

9 Belowground costs: hydraulic conductance

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There are three traditionally recognized functions of root systems: anchorage, water absorption, and procurement of mineral nutrients. More recently, production of growth regulators has been recognized as another important root function. In terms of survival advantage, the extremely high degrees of interaction and interdependence of these functions make it impossible to state that any one is more important than any other, or even that such a question really has any meaning. I shall confine my remarks to the water absorption function and arbitrarily treat that function as the sole benefit derived by a plant from its root system. It should be apparent, however, that because the other functions are also dependent on system size, most of the growth analysis will be relevant to them as well. Further, I shall not attempt a comprehensive review of this subject but shall use data primarily from my own laboratory on *Phaseolus vulgaris*, because similarly extensive data are difficult to find.

This chapter will be divided into two sections, the first dealing with root conductance as the benefit, and the second dealing with the cost to the plant of producing that water supply system. Specifically, the ultimate aim of this chapter is to estimate the cost of a unit of hydraulic conductance.

Benefits

Theory of hydraulic conductance

It has long been recognized that the flux of a fluid through a system (roots, pipes, etc.) can be described as the product of a driving force and some sort of conductance. The simplest kind of system is one in which the conductance is constant and the force-flux relationship passes through the origin. Unfortunately, root systems are generally not that simple. The main complicating factor arises because root systems accumulate solutes of various kinds at the expense of metabolic energy, thus creating osmotic gradients within the system. The relationships between

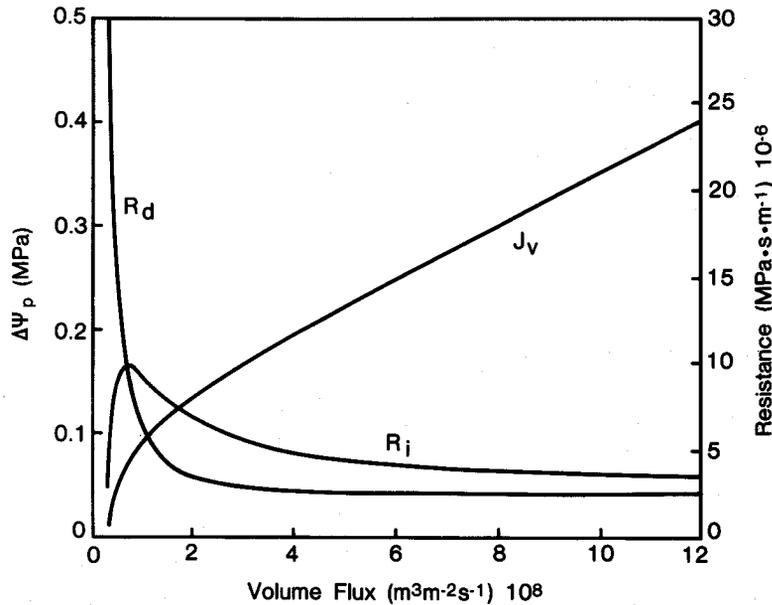


Figure 9.1. Total volume flux and instantaneous and differential resistance functions for a typical *Phaseolus* root system. $L_p = 4 \times 10^{-7} \text{ m s}^{-1} \text{ MPa}^{-1}$; $J_v^* = 1.5 \times 10^{-6} \text{ mol m}^{-2} \text{ s}^{-1}$; $\omega = 1 \times 10^{-6} \text{ mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$; $\sigma = 0.97$; $\Pi^e = 0.11 \text{ MPa}$.

the osmotic gradient and the hydrostatic gradient, usually the major driving force, are flux-dependent, so that depending on particular circumstances, the two forces may aid or oppose each other. The result of these interactions is a system with characteristics similar to those in Figure 9.1, which shows conductance (not a conductance coefficient) directly related to the flux rate. A great many problems arise in the interpretation of these relationships that are directly traceable to inconsistent and imprecise use of terminology, especially that related to conductance and resistance. For example, in discussing pressure- or tension-driven radial flow through roots, there are many ways in which the term "conductance" can be used in a single flux equation. Throughout the rest of this section I shall attempt to clarify this terminology and then discuss the interpretation of other relevant transport coefficients to define more clearly the water transport characteristics of a *Phaseolus* root system under different circumstances.

Water flow through whole root systems can be described adequately by the model we proposed several years ago (Fiscus 1975). This model was based on the well-known membrane transport relationship

$$J_v = L_p(\Delta P - \sigma\Delta\Pi) \quad (9.1)$$

where J_v is the volume flux in $\text{m}^3 \text{m}^{-2} \text{s}^{-1}$, ΔP is the pressure difference in MPa, $\Delta \Pi$ is the osmotic pressure difference in MPa, σ is the reflection coefficient or the osmotic efficiency, and L_p is the hydraulic conductance coefficient of the system in $\text{m}^3 \text{m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$. Please note that in order to make comparisons with the previous literature, the numerical value of L_p as given here is 0.1 times the value in $\text{cm}^3 \text{cm}^{-2} \text{s}^{-1} \text{bar}^{-1}$, a frequently used set of units. Also, J_v in $\text{m}^3 \text{m}^{-2} \text{s}^{-1}$ is 0.01 times the value in $\text{cm}^3 \text{cm}^{-2} \text{s}^{-1}$.

The relationship between xylem tension, included in ΔP , and water absorption is frequently nonlinear (Mees and Weatherley 1957; Lopushinsky 1961, 1964; Kuiper and Kuiper 1974; Fiscus 1975; Fiscus and Kramer 1975; Markhart et al. 1979; Sands et al. 1982). By examining the osmotic component of the driving force, we can discover possible reasons for the nonlinearity (Dalton et al. 1975; Fiscus 1975). If, for convenience, we use the van't Hoff approximation, we can write the osmotic difference in equation (9.1) as

$$\Delta \Pi = RT(C^o - C^i) \quad (9.2)$$

where R is the gas constant, T is the temperature in degrees Kelvin, and the C 's are the concentrations of solutes in mol m^{-3} outside the root and inside the xylem, respectively.

An important feature of equation (9.2) is that C^i is an inverse function of J_v and a direct function of J_s , the total solute transport rate, so that

$$C^i = J_s / J_v \quad (9.3)$$

Therefore, C^i , as a component of the driving force, is itself determined by the total volume flux.

