

CHAPTER 4C

Water Transport and Balance Within the Plant: Resistance to Water Flow in Roots

EDWIN L. FISCUS

*Agricultural Research Service, USDA
Fort Collins, Colorado*

I. INTRODUCTION

Water transport through root systems or segments of roots is frequently expressed in the plant physiological literature by the relationship

$$J_v = L_p (\Delta P_h - \sigma \Delta \pi), \quad [1]$$

which is the equation presented for irreversible volume flow through semi-permeable membranes (see Katchalsky & Curran, 1965). Here J_v is the flow of volume per unit area of root surface ($\text{cm}^3 \text{cm}^{-2} \text{s}^{-1}$), ΔP_h is the hydrostatic pressure difference between the outside and the inside (xylem elements) of the root (bars), σ is the dimensionless reflection coefficient or osmotic efficiency, and $\Delta \pi$ is the osmotic pressure difference between the inside and outside of the root (bars). The term L_p is the so-called hydraulic conductivity coefficient ($\text{cm}^3 \text{cm}^{-2} \text{s}^{-1} \text{bar}^{-1}$), which, unlike many expressions used in soils terminology, has the distance or length term absorbed into itself. Owing to the nature of the development of this relationship, the driving forces are expressed only as finite differences and not spatial derivatives (cf. Katchalsky & Curran, 1965; Chapter 10). In fact, the specific manner and anatomical structures over which these potential differences are dissipated is still a matter of controversy. Thus, Eq. [1] might be generally less useful if it were necessary to rigorously define the gradient. This distinction between a difference and a gradient is carried through to L_p , which, because the geometry of the system is not completely known, should properly be termed a conductance. In trying to establish some uniformity of terminology between plant physiology and other branches of science and engineering, we will refer to L_p as a conductance. One must bear in mind that other types of conductances are possible, depending on what parts of the system are considered unknown. We will use the symbol L_p for systems defined by Eq. [1], where the cross-sectional flux area is known, but not the gradient. The term conductivity will be confined to cases where the driving force is expressed as

a spatial derivative. The same considerations apply to the additional inverse coefficients, the resistivity, and the resistance. A flux density ($V l^{-2} t^{-1}$) may be defined by a conductivity or conductance, but a flux ($V t^{-1}$) only by a conductance. Further, we could make use of the hydraulic head concept, which is more widely used in soil sciences, and write Eq. [1] as

$$J_v = L_p (\Delta H - \sigma \Delta \pi), \quad [2]$$

where ΔH is the difference in hydraulic head ($\Delta H = \Delta h_p + \Delta h_g$), Δh_p is the difference in pressure head, and Δh_g is the difference in gravitational head. The notation used will not alter the sense of the following discussion.

It is generally considered to have been through the influence of the papers of Gradmann (1928) and van den Honert (1948) that the concept of resistance became part of the language of plant-water relations. However, Richter (1973) pointed out that it was really an earlier paper by Huber (1924) that was deserving of this credit. In any case, it was proposed that the flow of water through the various parts of the soil-plant-atmosphere continuum could be treated as a catena, analogous to the flow of current in an electrical circuit. This concept became established in the literature and came to be known as the *Ohm's law analogy*. The concept may be credited with stimulating much useful research in plant-water relations since its adoption. However, it did suffer from a serious shortcoming in that it was essentially an "instantaneous" concept, or was interpreted that way by many investigators. By "instantaneous" we mean that the value of the resistance to flow was calculated simply as the ratio of the instantaneous applied force to the instantaneous flux. Frequently implicit in the interpretation of such calculations are the assumptions that the relationship is linear and that it passes through the origin. So much confusion has been generated because of the difficulties inherent in the concept of the instantaneous resistance that we feel it is desirable to spend some time discussing two of the fundamental resistance concepts. The discussion will by no means be comprehensive.

