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WATER TRANSPORT

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INTRODUCTION

Plants were among the earliest organisms in the fossil record, but they did not colonize land until about 450 million years ago, or in the last 10% of the age of the earth. The delay was probably caused by the complexities of obtaining water in an inherently dry environment. Roots and an advanced vascular system were necessary to gather water while an epidermis and stomata were necessary to conserve it. Water had to move along a transport path consisting of many tissue types. Some tissues such as xylem were modified for water movement whereas others such as parenchyma were not. This complexity has caused researchers to view the system as a black box, at least initially, and approach the subject by measuring forces and determining the resulting water flows without knowing the precise nature of the flow path. Conceptually, this is no great problem, but it leaves open the possibility for variation between

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species adapted to different conditions and in turn the possibility for different experimental results.

In what follows, I will review some of these results for water transport in higher land plants. I shall not attempt to review the entire field because two reviews (74, 171a) and several books (79, 80, 152) give thorough overviews. To keep within reasonable limits, we will consider only liquid water transport. For discussions of water movement as a vapor, the reader is referred to recent reviews of vapor transport (23, 42) and the stomatal control of this transport (52, 68, 136, 174). The intriguing and related process of solute transport will be dealt with only as it relates to water movement. Moreover, even though water movement in the soil is an important aspect of water movement to the plant, it will be treated only where it directly affects the plant.

From a practical standpoint, plant water transport has always been of interest. Water must be moved to the leaves each day to replace what is lost by transpiration. This requires water potentials to decrease so that water will move into the plant from the soil. Cell enlargement, which is the primary means by which plants increase in size, is sensitive to these water potentials. Moreover, various aspects of plant metabolism may be affected. Therefore, for anyone interested in how water affects the growth and metabolism of plants, water transport becomes at least an avocation.

Our understanding of water transport became clearer after the field was put on a sound thermodynamic basis about 25 years ago (45, 79, 80, 152, 153). With the equilibrium concepts provided by thermodynamics, new methods of measuring water potential developed (13) that were based on equilibrium and used forces similar to those driving water through the plant. Now it is easy to observe diurnal fluctuations in water potential that move water to the shoot. The components contributing to these water potentials can be identified. Effects of soil water depletion, rehydration, and salinity can be readily studied. Because these methods have always been the most difficult aspect of research in this area, their development permitted studies not possible before, and these will be the focus of this review.

BACKGROUND

Water movement is governed by two fundamental factors: the driving force and the conductance of the flow path. The driving force originates from differences in solute concentration and pressure. As we will discuss more fully later (see Tissue Transport), differences in solute concentrations when displayed across a membrane express themselves as equivalent differences in pressure acting on the water adjacent to the membrane. Gravitational effects are also expressed as pressures that differ with position in the gravitational field. Solid surfaces, principally cell walls, exert forces on water that express themselves as local

tensions arising from the effects of surface tension at air-water interfaces and attractive forces at solid-water interfaces. At the high water contents usually found in cell walls, these surface effects can be described as negative pressures. Therefore, all the important forces driving water through the plant can be stated in solute and pressure terms expressed in units of pressure.

Thermodynamically, solute and pressure forces in plants and soils are most usefully described as free energy per unit volume (ergs/cm^3), i.e. the force per unit area (dynes/cm^2, pressure). These forces are described exactly by the water potential (ψ_w) which is the chemical potential (free energy/mol) divided by the partial molal volume of liquid water (18.0 cm^3/mol, considered a constant over the biological range of temperatures and concentrations). The ψ_w is generally expressed in units of bars, 1 bar = 10^6 dynes/cm^2 = 10^6 ergs/cm^3 = 0.987 atmospheres. The megapascal (= 10 bars) is being increasingly employed, but we will use the bar because of its convenient size.

Measurements of ψ_w are always compared to the reference water potential which is pure free water at atmospheric pressure, a defined gravitational position, and the same temperature as the system being measured. The reference is defined to have a water potential of O. Accordingly, ψ_w indicates how much the free energy differs from that in the reference state and is the sum of solute forces and local plus external pressure forces acting on the water:

$$\psi_w = \psi_s + \psi_p \qquad 1.$$

ψ_s is the osmotic potential and its value is always negative. ψ_p is the pressure potential and its value can be positive or negative depending on whether the pressure is above or below atmospheric. We shall ignore gravitational effects because they are important only in tall trees. We shall also ignore tissue having exceptionally low water contents, such as dry seeds, because the lack of a continuous liquid phase makes a description of the forces slightly more complex (although unaltered in principle). Note that in Equation 1 the surface effects are included in ψ_p. Thus, ψ_p represents forces resulting from external pressures, turgor, and local pressures. The local pressures are caused by interfacial effects in solids. Although this treatment provides a simple expression, the different origins of forces affecting ψ_p must be kept clearly in mind. In some systems, such as plant cells, all the forces in Equation 1 affect water movement. In others, such as soil where membranes are absent, only individual components (in this case local pressure) may affect water movement even though there are local differences in solute concentration.

As water moves along its flow path in response to these forces, it encounters a frictional resistance. To evaluate this resistance, it is of the utmost importance to know whether steady or transient flow is occurring. During steady flow, the situation is greatly simplified because the forces and flows remain constant and

the water content of the tissue does not change. Therefore, changes in tissue water content (capacitance) can be safely ignored, and only the resistance of the tissue need be considered. For single cells in a tissue transporting water in the steady state, the water flow across the plasmalemma can be related to the driving forces by:

$$J = Lp(\Delta\psi_p + \sigma\Delta\psi_s) \qquad 2.$$

where J is the water flow ($cm^3 \cdot cm^{-2} \cdot sec^{-1}$ based on membrane area), σ is the reflection coefficient expressing the ability of the plasmalemma to reflect solute (dimensionless, varies between 1 for a fully reflective membrane and 0 for a nonreflective membrane), Δ denotes the difference, in this case across the plasmalemma, and Lp is the hydraulic conductivity of the plasmalemma ($cm \cdot sec^{-1} \cdot bar^{-1}$). The hydraulic conductivity describes the degree to which hydraulic forces can move water through the main frictional resistance of the cell. This equation indicates that flow is proportional to force and that solute exerts a force according to the ability of the plasmalemma to discriminate between water and solute. If the plasmalemma is ideally differentially permeable, the discrimination is complete and σ is 1, in which case Equation 2 simplifies to:

$$J = Lp\ (\Delta\psi_w) \qquad 3.$$

Because metabolites and inorganic ions cross cell membranes slowly, σ approaches 1 in most situations and Equation 3 can be used, instead of Equation 2. Although not specifically indicated in Equations 2 and 3, water movement is directional. The direction is defined by the magnitude of the potential, water always moving toward the region of lowest potential.

If, on the other hand, flow is transient rather than steady, resistances and capacitances are involved. Capacitances contribute to transient flow because cell water content can change during the transient. This in turn causes ψ_w to change because the water potential is a function of cell water content. In single cells transporting water transiently, the kinetic behavior then depends on cell volume and its relationship to cell water potential. If no changes occur in cell solute content, the half-time ($t_{1/2}$, sec) for water transport resulting from a step change in the external water potential is given by the following equation (110):

$$t_{1/2} = V\ln 2/LpA(\epsilon - \psi_s) \qquad 4.$$

where A, V, and ϵ are the area of the plasmalemma (cm^2), volume of the cell (cm^3), and elastic modulus of the cell wall (bars), respectively. The term $V/(\epsilon - \psi_s)$ is a simplified version of the capacitance and gives the ψ_w (expressed in terms of $\epsilon - \psi_s$) for a particular cell V. The term LpA is the conductance for the cell. Let us define the capacitance as C and the conductance as L. The resistance R is then $1/L$ and Equation 4 becomes:

$$t_{1/2} = 0.693RC \qquad 5.$$

which shows a form analogous to that for simple electrical circuits. Expressed in these terms, the equation shows that transient water exchange by single cells follows the principles applicable to any finite system that can transport matter through a resistance to fill a capacitance.

Similar principles hold for tissues and plant organs except that the limiting area for flow is usually unknown, and it is almost always simpler to use the conductance/resistance expression than the hydraulic conductivity. Moreover, certain approximations need to be made to accommodate cell phenomena on a tissue level. First, because of the possibility for apoplast flow in tissues, parallel flows through the apoplast and the symplast might occur. However, if local equilibrium exists between the symplast and apoplast (110–112), the water potentials are the same at adjacent locations in the two paths, although potentials can differ from point to point in the tissue. Then, the properties of the two parallel paths can be combined in one conductance or resistance. Second, because it is difficult to determine the ψ_w of each cell in the tissue, ψ_w is usually not the water potential of an individual cell but rather an average for the tissue or water source. For steady flow, Equation 3 then becomes:

$$dV/dt = L(\Delta\psi_w) = \Delta\psi_w/R \qquad 6.$$

where dV/dt is the rate of water movement (cm^3/sec), L is the average conductance of the path between the source and the tissue or organ ($cm^3 \cdot sec^{-1} \cdot bar^{-1}$), and $\Delta\psi_w$ refers to the average water potential difference between the water source and the tissue rather than across the plasmalemma of a cell. This equation is frequently used to describe steady water movement through plants and plant parts.

Transient flow through tissues can be treated in a similar fashion. Providing that local equilibrium exists between the apoplast and symplast (110–112) and that the transport properties of the tissue are uniform, all the properties of the flow path can be combined in a single diffusion coefficient. The half-time for water transport after a step change in external ψ_w then has the general form:

$$t_{1/2} = Sl^2/D \qquad 7.$$

where D is the diffusivity (cm^2/sec), l is the distance for water movement through the tissue, and S is a constant that includes effects of tissue configuration (plane, cylinder, sphere, etc). The diffusivity is often used as the flow coefficient because the tissue is made up of small elements, the cells, that cause resistances to be distributed throughout the tissue. Because of this feature water movement is rather sensitive to tissue dimensions, requiring more time to move through large tissue than through small tissue.

Philip (125–127) defined the diffusivity of single cells of a tissue as $x^2/2RC$ where x is the length of the cells (110). Based on this relationship, Equation 7 can be simplified by expressing l in units of cell length ($l = nx$):

$$t_{1/2} = 2Sn^2RC \qquad 8.$$

Equation 8 for a tissue is analogous to Equation 5 for a single cell except that the time for water movement is proportional to the square of the number of cells that water must traverse in the tissue. Thus, the ratio of tissue/cell half-times (Equation 8/Equation 5) is about $2.89Sn^2$. This illustrates that, given the assumptions, the half-time for water movement in tissue is always longer than the half-time for single cells making up the tissue. As will be shown below, there is evidence that the assumptions are indeed valid.

These principles affect the way in which transport experiments are done. Although it is clear that conditions are rarely stable in nature, they can approximate a series of steady conditions. In the laboratory, steady conditions can be created systematically and the behavior of conductances for water transport can be studied. Alternatively, transient conditions may be used if capacitances are known, although assumptions about the configuration of the tissue are also necessary. In this simple form, the transient state approach is limited to conditions where the entire conductive tissue is involved in water movement during the time course of the transient. Investigators have often attributed nonlinear or hysteretic behavior in water transport to changes in the conductances of the flow path when in fact flow either did not involve the whole tissue or was not steady. This causes much confusion and should always be considered within the context of whether flow occurred uniformly and in the steady state or not.

