Reprinted from *Crop Science*
Vol. 21, Nov.-Dec. 1981, p. 909-913

Analysis of the Components of Area Growth of Bean Root Systems[1]

Edwin L. Fiscus[2]

ABSTRACT

Root and leaf surface areas were measured on green bean (*Phaseolus vulgaris* L. cv. Ouray) plants, with light intensity (photosynthetic photon flux density, PPFD) as the major growth variable, to determine how various sizes of roots are related to water transport and growth rates of whole-root systems. Plants were grown in aerated nutrient solution for 41 days in a greenhouse. Two light intensities were used: 425 and 320 µE m^{-2} sec^{-1}. Leaf area:root area ratios, distribution of root sizes, and the fraction of the total root surface area of each root class were determined. All of these parameters remained stable for plants with leaf and root areas greater than 1,000 cm^2 and they were unchanged by light intensity or growth rate. On the basis of previous data the mean root system hydraulic conductance (Lp) appeared to be keyed to plant size rather than age. The conductance was very low in small plants, increased about sixfold and peaked when the root systems reached approximately 1,000 cm^2 surface area. For plants larger than 1,000 cm^2, when the root size distributions were stabilized, conductance gradually declined, probably because of suberization or some other growth-related factor. Plants grown at lower light intensity showed the same pattern of relationships between root system size, root size distribution, and hydraulic conductance except that the overall Lp was consistently lower for plants of similar sizes.

Additional index words: Root water transport, Root growth model, Root conductance.

MODELING plant water transport characteristics through time requires knowledge not only of the specific root water transport coefficients and how they vary with time, but also of the extent of the system and the distribution of various sizes of roots within the system at any time. It is the purpose of this paper to present root and shoot growth data for *Phaselous* plants grown under two conditions of light intensity (PPFD) and to discuss how the distribution of various sizes of roots and their maturation might be related to the mean water transport coefficients and the growth rates for the whole root system.

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's solution (Robert B. Peters Co., Allentown, PA).[3] The solutions were continuously aerated and the plants were maintained in a controlled temperature greenhouse (27 ± 1.5 C). There was one plant per pot, the pots were topped off daily with tap-water, and the solutions were changed completely once a week. Supplemental sodium vapor lamps provided a mean midday flux density of 425 µE m^{-2} sec^{-1} throughout the experiment. A second set of plants was grown without the supplemental lighting, resulting in a mean midday flux density of only 320 µE m^{-2}sec^{-1}. Since these plants grew slower, they will be called the slow-growing plants, whereas the former will be called the fast-growing plants. Measurements were done on plants from 7 to 41 days after transfer to solution. The projected leaf area of each plant was measured with a L1-COR L13000 area meter.[3] The mean dry matter of the leaves and roots, when determined, was measured after drying them at 70 C.

The root system was visually divided into size classes according to their diameters. Since the classes were visually distinct without optical aids no further processing was necessary. A mean diameter for each size class was determined, then the total length of each class was estimated by Newman's line intersect method (4). The mean diameter and length allowed calculation of the surface area of each class. Total length and surface area for the entire system was obtained by summing the classes.

RESULTS AND DISCUSSION

Table 1 shows that the mean diameters for each of the classes (designated 1 to 4) are distinctive. Standard deviations of these means indicated there was little variation about each mean and virtually no overlap between them. Also, the standard error of the means showed that these mean diameters varied little between plants. It is, therefore, possible to use these mean diameters and the visual separation process in this species to determine the surface area of a whole root system or of a single class of roots. Because the same experimenter made the selections each time, there is no estimate of the possible variability due to individual perception.

In addition to the four root diameter classes indicated in Table 1, there was an additional class that contained the large primary root extending to the base of the stem. These remnants accounted for only a fraction of a percent of the total root surface area and were not included in the analysis.

The detailed analysis was confined to the fast-growing systems, and I shall use the slow growers later for comparison only. Generally, we found that the growth data of the whole plants, as well as their components, could be fit better with a power curve of the type

$$Y = At^B \qquad [1]$$

than with an exponential form, where Y is the magnitude of the property of interest at time t, in days, and A and B are regression constants. The growth constants and cor-

[1]Contribution from USDA-SEA-AR, Fort Collins, Colorado. Received 12 Feb. 1981.

[2]Plant physiologist, USDA-SEA-AR, Irrigation and Soil-Plant-Water Relations Research Group, Crops Research Laboratory, Colorado State Univ., Fort Collins, CO 80523.