We can further discover the roles of various solute transport components by examining the total solute flux relationship

$$J_s = \bar{C}_s(1 - \sigma)J_v + \omega\Delta\Pi + J_s^* \quad (9.4)$$

Equation (9.4) separates the total solute flux into three components, convective, diffusive, and active, each with its own distinctive coefficient.

Functional interpretation of parameters

The relationships in equations (9.1) and (9.4) were developed for and strictly apply to single-membrane systems, which the root is almost certainly not. And although we have repeatedly emphasized the operational interpretation of these relationships, some controversy has arisen from my use of the coefficients. Perhaps it would have been better to have altered them to indicate more clearly their functional nature when applied to roots. Not having changed the notation in the past, I shall take some

space here to clarify my use of these coefficients. Throughout, however, remember that the transport of any substance in any system can be described as the sum of the convective, diffusive, and active transport components, whether or not a membrane is involved. So, even if the notation were altered, the flux relationship would resemble equation (9.4) in form.

Convective solute flux. The \bar{C}_s term is usually taken as the average concentration of solutes across the membrane, with the restriction that the difference be small (Katchalsky and Curran 1974). Clearly, applying \bar{C}_s to flow across a root can be very risky, because (1) the root is a multiple-membrane system, (2) the concentration difference may be quite large, and (3) it is only under special circumstances that we can expect to estimate with any degree of reliability the actual concentration difference. For these reasons, we found \bar{C}_s to be inappropriate for describing convective solute fluxes through roots. We concluded that we really need a more functional definition of the convective term, one that will tell us how much of the external solutes are being conveyed to the root xylem as a result of being dissolved in the water that is moving in that direction. Convection in an open system can be described simply as the product of the volume flux and the concentration. However, when the solution crosses a barrier that in any way impedes the passage of one substance relative to the other, such as a semipermeable membrane, then we need a coefficient to describe the degree of retardation or filtration. The traditional reflection coefficient σ , just as it appears in equation (9.4), serves this purpose. But \bar{C}_s will now logically be replaced by C^o (Fiscus 1977), the external solute concentration, because we are interested only in how much of the solute passes the barrier with the water. In this way, we need not worry about the specific features of the barrier (or barriers) involved, but can describe it in terms of a measured reflection coefficient. The first term in equation (9.4) will therefore be altered to read $C^o(1 - \sigma)J_v$. Clearly, when $\sigma = 1$ there is no convection, and when $\sigma = 0$ the solute flux will not be restricted to any degree, an interpretation consistent with the development of the concept of the reflection coefficient, but one that must be kept carefully in proper context.

Diffusive and active solute flux. The diffusive and active components of J_s are also interpreted functionally, that is, as the sum of unknown processes operating somewhere between the exterior of the root and the xylem. J_s^* can be further expanded both by the usual Michaelis-Menten kinetics for isothermal conditions and by enlarging that treatment to span a range of temperatures, because temperature is an important environ-

mental variable affecting not only J_s^* but also L_p (Kramer 1942, 1948; Kuiper 1964; Markhart et al. 1979). However, these enhancements to the J_s^* term are beyond the scope and purpose of this chapter.

The coefficient of solute mobility in the membrane, ω , is in the nature of a diffusion coefficient. As such, it, too, is expected to vary with temperature, both because of the Q_{10} for diffusion and because of temperature-induced alterations in the fluidity of the cell membranes (Markhart et al. 1979; Markhart 1982).

Combined volume and solute flux

Substituting the modified equation (9.3) into equation (9.2) leads to the result (Fiscus 1977)

$$J_v = L_p \left[\Delta P + \frac{\sigma RT (J_s^* - \sigma C^o J_v)}{J_v + \omega RT} \right] \quad (9.5)$$

For values of L_p , σ , J_s^* , and ω determined experimentally (Fiscus 1977), a typical flow curve for a *Phaseolus* root system looks like Figure 9.1. Equation (9.5), from which Figure 9.1 is calculated, predicts several important features of this force-flux relationship. First, the overall flux curve will be nonlinear initially but will approach a limiting slope at high flow rates. This type of relationship has been demonstrated repeatedly for *Phaseolus* (Kuiper and Kuiper 1974; Fiscus 1975, 1977, 1981a), *Glycine* (Newman et al. 1973; Markhart et al. 1979), *Lycopersicon* (Mees and Weatherley 1957; Lopushinsky 1961, 1964), *Zea* and *Helianthus* (Newman et al. 1973; Boyer 1974), *Brassica* (Markhart et al. 1979), and *Pinus* (Sands et al. 1982). The limit of the slope is L_p , actually $1/L_p$ in the case of Figure 9.1. This limit will be discussed more fully later under the heading of the differential resistance. The second prediction is that the intercept of the curve at $\Delta P = 0$ is largely determined by J_s^* and is relatively insensitive to changes in L_p . A third and very important prediction is that extrapolation of the linear portion of the curve back to the ordinate should result in an intercept equal to $\sigma^2 \Pi^o$. That this does not usually happen was pointed out (Newman 1976) and forms the basis of the only serious criticism of the model.

Intermediate osmotic compartment. We attempted to address Newman's criticism and decided that there were two possibilities that had to be considered: (1) an external boundary-layer buildup that would increase Π at the root surface above the value in the bulk solution and (2) an intermediate compartment, although not with the characteristics he then proposed, acting in opposition to the flow. We concluded that the former explanation was unsatisfactory because the linear portion of the $J_v - \Delta P$