II. A CONCEPTUAL MODEL OF FLOW RESISTANCE

As an illustration of the resistance concepts, we will make use of the system in Fig. 1. Throughout, however, one must bear in mind that this system is only for illustration of the resistance concepts and may or may not bear any resemblance, real or analogous, to any particular part of the soil-plant-atmosphere system. This simple system consists of a vertical pipe with a nonlimiting inlet, four exit ports, and a pressure transducer at the bottom. At any time during the following discussion any combination of the exit ports may be closed to illustrate a particular point. The flow of water will occur from left to right and the efflux from the system, J_w , will be determined as a function of the pressure, P_h , at the base of the pipe. The measured pressure will, of course, depend only on the height, Z , of the water column, with the reference elevation, Z_o , being at the level of the

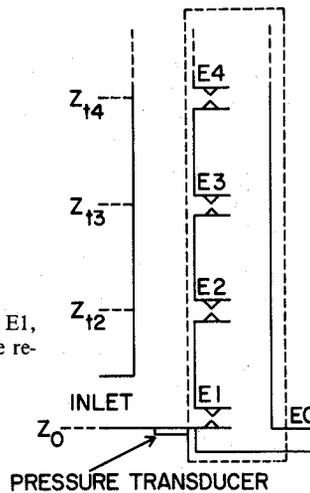


Fig. 1—Vertical pipe system with water outlet ports E1, E2, E3, and E4, and collective outlet at E0. The region within the dashed line is inaccessible.

transducer. The apertures of the exit ports may differ and only their relative sizes will be specified for each case considered. All efflux from the system will be collected at the outlet, EO, which will also be considered to be at Z_0 . Further, the area enclosed by the dashed lines will be inaccessible to measurement. As the simplest case, consider that all exit ports except E1 are closed. In this situation, the flow of water from the system, J_w , will be described by a straight line passing through the origin, line I in Fig. 2A. This line may be defined as

$$P_h = J_w r. \quad [3]$$

Obviously, the proportionality factor, r , may be calculated as P_h/J_w and is everywhere the same. The ratio P_h/J_w is also the tangent of the angle α formed by the horizontal axis and the force/flux line. For future reference, we will define $\tan \alpha (= P_h/J_w)$ as the instantaneous resistance. As it happens, $\tan \alpha$ is also the slope of the force/flux curve in this instance, and it is this slope, at any point, that we will define as the "differential" resistance. In this case, line I of Fig. 2B describes both resistance functions. Throughout the rest of this paper we will use r_i and r_d to mean the instantaneous and differential resistances, respectively.

Next, consider the situation where only port E2 is open and that it has the same aperture as E1. In this case, no water may exit the system until the threshold height (Z_{12}), therefore threshold pressure (P_{12}), has been reached (line II, Fig. 2A). Further increases in pressure beyond P_{12} result in the same proportional increases in flow as in line I. Line II may be described as

$$P_h = J_w r + P_{12}. \quad [4]$$

The differential resistance, $dP_h/dJ_w (= r_d)$, is the same for lines I and II, and one would not conclude from this that there was any difference in the apertures of ports E1 and E2. However, if one calculates the instantaneous