[3]Mention of companies or commercial products does not imply recommendation or endorsement by USDA over others not mentioned.

Table 1. Sizes and proportions of the various root diameter classes for the fast- and slow-growing plants. The percent of total root area figures are means for systems > 1000 cm² root area; sd is the standard deviation. Area weighted mean diameters are the mean values for all the systems calculated from equation [4]; n = 14.

Class	1	2	3	4	Area weighted mean
Fast growers					
d (cm)	0.0245	0.0540	0.0831	0.1159	0.0311
SD	0.0010	0.0015	0.0014	0.0030	0.0018
% of total root area	67.6	18.7	13.1	1.0	
SD	6.8	3.3	3.1	0.6	
Slow growers					
d (cm)	0.0254	0.0526	0.0818	0.1126	0.0317
SD	0.0020	0.0010	0.0020	0.0024	0.0027
% of total root area	65.7	21.4	10.1	2.4	
SD	7.1	3.3	3.6	1.5	

Table 2. Regression constants from equation 1 ($Y = At^B$) for fast and slow-growing sets of plants. Mean A_l/A_r values are calculated from all systems > 1,000 cm² root area, not from the 40 day values.

	A	B	r²	40 Day area	Mean A_l/A_r
				cm²	
Fast growers					
Total root area	1.0042	2.3701	0.975	6,293	
Class 1	0.2589	2.6525	0.966	4,598	
Class 2	0.6247	2.0139	0.898	1,052	
Class 3	0.3591	2.0597	0.916	716	
Class 4	0.0680	1.7343	0.481	41	
Projected leaf area	0.4947	2.5706	0.948	6,469	0.981 ±0.081
Slow growers					
Total root area	0.1938	2.5070	0.999	2,013	
Projected leaf area	0.1238	2.6031	0.999	1,832	1.073 ±0.222

relation coefficients are presented in table 2 for the surface area of the whole root system, each individual root diameter class, and for the projected leaf area.

The low r² value for the class 4 root growth curve resulted from the difficulty inherent in the line-intersect method when used on small samples. Class 4 roots, however, constituted a maximum of 6% and generally less than 2% of the total root system so that the relative errors introduced by the ill-fitting class 4 curve will be small. Constants for the total root surface area and for the projected leaf area for the slow-growing series are also given (Table 2). At 40 days of age these plants were only one-third as large as the fast growers.

The growth curves for total root surface area and projected leaf area are shown in Fig. 1. These two regression equations were plotted against each other (Fig. 2), showing that the resultant curve is nearly linear and that for these data a straight line would provide a good approximation of the relationship between them.

If I form the ratio of projected leaf area (A_l) to root area (A_r)

$$A_l/A_r = A_l/\sum_{m=1}^{4} \qquad [2]$$

where A_n is the area of root diameter class n, we can see from Fig. 3 that the ratio A_l/A_r is relatively constant except for plants less than approximately 1,000 cm² surface area. For smaller plants, A_l/A_r increases rather sharply from about 0.6. This initial increase, which is not obvious from Fig. 2 because it is obscured by scale, was caused by the root system development initially lagging behind the expansion of the large primary leaves and then rapidly catching up. As the plants exceeded 1,000 cm² in size, the value of A_l/A_r continued to rise but at a very low rate. The horizontal line in Fig. 3 indicates the mean value of A_l/A_r for plants larger than 1,000 cm² root surface area.

The proportions of the total root surface area that are accounted for by the various diameter classes may be calculated on a percentage basis as

$$P_n = (A_n/\sum_{m=1}^{4} A_n)\,100 \qquad [3]$$

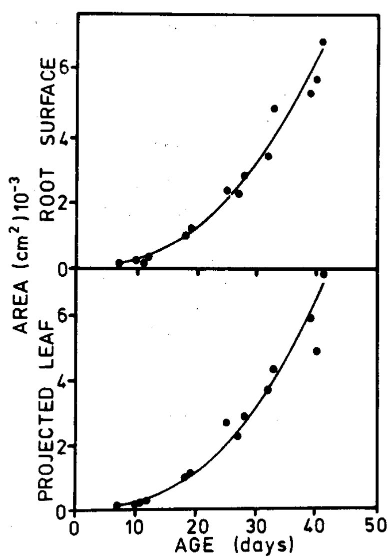

Fig. 1. Growth curves for projected leaf area and total root surface area for the fast-growing set of plants. Solid lines are least squares fits of data. Regression constants are listed in Table 1.