curve typically continued linearly up to at least 0.7 MPa (unpublished data). If boundary-layer buildup were a problem, we would expect to reach a point of diminishing slope long before that level of force (or flux: $J_v = 20 \times 10^{-8} \text{ m s}^{-1}$). The most likely explanation, at this time, involves an intermediate compartment, some of the characteristics of which we discovered while searching for explanations for certain growth regulator effects. We were able to show that a pool of solutes existed in *Phaseolus* roots that could be mobilized by abscisic acid (ABA) treatment (Fiscus 1981a). There appeared, in fact, to be two pools of sequestered solutes (Fiscus 1983), one of which, possibly the cytoplasm, had an ABA mobilization threshold at or below $10^{-10} \text{ mol ABA cm}^{-2}$ root surface, and the other, possibly the vacuole, with a threshold of $10^{-7} \text{ mol ABA cm}^{-2}$. The details of these pools are not essential now, but the important feature observed was that when the ABA treatments occurred and the pools of solutes were mobilized, there was a simultaneous increase in volume flux in proportion to the amount by which the expected intercept (just discussed) and the measured intercept differed. Thus, it appeared that the low-threshold pool was acting in opposition to the pressure-induced flow, and when that pool was mobilized, the entire $J_v - \Delta P$ curve was shifted by an amount that made it conform to Newman's intercept test. It appears, then, that there is an intermediate compartment between the root surface and the xylem containing normally nonmobile solutes that are asymmetrically distributed toward the interior of the root. This pool of solutes must be of a relatively stable size, because the intercept does not appear to shift much during the course of an experiment in which ABA is not involved. The implications of this for the model are quite simply that equation (9.5) will require that the bulk external osmotic pressure be replaced by an effective pressure (Fiscus 1977). Also, bearing in mind our discussion of the reflection coefficient, we shall need to use the actual bulk osmotic pressure when calculating that parameter from the limiting internal concentration as J_v approaches infinity (Fiscus 1977). Making these interpretational adjustments to equation (9.5) brings it very closely into line with experiment.

High fluxes and steady states. Finally, there are two very important points relating to the experimental determination of the parameters in equation (9.5): Almost all parameters need to be determined at high fluxes (Fiscus 1975, 1977, 1983; Markhart et al. 1979) and under steady-state conditions. It is only at high fluxes that we can expect to minimize artifacts that are largely due to our inability to determine concentrations deep within the root. Also, it is only at the steady states of volume and solute fluxes that we can minimize other artifacts, particularly hysteresis

effects (Kuiper and Kuiper 1974; Fiscus 1977) that are due to loading and unloading of solutes from the tissues adjacent to the conducting pathway. Because the exchange of ions between these tissues is slow, it may take several hours and a total volume turnover of 10 times (Markhart 1982; Fiscus 1983) to bring a root system to the steady state with respect to both fluxes.

Comparison of L_p values. Another question that is frequently raised concerning the model is how our solution-grown root systems compare with those grown in soil. Certainly they differ in appearance, the solution-grown ones being somewhat thinner and of a more uniform diameter. Functionally, however, as nearly as we can tell, with regard to their water conduction characteristics they act very much the same. The evidence for this is currently derived by comparison with the literature and is indirect. Conductance values calculated for soil-grown plants from data in the literature reveal that *Phaseolus*, *Glycine*, *Helianthus*, *Zea*, and *Gossypium* all fall within the same range: 0.8×10^{-7} to $6.1 \times 10^{-7} \text{ m}^3 \text{ m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ (Fiscus 1983). This is the entire range of values previously observed (Fiscus and Markhart 1979) for solution-grown *Phaseolus*. Another opportunity for comparison comes from a recent article (Fiscus et al. 1983) in which we estimated L_p in a model system designed to explain some peculiarities of whole-plant water transport reported by many authors. We estimated L_p as $4.3 \times 10^{-7} \text{ m}^3 \text{ m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$, a value that with minor refinements will provide a good fit to the whole-plant data (Boyer 1974) on which the estimates are based.

In addition to these comparisons there are theoretical reasons for believing that L_p values determined in a root-system pressure chamber are more realistic than those determined by osmotic methods or at low flux rates. The main reason for this is that the effects of both the intermediate osmotic compartment and any standing gradients in the system may be minimized at high fluxes. The real problem that we are trying to overcome at high fluxes is our ignorance of the axial distribution of the major parameters of the model. However, the experimental approach we use allows us to conclude that the values of L_p measured in the pressure chamber are accurate and relevant to whole-plant water flow models.

Differential resistance

Given that we can determine reliable values of L_p and can show how these values vary as the plant grows (Fiscus and Markhart 1979), we still have the problem of relating L_p to whole-plant water flow or whole-plant or even organ resistance or conductance. We would also like to relate

the various plant organ conductances and resistances to each other and to an overall plant conductance or resistance.

In a recent article, we discussed the concepts of instantaneous and differential resistances and conductances (Fiscus 1983) and concluded that the instantaneous concept, based on the Ohm's law analogy, was not of very great utility in dealing with plant water flow. These concepts differ in that the instantaneous resistance (based on a misinterpretation of Ohm's law) is simply the ratio of the force to the corresponding flux, whereas the differential resistance is the slope of the force-flux curve. For a system in which the force-flux relationship is linear and passes through the origin, these two concepts are interchangeable. However, many plant transport systems are not linear in nature, and their force-flux relationships do not pass through the origin. Figure 9.1 provides a useful example of how these concepts compare. The three curves on the graph are the volume flux, J_v , the differential resistance, R_d , and the instantaneous resistance, R_i . It is clear from examining the two resistance curves that experimental interpretation can vary considerably depending on which concept is used. In the one case (R_i), the resistance is seen to increase with the flux to a peak, after which point it decreases, slowly approaching the actual slope of the J_v curve as a limit. Because we have some intuitive notion about the meaning of the word "resistance," we might spend considerable time and effort searching for the cause of this outrageous behavior. In the other case (R_d), however, the resistance is seen to decrease continuously with increasing flow. In this instance, however, we can immediately discover the cause of the resistance change by examining the transport function and its derivative. For example, solving equation (9.5) for ΔP gives us

$$\Delta P = \frac{J_v}{L_p} - \frac{\sigma RT(J_s^* - \sigma C^o J_v)}{J_v + \omega RT} \quad (9.6)$$

which describes the force-flux curve in Figure 9.1. The slope of this curve, the differential resistance, is

$$R_d = \frac{d\Delta P}{dJ_v} = \frac{1}{L_p} + \frac{\sigma RT(J_s^* + \sigma \omega \Pi^o)}{(J_v + \omega RT)^2} \quad (9.7)$$

which is the curve labeled R_d in Figure 9.1. Immediately from equation (9.7) we can see that the hydraulic conductance coefficient L_p is only part of the resistance term, which is seen to decrease toward $1/L_p$ as a limit while the volume flux increases.

