the supplemental lighting with the result that the mean light intensity was reduced over the growth period (mean midday flux density = 320 μE m⁻² s⁻¹). During the experiment, the entire population of plants whose ages ranged from 7 to 41 days, was used. Before we used each plant, it was removed from the greenhouse and allowed to equilibrate in the laboratory overnight with the root system maintained at the temperature (25 ± 0.25 C), at which we made

1 This research was supported in part by National Science Foundation Grant PCM76-11142 to Paul J. Kramer of Duke University.

2 Abbreviations: Lp: hydraulic conductivity; QPL: root flow/unit leaf area; QPLm: root flow/unit leaf area at a pressure differential of 3 bars; Lam: total root system conductance; kr: root conductivity constant.

3 Mention of companies or commercial products does not imply recommendation or endorsement by the United States Department of Agriculture over others not mentioned.
the determinations. The next day, the shoot was cut off and the root system sealed into a pressure chamber, similar to that used by Lopushinsky (10) and others (3, 11). The chamber was filled with a nutrient solution of the same composition as that in which the plants were grown. Aeration was maintained via an air stone in the bottom of the chamber and a bleed-off valve in the top. The rate of exudation from the cut stem, which projected through a seal in the lid of the chamber, was measured at the steady-state under various levels of pressure. The relationship between the flow rate and the applied pressure, as described generally by equation 2, was then used to determine the value of Lp in the manner previously described by Fiscus (3). The leaf area of each plant was measured with a L1-COR L1-3000 area meter. The total root system length and surface area were estimated by modifying the Newman line intersect method (12), as described by Fiscus (3).

The data were processed with a Tektronix 4051 graphics system. Except for the growth data, Table I, the data were fitted with least squares polynomials. Because of the relatively large degree of data scatter, data were smoothed, rather than interpolated, during the fitting. Also, the linear transformation, \( T = mX + k \), was used to improve numerical accuracy where the \( X \) values were the independent variables and \( T \) was the transform. This transformation is simply a scaling procedure which makes the numbers similar in size, thereby reducing rounding errors. The regression coefficients for these polynomials, including \( m \) and \( k \), are given in Table II. The smooth curves shown in the figures were drawn from these polynomials.

RESULTS AND DISCUSSION

Projected leaf surface area \( (A_L) \), total root surface area \( (A_R) \), and root length \( (l_R) \) all exhibited typical exponential growth, described by a relationship of the type

\[
Y = Y_0 \exp(k_0t) \tag{3}
\]

where \( Y \) is the magnitude of the property of interest at time \( t \), in days; \( Y_0 \) is the value on the day the seedlings were placed in solution; \( t = 0 \); and \( k_0 \) is the relative growth rate of that property or the fractional increase per unit time per existing unit of that property. For example, the relative growth rate of leaf area would be expressed as \( \text{cm}^2/\text{cm}^2 \), or \( \text{cm}^2/\text{cm}^2 \) of existing leaf area. Table I shows the values of the relevant constants for leaf area, root surface area, and root length. Also shown are growth constants for the plants grown under reduced light intensities. The reduced light noticeably lowered the growth rate.

Comparison of the hydraulic conductivity \( (L_p) \) data from these two sets of plants revealed that root system size, rather than age per se, seemed to be the dominant factor controlling the water transfer characteristics of the systems. This is illustrated in Figure 1, where \( L_p \) is shown as a function of the total root surface area. Clearly the two data sets had similar forms and conductivities peaked at similar root system sizes, even though plants of similar size were widely divergent in chronological age, as calculations based on Table I showed. The \( L_p \) values of the slower growing plants seemed to fall consistently somewhat below those of plants of similar size from the faster growing set. We concluded that increased plant age or some factor associated with slower growth does have some effect on lowering \( L_p \), perhaps via increased suberization of the roots. However, system size seems to be the dominant factor. The regression line in Figure 1 was fitted only to the fast growing set of plants. Other figures in this paper will show data only from that set.

Figure 1 shows that the average \( L_p \) is constantly changing. Over the range of plant sizes we have examined, this range is about 7-fold from the lowest to the highest values. There are two major phases of change in \( L_p \) apparent in Figure 1, a rapid increase associated with the earliest stages of growth, which is followed by a more gradual decrease during the logarithmic growth phase. We can speculate that the early phase increase is caused by the rapid proliferation of new secondary and tertiary roots which we see at this growth stage. These smaller roots might initially be more highly conductive because of their smaller diameters, which result in a shorter path length and less resistance to flow between the root medium and the xylem. The smallest roots (mean diameter \( 0.025 \text{ cm} \)) continue to constitute the vast majority of the total surface area (70%) and the total length (85%) of the root systems during the logarithmic growth phase (unpublished data). It seems reasonable to suppose that these smaller roots are the major source of the gradual decrease in \( L_p \), possibly through suberization of their surfaces as the older roots age.