Where n is the diameter class number and P_n is the percentage of the total root area for that class. Figure 4 shows the results of such calculations for the four diameter classes. Class 1 roots are the only ones to show an initial rise from a relatively low 40% initially. The rapid rise is completed above a plant size of about 1,000 cm², and the value continues to rise, only much more slowly. The other three root size classes show, for the most part, more gradual decreases throughout the range. Table 1 shows the mean percentages of the four diameter classes for root systems larger than 1,000 cm².

When the total length and surface areas for each root class in a system are summed, one may calculate an area weighted mean diameter (d) for all roots in a system as

$$d = A_r/\pi \ell_r \qquad [4]$$

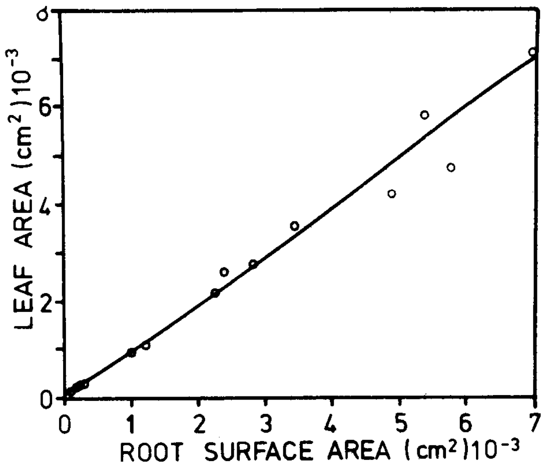

Fig. 2. Parametric plot of projected leaf area and root surface area as functions of time for the fast-growing series. Line results from plotting the leaf and root area curves of Fig. 1 against each other.

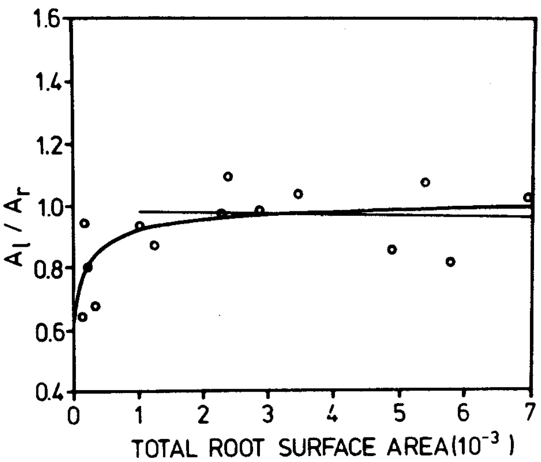

Fig. 3. Projected leaf area:root surface area ratio as a function of root system size for the fast-growing plants. Curve results from solving equations [2] for the various values of leaf and root areas. Straight horizontal line is the mean value for systems > 1,000 cm² root surface area.

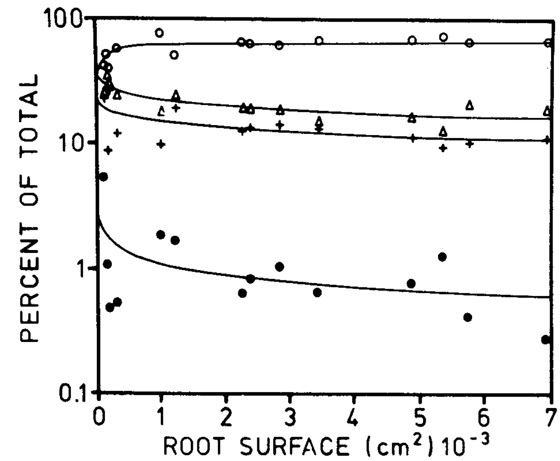

Fig. 4. Percentages of the total root area accounted for by each of the four root diameter classes in the fast-growing set. Solid lines were calculated from equation [3]. Mean percentages for systems > 1,000 cm² are given in Table 1. Open circles, root diameter class 1; triangles, class 2; crosses, class 3; closed circles, class 4.

