



# The Absorption of Water and Root and Stem Pressures

## INTRODUCTION

The continuous absorption of water is essential for the growth and survival of most plants because they lose large amounts of water daily, often even more than their own weight on hot, sunny days. Unless this is replaced immediately, they will die from dehydration. Only a few xeromorphs, such as cacti, with low rates of transpiration and a large water storage capacity, and plants very tolerant of dehydration can survive without immediate replacement of the water lost by transpiration. Thus, the mechanism of and factors affecting water absorption deserve careful attention. Furthermore, well-watered plants often develop root pressure, resulting in exudation of sap from wounds ("bleeding") and guttation. Other interesting exudation phenomena such as the flow of maple sap, latex, and oleoresin are discussed briefly, although they are not related directly to the absorption of water.

## ABSORPTION MECHANISMS

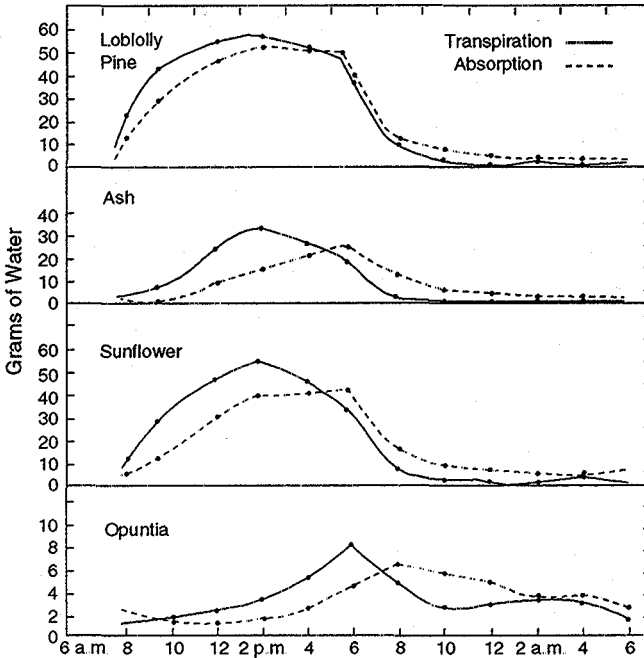
Absorption of water occurs along gradients of decreasing potential from the substrate to the roots. However, the gradient is produced differently in slowly and rapidly transpiring plants, resulting in two absorption mechanisms. Active or osmotic absorption occurs in slowly transpiring plants where the roots behave as osmometers whereas passive absorption occurs in rapidly transpiring plants where water is pulled in through the roots, which act merely as absorbing surfaces (Renner, 1912; Kramer, 1932). When the soil is warm and moist and

transpiration is slow, as at night and on cloudy days, water in the xylem often is under positive pressure (root pressure) as indicated by the occurrence of guttation and exudation of sap from wounds. This difference can be demonstrated by bending the stem of a plant below the surface of a container of a dye such as acid fuchsin and making a cut into it. If the plant is transpiring even moderately rapidly, dye will rush in and stain the xylem above and below the cut, but if the plant has been in moist soil and transpiring very slowly, the dye will not enter but sap is likely to exude from the cut. In moist soil, absorption at night and early in the morning is largely by the osmotic mechanism, but as daytime transpiration increases the demand for water in the leaves, absorption increasingly occurs by the passive mechanism and the osmotic mechanism becomes less and less important. The osmotic water absorption causing root pressure occurs only in healthy, well-aerated roots of slowly transpiring plants growing in moist soil, but passive intake of water can occur through anesthetized or dead roots, or in the absence of roots as in cut flowers or branches (Kramer, 1933). Osmotic absorption and some alternative explanations are discussed later in the section on root pressure.

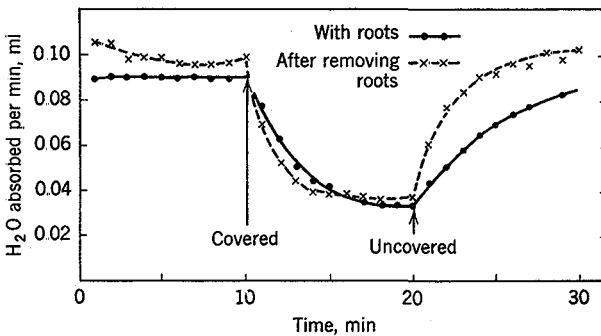
### Passive Absorption by Transpiring Plants

The force bringing about absorption of water by transpiring plants originates in the leaves and is transmitted to the roots or the lower end of cut stems through the sap stream in the xylem. Evaporation of water from leaf cells decreases their water potential, causing water to move into them from the xylem of the leaf veins. This reduces the potential in the xylem sap, and the reduction is transmitted through the cohesive water columns to the roots where the reduced water potential causes inflow from the soil (see Chapter 7 for details). In this situation water can be regarded as moving through the plant in a continuous, cohesive column, pulled by the matric or imbibitional forces developed in the evaporating surfaces of stem and leaf cell walls. Evaporation of water from the twigs and branches of bare deciduous trees and from cut flowers also causes upward flow in the xylem.