Related to the problem of steadiness of flow is the accurate measurement of the driving forces. Older methods generally relied on nonequilibrium techniques. In some popular methods, tissue was placcd in osmotica and the water loss or gain was noted. Alternatively, the kinetics of water exchange were measured. However, osmotica penetrate tissue slowly, so that not all cells are affected similarly by the solution (45, 75). Furthermore, solute exchange occurs between the cells and the solution, and the forces affecting water movement may then be altered (45, 75, 139). Therefore, solution methods generally should be avoided. These problems do not affect remote methods such as psychrometry where no solutions are in contact with the tissue. However, some forms of psychrometry also involve nonequilibrium measurements (e.g. measuring the rate of water evaporation from a thermocouple). This approach is subject to errors caused by resistances to diffusion of water vapor and differences in the size of the tissue (13, 19).

These problems can be avoided by measuring driving forces at thermodynamic equilibrium. The newer methods of measuring ψ_w depend on determining equilibrium pressures. The measurements are of three fundamental types: determinations of pressures in individual cells [pressure probe (70)], measurements of vapor pressures or pressures associated with excised tissues or organs [isopiestic psychrometer (19, 116), pressure chamber (10, 145)], and determinations of vapor pressures in intact tissues [isopiestic psychrometer (11,

20)]. Because the measurements are made at thermodynamic equilibrium, pressures present in the instrument equal the pressures present in the cell or tissue. For single cells, equilibrium during the measurement usually can be achieved within a few seconds (70). Longer equilibration times are necessary for tissues because of the multicellular nature of the flow path. These times may be on the order of minutes or, with whole plant organs, hours. It has been tempting to make nonequilibrium measurements particularly with whole organs (e.g., in the pressure chamber). In such a situation, the ψ_w that are reported may be for only one group of cells. On the other hand, when thermodynamic equilibrium is achieved in excised tissue, there can be no doubt that the water potential throughout the tissue is the same. Measuring the balancing pressure with a pressure chamber or the balancing vapor pressure by isopiestic thermocouple psychrometry in excised tissue assures that the instrument and tissue are in equilibrium with each other. This kind of measurement is independent of diffusion or transport factors or the geometry of the tissue being measured (13, 19).

Intact tissue poses a special measurement problem because of gradients in ψ_w that often exist. Thus, although the measurement technique may be at thermodynamic equilibrium with certain cells or with an average ψ_w of all the cells, the persistence of gradients clouds the interpretation. For gradients associated with transpiration, the enclosure of the tissue in a psychrometer raises the humidity around the tissue and inhibits transpiration, thereby changing the ψ_w gradients. In growing tissue, water uptake continues during the water potential measurement and ψ_w gradients persist. One way to explore gradient effects is to compare the ψ_w of intact tissue with the ψ_w of the same tissue after excision. Because the excised tissue clearly provides an average ψ_w at equilibrium, the comparison shows whether the intact measurement was above or below the average. In several comparisons where gradients were known to be present (11, 17a), the ψ_w were virtually at the average. In growing tissue, however, the comparison is complex (see section on Growth).

The development of thermodynamically sound methods of measuring the forces acting on water has not only allowed water transport to be studied more intensively but has provided a system of measuring plant/soil water status that is based on a physically defined reference. This permits experiments to be compared in quantitative ways not possible with any other approach, all of which are based on biological references. The methods allow measurements to be made remotely (thermocouple psychrometers) and rapidly (pressure chamber, pressure probe) on a variety of materials (thermocouple psychrometers) in the field or laboratory (pressure chamber, thermocouple psychrometer).

These advantages allow several questions to be investigated that previously were difficult. First, what is the mechanism of tissue water transport in tissues unmodified for water movement? Second, what is the relationship between

solute uptake and water uptake by roots? Third, what is the pathway for water movement through a leaf? Fourth, how is water uptake involved in tissue growth? Finally, how does water move through the intact plant?

TISSUE TRANSPORT

Here we are concerned with water movement through tissues that are not modified for water transport. These occur on the path through the root to the xylem and again from the xylem to the surrounding tissues of the shoot. The issue is particularly important for enlarging tissues because the cells are often small with relatively small vacuoles and can be far from the nearest mature xylem vessel. As a consequence, water may have numerous cell wall and cytoplasmic barriers to cross in order to move even short distances.

It is important to recall at this point that water can move either by bulk flow or by diffusion. For water within xylem cell walls, or protoplasts, the *water* concentrations are so uniform that only very small differences occur and diffusion plays a minor role, i.e. bulk flow predominates as long as there is a continuous liquid phase. However, across membranes, the type of water movement is less certain because it is not clear that a continuous liquid phase is present and there might be significant concentration differences. Robbins & Mauro (142) studied artificial membranes and found that bulk flow is the major mechanism of water movement through membranes having conductivities similar to higher plant membranes. This can be visualized as follows. Because membranes reflect solutes back into the solution, there is a sharp change in *solute* concentration at the solution side of the membrane. This step change forms a compensating tension in the water immediately within the conducting channels of the membrane (137). Tensions as large as 4 bars have been measured in these channels (96). Water moves in response to the tension in the membrane channels and ordinarily cannot be considered to diffuse. In effect, the membrane converts solute forces into pressure gradients that move the water by bulk flow through the channels. Thermodynamic treatments of water movement through membranes show that solute and pressure forces are equivalent, and the studies of Ray (137) and Mauro (96) provide a molecular and experimental rationale for this concept.

Because bulk flow is the dominant mechanism for water transport throughout the plant, there are certain constraints on the kinds of experiments that can be done. Experiments have been mainly of two types: (*a*) kinetic experiments in which water is driven through the tissue by the osmotic forces in the cells, or (*b*) marker experiments in which water is labeled with molecules expected to flow with the water. The principle of bulk flow is compatible with the first type of experiment but not with the second. This is because the kinetic experiments use the same forces and flows actually moving water through the plant, but marker experiments involve concentration gradients that were not present previously. The gradients are steepened if water evaporates and the markers are left behind.

This causes diffusional movement that can drive the marker molecules into regions not normally on pathways for bulk flow.

Just as troublesome is the inability of some markers to cross membranes. This automatically restricts the markers to the apoplast. For example, the accumulation of lead chelate in the walls of leaf epidermal cells led Tanton & Crowdy (160) to conclude that transpiration occurs primarily from the epidermis. This is at variance with the extremely slow rate of evaporation from epidermis that does not contain stomata, and is difficult to reconcile with the marked increases in evaporation from leaf surfaces when the cuticle or epidermis has been removed. Neither diffusional effects nor the likelihood of protoplast exclusion of the lead was considered by the authors. Similar arguments can be made about all marker experiments.

The studies unanimously showed that the markers were confined to cell walls of the tissue, especially in the epidermis and around the guard cells (2, 27, 44, 58, 158, 160, 163). Therefore, it was concluded that water moves through the cell walls, bypassing the protoplasts. This theory, often called the apoplast theory of water movement, is widely held. In view of the artifacts of the marker method, however, the conclusions seem unwarranted. The only instance where the interpretation of experiments with marker molecules seems unequivocal is in studies of the ability of the endodermis to act as a barrier to solute movement (115, 161). Here, diffusion is less of a problem and membranes play no part.

The use of deuterium or tritium-labeled water (88, 122, 123, 134, 135, 173) can avoid the problem of restriction of the marker to the apoplast, but labeled water will penetrate into diffusional space not normally a part of the bulk flow pathway because of the diffusion gradients created by large concentration differences of label. Moreover, the diffusion of labeled water is decreased by unstirred layers that depend on tissue size and internal geometry. The recognition of these limitations by Dainty (45) and Woolley (173) has discouraged further experiments of this sort.

An altogether different, kinetic approach to understanding the pathways of tissue water transport was used by Weatherley (171). He observed that after immersing previously transpiring leaves in water, there was a two-phase rehydration. The first phase was rapid, occurring in a few minutes, but the latter was slow and required hours. Weatherley (171) attributed the first phase to water movement in the cell walls and concluded that water bypasses the protoplasts by moving via the apoplast. However, Cowan & Milthorpe (43) point out that the amount of water moving in the first phase was considerably larger than the total volume of the apoplast so that other compartments, probably the symplast, were also involved. Thus, although the results of Weatherley (171) at first seem to confirm the experiments with marker molecules, on closer examination the rehydration kinetics are too complex to be interpreted at this time.

Since the experiments of Weatherley (171), the kinetic approach has ad-

vanced considerably. Mathematical methods have developed and were recently reviewed by Molz & Ferrier (110). We will not treat them in detail except to point out that the methods are based on concepts of Philip (125–127), who considered water to move through individual cells and aggregates of cells according to the hydraulic characteristics of the plasmalemmae. Cell aggregates were considered to transfer water from cell to cell. Thus, he did not treat the possibility of water movement in the apoplast.

Molz & Ikenberry (111) produced mathematical expressions to describe water movement both in the symplast and in the apoplast. Their expression, based on the conductance and cross-sectional areas of the individual paths, showed that water could move from cell to cell or could bypass cells depending on the individual characteristics of each path. Using a range of values for the characteristics of these paths, they concluded that for biologically relevant values, the protoplast would be virtually in equilibrium with the surrounding cell walls. This important concept, termed local equilibrium, simplifies our understanding of water movement. It suggests that if the water status of the apoplast can be measured, the water status of the protoplasts should be similar and vice versa. It does not imply that gradients in water potential are absent. Rather, the gradients exist over distances involving several cells.

It should be noted that if the apoplast is the main path for water flow, the apoplast must have a low resistance compared to the adjacent symplast. Only then can water in the apoplast bypass the symplast. Water would move through the apoplast to a protoplast where the main resistance would be encountered. The transport kinetics would approach those of single cells. On the other hand, if the apoplast is not of such low resistance, flow would be forced through the symplast or from cell to cell across each cell wall and plasmalemma. The transport kinetics would be slower than for a single cell. The kinetics would be describable by equations like 7 and 8. A comparison of tissue kinetics with single-cell kinetics then provides an unambiguous test of whether water moves predominantly via the apoplast or via the symplast or cell-to-cell paths.

It is essential to recognize that, according to this test, slow kinetics for the tissue compared to the cells indicates that apoplastic flow *cannot* predominate. This is because the protoplasts would have time to exchange water with the apoplast. The apoplast water would then be entering the protoplasts—not bypassing them—and it would be impossible for water to travel far through the apoplast alone.

Early measurements of these kinetics involved placing cells and tissues in osmotica of various sorts (154). However, there is evidence that the measurements contain errors resulting from solute exchange and unstirred layers of solution surrounding the cells (75, 139). Subsequently, the development of the miniature pressure probe (70) provided a way to avoid these problems and had the further advantage that measurements could be made in individual cells in situ.

The pressure probe was used to inject water into a cell, and the turgor was measured as water moved in response to the pressure pulse (70). The data showed that higher plant cells have hydraulic conductivities on the order of 10^{-6} cm·s^{-1}·bar^{-1}, although some cells exhibit hydraulic conductivities an order of magnitude higher or lower than this median figure (156). For hydraulic conductivities of this order, local equilibrium will occur (110–112). Measurements with the probe are somewhat hampered by the need to know the cell dimensions, and temperature changes can sometimes be a problem. However, the principle is inherently sound and the directness of the measurements avoids sources of variability that affect other methods.