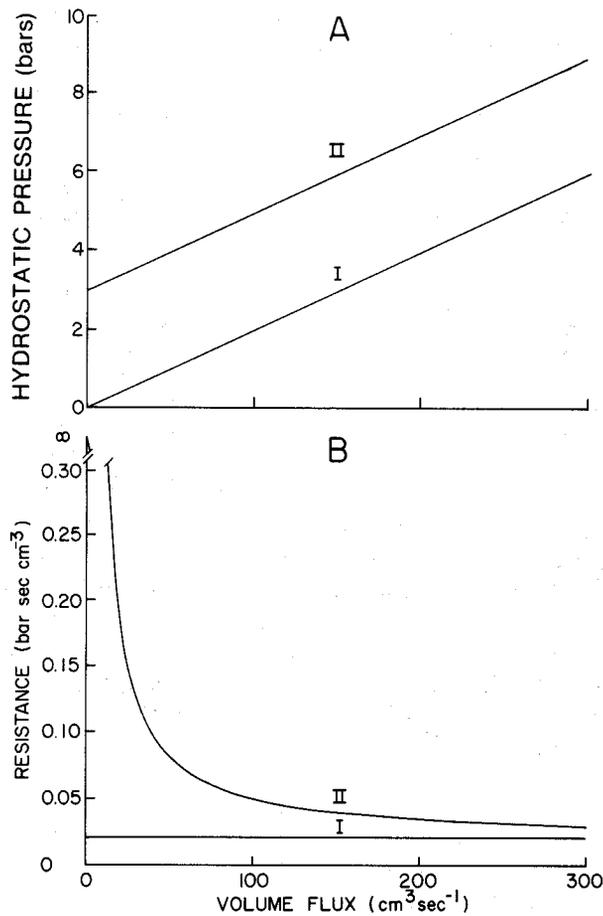


Fig. 2—Plot of pressure at base of pipe against volume flux (A), and system resistances against volume flux (B). In each plot line I is for the case when only pore E1 is open, and line II is when only pore E2 is open.

resistance for line II of Fig. 2A, quite a different picture emerges. The instantaneous resistance (line II, Fig. 2B) may take on any value between infinity as $J_w \rightarrow 0$ and the differential resistance value as J_w becomes infinite. Such a resistance function may clearly be erroneously interpreted as showing nonlinear flow characteristics. As a result, much time and effort may be expended searching for the causes of this nonlinearity when in fact it does not exist.

To further illustrate the pitfalls of the instantaneous resistance concept, consider one further example. In this example, E1 is closed and E3 and E4 have identical characteristics, which include much larger apertures than E2. In the first instance, E4 is closed and the flow curve will look like line I in Fig. 3A.

In the second instance, E3 is closed and E4 is opened so that flow will resemble line II of Fig. 3A. The corresponding differential resistance func-

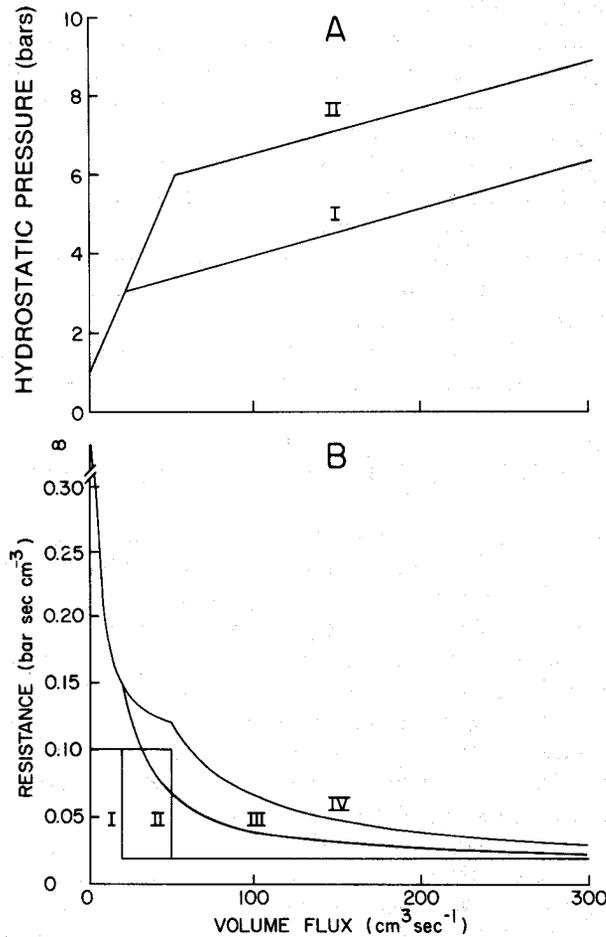


Fig. 3—Plot of pressure at base of pipe against volume flux (A), and system resistances against volume flux (B). Lines I & III are for cases when E2 and E3 are open, and lines II & IV when E2 and E4 are open. The relative apertures are E3 and E4 > E2.

tions will look like lines I and II of Fig. 3B. These lines clearly indicate that the only difference between the two systems is in the height of the ports. The instantaneous resistance functions, lines III and IV of Fig. 3B, not only suggest two highly nonlinear systems, but substantial differences between them. Unfortunately, the instantaneous resistance functions also tend to mask the essential difference between the two cases. In short, the differential resistance function clearly and concisely conveys the behavior of the system, whereas the instantaneous concept tends to mask the particularly relevant features.