As shown in Fig. 6.1, passive absorption often lags quantitatively behind transpiration during the day, indicating the existence of resistances to water flow and capacitance or water storage in the system. Resistance may exist at several points, but the most important site usually is in the living cells of the roots. This is indicated by the fact that the removal of roots from shoots exposed to sun is followed by an increase in the rate of water absorption in a variety of herbaceous and woody plants ranging from sunflowers (Kramer, 1938) to pine trees (Running, 1980) to paddy rice growing in water (Hirasawa *et al.*, 1992). An example is shown in Fig. 6.2. Water storage in the parenchyma cells of various organs is responsible for most of the capacitance effect and the absorption lag.



**Figure 6.1** The lag of absorption behind transpiration on a hot summer day for four different kinds of plants growing in soil supplied with water by an autoirrigator system that permitted measurement of both water loss and water uptake. Note the evening maximum in transpiration of *Opuntia*, which is a CAM plant, and the midday decrease in sunflower, probably caused by a temporary water deficit and partial closure of stomata. From Kramer (1983), after Kramer (1937).



**Figure 6.2** Removal of roots decreases the lag of absorption behind transpiration for sunflower plants in a dilute nutrient solution. Absorption of intact plants was measured for 10 min. The shoots were then covered for 10 min to reduce transpiration and uncovered for another 10 min. The root systems were then removed and the experiment was repeated. From Kramer (1983), after Kramer (1938).

### Osmotic Absorption and Root Pressure

It was stated earlier that positive pressure in slowly transpiring plants often develops in the xylem sap, resulting in exudation (often termed "bleeding") from cut or broken stems. Hales (1727) measured this pressure and there has been interest in the problem from the 18th century to the present. Some confusion has resulted from failure to distinguish between such diverse phenomena as root pressure, stem pressure, guttation, and exudation from nectaries. It also is necessary to distinguish between exudation caused by root pressure as in birch, grape, and many herbaceous plants and that caused by stem pressure as in maple or by wounding as in agave and palm. The older literature was reviewed by Kramer (1945, 1949, Chapter 7).

There are three groups of explanations for root pressure: secretory activity of the root cells, electroosmosis, and the assumption that the roots behave as osmometers.

*Secretion or Nonosmotic Theories.* Ursprung (1929) and others suggested that the water potential is lower on the inner than on the outer side of root cells, resulting in an inward movement of water. This explanation appears to have been revived by Borisova (in McMichael and Persson, 1991). However, it seems very unlikely that significant differences in water potential can be maintained on opposite sides of cells in slowly transpiring plants, and interest in this theory has waned. In the 1940s and 1950s there was renewed interest in the possibility of nonosmotic movement of water in cells and roots. This resulted from observations, such as those of Van Overbeek (1942) and Ginsburg and Ginzburg (1970), that the osmotic potential of exudate from detopped root systems often is higher than the osmotic potential of the solution required to stop exudation (see Kramer, 1983, p. 221, and Mozhaeva and Pilschshikova, 1979, for references). This difference was attributed to some kind of nonosmotic force causing water movement. However, other investigators pointed out that roots are not completely impermeable to solutes, also that considerable salt is removed from the xylem sap as it moves up through the roots and the lower part of the stem. This can result in the concentration of solutes in the xylem sap being significantly higher in the roots than at the stem stump where it usually is collected (Klepper and Kaufmann, 1966; Oertli, 1966). This explanation of the discrepancy was disregarded by Schwenke and Wagner (1992) who proposed a complex explanation of exudation based on turgor-regulated changes in permeability of cell membranes. They also reported strong short-term pulses in exudation previously unobserved. Fiscus (private communication) suggested that if ion uptake is greater toward the root apex than toward the base and water enters along the entire length of the root, the concentration in the xylem solution will become increasingly dilute toward the base of the root. This gradient in concentration might explain some of the discrepancies in the literature.