The relationships between \( L_p \) and root length \( (l_R) \), root area \( (A_R) \), and leaf surface area \( (A_L) \) have forms similar to Figure 1. Table II lists the regression coefficients for all three of these relationships.

Two other interesting ways of considering these data are first to see how the root flow per unit leaf area varies with plant size; and second to determine the relationship between the total system conductance and plant size.

The root flow per unit leaf area \( (Q_{PL}) \) is defined as the total flow of exudate from the root system divided by the projected leaf surface area. Pressure differential must also be given so that comparisons may be made between plants. We have arbitrarily chosen that flow which occurs under a \( \Delta P = 3 \text{ bars} \) and have designated the QPL at this \( \Delta P \) as \( Q_{PL3} \). Therefore,

\[
Q_{PL3} = Q_3/A_L \tag{4}
\]

where \( Q_3 = J_{xP} \text{ in cm}^3/\text{liter} \text{ s}^{-1} \) at \( \Delta P = 3 \text{ bars} \), and the leaf area \( A_L \) is in \( \text{cm}^2 \).
The coefficients fit the polynomial $Y = a + BT + cT^2 + dT^3 + eT^4 + fT^5$ where $T$ is the X-data transform = $mx + k$. For example, to calculate $L_R$ for a root area of 3,000 cm$^2$, $T = 5.869405 \times 10^{-4}$, 3,000 - 0.208569. The coefficients $a$, $b$, $c$, etc. are substituted into the generalized polynomial along with the value of $T$ and $L_R$ is calculated.

<table>
<thead>
<tr>
<th>$Y_X$</th>
<th>$L_P/A_R$</th>
<th>$L_P/A_l$</th>
<th>$L_P/A_t$</th>
<th>QPL1/A_R</th>
<th>QPL1/A_l</th>
<th>QPL1/A_t</th>
<th>k/A_R</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r^2$</td>
<td>0.937</td>
<td>0.940</td>
<td>0.939</td>
<td>0.973</td>
<td>0.985</td>
<td>0.939</td>
<td></td>
</tr>
<tr>
<td>$a$</td>
<td>2.063725X10^{-6}</td>
<td>2.069940X10^{-6}</td>
<td>2.014440X10^{-6}</td>
<td>5.446010X10^{-6}</td>
<td>8.031385X10^{-3}</td>
<td>1.166965X10^{-6}</td>
<td></td>
</tr>
<tr>
<td>$b$</td>
<td>-5.685751X10^{-7}</td>
<td>-5.443276X10^{-7}</td>
<td>-3.314567X10^{-7}</td>
<td>-1.297721X10^{-6}</td>
<td>6.696497X10^{-4}</td>
<td>-2.555112X10^{-7}</td>
<td></td>
</tr>
<tr>
<td>$c$</td>
<td>9.570641X10^{-6}</td>
<td>1.045545X10^{-6}</td>
<td>1.070686X10^{-6}</td>
<td>2.027936X10^{-6}</td>
<td>1.754717X10^{-4}</td>
<td>3.263999X10^{-7}</td>
<td></td>
</tr>
<tr>
<td>$d$</td>
<td>-6.641282X10^{-7}</td>
<td>-6.920519X10^{-7}</td>
<td>-9.057525X10^{-7}</td>
<td>-4.022234X10^{-7}</td>
<td>8.619097X10^{-4}</td>
<td>-2.369057X10^{-7}</td>
<td></td>
</tr>
<tr>
<td>$e$</td>
<td>-1.990026X10^{-7}</td>
<td>-2.112148X10^{-7}</td>
<td>-2.118823X10^{-7}</td>
<td>-3.353373X10^{-7}</td>
<td>-4.658780X10^{-4}</td>
<td>-2.112148X10^{-7}</td>
<td></td>
</tr>
<tr>
<td>$f$</td>
<td>1.948762X10^{-7}</td>
<td>2.020778X10^{-7}</td>
<td>2.417357X10^{-7}</td>
<td>1.212130X10^{-7}</td>
<td>6.466731X10^{-4}</td>
<td>6.466731X10^{-4}</td>
<td></td>
</tr>
<tr>
<td>$m$</td>
<td>5.869405X10^{-4}</td>
<td>5.908157X10^{-5}</td>
<td>5.576467X10^{-4}</td>
<td>5.869405X10^{-4}</td>
<td>5.576467X10^{-4}</td>
<td>5.576467X10^{-4}</td>
<td></td>
</tr>
<tr>
<td>$k$</td>
<td>-2.085693</td>
<td>-2.072906</td>
<td>-2.052976</td>
<td>-2.085693</td>
<td>-2.052976</td>
<td>-2.052976</td>
<td></td>
</tr>
</tbody>
</table>

**FIG. 2.** QPL$_3$ as a function of root system size. Solid line is fifth degree least squares polynomial fit. Polynomial coefficients are given in Table II.