At this point it may be useful to recap the various uses of the terms "resistance," "resistivity," "conductance," and "conductivity." We have described briefly the instantaneous and differential resistances, and by the

same reasoning there must also be differential and instantaneous conductances. Also, there is the hydraulic conductance coefficient L_p , which when applied to root systems may be modified, depending on which root dimension we want to relate to the water flux. Any of the dimensions may be useful under different conditions, and they are equally correct as long as they are clearly defined. Thus, we can with equal validity have a flow based on unit area, unit length, or even unit volume if we wish. The real problem arises when the concepts are mixed indiscriminantly, such as measuring the instantaneous resistance and then equating it with $1/L_p$, however defined.

Also from equation (9.7) we can draw some inferences about how R_d might vary with changes in all the parameters of the equation. The equation does in fact suggest which parameters might be most profitably manipulated to achieve some desired end. For instance, in the past it was common practice to use natural root-pressure exudation rates ($\Delta P = 0$) to determine L_p values. Notwithstanding the standing gradient effects, it is easy to show (Fiscus 1975, 1977, 1981a) that the volume flux rates in such a system are determined almost entirely by J_i^* and should be very insensitive to changes in L_p over a wide range.

Without belaboring the point any further, we can conclude this section by stating that in addition to providing us with experimentally testable hypotheses, the differential resistance concept also provides a common link that joins transport processes throughout the whole plant (Fiscus et al. 1983) and allows a unified physical treatment of diffusive, convective, and active transport processes in the liquid and vapor phases of the entire system.

Having defined the various kinds of conductances and resistances and briefly indicated their use, we shall now make some estimates concerning the cost to the plant of producing these facilities for water uptake and transport.

Costs

In earlier work we found that the *Phaseolus* root system could be divided into four very distinctive size classes according to external diameter (Fiscus 1981b). The variability in diameters was such that there was practically no overlap between the size classes, and it became a relatively easy, though tedious, task to measure the contribution of each class to the total root surface area. We also found that once the plants had reached a size of about 0.1 m² total root area, the proportions of the various size

classes remained relatively constant. Because of this constancy, we were able to use average values for plants larger than 0.1 m² for many of our calculations and for some purposes will continue to do so here.

Growth model

Growth of the projected leaf area, the area of each root size class, and the total root area can be described by an exponential sigmoid function of the form

$$A = \frac{a}{1 + be^{nt}} \quad (\text{m}^2) \quad (9.8)$$

where t is the time in days, a is the maximum area, and b and n are growth coefficients given in Table 9.1. Although we used a simple power function in previous work, it is not generally considered a good growth model because it does not account for maturity and senescence effects. So we replace the power function with equation (9.8) and fit our previous data (Fiscus 1981b) to that function.

Although the root surface area is the geometric parameter we think most relevant to determining rates of water absorption, accounting for the energy necessary to produce that surface area requires some relationship between rates of dry-matter and surface-area accumulation. We can start with the fundamental relationships

$$M = \rho V \quad \text{and} \quad V = \frac{Ad}{4} \quad (9.9)$$

where M is the dry matter in g, ρ is the dry weight (DW) density in g dry matter [cm³ fresh volume]⁻¹, V is the volume in cm³, A is the surface area in cm², and d is the mean diameter for each root class or for the whole root system in cm. Values for ρ and d are taken from previous work (Fiscus 1981b). Combining relationships (9.8) and (9.9), we get for M , in g, as a function of time,

$$M = \frac{\rho d}{4} A = \frac{\rho da}{4(1 + be^{nt})} \quad (9.10)$$

and for the rate of dry-matter accumulation,

$$\frac{dM}{dt} = - \frac{\rho dabne^{nt}}{4(1 + be^{nt})^2} \quad (9.11)$$

in g DW day⁻¹.

From the relationships (9.9), simple geometry allows us to form the area/dry-matter ratio

$$A/M = 4/\rho d \quad (9.12)$$

Table 9.1. Geometric dimensions and energy and mass relationships for solution-grown *Phaseolus* root systems^a

Size class	Diameter (cm)	A/M (cm ² g ⁻¹)	% of class 1	A/E _b (cm ² kJ ⁻¹)	a	b	n	r ²
1	0.0245	1458	100	91.1	0.560	130	-0.15	0.98
2	0.0540	661	45.3	41.3	0.155 ^b	80	-0.13	0.89
3	0.0831	430	27.5	26.9	0.108 ^b	30	-0.10	0.92
4	0.1159	308	21.1	19.2	0.128	20	-0.07	0.61
Total	0.0311	1148	78.7	71.7	0.90	85	-0.13	0.97
Leaf area (m ²)					0.79	125	-0.15	0.96

^a The average energy content of the dry matter is 16.01 kJ [g DW]⁻¹. Note that the coefficients *a*, *b*, and *n* give the areas in m².

^b Coefficients *b* and *n* were fitted for a value of *a* picked to be consistent with the size class proportions discovered earlier (Fiscus and Markhart 1979).

which allows us easily to see that the smallest size class makes by far the most efficient use of dry matter in the production of surface area. The figures for each size class and the total are summarized in Table 9.1, where for purposes of comparison the *A/M* ratios are given as percentages of class 1 roots.

Required energy. To obtain an estimate of the total energy required to build and maintain the root water transport capacity for the plant, we must consider three factors: the energy content of the building blocks (*E_b*), the energy required to assemble them into cellular structures and to drive cell expansion (growth respiration, *R_g*), and the energy required to maintain the structures (maintenance respiration, *R_m*). Several assumptions and extrapolations are necessary to sort out these various components of energy input. As a starting point we shall assume a constant rate of maintenance respiration equal to 319 J [g DW]⁻¹ day⁻¹ (Penning de Vries 1975a) (equal to 20 mg glucose [g DW]⁻¹ day⁻¹). Given *R_m* and assuming that *R_g* (J [g DW]⁻¹ day⁻¹) is also constant, we can estimate a value for *R_g* from Figure 9.2. This figure is the oxygen consumption rate for an entire *Phaseolus* root system measured diurnally at approximate hourly intervals. An estimate of the integral over 24 hr divided by time provides us with an average for the total respiration rate for this period, assuming a respiratory quotient of 1. Calculations based on this figure are given in Table 9.2, where the most significant number for our purposes is *R_g*.