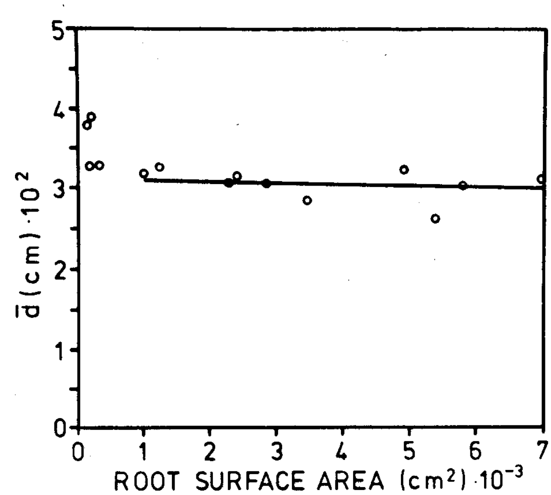

Fig. 5. Area weighted mean diameters for the fast-growing root systems calculated from equation [4]. Regression line is for plants > 1,000 cm² root surface area.

where A_r and l_r are the total area and length respectively of the root system. As seen from Fig. 5, except for small plants, generally less than 1,000 cm² root area, d remains relatively constant. The average value of d for plants whose surface areas were greater than 1,000 cm² is indicated by the regression line and approximates 0.0311 cm. The stability of d over the range of plant sizes encountered reflects the stability of the sizes and proportions of the various classes of roots within the systems. A plot of the root surface area vs. root length (Fig. 6) will yield another figure for d from the slope of the line (slope = πd). In this case d equaled 0.0303 cm. Calculation of the ratio A_r/l_r from Fig. 5 and equation [4] gives 0.098 and from Fig. 6, 0.095 cm² area cm⁻¹ length. Both Fig. 5 and 6 demonstrate that d and A_r/l_r are stable over most of the range of interest.

Since the sizes, proportions of the various classes of roots, and the leaf area-root area ratios remain relatively stable for plants larger than 1,000 cm² root or leaf area, we may simplify the following few calculations by using mean values for systems larger than the specified 1,000 cm².

A mean volume (V_R) for the root systems larger than 1,000 cm² area can be calculated as

$$V_R = dA_r/4 \qquad [5]$$

where A_r is the mean root system area (= 3621 cm²) and d is the average of the area weighted mean diameters in Fig. 5 (0.0311 ± 0.0018 cm). The result is a mean root system volume of 28.15 cm³. Of course, the volume of

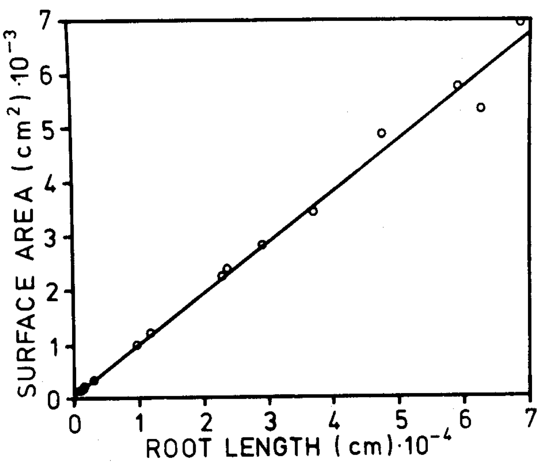

Fig. 6. Root surface area as a function of root length. Solid line is from linear regression with the slope = $\pi\bar{d}$, providing another value for $\bar{d}$.

each root system may be calculated separately and the average taken, with the result that V = 28.38 cm^3. The mean oven dry weight for the same systems is 3.151 g, so a root system mean dry weight density, ϱ_{DW}, of 0.112 g cm^{-3} may be calculated. Because of the difficulty of assessing the proper degree of dryness when obtaining the weight of fresh roots, particularly those grown in nutrient solution, a fresh weight density was not measured. However, it is possible to calculate such a density by assuming that the average tissue water content of the roots is similar to that of the stems and leaves. The mean water content of the stems and leaves were 87.6 and 88.7%, respectively. Taking the average of these two numbers, we can calculate the fraction dry weight, which, when divided into ϱ_{DW}, yields a fresh weight density, ϱ_{FW}, of 0.945 g cm^{-3}. Table 3 summarizes the various mean fresh and dry weights for the roots, stems, and leaves.

The proportions of the various plant parts on a dry weight basis are relatively stable, the leaves constituting over half (55.8%) of the total dry weight. The total for the aboveground parts is 78.1%, resulting in a dry weight shoot to root ratio of 3.57:1.

Having established the relative stability of the sizes, proportions of the various roots, the various shoot:root ratios, and dry matter distributions for the fast-growing plants, we can now compare these figures with the other set grown under lower average light intensities. Since we did not measure dry or fresh weights for these plants, I shall deal only with the geometric parameters and, other than the growth equations, only with means of those systems larger than 1,000 cm^2 root surface area.