Steudle & Jeschke (155) used the pressure probe to compare single-cell and whole-root kinetics in barley. This elegant work showed that hydration was fast for the cells but slow for the roots. Similar comparisons of single-cell and whole-tissue kinetics using psychrometers showed that the successive removal of organs from a sunflower plant increased the rate at which the leaves rehydrated, indicating that water moved in series through each successive organ (12). The rehydrations were slower than for the isolated leaf cells (17) and required minutes to hours for completion (12, 15). The tissue kinetics could be described by an equation based on the series movement of water from cell to cell (12, 15). Molz and his coworkers found similar kinetics for the rehydration of stems using position-sensitive transducers (113, 114). Tyree and his coworkers found slow efflux kinetics in intact *Fagus* (165) and sunflower leaves (166) using a pressure chamber. However, in the sunflower leaves (166), the kinetics of hydration were complex and involved vascular resistance (but see section on Leaf Water Transport).

The accumulating kinetic evidence (17, 155) is nearly unanimous in supporting the notion that tissues transport water at rates much slower than for single cells in the same tissue and that tissue kinetics are slow in general (12, 113, 114, 165, 166). Therefore, water likely moves from cell to cell either through the symplast or through cell wall-plasmalemma barriers, and local equilibrium should occur between the protoplast and surrounding cell wall. This does not exclude apoplast water movement, which probably also occurs (110--112), but the apoplast appears not to be the dominant path.

More kinetic studies are needed. We would like to know whether there are species or tissue differences in the characteristics of flow. Thus far, it has only been possible to study tissues with large cells with the pressure probe because of limitations in the method. In these tissues, the apoplast is often only a small fraction of the total tissue volume. It will be exciting to learn whether tissues having larger apoplast volumes display cell-to-cell transport.

ROOT WATER TRANSPORT

Water enters roots most rapidly in the region just behind the zone of elongation. Hansen (66) exposed individual 1 cm regions of single attached wheat (*Triti-*

cum) roots to water. He found that the highest conductivity occurred 2 cm behind the root tip and extended to about 6 cm behind the tip, a result similar to that reported by Brouwer (21) for *Phaseolus*. Hansen (66) attributed the high conductance to the presence of mature xylem vessels and noncuticularized tissue surfaces. Outside of this 4 cm region, the conductance decreased markedly.

At the same time that water enters roots, solutes enter from the soil solution. Once inside the root, most of the water and much of the solute pass to the root xylem and then to the shoot. The amount of entering solute is osmotically significant so water enters the root not only in response to tensions in the xylem solution generated by the shoot but also in response to osmotic potentials in the xylem solution generated by solute uptake. During periods when transpiration is low, tensions in the xylem solution may disappear and water may enter solely because of these osmotic potentials. Positive pressures, i.e. root pressures, can result.

Solute uptake requires metabolic activity whereas water movement is a passive process in roots. This difference implies that water flowing through the root can dilute the solution in the xylem depending on how fast the water is moving. Considerable evidence shows that this occurs (50, 85, 97, 147, 148) with a range of ions. In a detailed study of nitrate transport to the shoot (147, 148), for example, nitrate movement into the xylem was independent of water movement, and the xylem concentration of nitrate varied inversely with the rate of water transport through the root. However, at very low water fluxes, it became dependent on water flow. The authors (147, 148) attributed the dependency at low fluxes to the build-up of high nitrate concentrations (approaching 40 mM) in the xylem that could have inhibited further nitrate uptake.

Because water transport through roots is driven by osmotic and pressure forces that can interact in this way, the measurement of transport properties is complex. A recurrent problem is the apparent change in conductance of the roots as rates of water movement vary (85, 97). It has been difficult to account for this behavior strictly in terms of the hydraulic properties of membranes. However, Dalton et al (46) and Fiscus (53) considered the interaction between solute and water flows and showed theoretically that the conductance could appear to change when in fact it was constant. The apparent change was caused by the diluting effect of water on solute concentrations in the root xylem and could be attributed entirely to this interaction between water and solute transport. Moreover, they (46, 53) showed that the conductance to water can be assessed most easily at high rates of water flow where solute concentrations are negligible in the xylem.

One possible problem with this approach is that pressures of several bars (often in the range of 2–5 bars) must be applied to the external solution to attain high rates of water flow and, in principle, these might alter the conductance

properties of roots. However, pressures in this range produce flows that are comparable to those in rapidly transpiring plants, and the pressures are similar in magnitude to the tensions in the xylem solution occurring naturally. Therefore, the conductance properties of the roots probably are close to those in the intact system.

These landmark papers clarified an important aspect of root behavior. However, they were criticized by Newman (121) on the grounds that the mathematical formulations often predicted higher concentrations than expected in the external root medium. Fiscus (54) subsequently showed that the external concentrations next to roots are likely to be higher than the bulk concentrations in the medium because of ultrafiltration. This would tend to increase the concentration of solutes in the unstirred layers of solution immediately next to the transporting membranes of the root cells, and thus it is not surprising that the predicted concentrations were higher than in the bulk phase.

Fiscus and his colleagues have since measured root conductance at high flow rates, as required by the theory. In one study, Fiscus & Markhart (57) found that the conductance of *Phaseolus* root systems increased as the plants grew. The increase was caused mostly by the growth of the root system because the conductivity changed only slightly when based on a unit of root surface. It is also noteworthy that the root conductance per unit leaf area changed only slightly as well. This indicates that the plants produced new conductive root tissue roughly in proportion to new leaf tissue. In dry soil, however, root growth often outstrips shoot growth (79, 80), so this conclusion probably is not a generalization for all growth conditions.

Markhart et al (92) made a comparative study of the root conductance of chill-sensitive soybean *(Glycine)* and chill-tolerant broccoli *(Brassica)* using the same high-flow methods discussed above. The roots of the chill-tolerant species responded to cool temperatures as though there was a single activation energy associated with water movement. On the other hand, roots of the chill-sensitive species showed an increase in activation energy at temperatures below 14 degrees. Interestingly, the increase in activation energy could be shifted to lower temperatures by growing the chill-sensitive species at low temperatures. This indicates that the chill sensitivity could be relieved somewhat by low temperature acclimation. The increase in activation energy was interpreted in terms of a reaction or structural property, perhaps in cell membranes, that affected the conducting path at the low temperatures. The cause of the conductance behavior of the roots was investigated by measuring the total fatty acids in the root systems (93). The level of unsaturation was not correlated with the differences between species, but it increased during the acclimation of the plants to chilling temperatures. High quantities of unsaturated fatty acids in membrane phospholipids are proposed to prevent phase transitions at chill temperatures and maintain the fluidity and passive conductance properties of membranes (5, 87). Markhart et al (93) attributed the lowered conductance of

the chill-sensitive species below 14 degrees to a phase transition in the phospholipid fraction of the membranes. However, because they measured only total fatty acids rather than fatty acids in the membrane phospholipids, this conclusion seems somewhat speculative, particularly in view of the lack of correlation between species.

Another aspect of water transport through roots has attracted attention recently since Glinka (61, 62) showed that high abscisic acid (ABA) concentrations increased the rate of water movement through sunflower *(Helianthus)* roots. Roots have a low conductance for water compared to the vascular system of the plant and represent an important rate-limiting barrier to water movement (6, 12, 15, 16, 76, 77). ABA concentrations vary in plant tissue, increasing at low water potential in many tissues. Roots of several species are reported to synthesize ABA in response to dehydration (170). However, the ABA content was expressed on a fresh weight basis (170) which would inflate the amount of apparent synthesis. The data of Milborrow & Robinson (105) were expressed on the basis of turgid weight and should not have been affected by this problem. The data showed little dehydration-induced ABA synthesis in sunflower or avocado *(Persea)* roots.

The measurements of Glinka (61, 62) were performed on roots that were exuding either naturally or under slight suctions. Thus they were accompanied by high solute concentrations in the exudate, which complicates the calculation of conductance. Nevertheless, the calculations indicated that the root conductance to water increased in the presence of ABA. Karmoker & Van Steveninck (72) reported similar results for *Phaseolus*. Fiscus (55) was unable to confirm these increases when he used high flow rates to minimize the effects of high solute concentrations. The experiments were done for 24 h so that long-term effects would have been detected. However, the ABA concentrations he employed appear to have been higher than those occurring physiologically even at low tissue water potential. Pitman & Wellfare (128) also were unable to find a long-term effect on root water transport over a range of concentrations of ABA, but their experiments were done with freely exuding roots and, although they attempted to correct for the effects of concentration, direct measurements at high rates of water transport would have been preferable.

Given the uncertainty in ABA synthesis by roots and the lack of agreement about ABA effects on conductance, it is difficult to reach a conclusion. We need experiments that are based on good measurements of root conductance and tissue water status at realistic concentrations of ABA in experiments of sufficiently long duration to avoid transient effects.

LEAF WATER TRANSPORT

The exact sites where water evaporates are not known for leaves. One feature that is clear is that most water evaporates from inside the leaf, passing through

the stomata to the outside, and only a small amount evaporates directly from the epidermis, depending on the relative diffusive resistances of the cuticle and stomata. It is also clear that large amounts of water can be involved: a rapidly transpiring sunflower leaf loses the equivalent of the entire leaf water content every 20 minutes! The movement of water vapor out of the leaf follows well-known laws of diffusion (23, 42, 52), but the movement of liquid water to the evaporating sites is much less understood.

The rapid rate of movement that would be necessary to replenish the evaporating sites has led to the thought that the evaporating surfaces might undergo incipient drying, reducing evaporation and preventing excessive water loss from the leaf. Farquhar & Raschke (51) investigated this possibility by supplying helium to one side of amphistomatous leaves from several plant species and comparing its diffusion through the leaf with the diffusion of water vapor out of the leaf. Because the leaves had stomata on both sides, water vapor at most would traverse half the thickness of the leaf before reaching the epidermis, and the diffusive resistance for water would be no more than half that for helium. If the diffusive resistance were larger, the result could only be attributed to the nature of the evaporating surface because all other characteristics of the diffusion path were identical for the two gases. This ingenious experiment had the advantage that the plant and its transport systems were left entirely intact. The data showed that the diffusive resistance for water vapor was slightly less than half that for helium. Farquhar & Raschke (51) concluded that the replenishment of the evaporating sites was sufficient to prevent incipient drying. Thus, the evaporating sites within leaves may be considered to be completely wetted and the vapor pressure of the surface virtually saturated at the water potentials usually present.

The fact that the diffusive resistance for water vapor was almost half that for helium is important in another context. The resistance of the intercellular space system is significant in leaves (23). The through-diffusion of helium would include this resistance. Since water vapor encountered almost half the resistance for the through-diffusion of helium, the path for water vapor should have been about half as long as for helium. Although Farquhar & Raschke (51) did not comment on this behavior, it implies that the evaporating sites were deep within the leaf and close to the vascular system. If so, the liquid transport path from the xylem to the evaporating sites would be short, and the vapor transport path to the leaf surface would be long. If the liquid path is short, its resistance could be low.