Now we shall turn our attention to the energy content of the assembled structures. To do so requires some assumptions about the proportions of

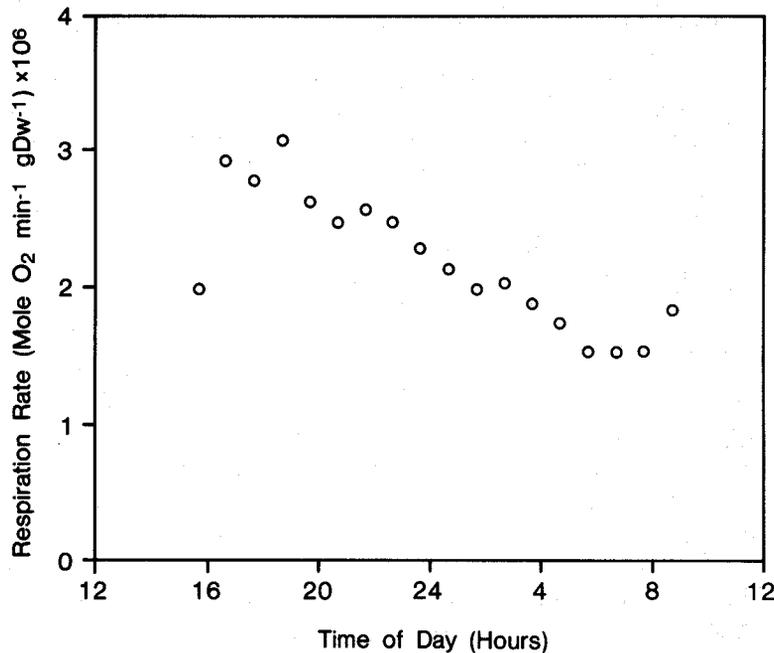


Figure 9.2. Diurnal changes in respiration rate for an entire *Phaseolus* root system. The plant was 18 days old, with a leaf area of 0.14 m² at the beginning of the experiment.

proteins, lipids, and carbohydrates in the tissues. Because most plant vegetative tissues are composed of 1% to 5% nitrogen (Bonner and Galston 1952), we assume a value of 3%, and that this is mostly protein, which on average is 16% N. This gives us a protein content of about 19% of the dry weight. Lipids generally compose 5% or less of the dry weight of vegetative organs (Bonner and Galston 1952), and so we also choose an average value of 3% for that component. Mineral ions may compose a further 5% of the dry weight but will be considered to be an integral part of the system and as such not possessed of structural energy in the same sense as we are considering the other components. The remainder of the dry weight (73%) is assumed to be carbohydrate.

Table 9.3 summarizes calculations of the average energy content of the dry matter based on standard bomb-calorimeter combustion values for lipid, protein, and carbohydrate (White et al. 1959) and the foregoing assumptions regarding composition.

Because part of the growth energy finds its way into the structure of the system in the form of chemical bonds, linking carbohydrate and protein subunits, for example, we must somehow account for the relationship

Table 9.2. Respiratory components and other relevant data for the *Phaseolus* root system used in Figure 9.1

		Total glucose equivalents (mg)	Energy
Total consumed	$2.61 \times 10^{-3} \text{ mol O}_2$	78.4	1,249 J
Dry weight	0.88 g		
dM/dt	0.109 g day^{-1}		
Respiration (maintenance) (R_m)	20 mg glucose [g DW] $^{-1}$ day $^{-1}$	17.6	319 J [g DW] $^{-1}$ day $^{-1}$
Respiration (growth) (R_g)	558 mg glucose [g DW] $^{-1}$	60.8	8,888 J [g DW] $^{-1}$

between the energy contents of the building blocks and the final structure and the respiratory energy necessary to assemble the components. To this end we can start by expressing the total energy of the system (E_s) as

$$E_s = E_b + E_a \quad (9.13)$$

where E_a is the energy incorporated into the structure during assembly of the building blocks, and E_b is the energy content of the building blocks.

As a first attempt to separate these components we shall examine the situation with regard to the carbohydrates, because they constitute the largest percentage of the dry matter, and specifically we shall examine cellulose, because that is frequently the largest carbohydrate component present.

Taking the combustion value for glucose as 15.69 kJ g^{-1} and that of cellulose as 17.58 kJ g^{-1} (Crampton and Lloyd 1959), we can see an increase in energy of the cellulose over the glucose building blocks of 1.9 kJ g^{-1} or about 12%. We shall now proceed under the assumption that a similar figure applies to assembly of the lipid and protein components. This may not be an especially good assumption, but the proportions of lipid and protein are relatively small compared with carbohydrate, and so the error may be minor.

Although the 1.9 kJ g^{-1} just calculated for E_a is energy we may measure as part of E_s , in order to separate it from the respiratory energy expenditures from whence it came we must subtract it from E_s and deal only with E_b when further considering rates of energy incorporation into dry matter. That is, E_a is accounted as part of R_g rather than as part of E_s . Leaving E_a as a part of E_s , for accounting purposes, would require that we know the efficiency of incorporation of respiratory energy into dry matter. Al-

Table 9.3. Assumed composition and energy content for typical vegetative tissues

Component	Fraction	Combustion value (kJ g ⁻¹)	Tissue energy content (kJ [g DW] ⁻¹)
Protein	0.19	22.18	4.21
Lipids	0.03	38.92	1.17
Minerals	0.05		
Carbohydrates	0.73	17.16	12.53
Total	1.00		(E _b) 17.91

though the latter approach to the problem is just as viable, we choose the former as being more convenient at this time.

Carrying out the calculation indicated by equation (9.13) gives us an energy value of 16.01 kJ [g DW]⁻¹ for the building blocks (E_b). It is of interest to note that this value is within 2% of the energy value for glucose and within 2% of the average energy value for plant dry matter cited by Gates (1980). This fact may or may not be strictly fortuitous, but in any case this was the number used to calculate A/E_b in Table 9.1.

Direct PAR. Finally, we shall compare the energy required for the establishment and functioning of a root system to the total amount of radiant energy, in the form of direct PAR, available to (incident on) the plant. For simplicity we shall consider only the direct radiation and leave as an exercise for the reader the more refined calculations.