First, reference to the regression constants of Table 2 reveals that those plants grown under reduced light grew considerably more slowly. In fact, at 40 days of age the fast-growing plants were about three times as large as the slow-growing plants of the same age. However, Table 1 shows that there is practically no difference in the mean diameters of the four major root size classes between the two sets of plants. Not only are the diameters the same, but neither the area-weighted mean diameters nor the

Table 3. Densities and miscellaneous parameters for the fast-growing plants. Values, except percent of total DW, were calculated from the means for plants > 1,000 cm^2 root area.†

Parameter	Roots	Stems	Leaves
Area (cm^2)	3,621.0	--	3,564.0
Volume (cm^3)	28.153	--	--
Dry weight (g)	3.151	3.208	7.865
Fresh weight (g)	--	25.871	69.605
ϱ_{DW} (g cm^{-3})	0.112	--	--
mg DW cm^{-2} (total area)	0.87	--	1.10
mg FW cm^{-2}	--	--	9.76
Percent of total DW ± SD	21.9 ±2.4	22.3 ±0.9	55.8 ±2.4
ϱ_{FW} (g cm^{-3})	0.945	--	--

† ϱ is density; DW is dry weight; FW is fresh weight.

mean percentage of the total surface area accounted for by each class differed between the sets. Furthermore, the ratio of projected leaf area to root surface area in the slow-growing plants, 1.073 ± 0.222, was not significantly different from the faster-growing plants.

We showed in an earlier paper (2) that, for these same sets of plants, the mean root system hydraulic conductance L_p (= cm^3 water cm^{-2} root area sec^{-1} bar^{-1}) changed with root system size in a complex manner. Very young plants had low L_ps, which increased rapidly to a maximum for plants somewhat less than 1,000 cm^2 root surface area. After this early peak L_p again declined with increasing plant size until a final brief increase was noted in the largest plants. We found that the L_ps for the slower-growing set of plants followed the same pattern but were somewhat lower when plants of similar sizes were compared. The peak L_p appeared to occur at approximately the same plant size for both plant sets. The differences in L_p between the two sets were much more apparent when comparisons were made between plant sets on the basis of age. This led us to conclude that the pattern of change in L_p was keyed more to plant size than age.

Curiously, L_p seemed to peak at about the same time that the proportions and mean dimensions I have been discussing in this paper became stabilized. This led me to speculate that the initial rapid increase in L_p was caused by the rapid proliferation of class 1 roots during early growth (Fig. 4). Once the proportions of the roots became stabilized, the subsequent decline in L_p must have been due to suberization or some other process associated with maturation of the roots. It appears that the effect of lowered growth rate, insofar as affected by light intensity, had very little to do with the average dimensions and distribution of the classes of roots in the systems. Unfortunately, lack of dry weight data makes direct comparison impossible, but the constancy of the shoot:root surface area appears contrary to the results of Brouwer and De Wit (1), who showed substantial increases in the dry weight of *Phaseolus vulgaris* leaves relative to roots under low light conditions. However, for the purposes of modeling water fluxes the areas and not the weights are probably more important because they are fundamental to the control of nutrient and water transport.

The nature of the optimum relationship between the shoot and root system, and the size distribution of the roots, will depend on the specific environment and is expected to vary widely. This might be especially true under conditions where variables such as soil texture, water supply, aeration, or others may considerably alter the aspect of the roots. These environmental variables may be thought of as limiting the expression of the plants' genetic makeup. But since the soil and nutritional variables have been eliminated or controlled, and since the plant relations appear to be relatively stable in this study, they might provide a basis for selection during breeding or at least as a valuable point of reference when examining the response of plant growth to its environment (see Hackett (3) for further discussion of this point).

REFERENCES

1. Brouwer, R. and C.T. De Wit. 1969. A simulation model of plant growth with special attention to root growth and its consequences. p. 224-244. *In* W.J. Whittington (ed.) Root growth. Butterworths, London.
2. Fiscus, E.L., and A.B. Markhart III. 1979. Relationships between root system water transport properties and plant size in *Phaseolus*. Plant Physiol. 64:770-773.
3. Hackett, C. 1969. Quantitative aspects of the growth of cereal root systems. p. 134-147. *In* W.J. Whittington (ed.) Root growth. Butterworths, London.
4. Newman, E.I. 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3, 139-145.