In support of this idea is the high resistance that liquid water encounters when it is forced to move long distances in the leaf mesophyll (16, 17, 149, 165). In rehydrating leaves, water must move into all the cells, and consequently the paths through the mesophyll are long. Rehydrating sunflower leaves transported water much more slowly than during transpiration despite the presence of larger driving forces (lower water potentials) during the rehydration (16).

Moreover, the efflux of water under pressure gave similarly low rates of water transport, so the effects were similar whether water was entering or leaving the mesophyll (16, 17). Tyree et al (166) also found slow rehydration in sunflower leaves but were unable to fit the kinetics with an appropriate model nor show that most of the resistance to water transport was in the leaf mesophyll because the leaf xylem had a large and variable resistance. The leaves had been previously dehydrated with high pressure. It is possible that these pressures forced air into the vascular system, disrupting liquid continuity and causing a high vascular resistance. Indeed, recent studies (167, 168) of the formation of air emboli in the vascular system of *Thuja* twigs showed few emboli if the twigs were exposed to high pressures beforehand. This suggests that the pressure could have forced gas into the vascular system, thus decreasing the number of emboli that could be counted subsequently.

Isolated mesophyll cells from sunflower leaves displayed dehydration kinetics much shorter than for the intact leaves (17), and the kinetics were consistent with hydraulic conductivities of about 10^{-6} $cm \cdot sec^{-1} \cdot bar^{-1}$ for the cells, or about the same as in most higher plant cells (156). Also, Tyree & Cheung (165) calculated the hydraulic conductivity of mesophyll cells from *Fagus* leaves in a pressure efflux experiment and concluded it was on the order of 10^{-6} $cm \cdot sec^{-1} \cdot bar^{-1}$. Importantly, the cell walls of *Fagus* leaves appeared to have a specific hydraulic conductivity (not the same as hydraulic conductivity because of difference in definition required for cell walls) of about 5×10^{-10} $cm^2 \cdot sec^{-1} \cdot bar^{-1}$ which is low enough that most of the water would flow from cell to cell rather than through the apoplast of the mesophyll (165). This mode of transport was also suggested by the earlier finding (12, 15) that leaf hydration could be fitted by a model that assumed cell-to-cell transport. These results indicate that water moving through leaf mesophyll could not go far at the rates occurring during transpiration without requiring unrealistically low water potentials. Therefore, the bulk of the water moving through the leaf may evaporate from sites close to the veins. This would cause the vapor to diffuse through almost half the thickness of the leaf, bypassing some of the leaf mesophyll.

The results of these papers raise fundamental questions. Why is the resistance to water transport so high in leaf mesophyll? If water bypasses some cells in the leaf when transpiration occurs, how do bypassed cells avoid dehydration?

The finding that mesophyll cells display hydraulic conductivities typical of those of other higher plant cells indicates that the high resistance of the tissue is not caused by unique transport properties of the cells. However, the fluxes of water occurring during transpiration can be enormous. For a sunflower leaf turning over its entire water content every 20 minutes, the flux through cells close to the veins must be even larger because all the water exchanged by the

leaf must pass through them. As the number of cells in a sunflower leaf exceeds the number next to the veins by at least tenfold (17), the water content of the cells next to the veins would turn over in 2 minutes or less. For such a cell having average dimensions of about 20 μm diameter and 50 μm length, the water potential difference across the cell would need to be about 6 bars (calculated from Equation 3) to accomodate the flux (cell volume = 16 picoliters, cell surface = 0.37×10^{-4} cm^2, hydraulic conductivity = 10^{-6} cm·sec^{-1}·bar^{-1}, two cell wall-plasmalemma layers tranversed, turnover time for cell water = 2 min). If this water was transported through several cells before evaporating, unrealistically large gradients in water potential would be necessary. Therefore, it seems likely that these fluxes pass only a short distance before evaporation occurs.

In this case, the outlying cells would need protection from excessive evaporation. The presence of water vapor at high concentrations in the intercellular spaces would protect mesophyll cells somewhat. However, additional protection might be provided by internal cuticle. Cuticle extends around the stomatal guard cells and into the leaf, lining the undersurfaces of epidermal cells and possibly coating surfaces of nearby mesophyll cells. Figure 1 shows an example from an isolated pear *(Pyrus)* cuticle prepared by Dr. M. J. Bukovac. The extension of the cuticle to the underside of the epidermis is clearly visible. This cuticle should represent a significant barrier to evaporation from guard cells and epidermal cells and, if it extends onto the mesophyll, should decrease dehydration in those cells most likely to be bypassed by liquid water at the fluxes occurring during transpiration.

It should be noted that this theory does not exclude the possibility of evaporation directly from the epidermal and outlying mesophyll cells. It indicates only that the evaporation would be slowed to a rate that could be sustained by liquid water movement through a mesophyll tissue of comparatively high resistance.

Figure 1 Isolated pear *(Pyrus)* leaf cuticle. Outer surface is up. Note that the cuticle extends around guard cells to underside of epidermis. Cuticle preparation by Dr. M. J. Bukovac, Dept. of Horticulture, Michigan State University.

Within this concept, it is likely that the epidermis and guard cell apparatus would be uniquely sensitive to the humidity of the air. The high resistance of the mesophyll would restrict water flow to the guard cell complex or perhaps to the epidermis as a whole, but water loss close to the stomatal complex would be kept from becoming excessive by the cuticle. Thus, epidermal cells might change in water status without much change in the water status of the bulk mesophyll. Direct measurements of the water status of the epidermis are needed. These measurements could go far toward answering whether the epidermal water status is affected by changes in air humidity and whether these changes display any independence from the water status of the bulk leaf.

The water supply to the epidermis of leaves has been of interest because the stomatal apparatus is located there. The guard cells of the stomata must obtain ions and water from the surrounding epidermis in order to function (68, 136, 174). Moreover, the guard cells respond to low water potentials (48, 68, 136, 174) and changes in atmospheric humidity (82, 86, 146) and may lose water directly by evaporation (88–91, 98). Therefore, water transport must be sufficient to permit not only stomatal function but also replacement of the water that is lost.

The evaporation of water from the guard cells and adjacent cells has been termed peristomatal transpiration (see review 91), and there is evidence that the transpiration from this region is more rapid than from other parts of the epidermis (88–90, 150). Maercker (88) supplied tritiated water to leaves and found more label in the vicinity of the guard cells than in the surrounding epidermis when the disintegrations of the tritium were collected by a photographic emulsion coating the epidermis. She also used hygroscopic coatings that changed optical density upon hydration (89), and the results obtained with them resembled the results with the tritium label. These experiments gave clear results but may be subject to the same diffusion problems described earlier for marker molecules (see section on Cell-to-Cell Transport), i.e. diffusional space may be entered that normally would not be part of a bulk flow pathway because the experiments involved long times and possible concentration gradients. However, Maier-Maercker (90) demonstrated that water deficits are more severe in cells close to the guard cells than in cells farther away because the walls of the subsidiary cells wrinkled upon exposure of the epidermis to low humidities, suggesting turgor loss. This effect was most apparent when the guard cells were opening. Upon stomatal opening, the subsidiary cells gradually rehydrated. It therefore seems that transpiration could be more rapid in the vicinity of the stomatal apparatus than in other regions of the epidermis, although it would be desirable to know the solute content of these cells during shrinkage and swelling and whether membrane characteristics of the cells were changed. Rapid changes in solute content can occur in stomatal guard cells when water potentials are low (48), and Lösch & Schenk (86) found that solutes were lost from guard cells about an hour after stomatal closure by low humidities.

On the other hand, Sheriff & Meidner (149) interpreted the conductivities observed in leaves of *Tradescantia* in terms of a close connection between the leaf xylem and the epidermis. They view this path as having a low resistance compared to the mesophyll tissue so that water would bypass the mesophyll cells through vascular connections to the epidermis. However, their conclusions relied on differences in conductances of leaf tissue with and without epidermis that, on inspection, were not statistically significant. Their measurements of epidermal conductance (99, 149) were also subject to the possible movement of water films along the surface of the isolated tissue rather than along pathways normally used in situ. Therefore, although there may be preferred paths for liquid water as it moves from the veins to the epidermis (98, 99, 149, 150), more work will be required before the paths are known with certainty.

Others (133, 169) have used mathematical models to calculate where evaporation occurs most rapidly in the leaf. These have invariably indicated that evaporation is most rapid from the guard cells and the mesophyll cells beneath the epidermis and closest to the stomata. A physical model of the stomatal cavity lined with wet filter paper showed that evaporation occurred most rapidly from those surfaces close to the stomatal pore (100). These results extend the concept of peristomatal transpiration to the interior of the leaf. Indeed, the implication is that the majority of the liquid water moving through the leaf would have to reach evaporation sites close to the underside of the stomata. If the internal surfaces of the leaf are uniformally wet where they are in contact with air, as was assumed by these investigators (100, 133, 169), these conclusions seem inevitable. The diffusive resistance for water vapor is smallest for those molecules closest to the stomatal pore, and thus the flux would be greatest from nearby evaporating sites.

The question therefore becomes: are the internal surfaces uniformly wet? Although the data of Farquhar & Raschke (51) indicate that the evaporating sites are *fully* wet, not all internal surfaces need to be evaporating. Indeed, the comparability of the diffusive resistances for water vapor and helium (see above) suggest that evaporation does not occur primarily from the superficial tissues or cells of the leaf. The cuticle is one means by which the site of evaporation might be modified inside the leaf. Neither the mathematical models (133, 169) nor the physical model (100) took the effects of internal cuticle into account. It would be useful to have measurements of the amount and location of the internal cuticle and how it changes the transpiration characteristics of the leaf. If plants can alter the location of the evaporation sites by altering the extent of internal cuticle, the result could be not only a protection of cells close to the guard cell complex but also an alteration of the diffusive resistance to vapor movement within the leaf.

GROWTH

The enlargement of plants is almost entirely attributable to an increase in cellular water content. The process depends on the simultaneous uptake of water, extension of the cell walls, and accumulation of solute. Enlargement is initiated when the walls are loosened by metabolic events, and a turgor-driven extension follows (35, 36, 159). As extension occurs, turgor decreases and creates a lowered water potential within the cells. This low water potential causes water to enter the cells, enlarging them. Because of wall extension, turgor and water potential are lower during growth than when the walls have not been loosened and growth is not occurring. During this process, solute must continually accumulate if dilution of the cell solution is to be prevented. The solute maintains the osmotic potential necessary to generate the turgor for wall extension and the water potential for water uptake.

The role of turgor in extending the walls is well documented. Cleland (33) showed that a minimum turgor, usually termed the yield threshold (Y), had to be exceeded before wall extension occurred. Green et al (63) interpreted the growth of *Nitella* in terms of ($\psi_p - Y$), i.e. a turgor increment that extends the walls. This work confirmed the earlier findings of Probine & Preston (130), who showed that isolated cell walls of *Nitella* required a force above a minimum before irreversible extension of the walls occurred. Wall extensibility was a function of the rate of elongation occurring before the walls were isolated, which indicated that wall structure had been altered by cellular metabolism such that extension by turgor could take place.

There is evidence that Y, which is a cell wall property, can be changed by metabolic activity. Thus, Green et al (63) observed changes in Y that required about 30 min in *Nitella* and were sensitive to metabolic inhibitors. Y appeared to be controlled simultaneously by a hardening that was nonmetabolic and a loosening that was controlled by metabolism.