Measurements of the projected canopy area provide us with a good measure of the leaf area exposed to direct radiation. Figure 9.3 is a plot of the relationship between the shadow area of the canopy and the total projected leaf area for a small population of plants covering the range of sizes of interest to us. The linear correlation is quite good, especially for plants larger than 0.1 m², so that the area exposed to direct radiation at any time can be calculated by combining the equation for Figure 9.3 and equation (9.8) to yield

$$A_{ID} = k + \frac{ma}{1 + be^{at}} \quad (9.14)$$

where A_{ID} is the shadow area (leaf area exposed to direct radiation), k and m are the intercept and slope, respectively, in Figure 9.3, and a and b are as before.

The daily average integral of the light intensity for the relevant green-

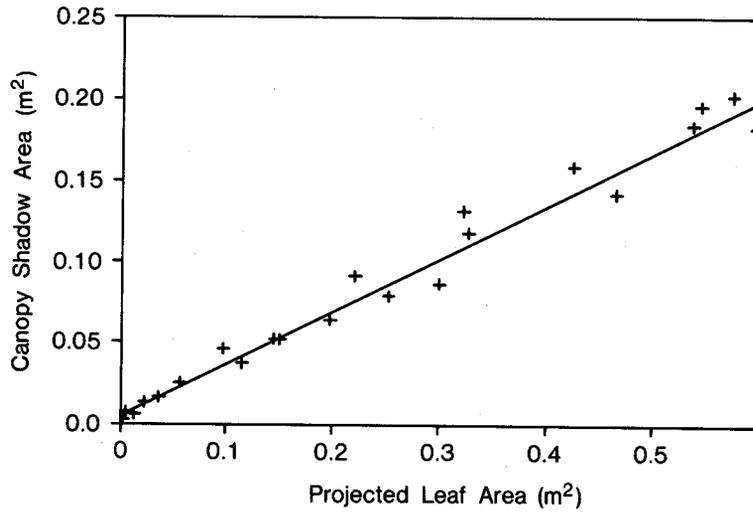


Figure 9.3. Measured canopy shadow area as a function of total projected leaf area used to calculate the direct radiation. $A_{ID} = k + mA_i$; $k = 4.603 \times 10^{-3}$; $m = 3.319 \times 10^{-1}$; A_i is given by equation (9.8).

house growth conditions was $12.4 \pm 1.5 \text{ mol m}^{-2}$, about 20% of the outdoor summertime maximum for this location. Using the conversion factor of $4.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ of $\text{PAR} = 1 \text{ watt m}^{-2}$ (Biggs and Hansen 1979) yields an average daily energy incident on the leaves of 2.7 MJ m^{-2} . The total energy incident on the plant in the form of direct PAR in MJ day^{-1} is the product of this figure and the leaf area exposed to direct radiation:

$$\frac{dE_i}{dt} = A_{ID}(2.7 \text{ MJ m}^{-2} \text{ day}^{-1}) \tag{9.15}$$

Efficiency of energy use. The efficiency with which direct radiation is used to form a root system can be defined as the ratio of the rate of energy incident on the leaves (dE_i/dt) to the rate of total energy usage by the root system (dE_T/dt). In this sense, E_T is the total of the energy of the building blocks used to make the system (E_b), the growth energy required to assemble those blocks into roots (R_g), and the energy necessary to maintain the existing system (R_m). We can therefore write for the daily rate of energy use

$$\frac{dE_T}{dt} = E_b \frac{dM}{dt} + R_g \frac{dM}{dt} + R_m M \tag{9.16}$$

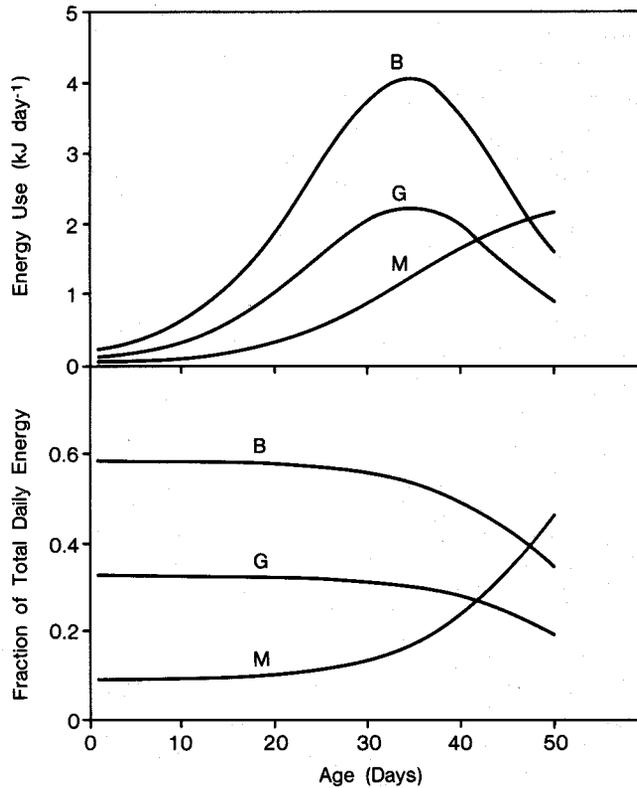


Figure 9.4. Proportions of the energy content and growth and maintenance energy expenditures as functions of plant age as calculated from equation (9.16). B: $E_b (dM/dt)$. G: $R_g (dM/dt)$. M: $R_m M$.

Rearrangement and substitution of equation (9.10) for M and equation (9.11) for dM/dt gives the total daily rate of energy consumption by the root system as

$$\frac{dE_T}{dt} = -\frac{\rho d a b n e^{nt}}{4(1 + b e^{nt})^2} \left[E_b + R_g - \frac{R_m(1 + b e^{nt})}{b n e^{nt}} \right] \quad (9.17)$$

where R_g and R_m are the growth and maintenance respiratory coefficients given in Table 9.2.