If all that we desire is to reproduce the force/flux curve, then calculating the instantaneous resistance will serve, and so will a commercial copy machine. In neither case will the procedure tell us anything about what makes the plant system operate as it does. The concept of instantaneous resistance does not provide us with any insights concerning how the system

should respond to environmental parameters that might be related to the resistance, nor does it provide us with any physiological hypotheses to test. At best one might reason out similar qualitative mechanisms from both resistance functions, however, assigning values to physiological parameters on that basis may lead to quite different conclusions quantitatively.

To be sure, a more logical choice in the preceding examples would have been to measure the flow through each exit port as a function of the pressure drop across that port. The total flow would then be the simple sum over all the operating ports. However, we have stated that these areas are inaccessible. So, too, it is often the case in biological systems that we are not able to measure the relevant forces at their sites of action. Also, it is frequently not clear what driving forces are acting in a system nor even where they are acting. This, too, has been a source of confusion over the years.

III. RESISTANCE TO FLOW IN THE PLANT SYSTEM

The general principles of the differential resistance should be equally applicable to water fluxes in any part of the soil-plant-atmosphere continuum. However, there are parts of the system where more than one force, flux, or pathway may be operating. In these cases, interpretation of the force/flux relationships becomes more difficult and it is in these cases that it is especially important to avoid the additional confusion that arises through the use of the instantaneous resistance concept.

To illustrate how the use of the instantaneous rather than differential resistance may lead to erroneous conclusions in biological systems, we will cite two examples. The first of these deals with the relationship between leaf and root resistances, and the second deals only with radial root resistance.

In the first example the relationships between leaf water potential and water absorption rates were determined in attached and detached leaves of sunflower (Boyer, 1974). The objective was to determine whether the large variable plant resistance resided in the leaves or the roots. In the case of attached leaves the investigator observed a force/flux relationship similar to our Fig. 3A, line I or II. The pattern observed for detached leaves was similar to our line II of Fig. 2A.

Calculations based on these data [(Boyer, 1974) Fig. 2A and 2B] showed large changes in r_i in both the attached and detached leaves. Because of the large change in r_i of the detached leaves, the investigator concluded that the major variable resistance to flow within the plant resided in the leaves. However, examination of the differential resistance characteristics of his data reveals that (i) there is an approximate sixfold change in r_d in the attached leaves over the range of water absorption rates examined, (ii) over the same approximate range of flux rates there is practically no change in r_d for the detached leaves, and (iii) for the higher absorption rates encountered, r_d for the attached leaves is about 2.6 times larger than r_d for the detached leaves. Therefore, on the basis of r_d , one must conclude that the major resistance lies not in the leaves but in some other part of the plant,

probably the roots. In fact, the data under discussion show that at high flux rates the leaf r_d is approximately 38% of the total system r_d and only 6% of the total r_d at low flux rates. In this instance the use of r_i was totally misleading.

The second example deals with the volume flow through detopped root systems in response to an applied hydrostatic pressure. The details of the experimental technique may be found in Lopushinsky (1964) and Mees and Weatherley (1957). Basically, the technique consists of severing the shoot from the root system and sealing the roots in a chamber with the stump protruding through the lid. A source of water and nutrient ions is made available and the rate of solute and water flow from the stump measured under various levels of hydrostatic pressure in the chamber. The technique was developed to simulate the high rates of volume flow through the root system that the intact plant may generate during conditions of rapid transpiration. Even though we can succeed in producing high flow rates in this manner, the crucial question remains as to whether or not the root system conductances measured under these conditions are comparable to those that exist in the intact plant. We will approach this question later and will, for now, accept that the technique is valid.