By comparison with the evidence that turgor drives cell wall extension, attempts to detect a lowered water potential in enlarging tissue have had varied success. Early efforts (4, 22, 24, 25, 33, 34) depended on immersion of tissue segments in concentrated solutions and determination of the solution water potential that prevented enlargement. This approach suffered from problems mentioned earlier (see Background and Tissue Transport sections) because of long incubation times, solute penetration, unstirred layers of solution, and in addition the need to prevent growth in order to measure water potential. Kinetic measurements of the rate of equilibration of tissue segments with isotopically labeled water (122, 123) or with solution (139) were subject to similar problems (139).

It should be noted that most studies of cell enlargement and the mode of action of growth regulators have been conducted with tissue segments immersed in solution. Osmotic disequilibria are hard to detect under these conditions and have generally been ignored or have been tested by observing the

hydration kinetics of the tissue in the solutions. However, the effects of unstirred layers of solution and solute exchange make the kinetics difficult to interpret. The problem is worsened by the simultaneous enlargement of the tissue that obscures the initial and final stages of the kinetics. Therefore, little is known about osmotic disequilibria in these experiments, and in consequence little can be concluded about the mode of action of growth regulators in water-driven aspects of cell enlargement.

The best early estimates of the water potentials associated with growth appear to have been obtained from the kinetics of water uptake by previously dehydrated tissue (139). These kinetics suggested that enlarging tissue required a water potential 1 to 1.5 bars below the water potential of the external solution in order to supply water to the enlarging tissue. Subsequently, isopiestic thermocouple psychrometry was used to measure directly the water potential during growth in growing regions of intact plants (11, 20, 31, 109, 172). The water potentials were 1.5 to 4 bars below those of the vascular system and were not observed in the mature tissue of growing plants. Therefore, it is clear that there are significant osmotic disequilibria in the growing tissues.

It is possible to place these results with intact plants into a conceptual framework using a theory of cell enlargement from Lockhart (84). The basic tenets are that enlargement requires a high enough turgor to extend the walls and a low enough water potential to provide water for the enlargement process. The osmotic potential must be sufficiently low to allow both these requirements to be met simultaneously. For tissues, enlargement properties remain constant when enlargement occurs at a steady rate, but they vary with position in the tissue because of water potential gradients involved in moving water to the enlarging cells. For many studies, however, growth rates are measured as average rates for the entire enlarging region. Therefore, average tissue water potential, osmotic potential, and turgor are often adequate to describe the enlargement process. Accordingly, the steady rate of tissue enlargement is related to the average wall extensibility (m) and average turgor that extends the wall by the equation (63):

$$\frac{dV}{dt}\,\frac{1}{V} = R = m(\psi_p - Y) \qquad 9.$$

where V is the volume of enlarging tissue (cm^3), R is the relative growth rate (s^{-1}), Y is the average yield threshold (bars), and m has units of $sec^{-1} \cdot bar^{-1}$. This equation represents the demand for water resulting from the extension of the walls by the turgor increment ($\psi_p - Y$).

The steady rate of water uptake necessary to support cell enlargement is related to the average tissue conductance for water (L) and average water potential difference between the water source and the protoplasts in a fashion similar to that in Equation 6. For most plant tissues, the water source is the xylem and thus:

$$\frac{dV_w}{dt}\frac{1}{V_w} = R = L(\psi_o - \psi_w) \qquad 10.$$

where V_w is the volume of water in the enlarging tissue (cm^3), ψ_o is the water potential of the xylem (bars), ψ_w is the average water potential of the elongating tissue (bars), and L has units of $sec^{-1} \cdot bar^{-1}$. Equation 10 is not identical to Equation 6 because the water transport is expressed in terms of the volume of water in the growing region. This is a relative rate of transport whereas Equation 6 described transport as an absolute rate. This changes the units of L but not the fundamental meaning. Similarly, V_w of Equation 10 is not identical to V of Equation 9 because V_w involves only water volume whereas V involves intercellular space as well as water volume. The differential forms are equivalent, however, and R of Equation 10 equals R of Equation 9. Equation 10 represents the supply of water for cell enlargement. The water potential difference ($\psi_o - \psi_w$) has been called the growth-induced water potential (109) or growth-sustaining water potential (151) that drives water inflow.

Growth R therefore depends on a water demand function and a water supply function which, because they act simultaneously, can be combined. Substituting Equation 1 in Equation 9 and combining Equations 9 and 10 to eliminate ψ_w gives:

$$R = \frac{mL}{m+L}(\psi_o - \psi_s - Y) \qquad 11.$$

which is the combined rate equation governing tissue enlargement (20, 84, 138) and showing both the effects of wall extensibility and water conductance. The factor ($\psi_o - \psi_s - Y$) is the net osmotic force for growth and represents the maximum osmotic force ($\psi_o - \psi_s$) diminished by Y. The coefficient $mL/(m + L)$ determines the rate of tissue enlargement at a particular ψ_o. When m is large, the coefficient approximates L, which then controls growth. When L is large, the coefficient approximates m, which controls growth. Although this form of the equation does not show ψ_p explicitly, the involvement of turgor in cell enlargement is implied by ψ_s according to Equation 1.

Figure 2A, B shows Equations 9 and 10 and Figure 2C shows the combined expression (Equation 11) in diagrammatic form and illustrates that enlarging tissue has a water potential defined by the intersection of the lines formed by Equations 9 and 10 when growth occurs steadily. It is obvious that plants may differ with respect to their tissue water potential and growth depending on the water supply and demand. When L is large, ψ_w is close to ψ_o and the growth rate is large at a particular m. When m is large, ψ_w is close to the water potential at Y and growth rate is large at a particular L. Therefore, ψ_w may be anywhere between ψ_o and the water potential at Y. As a result, the growth-induced water potential ($\psi_o - \psi_w$) can vary and be modified either by the activity for growth, which affects ψ_w, or by the potential of the water source, which affects ψ_o.

The relative magnitudes of m and L may be compared by setting Equation 9 equal to Equation 10:

$$\frac{m}{L} = \frac{(\psi_o - \psi_w)}{(\psi_p - Y)} \qquad 12.$$

This relationship shows that simple measurements of $(\psi_o - \psi_w)$ and $(\psi_p - Y)$ in the intact tissue at steady state can indicate whether cell enlargement is limited by water conductance ($m/L > 1$), wall extensibility ($m/L < 1$) or both ($m/L = 1$).

The measurement of these rate-controlling parameters can be made in intact enlarging tissue by thermocouple psychrometry. Because the tissue remains attached to the plant, growth can occur steadily during the measurement. The tissue water potential is measured in the usual way (11, 20), and tissue osmotic potential is also measured on the cell solution after freezing and thawing the same tissue to break the cell membranes. Although this loss of compartmentation mixes all the solutions in the tissue, notably dilute ones in the cell wall with concentrated ones in the protoplast, the effects are small because the walls consist of only the primary wall which is a small proportion of the cell volume at this stage of development. The turgor can then be calculated from Equation 1 for the intact tissue. The relative growth rate can be measured with methods of evaluating increases in water content as tissue increases in size, usually from fresh weight and dry weight determinations and area or length measurements. The most difficult term to evaluate is the yield threshold Y. Measurements have involved soaking tissue segments in solutions, which gives rise to the sorts of problems described above (33, 34), or withholding water and determining the turgor at which growth stops (11, 95, 131). The measurements require several hours or days during which Y might change.

In principle, however, it should be possible to measure Y by excising enlarging tissue in air. Upon excision, the water in the xylem is rapidly depleted and its water potential falls until it equilibrates with the water potential of the surrounding cells, preventing water entry into these cells. Since turgor remains large enough to extend the walls but no water can enter, the walls should relax, and turgor should decrease to Y. Figure 2D shows that the change resulting from excision should be a depletion of xylem water and a movement of xylem water potential and tissue turgor to the right until $\psi_o = \psi_w = (\psi_s + Y)$, where enlargement ceases. The turgor increment measurable by this decrease is $(\psi_p - Y)$. This approach has the advantage that Y can be evaluated in only a short time and on the same tissue that all the other parameters are measured.

Recently, Equations 9 to 12 were evaluated using a newly designed guillotine thermocouple psychrometer that allowed the water potential to be monitored continuously during elongation of intact tissue and after excision of the tissue (17a). The turgor decreased to Y within about 5 min in accordance with

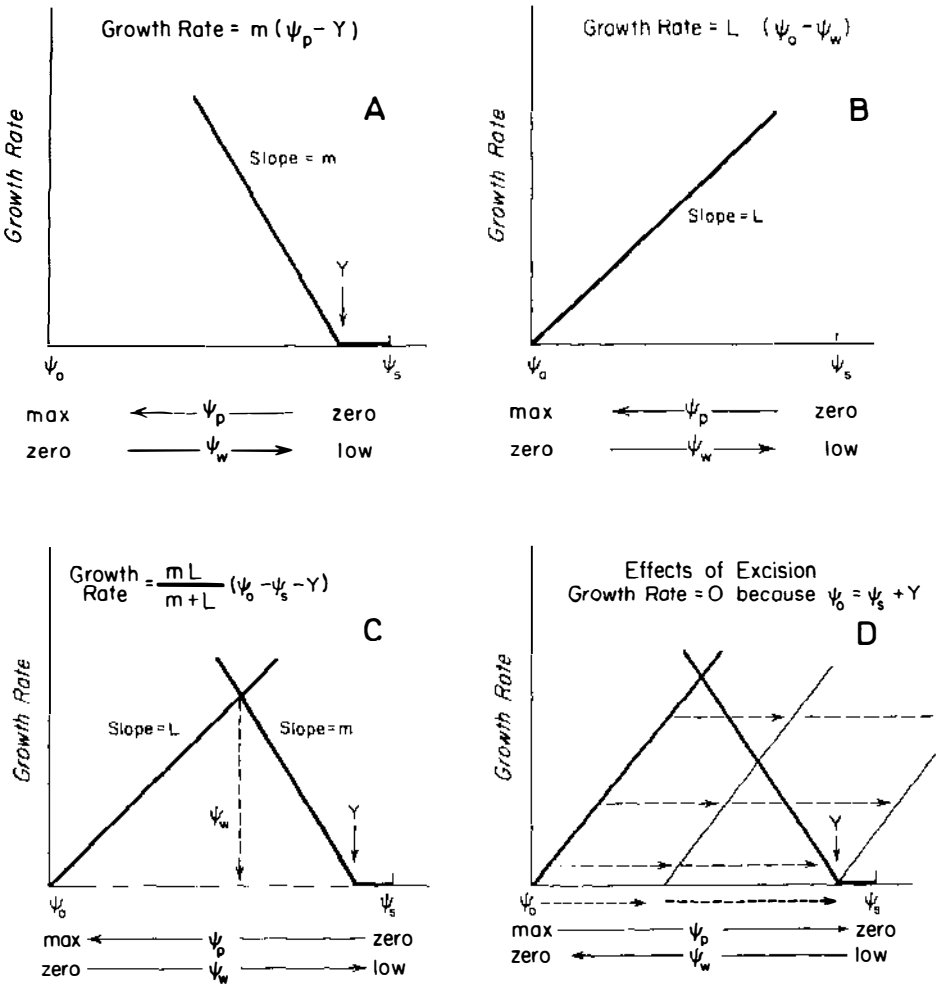

Figure 2 Diagrammatic representation of Equations 9 to 12 showing effects of (A) wall extensibility m, (B) water conductance L, (C) both wall extensibility and water conductance, and (D) effects of depletion of water supply by plant tissue that is enlarging steadily. In (D), depletion causes the water potential of the water source (ψ_o) to move lower (to the right) until $\psi_o = \psi_w = \psi_s + Y$, where wall extension ceases. This change can be used to measure Y. Among the factors that cause depletion are (*a*) the use of water in the soil without replenishment or (*b*) the use of water in the xylem after excision of the tissue in air. Y is most accurately measured when depletion is rapid, as in (*b*).

the theory shown in Figure 2D. The turgor increment ($\psi_p - Y$) was about 0.9 bars in soybean stems (hypocotyls). This indicates that turgor was not far above Y when rapid growth was occurring. The value of Y was about 4.4 bars in these stems, which shows that the cells required quite high turgor before enlargement could begin. The measurements of Y are similar to some made recently with the pressure probe (40a).

