Relationships between Root System Water Transport Properties and Plant Size in *Phaseolus*[1]

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ABSTRACT

Root system hydraulic conductivity (L_p) was measured on *Phaseolus* plants of different ages and sizes. Data analysis showed that L_p changed in a complex manner depending on plant size. As the plants increased in size, L_p increased initially then gradually decreased followed by a final modest increase. Values for L_p ranged between 0.8×10^{-6} and 6.1×10^{-6} centimeter per second per bar. Relationships between the root flow per unit leaf area at a pressure differential of 3 bars (QPL_3), as well as the total root system conductance (L_R), and plant size were also examined. Values for QPL_3 varied with plant size, somewhat like L_p. L_R values continuously increased with plant size at rates which depended on the growth rate of the root surface area as well as L_p. Comparison of our data with the root conductivity constant (k_r) of Taylor and Klepper (1975 Soil Sci, 120: 57–67) showed good agreement. The observations on *Phaseolus* were also confirmed for *Glycine*. Values for L_p and k_r of both species were within the same range.

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

$$J_v = L_p (\Delta P - \sigma \Delta \Pi) \qquad (1)$$

where the flow of volume, J_v, is in cm^3 cm^{-2} s^{-1}; the hydrostatic pressure difference ΔP, is in bars, as is the osmotic pressure difference $\Delta \Pi$; σ is the dimensionless reflection coefficient or osmotic efficiency factor; and L_p is the hydraulic conductivity coefficient in cm^3 cm^{-2} s^{-1} bar^{-1}.

Taking into account the fact that the osmotic pressure difference is a function of the total volume flow, J_v, as well as the solute flux, J_s, 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^a, is of the form

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

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 J_v increases and that at high flow rates R^a approximates $1/L_p$. This relationship at high flow rates provides a convenient method for estimating an average L_p value either for an entire root system or for any particular segment of a system.

Values of L_p,[2] 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 L_p 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.[3] 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

[2] Abbreviations: L_p: hydraulic conductivity; QPL: root flow/unit leaf area; QPL_3: root flow/unit leaf area at a pressure differential of 3 bars; L_R: total root system conductance; k_r: 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 L_p, 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, $T = mx_i + k$, was used to improve numerical accuracy where the x_i values were the independent variables and T was the transform. This transformation is simply a scaling procedure which makes the numbers similar in size, thus 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

$$Y = Y_o \exp(k_y t) \qquad (3)$$

where Y is the magnitude of the property of interest at time t, in days; Y_o is the value on the day the seedlings were placed in solution, t = 0; and k_y 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 cm^2 new growth per 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

Table I. *Plant Exponential Growth Curve Constants for Intense (Fast Growing) and Reduced (Slow Growing) Light Conditions*

The constants are to be inserted in equation 3. For example, the projected leaf area at any day t is given as $A_L = A_{L_o} \exp(k_{A_L} t)$. The correlation coefficient is r.

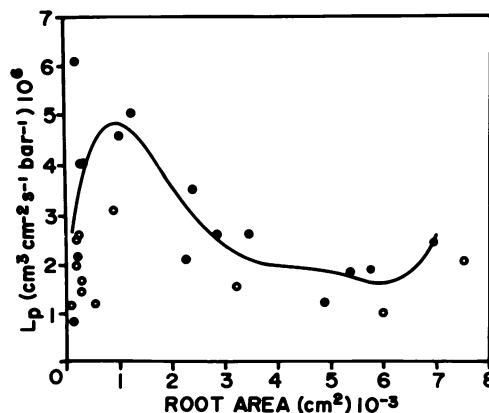| Light	k_{A_L}	k_{A_R}	k_{l_R}	A_{L_o}	A_{R_o}	l_{R_o}
				cm^2	cm^2	cm
Intense	0.1225	0.1138	0.1196	64.8	88.1	747.3
r^2	0.9280	0.9372	0.9377			
Reduced	0.0881	0.0958	0.1033	39.8	23.6	151.4
r^2	0.9798	0.9693	0.9654			

Fig. 1. Relationship between L_p and root system surface area. Solid line is fifth degree least squares polynomial fit. Polynomial coefficients are given in Table II. (●): fast growing plants, (○): slow growing. Line was fit to fast growing plants only.

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 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 (QPL) 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 ΔP of 3 bars and have designated the QPL at this ΔP as QPL_3. Therefore,

$$QPL_3 = Q_3/A_L \qquad (4)$$

where $Q_3 = J_v A_R$ in cm^3 (liquid) s^{-1} at ΔP = 3 bars, and the leaf area A_L is in cm^2.