The nonlinear nature of the pressure-induced flow through detopped root systems led some workers to conclude that L_p (eq. [1]) was changing. We were able to show (Fiscus, 1975, 1977) that even though the differential resistance was changing, it was possible for this to occur while L_p remained constant. Because we were able to express r_d in terms of physiological parameters, we were able to demonstrate that the nonlinear nature of the flow could be accounted for on the basis of a variable osmotic difference term, while L_p could remain constant. That is to say that the differential resistance was shown to be a function of interacting forces and fluxes. It is clear that in such a case calculation of r_i was a meaningless exercise. In addition, we were able to show that L_p could be calculated as the reciprocal of the limiting r_d at high flow rates. This last point brings us to another area of confusion regarding resistance terminology, and that arises because of the penchant of some workers for freely using a reciprocal relationship between conductance and resistance. There is a natural proclivity to do so when the concept of instantaneous resistance is invoked. However, in many cases, the use of conductance and resistance in this manner can be very misleading [cf. Fiscus & Kramer (1975)]. Where the concept of differential resistance is used, it is frequently quite clear that such reciprocal usage may cause great problems. Here again, frequently implicit in the use of this reciprocal relationship is the assumption that the force/flux relationship is linear and passes through the origin, so that the instantaneous conductance can therefore be just as meaningless as the instantaneous resistance.

Criticism of our original nonlinear root-water flow model by Newman (1976b) is valid and, we think, will lead to modifications, although not exactly as he suggests. We feel now, as we stated then (Fiscus, 1975), that the basic effects we elucidated regarding coupled solvent/solute flow in root systems and the differential resistance characteristics will remain valid, even

though the details of the system may change with regard to the number of compartments necessary. In the original model (Fiscus, 1975), we used the term "apparent" resistance but have since come to believe that the term "differential" resistance is more descriptive and far preferable.

In addition to the confusion created by the use of the instantaneous resistance, there are several other somewhat controversial problem areas in plant-water transport research that we feel are worthy of brief mention. Most of the following remarks will be confined to root-water transport and will be presented as they occur to us. The list will not be comprehensive.

A. Radial vs. Axial Resistance

We have previously assumed that it is the resistance to radial water flow that controls the overall flux patterns in our root systems. By radial water flow we mean only that which occurs between the root surface and the xylem elements. That the radial resistance is limiting in our systems is strongly supported by the temperature response of root water flow under a constant pressure. The early work of Kramer (1942, 1948), Kuiper (1964), and, more recently, Markhart et al. (1979) generally show a temperature response that is much greater than can be accounted for on the basis of viscous flow phenomena. More important, the sharp breaks in the Arrhenius plots of the responses in many of these instances are characteristic of membrane phase transitions or some form of metabolic mediation. So far as we know, there is no evidence to indicate that membrane properties control the axial flow of water along significant portions of a root. Also, the many examples of metabolic-inhibitor treatments slowing root water transport suggest that something other than the axial resistance is limiting in those instances. This is not to suggest that axial resistance cannot be limiting, especially in species with smaller vessels and longer roots. None of the roots in any of our studies on beans and soybeans was longer than 3 m.

B. Driving Force for Radial Flow

Failure to distinguish between systems driven by an external pressure excess and those driven by an internal pressure reduction (tension) can be misleading. In an intact transpiring plant the xylem tension (ψ_{px}), as well as the leaf water potential (ψ_L), is not merely a result of the atmospheric demand and the root conductance. It is also a function of the osmotic phenomena opposing (or aiding) flux at the root-water flow barrier. One therefore would expect the relationship between ψ_L (or ψ_{px}) and the root water flux to be nonlinear in a manner similar to the relationship between J_v and ΔP_h (Eq. [1]; Fiscus, 1975, 1977; Fiscus & Kramer, 1975), assuming that the root medium is unchanged and ignoring any longitudinal losses. This nonlinearity does not require "leaky" membranes (Aston & Lawlor, 1979) or changes in L_p (Michel, 1977), but is due in general to the coupling of water and solute transport in the roots.