The three components of equation (9.16) were calculated and plotted in Figure 9.4. The first term, dE_b/dt , is the rate of incorporation of new material into the roots and is the product of the rate of dry-matter increase and the average energy content of that dry matter (Table 9.1). Term two is the energy required to assemble the dry matter into root tissue and con-

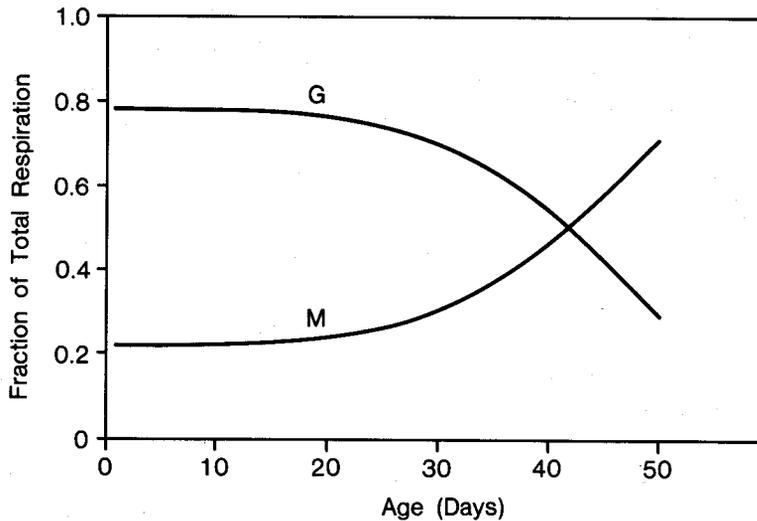


Figure 9.5. Partitioning of total respiratory energy use between growth (G) and maintenance (M).

tains the growth respiratory coefficient and the rate of increase of dry matter. Finally, the third term is the energy required to maintain the existing system and is the product of the maintenance respiratory coefficient and the quantity of dry matter present at any time.

As expected, the energies of the building blocks and the growth component decline as the plant approaches maturity. Maintenance energy, however, continues to increase, approaching a plateau of about 2.5 kJ day^{-1} . As a proportion of the total energy use by the roots, maintenance goes from about 10% during early growth to about 50% at day 50.

The calculated growth and maintenance components are broken out for comparison with each other in Figure 9.5.

Now we can form the efficiency ratio (dE_T/dE_i) simply by dividing equation (9.17) by equation (9.15). Figure 9.6 is a plot of both the components and the efficiency, which is seen to range from about 0.5% to a little over 3%, with an arithmetic mean of $2.2 \pm 0.8\%$.

Cost of conductance

The final point we are now able to address is the question of the energy cost per unit of total root-system conductance. Because the differential conductance (Fiscus 1983) varies with the flow rate, we shall examine only the average hydraulic conductance coefficient (L_R). L_R is the

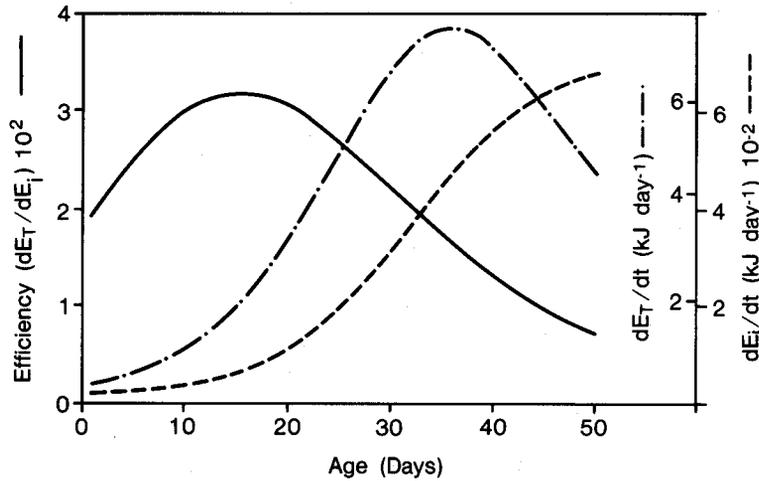


Figure 9.6. Rates of direct-radiation input (dE_i/dt) and total energy usage by the root system (dE_T/dt) and the ratio of the two (efficiency).

product of the hydraulic conductance (L_p) and the root surface area. The units of L_R are $m^3 s^{-1} MPa^{-1}$, and the curve in Figure 9.7 was constructed from previous data (Fiscus and Markhart 1979).

The conductance of the root system changes with time, but at any particular time its value is related to the energy expended to build and maintain the system up until that time. For this reason we have chosen the integral of the daily rate of energy usage (dE_T/dt) as the appropriate figure to compare with L_R . The integral can be formed from equation (9.17) and is

$$E_T = \frac{\rho da}{4(1 + be^{nt})} \left[E_b + R_g + R_m(1 + be^{nt}) \cdot \left(t - \frac{\ln(1 + be^{nt})}{n} \right) \right] + C \quad (\text{kJ}) \quad (9.18)$$

where C , the integration constant, is -87.93 kJ. For curiosity's sake, the direct-radiation integral can be formed from equation (9.15),

$$E_i = 2,700 \left[k + ma \left(t - \frac{\ln(1 + be^{nt})}{n} \right) \right] + C \quad (\text{kJ}) \quad (9.19)$$

where C is -22.8 MJ.

The ratios of equations (9.18) and (9.19) to L_R were formed and plotted in Figure 9.8 as functions of plant age. Both functions are seen to cycle, starting out high, because the early conductance is so low, reaching a

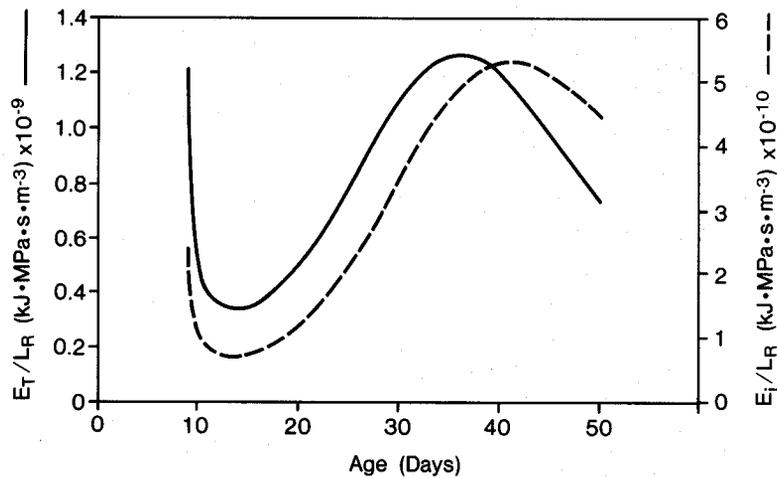


Figure 9.8. Cumulative energy input per unit of conductance. Energy is given both as the total used (E_T) and the total direct radiation (E_i). Means and standard deviations are $E_T/L_R = 8.5 \times 10^8 \pm 3.3 \times 10^8$ and $E_i/L_R = 3.17 \times 10^{10} \pm 178 \times 10^{10}$.