Table II. *Polynomial Regression Coefficients for the Various Relationships Discussed*

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_p for a root area of 3,000 cm^2, $T = 5.869405$ (10^{-4}) $3,000 - 2.085693$. The coefficients a, b, c, etc. are substituted into the generalized polynomial along with the value of T and L_p is calculated.

| Y:x	L_p:A_R	L_p:l_R	L_p:A_L	QPL_3:A_R	L_R:A_L	k_r:A_L
r^2	0.937	0.940	0.939	0.973	0.985	0.939
a	2.063725X10-6	2.069940X10-6	2.014440X10-6	5.446010X10-6	8.031385X10-3	1.166965X10-6
b	−5.685751X10-7	−5.443276X10-7	−3.314567X10-7	−1.297721X10-6	6.696497X10-4	−2.555112X10-7
c	9.570641X10-7	1.045545X10-6	1.007668X10-6	2.027936X10-6	1.754717X10-4	3.263099X10-7
d	−6.641282X10-7	−6.920519X10-7	−9.057525X10-7	−4.022234X10-7	8.619097X10-4	−2.369057X10-7
e	−1.990028X10-7	−2.215249X10-7	−2.118282X10-7	−3.435373X10-7		−4.658780X10-8
f	1.948762X10-7	2.020778X10-7	2.417375X10-7	1.123040X10-7		6.466731X10-8
m	5.869405X10-4	5.908157X10-5	5.576467X10-4	5.869405X10-4	5.576467X10-4	5.576467X10-4
k	−2.085693	−2.072906	−2.052976	−2.085693	−2.052976	−2.052976
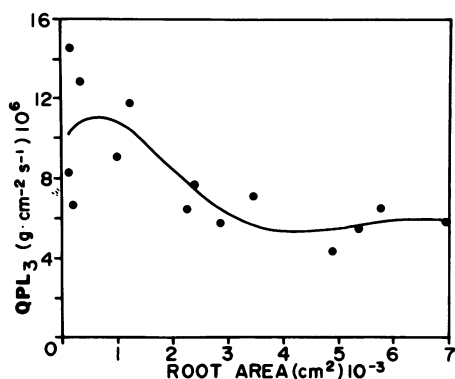
Fig. 2. QPL_3 as a function of root system size. Solid line is fifth degree least squares polynomial fit. Polynomial coefficients are given in Table II.

QPL_3 peaks early followed by a gradual decrease to a fairly steady level (Fig. 2). This pattern, of course, resembles that encountered for the change of L_p with leaf surface area. The significance of the decrease in the second stage is that the older plants must develop a greater driving force to move as much water per unit leaf area through the root system. It is now important to recall that Q was averaged over the projected leaf area and not the total leaf surface area so that QPL_3 will appear high in relation to actual transpirational flux densities. Also, implicit in this calculation is that the total water loss is evenly distributed over the total leaf area. While this may be approximately true for the younger plants, mutual shading and senescence will certainly reduce the demand on the older leaves and alter their response to that demand.

Of more importance to the plant, perhaps, is the relationship between the leaf area and the total root system conductance. The root system conductance (L_R) in cm^3 s^{-1} bar^{-1} may be defined as

$$L_R = L_p A_R , \qquad (5)$$

and the nature of its relationship to leaf area is shown in Figure 3. Probably the relationship may be divided into three phases. The first, which occurs at leaf areas of less than 1,000 cm^2 is steep. This is followed by a lower rate of increase between 1,000 and 5,500 cm^2 beyond which the rate of increase seems to steepen again. Each of these phases may be explained by examining the relationships between the plant age and L_p and A_R. Plant age was chosen simply as the most convenient parameter linking L_p and A_R. Since L_R is the product of L_p and A_R (equation 3), Figure 4 may be interpreted as a plot of the components of L_R. The initial steep increase in L_R (Fig. 3) is almost solely due to the large increase in L_p with age, or leaf area, of the younger plants. As the plants grow larger, the decrease in the average L_p is more than offset by the rapid increase in the total root area (Fig. 4). Thus, the total system conductance continues to increase with age, although at a lower rate than initially. The last phase of rapid

increase in L_R in the oldest plants was due to an increase in L_p, which was amplified by a concurrent rapid increase in root area.

When comparing Figures 3 and 4 it might be helpful to remember that: (a) the leaf area is the same order of magnitude as the root area; and (b) because of the exponential relationship between root and leaf area and age, the form of the relationship between L_R and A_L (Fig. 3) will be compressed toward the origin as compared with the values of L_R versus plant age.