**FIG. 3.** Total root system conductance as related to leaf area. Solid line is third degree least squares polynomial fit. Polynomial coefficients are given in Table II.

**FIG. 4.** Root area and hydraulic conductivity as functions of plant age. (○): $L_p$. Line fitting $L_p$ is the fifth degree polynomial with coefficients $a = 3.524362 \times 10^{-4}$, $b = -2.245776 \times 10^{-3}$, $c = 9.883224 \times 10^{-2}$, $d = 5.270597 \times 10^{-1}$, $e = -1.507935 \times 10^{-2}$, $f = 3.370160 \times 10^{-4}$, $m = 0.1176470$, and $k = -2.823529$. These coefficients fit the generalized polynomial given in Table II. (□): Root area. Line fitting them was calculated from coefficients given in Table I.
which in the field, are much more accessible. We naturally question, though, how the root properties we measure in the laboratory compare with those in field-grown plants. Unfortunately, we have no parallel data on Phaseolus, but the data of Taylor and Klepper (17) on Gossypium grown in the Auburn Rhizotron (16) provided us with an opportunity for comparison. We would at least like to know if the hydraulic conductivities that we measured on solution-grown plants resembled those grown outdoors in soil.

Taylor and Klepper (17) used a radial flow equation based on the models of Philip (15), Gardner (4), and Cowan (1). The steady-state rate of water uptake per cm length of root, q, in cm$^3$ cm$^{-1}$ day$^{-1}$ was given by

$$q_r = \frac{-2\pi k_s (\psi_1 - \psi_2)}{\ln(r_{cil}\gamma_{root})}$$

where $k_s$ is the soil hydraulic conductivity in cm day$^{-1}$; $\psi_1$ is the pressure potential at the root surface in cm of water; $\psi_2$ is the pressure potential of the soil water in cm at a distance $r_{cil}$ from the center of the root; $r_{cil}$ is the radius of the soil cylinder in cm through which water is moving to the root, and $r_{root}$ is the root radius in cm. Following Taylor and Klepper (17), we moved the inner boundary of the system to the outer edge of the xylem so that $\psi_1$ is replaced by $\psi_{xylem}$ and $r_{root}$ by $r_{stele}$, which we also assumed to be two-thirds of the root radius. For solution-grown plants, like we used, $\psi_2$ will have the value of the nutrient solution, and $r_{cil}$ becomes the root radius, $r$. We may now use our flow measurements to calculate $k_r$, another root system hydraulic conductivity in cm day$^{-1}$.

$$k_r = \frac{r_{stele}}{\ln(r_{root})}$$

Figure 5 shows the results of such calculations plotted as a function of leaf area. As the plant system increases in size, $k_r$ substantially changes. We observed a similar pattern when $k_r$ was plotted against root surface area or root length—an initial increase in $k_r$ followed by a decrease and then a more gradual increase.

The smoothing techniques used in treating some of these data tended to mask, by design, significant rapid changes in some parameters. The rapid changes in $L_p$, which occur during early growth, for example, were all but wiped out (e.g. Figs. 2 and 5). The polynomial coefficients in Table II should be used with the realization that they are only approximations and do not precisely represent plant behavior. Also, extrapolation of the polynomials beyond the limits shown in the figures can be extremely misleading.

The calculations of Taylor and Klepper (17) on the data of Lawlor (9) and Hansen (5) for transpiring wheat plants in solution culture yielded values for $k_r$ of $5.8 \times 10^{-6}$ and $4.0 \times 10^{-6}$ cm day$^{-1}$, respectively. Using the data of Klepper (8) for detached corn root tips, Taylor and Klepper (17) also calculated $k_r = 0.4 \times 10^{-6}$ cm day$^{-1}$. Values of $k_r$ for our solution-grown bean plants ranged from 0.8 to $4 \times 10^{-6}$ cm day$^{-1}$, which compared quite favorably with those of Taylor and Klepper (17). Also, Taylor and Klepper (17) calculated $k_r$ of about $10^{-6}$ for their soil-grown plants. Again, this compares favorably with the values we obtain with our system. It seems, at least on the basis of these comparisons, that solution and soil-grown plants have similar conductivites and that the data for the species examined all seem to fall within the same order of magnitude.

We have similar data for solution-grown soybeans, Glycine max L. mer. (cv. Ransom). Although these data are not as extensive as those for Phaseolus, the patterns of change of $L_p$ and $k_r$ with plant size seem similar. The $L_p$ values encountered ranged from 2.2 to $5.6 \times 10^{-6}$ cm$^2$ s$^{-1}$ bar$^{-1}$, which is somewhat narrower than that for Phaseolus, but we made no measurements on comparably small soybeans, where we encountered the greatest range of values. This same population of soybean plants showed $k_r$ values, using the same assumptions as before, ranging from 1.2 to $3.7 \times 10^{-6}$ cm day$^{-1}$.

**LITERATURE CITED**