Even if we include the aboveground portions, which in this case constitute the other three-fourths of the plant dry matter (fractional dry weight of roots:stems:leaves = 0.222:0.226:0.552), the total efficiency, as defined earlier, will still average only about 9%. If we accept the assumption that leaves not receiving direct radiation produce adequate photosynthate to meet the demands of maintenance respiration (Tanner and Sinclair 1983), then the efficiency of use of direct radiation will fall even more.

Our assumptions about root composition may be erroneous, but it seems unlikely that the values will be too far wrong. Direct comparisons are difficult, but previously published compositions of leaf material (Penning de Vries 1975b) give us cause for optimism. The composition given is 25% nitrogenous compounds, 66.5% carbohydrates, 2.5% lipids, and 6% for minerals and lignin. The respective estimates for the root composition given in Table 9.3 are 19%, 73%, 3%, and 5% for minerals. Later Kjeldahl analysis on plants grown under similar conditions showed 3.04%, 2.50%, and 3.96% Kjeldahl N in the roots, stems, and leaves, respectively. These values work out to 19%, 15.6%, and 24.8% protein. The 19% value for roots is exactly what we estimated, and the 24.8% for the leaves is very close to the value given by Penning de Vries. We think that the nearly 6.5% difference between his value for leaf carbohydrate and our estimate for root carbohydrate is very nearly balanced by the almost 6% difference between the root and leaf percentage protein compositions shown by

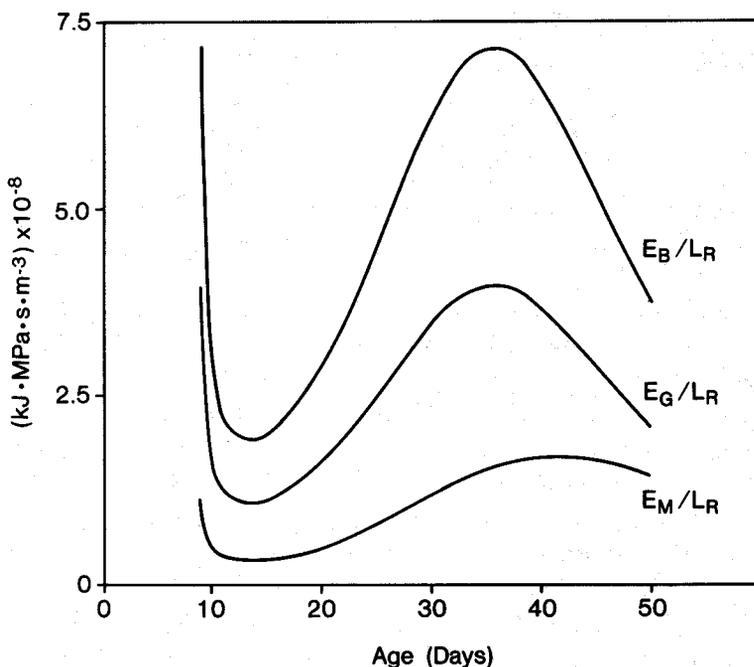


Figure 9.9. Cumulative energy input per unit of conductance broken down into construction materials (E_B), growth energy (E_G), and maintenance energy (E_M). Means and standard deviations are $E_B/L_R = 4.76 \times 10^8 \pm 1.84 \times 10^8$; $E_G/L_R = 2.64 \times 10^8 \pm 1.02 \times 10^8$; $E_M/L_R = 1.08 \times 10^8 \pm 0.53 \times 10^8$.

Kjeldahl analysis. We therefore believe that our estimates of composition, no matter how crudely derived, are reasonable.

Our assumption about the value of R_m may also prove erroneous, but it and the resulting value of R_g determined from experiment are not out of line with those of other workers (Evans 1975). It is more likely, however, that our assumption of their constancy will prove false.

Water and nutrient absorption and transport are inextricable. However, one might just as easily choose to view the root system as though its main function were nutrient uptake and everything else merely a consequence of that function. The energy actually expended to extract nutrients from the soil is included in R_m (Penning de Vries 1975a) and constitutes about 15% of R_m in the case of our plants. Therefore, nutrient uptake constitutes only 1–2% of the total energy used by the root system until growth begins to decline (Figure 9.4). Of course, the apparatus of extraction must exist, and so all the growth-related expenditures should be included in the cost of extracting nutrients from the soil.

Table 9.4. Average integrals from Figures 9.8 and 9.9 given in various units^a

Units	E_T/L_R	E_B/L_R	E_G/L_R	E_M/L_R
kJ MPa s m ⁻³	8.5×10^8	4.76×10^8	2.64×10^8	1.08×10^8
mg glucose MPa s cm ⁻³	5.42×10^4	3.03×10^4	1.68×10^4	6.88×10^3
g DW MPa s cm ⁻³	53.1	29.7	16.5	6.7

^a Values used for conversions were 15.69 kJ g⁻¹ glucose and 16.01 kJ g⁻¹ DW.

Considering the quantities of plant growth regulators formed in the roots, the energy expenditures specifically involved in those activities are probably negligible.

The function of anchorage is a much more slippery proposition to analyze. In some respects, anchorage might be viewed as a secondary benefit deriving from the plant's water- and nutrient-extracting activities. Secondary growth necessary for support and anchorage of larger plants may simply be the consequence of generating a water supply system adequate to meet the needs of the foliage. However, the existence of the additional root functions of support, nutrient uptake, and hormone secretion means that our estimate of the direct cost of the hydraulic conductance may be an upper limit for the actual cost, because the costs of the other functions have been included.

In short, no matter how we choose to view the root system functionally, the cost of building and maintaining it will be the same.

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