C. Radial Pathway(s)

Just as there can be interaction between different forces and fluxes in root systems, it is also possible for interactions to occur between alternate pathways for water movement in a system. The pathway of radial water movement has been the subject of controversy for years. The reviews by Newman (1974, 1976a) present as many of the alternate views as one is likely to find. The choice between pathways is seen primarily as between the cell-wall-endodermal pathway and the symplastic pathway. Unfortunately, there still has been no accumulation of the types of data that will allow an unequivocal choice between these alternate radial pathways, nor is it clear whether an "either/or" situation exists. Also, there is no reliable information indicating whether or how much the various solvent and solute fluxes might be proportioned between alternate pathways, and how this proportioning might be affected by changes in the total volume flux through the root system. Fortunately, for many purposes and analyses, it is not necessary to identify specific structures. We need only know how the systems act compared with some theoretical system with ideal properties. For example, we find that in many ways, root systems act like nothing more than semipermeable membranes with the ability to transport solutes at the expense of metabolic energy. We may, therefore, assign other membrane-related properties to root systems, even though we may not know what structure or combination of structures is responsible for these properties. Ultimately our goal is to identify and model these specific structures.

D. The Steady State

Throughout this discussion we have made implicit use of several steady-state concepts without defining or further elucidating this particular concept. Generally, the steady state is thought of as a situation in which the particular flux being examined does not change with time. In the literature, one finds numerous instances, indeed the majority of cases, in which criteria for the steady-state are never defined and the unchanging flux only implied.

When dealing with complex biological systems, it seems desirable to try and establish, in each case, rather rigid criteria that define the steady state. This is especially important in systems where more than one force or flux interact and especially where alternate pathways may be involved. In these situations it seems desirable to specify that all interacting forces and fluxes are in the steady state. This last statement is obviously relevant to plant systems in general and especially to those in the field where major environmental influences cannot generally be controlled. Lack of a true steady state is particularly troublesome in field experiments designed to determine physiological water-transport coefficients. For example, changes in wind speed, direction, solar radiation, humidity, air or soil temperatures, stomatal resistance, or even the age of the plant part itself could all, or any individually, upset the delicate steady state.

In fact, it seems unlikely that true steady-state conditions ever can exist in nature owing to the diurnicity of the system and the fact that it is continually changing size. It is not at all clear that any sort of transient analysis could be any more useful at this time. This is primarily because in a growing biological system, we would expect each response to be influenced by the special history of the individual system. That rather rigid steady-state criteria are necessary, even in the laboratory, may be illustrated by the recent work of Bunce (1978) on soybeans and cotton. He found that in both species leaf water potential did not reach steady values until 3 hours after the transpiration rate had ceased to change. It is clear that if the transpiration rate had been used as the sole steady-state criterion, interpretation of the observed relationships could easily become confused.

E. Induction and Hysteresis

Another area related to the steady-state problem is the so-called induction and hysteresis involved in water flow through root systems. The name "induction" was bestowed by Kuiper (1974) and derives from the fact that when root systems of some species are subjected to stepwise changes in hydrostatic pressure, the flow rate does not immediately reach a new steady value. Rather, there is a period of time, frequently several hours, during which flow increases gradually to its new steady state. Conversely, when the pressure is decreased suddenly, the new steady flow rate may not be achieved immediately (induction) and may sometimes be observed to be somewhat higher than the original rate at that same pressure (hysteresis). Both of these phenomena have been attributed to some effect of flow rate on the hydraulic conductance of the system. Our observations and those of Markhart et al. (1979) indicate that when sufficient care is taken to achieve steady-state rates of solute as well as solvent flux, we do not observe hysteresis. In addition, we feel that the gradual rather than stepwise changes in flow rate when the pressure is changed may be due to the time required for the solute fluxes, and thus the osmotic forces, to come to the steady state, rather than to changes in the hydraulic conductance.