Inasmuch as this method (17a) allows the tissue conductance for water and the wall extensibility to be compared, it can determine whether the water supply or the water demand for wall extension is most rate-limiting for growth. For the soybean stems used in the study, ($\psi_o - \psi_w$) was about 1.5 to 2.5 bars. Because ($\psi_p - Y$) was 0.9 bars, L and m were about the same magnitude and, according to Equation 12, m/L approximated 1. Thus, conductance (supply) and extensibility (demand) co-limited the rates of stem elongation.

It must be emphasized that the theoretical analysis of growth in Equations 9–12 applies only to the steady state. If growth departs from the steady state, as when the tissue is excised, the analysis cannot be used until new steady state conditions are established. Nevertheless, even in transient conditions, the concept remains valid that growth ceases if ψ_p decreases to Y or ψ_o decreases to ψ_w. Therefore, the excision experiment represents a convenient way to measure Y (Figure 2D).

An alternate method attempted to use transient conditions to determine the factors limiting rates of cell enlargement (37). It relied on changes in turgor occurring during changes in growth rate and had the advantage of being simple, but because it measured only turgor, other parameters in Equation 11 (Y, ψ_s, ψ_o) could change without detection. Therefore, the results obtained in this fashion are somewhat ambiguous.

The measurements of ($\psi_o - \psi_w$) in enlarging tissue imply that the resistance to water movement through the entire tissue is significant (109; see also 40). Molz & Boyer (109) calculated the magnitude of ($\psi_o - \psi_w$) from the properties of single cells in the tissues. These calculations indicated that for single, isolated cells having hydraulic conductivities of 10^{-6} cm·sec^{-1}·bar^{-1} (typical of higher plant cells), the water potential would need to be only about 0.1 bar below the water potential of the surroundings in order to supply water for rapid cell enlargement (local equilibrium). However, for cells in tissues, the surrounding cells add additional resistance, and the cell water potential would need to be several bars below that of the water supply in order to supply water for enlargement. The comparatively large size of ($\psi_o - \psi_w$) is caused by the necessity for cells close to the xylem to transport water much faster than for their own needs alone. For stem tissues, the radial symmetry also forces the initial transport out of the xylem to pass through only a few cells to the entire surrounding population, and particularly large gradients may develop. Molz & Boyer (109) measured the sorption kinetics of soybean stem tissue and presented measurements of ($\psi_o - \psi_w$) as two ways of testing the theory. In each

test, average tissue water potentials were between −1 and −3 bars. This work confirmed that significant water potential disequilibria were associated with tissue enlargement and provided a physical explanation for why they occur.

Silk & Wagner (151) extended the work to a three-dimensional analysis of water entry into roots during growth. Their conclusions were similar except that, because water entered both from the vascular system and the surrounding soil, the water flow pathways were shorter than in stems, and the water potential differences required to move water for growth were smaller, rarely exceeding 1 bar.

Recently, a combination of intact and excised tissue was used (172) to explore the water potentials of elongating regions throughout the maize plant (root, stem, leaves, and silks). They were between −2 and −4 bars and, as ψ_o varied during the day because of transpiration, ψ_w in the enlarging tissue changed in parallel. The adjustment of ψ_w to ψ_o was brought about by solute transport to the enlarging tissue that increased concentrations sufficiently within the cells to lower ψ_s. This diurnal osmotic adjustment also maintained ψ_p constant. Therefore, despite diurnal fluctuations in ψ_o, both $(\psi_o - \psi_w)$ and ψ_p remained virtually constant and favorable for growth.

These measurements together with the theoretical analysis (see especially Equation 12) indicate that water potential disequilibria are large enough to cause cell enlargement to be rate-limited at least in part by the water conductance (supply) in intact plants. This conclusion implies that changes in ψ_o can alter $(\psi_o - \psi_w)$, and the growth rate may be rapidly altered without a change in turgor when ψ_o fluctuates. This is an important principle. It arises from the necessity for a water potential disequilibrium to supply water for steady cell enlargement. Any transient change in the disequilibrium should be quickly reflected in a change in growth rate without any requirement for an immediate change in turgor or other factors normally affecting growth. Eventually, of course, turgor should respond as new steady conditions are established. There are two recent studies (94, 104) in which growth was inhibited at low water potentials without a detectable change in turgor of the enlarging tissue. It therefore seems possible that a change in $(\psi_o - \psi_w)$ could have been involved, at least in the early phases of growth reduction.

Solute transport is another aspect of growth in the intact system that can change with changing external conditions. At low water potentials, solute transport may continue but may exceed solute use so that osmotic potential decreases, i.e. osmotic adjustment occurs (94, 101, 102, 104 are examples). As a result, turgor remains higher than would otherwise be the case. Solute accumulation can be so extensive that turgor does not decrease at low water potentials (94, 104). Thus, it is possible for growth to be inhibited without detectable changes in turgor both in the short term and in the long term (94, 104).

Boyer & Wu (20) studied how $(\psi_o - \psi_w)$ responded to changes in the supply of auxin because of the possibility that auxin could affect the conductance of

tissue for water (4, 122, 159). They determined the water potential and growth of tissue before and after removing the auxin supply. The ($\psi_o - \psi_w$) changed little despite large changes in growth rate caused by auxin, and they concluded that the tissue conductance must have changed. However, they used tissue segments excised in air for most of their measurements and, in view of the effects of this type of excision on the water potential (see above), the measurements may have represented the water potential at Y rather than the water potential of intact tissue. Cosgrove & Cleland (38) failed to find an effect of auxin on pressure-induced changes in growth rate and concluded that auxin had little effect on tissue conductances to water. Therefore, the effects of auxin on water transport need further investigation.

It should be noted that throughout this application of growth theory to intact plant tissues, it has been assumed that the flow path through the tissue has a significant friction caused by the necessity of outer cells of the growing region to drag water from the xylem through many intervening cells in the growing region. This idea has been challenged by Cosgrove & Cleland (39), who suggest that the potentials associated with growth are caused by solute in the cell walls. In this case, frictional resistances would be small and the water potential of the cell walls and protoplasts would be held low by the osmotic potential of the apoplast solution. Indeed, these investigators (39) found that hydraulic conductivities of cortical cells in pea stems were larger than in most higher plants when measured with the pressure probe, and they concluded that calculated frictional resistances would be small in these stems. However, this is at variance with conclusions of an earlier study in the same system using similar techniques (40). Moreover, measurements of hydraulic conductivities of cortical cells may not apply to other cells in the elongating region, particularly the small cells adjacent to the vascular tissue where substantial resistances could be present.

In addition to the measurements of hydraulic conductivities, these workers (39) measured the solutes in the apoplast solution by three different methods. First, they flooded the intercellular spaces of growing pea stems with water, removed this water by centrifugation of stem segments or by pressurization of roots of intact seedlings, and measured the solute content. The concentration in the original cell wall solution was calculated from independent measurements of the volume of water that had been used to fill the intercellular spaces. Second, exudate was collected from the cut surface of stem segments that had been pressurized and the concentration of the exudate was measured. Third, the turgor pressure of enlarging cells was measured with the pressure probe at high and low temperatures on the assumption that low temperatures would not alter the osmotic potential of apoplast solutes significantly but would alter the movement of water through any frictional resistances in the tissue. The first two measurements indicated that apoplast solute concentrations were equivalent to -2 to -3 bars, and the temperature experiments showed little change in turgor, which is consistent with low frictional resistances in the tissue.

Each of these measurements is likely to be compromised by important problems, however. First, the flooding of the intercellular spaces with water should upset equilibria between free solutes and sorbed or compartmented solutes. Thus, apoplast water would have been diluted by the water flooding the intercellular spaces, and sorbed or compartmented solutes would tend to be released to this water until a new equilibrium occurred. Measuring the solutes in the solution in the intercellular space would reflect not only solutes that had been free in the apoplast but also solutes that had been released from the cell walls or from compartments in the cells. Second, the expression of exudate under pressure from cut segments has the possibility of contamination by solutes released from the phloem, which was also exposed at the cut surface where the solution was collected. Third, turgor was measured for only 5 min after temperature was lowered, which might not allow sufficient time for transmission of temperature-induced changes in turgor throughout the tissue. Tissue generally requires long times (on the order of 20–200 min) before new stable water potentials and turgors are established (12, 16, 17, 95, 109, 113, 114, 143, 155, 165, 166).

Although the experiments of Cosgrove & Cleland (39) were designed to test whether significant solutes are present in the apoplast of enlarging tissue, the problems in each experiment tend to overestimate the quantity of solute and underestimate the amount of frictional resistance. It is well to note that pressures of about 2 bars are required to move water out of enlarging tissue (11). Pressures of this magnitude are expected if frictional resistances dominate and are difficult to reconcile with the concept of Cosgrove & Cleland (39). It will be particularly important to explore whether apoplast solutes contribute significantly to the water potentials of growing tissue by using pressures to measure the extent of osmotic disequilibrium and other methods that will not upset equilibria between bound and free solutes.

Most of our understanding of cell enlargement is predicated on experiments showing that turgor extends cell walls according to the degree of wall extensibility. Yet experiments with intact plants indicate that rapid changes in water supply can cause rapid changes in growth rates without necessarily changing turgor wall extensibility. Moreover, longer-term changes in water supply are confounded by changes in osmotic potential that maintain turgor in intact plants. Thus, we must look beyond turgor for additional explanations of how growth can change. Many of the specialized characteristics of growth in intact tissue can be observed only with difficulty in single cells or in tissue segments bathed in solutions, but they can have important consequences for the control of growth rates.

WHOLE PLANTS

Water transport through whole plants is complicated by several types of flow occurring simultaneously. Most water is lost by transpiration during the day.

Smaller amounts are devoted to cell enlargement, cell metabolism, and phloem transport. At night, transpiration is diminished and the small amounts may become the dominant flows. We shall consider all of the smaller flows together as "growth" for which water uptake for cell enlargement is the major component.