Knowing the relationship between leaf surface area and root system conductance (Fig. 3) or conductivity (Table II) increases our ability to predict water uptake rates from shoot characteristics,
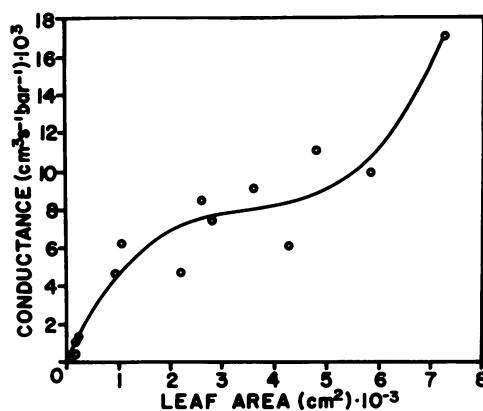

Fig. 3. Total root system conductance as related to leaf area. Solid line is third degree least squares polynomial fit. Polynomial coefficients are given in Table II.
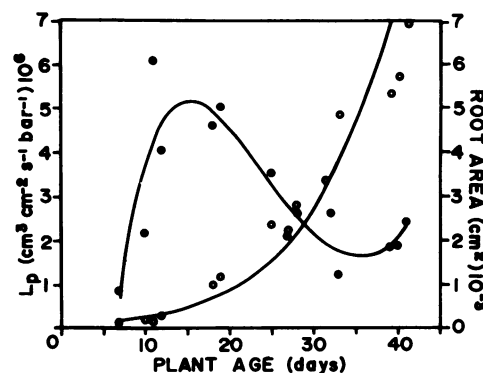

Fig. 4. Root area and hydraulic conductivity as functions of plant age. (●): L_p. Line fitting L_p is the fifth degree polynomial with coefficients $a = 3.524362 \times 10^{-6}$, $b = -2.245776 \times 10^{-6}$, $c = 9.883224 \times 10^{-8}$, $d = 5.270597 \times 10^{-7}$, $e = -1.507935 \times 10^{-7}$, $f = 3.370160 \times 10^{-8}$, $m = 0.1176470$, and $k = -2.823529$. These coefficients fit the generalized polynomial given in Table II. (O): 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_r in cm^3 cm^{-1} day^{-1} was given by

$$q_r = \frac{-2 \Pi k_s (\Psi_r - \Psi_s)}{\ln(r_{cyl}/r_{root})} \qquad (6)$$

where k_s is the soil hydraulic conductivity in cm day^{-1}; ψ_r is the pressure potential at the root surface in cm of water; ψ_s is the pressure potential of the soil water in cm at a distance r_{cyl} from the center of the root; r_{cyl} 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 ψ_r is replaced by ψ_{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, ψ_s will have the value of the nutrient solution, and r_{cyl} becomes the root radius, r_r. We may now use our flow measurements to calculate k_r, another root system hydraulic conductivity in cm day^{-1}.

$$k_r = - \frac{q_r \ln\dfrac{r_{root}}{r_{stele}}}{2 \Pi (\Psi_{xylem} - \Psi_{solution})} \qquad (7)$$

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.

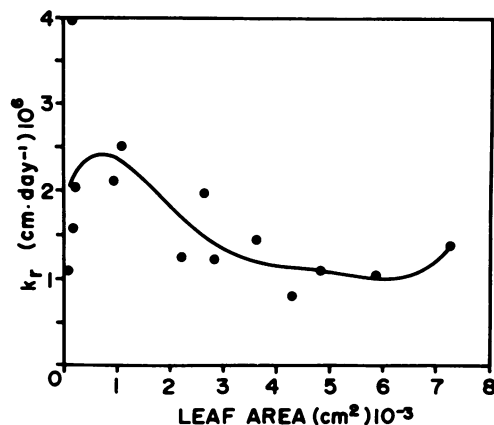The smoothing techniques used in treating some of these data

Fig. 5. Root conductivity calculated after Taylor and Klepper (17) as a function of leaf area. k_r was calculated for the flow rate at $\Delta P = 3$ bars. Points are data; solid line is fifth degree least squares polynomial fit. Polynomial coefficients are given in Table II.

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 × 10^{-6} and 4.0 × 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 × 10^{-6} cm day^{-1}. Values of k_r for our solution-grown bean plants ranged from 0.8 to 4 × 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 conductivities 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. merr. (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 × 10^{-6} cm^3 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 × 10^{-6} cm day^{-1}.

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