F. Soil- vs. Solution-Grown Roots

Most of our discussion of root systems has dealt with those grown in growth chambers or greenhouses in nutrient solution. We must finally address the question of how these systems act compared with soil-grown systems. Unfortunately, the comparisons cannot be direct, since extant data were generally not gathered for the same purpose. However, we may make some rough comparisons based on observed flow rates, measured potential differences, and assumed root-area/leaf-area ratios. We will compare other data with those of Fiscus and Markhart (1979) for beans and soybeans. The hydraulic conductances measured according to Fiscus (1977) ranged from 0.8×10^{-6} to 6.1×10^{-6} $\text{cm s}^{-1} \text{bar}^{-1}$ for beans, and from 2.2×10^{-6} to 5.6×10^{-6} $\text{cm s}^{-1} \text{bar}^{-1}$ for soybeans. These determinations varied considerably

because of differences associated with root system size and age (Fiscus, 1979).

For comparative purposes, we may draw on several pieces of data in the literature. First, we can take the single soil-grown sunflower root system used by Boyer (1974) in the pressure chamber and estimate an L_p based on his Fig. 4 and a 1:1 root-area/projected-leaf-area ratio. The result, based on an estimate of the limiting differential resistance, is $L_p = 1.8 \times 10^{-6} \text{ cm s}^{-1} \text{ bar}^{-1}$, which is well within the range of our measurements.

Another opportunity for comparison is presented by the work of Neumann et al. (1973) on corn, sunflowers, and soybeans grown in a silica rooting medium. Here again we will assume a 1:1 root/leaf area ratio and that the root transport characteristics control the overall flow pattern within the plant. Based on these assumptions, the inverse of the limiting differential resistance (L_p) may be calculated from their figures. For soybeans the L_p are found to range from 0.8×10^{-6} to $2.3 \times 10^{-6} \text{ cm s}^{-1} \text{ bar}^{-1}$. For sunflowers, this range is 0.8×10^{-6} to $2.2 \times 10^{-6} \text{ cm s}^{-1} \text{ bar}^{-1}$, and the normalized composite (Neumann's Fig. 3) yields a value of $1.2 \times 10^{-6} \text{ cm s}^{-1} \text{ bar}^{-1}$ for corn.

In addition to these data, a further comparison made by Fiscus and Markhart (1979) also shows that, based on the flow rates encountered in our experiments, root system coefficients may be calculated by the method of Taylor and Klepper (1975), which are similar to the value of $1 \times 10^{-6} \text{ cm d}^{-1}$ they calculated for their cotton plants grown outdoors in soil.

The above comparisons indicate, at least within the large degree of uncertainty inherent in such maneuvers, that soil- and solution-grown root systems may act in a very similar manner with respect to their water-transport properties.

IV. SUMMARY

In most plant systems the stomata control the loss of water from the plant. However, it is the rate of water transport to the leaves that controls, to a large degree, the stomata. Of course it is the root-water-transport characteristics that control the flow to the leaves, so there is adequate rationale for expecting to be able to genetically manipulate the water transport in the plant by selecting for root characteristics. However, it is not root resistance alone that must be selected but eventually combinations of root resistance and stomatal response. Thus far there is very little firm data concerning the interactions of root resistance and stomatal response characteristics, and for this and other reasons it is not always clear what constitutes a desirable water-transport trait. It will probably develop that a wide range of combinations, from plants that offer practically no impedance to water flow to those that severely restrict it, will be useful in various production situations.

Production strategy will also be important in that different transport characteristics will be desirable, depending upon whether we wish to maximize production or to stabilize it.

Finally, we cannot deal with water transport exclusive of other plant functions. We may be successful in selecting for L_p , for example, and find

that the system is dominated by growth rates and patterns. A high value of L_p is useless if the plant is unable to explore an adequate volume of soil or if the cost in terms of growth-related resources is too high.

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