During nonsteady flow, one must also consider water movement for rehydration and dehydration of the tissue. This water can be considered to be stored in tissue capacitances. It is not a part of the transpiration or growth components. Each day as transpiration begins, the plant dehydrates (tissue capacitance loses water) and the water potential decreases until water enters the plant rapidly enough to prevent further dehydration. The reverse happens as the day ends. Thus, leaf water content and leaf water potential rise and fall diurnally.

The conservation of mass requires that each of these flows be additive with due regard to whether water is entering, leaving, or being stored by the plant (16). Accordingly:

$$A + T = G + H \qquad 13.$$

where A and T are the fluxes for absorption and transpiration, and G and H are the storage fluxes for growth and hydration-dehydration, respectively. In Equation 13, A represents the total water gained by the plant. T is the total water lost by the plant. The sum of A (positive) and T (negative) is the flux available for growth and changes in hydration. G is always positive or zero whereas H can be positive or negative depending on whether the plant is hydrating or dehydrating. Although G is considered a storage term similar to that for H, the two terms differ because growth can occur continually and often is localized whereas hydration is a transient phenomenon that can occur anywhere in the plant. The fluxes are most usefully described in terms of the total flow per plant (cm^3/sec^{-1}). They can also be expressed on the basis of unit area of leaf or some other surface ($cm^3 \cdot cm^{-2} \cdot sec^{-1}$) if due attention is given to the effects of branch points (141).

If we consider steady conditions, these concepts are simplified because the water status of the plant is a constant. The water potentials do not change with time, and H is zero. Thus, in the steady state:

$$A + T = G \qquad 14.$$

This equation states that water absorption must exceed transpiration sufficiently to also supply water for growth. Growth proceeds at a rate that is permitted by the water potentials necessary to bring this equation to a steady state (see section on Growth), i.e. to bring absorption to a level that replenishes the evaporating surfaces and supplies the water for G. Leaf water potentials decrease until this occurs, after which they become constant.

Because T can vary, it is possible to simplify this relationship even further by choosing nontranspiring conditions, in which case:

$$A = G \qquad 15.$$

On the other hand, when transpiration is rapid, the water potentials within the plant may be so low that G approaches zero. In this case:

$$A = -T \qquad 16.$$

Equations 13–16 suggest simple ways to study the component flows in whole plants. However, each flow has its own set of component forces and one must distinguish which force applies to which component flow.

Water flow through plants must generally be studied in the whole organism because detached parts often do not simulate the factors controlling flow in the intact system. Detached parts by their nature have open ends with exposed vascular tissue and intercellular spaces. When pressure is applied, water can infiltrate the intercellular spaces and can lead to water movement through the apoplast that would not have occurred in the intact plant (154a). When tensions are applied, air can leave the intercellular spaces which may prevent large tensions from being applied because the exiting air bubbles break the liquid continuity between the tissue and the measuring equipment.

The difficulty of duplicating whole plant behavior in detached plant parts centers on the vascular system, where vascular continuity plays an important role. Normally, it is a completely closed system and pressures may vary widely from somewhat above atmospheric (up to perhaps 4 bars due to root pressures) to well below atmospheric (−30 to −60 bars when transpiration is rapid or there are low soil water potentials). At these extremes, water may exude from the edges of leaves at positive pressures (guttation) and exceed the water requirements of the plant, or the xylem water columns may rupture at large tensions (embolism) so that flow undersupplies the plant. Therefore, it has been necessary to separate the conditions under which transport is studied into those where soil water potentials are high, thus avoiding extreme vascular tensions, and those where soil water potentials are low and large tensions occur.

High Soil Water Potentials

The relationship between leaf water potential and water transport has been studied extensively since the newer methods of measuring tissue water status became available. Most investigators varied transpiration and measured the leaf water potential when the roots were in nutrient media or soil of high water content. Weatherley and his coworkers (157, 164) showed that leaf water potential decreased by a large amount as transpiration became more rapid but, at higher rates of transpiration, further decreases became less. The slope of the relationship represented the conductance of the flow path and, because the slope was nonlinear (i.e. not straight), these investigators concluded that the conductance was flow-dependent. They attributed the nonlinearity to the roots since the roots represent a major resistance to water movement in transpiring plants. However, others removed the roots and stem from the experimental

leaf, but leaf water potential continued to show the same nonlinear behavior (16, 129). Moreover, water transport through the roots showed only a slight nonlinearity in comparison to water transport through the leaves (16). This result showed that the nonlinear relationship could not be caused by the roots, although the roots might have contributed slightly to the effect.

The presence of nonlinearities in the relationship between transpiration and leaf water potential was confirmed under field conditions (71). Meyer & Ritchie (103) also observed nonlinearities but had difficulties establishing steady state conditions. Aston & Lawlor (3) found extreme nonlinearities in a laboratory study. They concluded that changes in the root conductance could account for this behavior but presented no root data. The leaf water potentials were estimated from leaf water contents determined with a beta gauge, which is known to be insensitive to small changes in water content (118) and could have caused some of the nonlinearity. Black (6–8) observed nonlinearities that continued when the roots were absent, thus confirming earlier observations (16, 129).

Some of these investigators (6–8, 71, 103) did not demonstrate that steady transpiration and water potentials had been achieved in their measurements. Bunce (22a) showed in soybean and cotton *(Gossypium)* that nonlinearities were less when longer times were used to establish steady conditions. This illustrates the importance of conducting measurements in the true steady state in this type of experiment.

In contrast, Hailey et al (64) and Neumann and his coworkers (47, 117) observed linear relationships between leaf water potential and transpiration in whole plants of several species. The experimcnts were conducted under steady flow conditions and used either the pressure chamber or psychrometer to measure leaf water potential. Thus, the methods were similar to those of investigators who carefully used steady state conditions but observed nonlinearities (16, 157, 164). It is important that the linear behavior found by Hailey et al (64) and Neumann and coworkers (47, 117) was often in older plants and always involved mature, fully expanded leaves. Therefore, it appears tht linearity was associated with a lack of leaf growth.

These studies when taken together show that nonlinear behavior is a frequent but not constant property of water transport in intact plants. However, when nonlinearity is present, the primary site is in the leaves and not the roots. This raises the question of how the leaf conductance could vary, in some cases by more than an order of magnitude, as the flow through the leaf varies. Related to this question is the occasional nature of the nonlinearity: why is it present at some times and not at others?

Most investigators have considered steady transpiration to be a measure of the rate of water flow through the plant. This ignores other component flows, notably the one for growth. The small flows of water associated with growth

could have their own set of driving forces, complicating the relationship between transpiration and leaf water potential. Furthermore, growth might be present at some times and negligible at others.

This possibility was tested (16, 17) by conducting steady state experiments with sunflower plants that were nontranspiring, i.e. $A = G$, or that were transpiring so fast that leaf water potentials completely inhibited leaf growth, i.e. $A = -T$ (Equations 15 and 16). Although the complete relationship was nonlinear, it became linear when the plants transpired fast enough to inhibit leaf growth (see Figure 3B and 3C). The conductances calculated from the fluxes and water potentials were markedly different for the growing and nongrowing condition, both in the intact plant and in the detached leaf. Furthermore, the difference in conductances fully accounted for the nonlinearities observed in intact sunflower plants at varying rates of transpiration. Therefore, the change in plant conductance was only apparent and associated with the transition from one component flow (G) to another (T).

The unexpectedly small conductance of the plant when $A = G$ compared to $A = -T$, although accounting for the nonlinearity effects, raises the question of why the conductance should be so different for the growth and transpiration components. Either the conductance of the flow path through the leaf changed as flow changed from one component to the other or each component followed a different path having its own conductance. These possibilities were tested (16, 17) by measuring water transport in rehydrating and dehydrating leaves on the assumption that leaf rehydration would involve all the leaf cells and water would follow the same path as during growth. Regardless of whether leaves were hydrated by water uptake through the petiole or dehydrated by pressurizing the lamina, flow rates were much less than those for transpiration even when the driving forces were unrealisitically high. Therefore, it was concluded that the growth path could not support the large flows for transpiration and the paths for growth and transpiration must be different.

Subsequently, Fiscus et al (56) proposed a model to account for these complexities by considering water to be partitioned between component flows for growth and transpiration and water to interact with solute movement through the roots. Figure 3 shows the nonlinearities predicted by the model (Figure 3a–c) and how they compare with the data of (16, 17) and (117) (Figure 3A–C). The comparison is close enough that the model provides a theoretical rationale for the change in conductance from that for growth to that for transpiration and will probably become a valuable interpretive tool.

Many of the concepts that apply to water transport for transpiration and growth are similar to those for water transport in leaves (see section on Leaf Water Transport). To reiterate briefly, water lost by transpiration might evaporate from sites close enough to the xylem that the liquid flow path would be short and have a high conductance. Cells far from a vein would be bypassed by

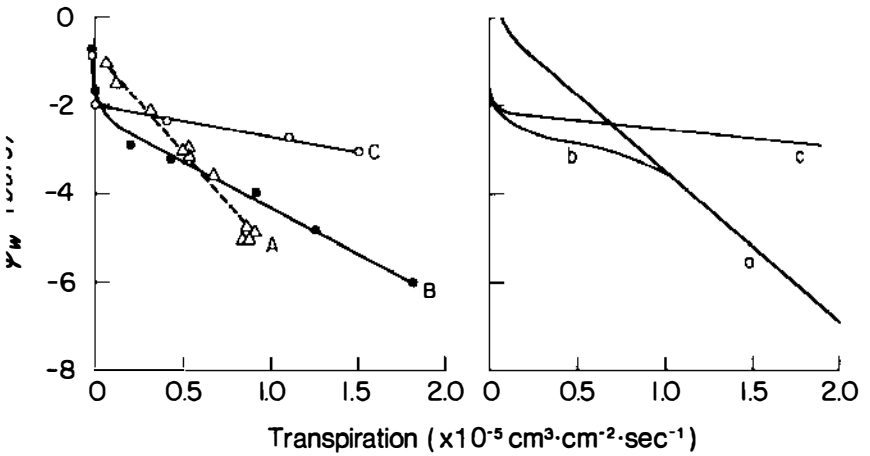

Figure 3 Leaf water potentials at various rate of transpiration. (A) Linear response measured in nongrowing leaves of old sunflower plants (117); (B) nonlinear response in growing leaves of young sunflower plants (16, 17); (C) nonlinear response in growing detached leaves of sunflower plants (16, 17). (a to c) are simulations conducted by Fiscus et al (56) for the experiments in (A to C). Note that curves B and C cross the ordinate, indicating that transpiration is zero and the only water movement is for growth. Most of the nonlinearity in B and C occurs at this cross-over.

the water involved in transpiration and would be surrounded by water vapor being transported to the leaf exterior via the intercellular spaces. These outlying cells would be protected not only by the high humidity but possibly by internal cuticle (Figure 1) that may coat them. This would have the effect of causing the growth path (the entire mesophyll and epidermis) to be long by comparison with the transpiration path. A low conductance for the growth path and a high conductance for the transpiration path would result.

An important principle to come out of this work is that, in intact plants, the location of the rate-limiting resistance to water flow differs according to what kind of water transport is occurring. If water moves only for transpiration, the root represents the rate-limiting resistance. If water moves only for growth, the growing tissue itself represents the rate-limiting resistance even though water must flow through the root to reach the growing tissue. This is because the resistance of the growing tissue is so much higher than that of the root. This implies that altering the flow characteristics of the roots will alter growth only when transpiration occurs and then only by affecting the water potentials of the growing tissues. When transpiration does not occur, altering root flow characteristics should have little effect on growth. This is because the flow to the site of cell enlargement is rate-limited by the high resistance of the growing tissue, and the resistance of the root, being smaller, can change without consequences for growth. Indeed, if one removes the roots from a nontranspiring plant by cutting under water, the shoot growth rate is hardly affected (20). These

principles apply because the resistances to water flow for growth and transpiration are so different. If they did not differ, water movement for growth would be co-limited by the roots and by the path through the growing tissue. Of course, altering root characteristics in other ways that change the production of plant growth regulators or nutrient accumulation from the soil will often affect the growth of the shoot, but these are slow and indirect in comparison to the direct effect of changing the resistances to water movement through the roots.

Apart from these ideas of pathways for water transport, studies of the relationships between water movement and driving forces have provided new information about root function. There is considerable evidence that varying the water transport characteristics of roots can alter the water potentials of the leaves during transpiration. Previous exposure of the roots to dry soil (78, 117), the occurrence of suboptimal temperatures (73), the presence of mycorrhizae (143, 144), the *N* (131) and *P* (132) status of the plant, and the age of the plant (57) can affect the ability of the roots to supply water to the shoot. Often the effects cannot be attributed to differences in root size (131, 144). This suggests that the differences can lie at the cellular level, perhaps at the endodermis where water apparently flows through a wall-cytoplasm barrier (115, 161), or perhaps throughout the cells and tissues external to the xylem.

An example is the mycorrhizal association, which can increase the conductance of root systems (143). In the most common type (endotrophic), the hyphae penetrate individual cells in the root cortex and form an extensive hyphal network in the soil. However, when the hyphae were preferentially killed, the conductance of soybean roots did not change (144). Because there were no differences in root size attributable to the mycorrhizal infection and the effects could be simulated by feeding high *P* levels to the nonmycorrhizal roots, mycorrhizae probably caused high root conductance by enhancing the *P* nutrition of the roots and therefore the transport properties of the host root tissues (144).

The possibility of genetically modifying root systems to benefit agriculture has been investigated by several groups. Genetic differences in rooting density and depth are well known within species. Burton et al (26) successfully selected bermuda grass types with deeper rooting that enhanced pasture production under dry conditions. The deep rooting was best for regions with intermittent rainfall because high production could continue longer in the absence of rain but the soil could be replenished occasionally. Under dry land conditions, however, Passioura (124) demonstrated that wheat forced to rely on only one seminal root yielded more than wheat that was allowed to develop with a full complement of roots. Presumably, plants with pruned roots were kept somewhat water deficient in the early part of the growing season. The resulting water conservation made more water available late in the season when grain growth occurred.

It is perhaps significant that the selection for high yields in certain grain crops has affected rooting densities so that the shoot water status is in turn altered. In one study of new and old soybean cultivars (18), higher leaf water potentials during midday were associated with the newer soybean cultivars. These in turn were associated with higher yields and denser rooting. Thus, plant breeders appear to have selected for more suitable root systems and more favorable midday leaf water potentials by selecting for higher yields.

Another important application of the principles of water transport has been in forest production. Leaf water potentials are frequently low enough to affect leaf metabolic activities in trees, but there are problems not only with characterizing the water status of the large shoots but also in measuring water movement through them. Elfving et al (49) overcame some of these problems by using the principle that transpiration is the product of the leaf diffusive conductance to water vapor and the vapor concentration difference between the leaf evaporating surfaces and the bulk air. Since each of these parameters can be measured in leaves and the air surrounding them, all the information necessary to determine transpiration could be obtained. By comparing the relationship between water potential and transpiration in nonlimiting soil conditions with those when soil water and temperature were varied, the soil conditions that were limiting for root water transport could be identified. This useful idea has been tested in citrus both in the field and in the laboratory by Camacho-B et al (29, 30) and in spruce by Kaufmann (73). Interestingly, root conductances in spruce (a chill-tolerant species) were relatively unaffected by soil temperatures as low as 8°C, but in citrus (a chill-sensitive species) root conductances were reduced when soil temperatures were below 15°C (73).

Another method of measuring water transport in large trees is the heat balance method of Cěrmák and his coworkers (32, 81). Heat is added to part of a stem in an amount that elevates the temperature of a downstream sensor (above the heated area). The amount necessary to hold the temperature constant varies in proportion to the flow. An advantage of this method is that it approaches steady state and can be corrected for the contributions of the nonflowing portion of the stem. Comparisons with transpiration measured directly in smaller plants have been promising.

Low Soil Water Potentials

When soils become water depleted, water transport diminishes. This occurs in part because the conductance of the soil decreases as water withdraws from the pore lumina, decreasing the cross-sectional area for water flow. The tortuosity of the path increases and contributes to the decrease in soil conductance. Furthermore, shrinkage may occur both in the soil and in the roots (69), which decreases the soil contact with the roots. Thus, the entire path through the soil to the surface of the root becomes less conductive, often by several orders of

magnitude [see (59) for some examples in different soil types]. Several theoretical treatments and direct measurements of the soil conductance have led to the notion that the rate-limitation for water movement is in the soil under these conditions (41, 59, 60, 175), probably at the soil-root interface (67, 162). Other work (1, 65, 66, 83, 119, 120, 140, 162) concluded that even with the changes in soil properties, the rate-limitation might be in the plant. However, in none of this work were the changes occurring in the plant and in the soil determined directly but rather by inference from calculated water transport properties.

Recently, the conductance of the soil was compared to that of soybean plants by directly measuring rates of water movement and water potentials in both segments of the flow path as the soil dried (9). The data were collected when flow approximated the steady state, and thermocouple psychrometry was used to evaluate the water potentials throughout the soil-plant system. The data showed that the conductance of the plant decreased at the same time the conductance of the soil decreased. The conductance of the plant was always less than the conductance of the soil regardless of the soil water content, indicating that water movement through the soil-plant sytem was limited more by the plant than by the soil.

The decrease in conductance of the plant is difficult to understand if the water flow pathways remain water filled to the same extent as when water potentials are high. A possible reason for the decreased plant conductance was breakage of xylem water columns and emptying of the vessels. It was proposed that (9) because the xylem water comes under increasing tension as leaf water potentials drop in response to drying soil, the water columns begin to rupture and form gas-filled emboli that render the vessels relatively inactive. This would form an additional resistance to water transport to the shoot.

Direct evidence of vascular blockage has been found in sunflower below water potentials of about -15 bars (14). The blocked vascular tissue could be removed under water and rapid transport resumed in the remaining tissue (14). The blocked tissue had larger diameter xylem vessels than the remaining tissue, which may indicate that the larger the diameter, the more prone is the vessel to rupture of the water column. Also, Byrne et al (28) found discontinuities in the vascular system of plant roots from dehydrating soil. They froze the root tissue and measured the ability of air to pass through the roots in the frozen state. At root water potentials below about -10 bars, air-filled vessels could be detected, indicating that the root vascular system was progressively emptying of water.

Milburn (106–108), and later Tyree and coworkers (167, 168), used acoustic techniques to detect breakage of water columns in *Ricinus* and *Thuja*. The breakage began at leaf water potentials of about -8 to -10 bars and became progressively greater until, below about -20 bars, the rate of vascular disruption decreased once again because most of the vessels had become empty.

This important work indicates that water columns begin to rupture at moderate tensions (8 to 15 bars) in plants. The tensions are considerably less than can be achieved in the laboratory where water withstands tensions of at least 300 bars [see (80) for a discussion of the experiments]. Perhaps gases dissolve in vascular water and cause emboli at tensions below the maximum achievable when water is gas-free and tested in the laboratory.

The tensions at which emboli occur probably differ between species and growth conditions. If emboli form most readily in vessels of large diameter (14), plants grown under water-deficient conditions, which tend to develop smaller diameter vessels, may be less prone to form emboli than plants grown under favorable conditions. Also, the composition or structure of the vessel walls might influence the tensions at which emboli form.

It is interesting that vascular emboli disappear gradually when water is restored to the soil (14). The recovery depends on transpiration low enough not to exceed the impaired ability of the vascular system to supply water to the shoot. For this reason, leaf water potential recovers fastest and most completely under nontranspiring conditions such as occur during prolonged rains and cloudy periods. Vascular repair presumably occurs because tension on the xylem water is relieved, the gases in the vascular emboli redissolve in nearby water, and the water columns reconnect as the gases become fully dissolved. However, more work on embolus formation and repair is needed before we will fully understand why it occurs, the conditions involved, and the physics of the process.

CONCLUDING REMARKS

Progress in understanding water transport has accelerated during the last 15 years because methods have developed for measuring the forces driving water through plants. Of the principles that have emerged, several stand out as particularly fundamental. These are:

1. The cells of higher plants have hydraulic conductivities centering on 10^{-6} $cm \cdot sec^{-1} \cdot bar^{-1}$.
2. At water potentials expected for cells in a tissue, protoplasts having these hydraulic conductivities will be in near equilibrium with their cell walls (local equilibrium). Gradients in water potential will be distributed over larger distances.
3. Water influx and efflux follows slower kinetics from tissue than from cells making up the tissue. This indicates that water must be moving from cell to cell rather than primarily through the apoplast.
4. When the only significant water transport is for replacing the water lost by transpiration, water movement is linearly related to the water potential driving force.

5. When water moves through the plant for growth, the growing tissue itself represents a large resistance that exceeds the resistances in the transpiration path. The resistance of the growing tissue arises from the cell-to-cell nature of water transport through tissue, not from special transport properties of the cells.
6. The resistance to water flow through the plant is not flow dependent but often appears to be as water flow changes from that for growth to that for transpiration. The apparent change in resistance results from the different paths for the two flows, each with its own resistance.
7. Cell enlargement in tissue is associated with water potential disequilibria that are somehow related to the growth process. This is in contrast to single isolated cells, where disequilibria are negligible during enlargement.
8. The resistance to water flow through roots is not flow dependent when due regard is given to the interactions between solute and pressure driving forces. Nevertheless, it is sensitive to conditions altering root cell metabolism.
9. Plants are the dominant resistance in the soil-plant system when water is abundant. They remain the dominant resistance as the soil dries primarily because the resistance increases inside the plant. The increase is possibly the result of rupture of the vascular water columns as the columns come under increasing tension. When tensions are relieved, the columns undergo gradual repair. Rupture of vascular water columns appears to be rare when plants are well supplied with water.

There are many aspects of water transport that remain to be explored. The apoplast contribution to water transport needs better evaluation. The position of leaf evaporating sites needs to be known with more certainty. We do not understand the origin of water potential disequilibria during growth nor the entire role they play in the growth process. Of particular interest is how growth is controlled in the intact plant and how transpiration affects the partitioning of water between water loss by evaporation and water gain for cell enlargement. We need more information about vascular emboli.

The answers that emerge are likely to influence our concepts of how root and shoot growth are controlled and how shoot water deficits can be modified, with important consequences for agriculture and forest management. Now that techniques for measuring the driving forces are at hand for investigating both tissue and cell behavior, the necessary experiments are possible and we may look forward to additional information in the near future.

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