*Electroosmotic Theories.* Various investigators have attributed root pressure to electroosmotic transport of water into the xylem (Keller, 1930; Heyl, 1933). Water can be moved across a membrane under an applied electric current, with the direction being toward the pole with the same charge as the membrane. The interior of roots are electrically negative to the exterior and cellulose membranes are negatively charged so water should move inward. Interest in electroosmosis was renewed by Fensom (1958) who observed correlations between cycles of root pressure exudation and bioelectric currents, and Tyree (1973) suggested it as an alternative or supplement to the osmotic theory. However, it is doubtful if electroosmosis can cause significant net water movement in plant tissue because the high permeability of plant cells allows water to leak out almost as rapidly as it is moved inward (Ordin and Kramer, 1956; Dainty, 1963; Slatyer, 1967, pp. 174–175).

*Osmotic Theories.* The most satisfactory explanation of root pressure assumes that it is an osmotic process in which roots function as osmometers because of accumulation of solutes in the xylem sap. This view is supported by the pressure probe experiments of Steudle and Frensch (1989) and data in Chapter 3. Most of the solutes are moved into the root xylem by an active ion transport system, but some may be released by the disintegration of protoplasts in maturing xylem vessels (Hylmö, 1953; Kevekordes *et al.*, 1988) and some are carried into roots by the transpiration stream. Cortes (1992) speculated that ions are released in the root interior because of the decreased membrane potential across the cortex.

It is well established that the occurrence of root pressure is correlated with the accumulation of salt in the root xylem. It develops only if root systems are healthy, provided with a supply of minerals, and kept well aerated and at a moderate temperature. Root pressure exudation ceases when root systems are subjected to low temperature, inadequate aeration, dry soil, or an inadequate supply of minerals, as when they are immersed in distilled water.

The principal problem is the location of the differentially permeable membrane permitting solute accumulation in the stele and the development of osmotic pressure. It generally is assumed that in roots which have not undergone secondary growth the endodermis functions as the differentially permeable membrane. This usually may be true, but root pressure was demonstrated in maize roots from which the cortex had been removed, destroying the endodermis (Yu, personal communication). Steudle *et al.* (1993) found that penetrating the endodermis caused a large, but temporary, decrease in root pressure. Ginsburg and Ginzburg (1970) removed cylinders of cortical tissue from maize roots and used them as osmometers to produce osmotic pressure, and Shone and Clarkson (1988) used hypodermal sleeves from maize roots to study the radial flow of water. Thus, it appears that the cortical parenchyma or the

pericycle and stelar parenchyma can function as a multicellular osmotic membrane, although probably not as effectively as in an intact root (Atkins, 1916). Clarkson (1993) discussed root structure with respect to the inward transport of solutes and water and considered plasmodesmata in the symplast pathway, but Rygol *et al.* (1993) questioned the conventional view of inward flow.

Little attention has been given to the location of the differentially permeable membrane in woody roots that have lost their cortical parenchyma and endodermis during secondary growth. It must be present because fully suberized grape (Queen, 1967) and conifer root systems (Lopushinsky, 1980) exhibit root pressure. Also, application of pressure increases water flow through suberized pine roots more than salt movement (Chung and Kramer, 1975). It seems possible that the cambial region serves as a salt barrier in woody roots because its cell walls are too thin to permit significant leakage into the apoplast. However, this problem needs more study.

### Relative Importance of Osmotic and Passive Absorption

There are differences in opinion concerning the importance of osmotic absorption of water and the accompanying root pressure. Fensom (1958), Minshall (1964), Rufelt (1956), and others claimed that it is quite important. Rufelt (1956) and Brouwer (1965) claimed that osmotic absorption operates in series with passive absorption, but it seems more reasonable to regard it as operating in parallel. Furthermore, positive pressure disappears as transpiration increases and increased water flow lowers the solute concentration in the root xylem. Others suggest that it plays an essential role in refilling xylem vessels with water that have become filled with gas by cavitation during periods of rapid transpiration or freezing weather. This is discussed in Chapter 7. Palzkill and Tibbits (1977) claimed that root pressure flow is essential to supply calcium to slowly transpiring tissues such as leaves in the interior of cabbage heads.

Our view is that root pressure results from the accumulation of solutes in the stele of roots and that any beneficial results are largely incidental. Intact transpiring plants can absorb water from drier soil and more concentrated solutions than can detopped root systems (Jäntti and Kramer, 1957; McDermott, 1945). Also, the volume of exudate usually is only a small percentage of the volume of water lost by transpiration, and no root pressure exists in the roots of rapidly transpiring plants (Fig. 6.3). The early history of root pressure phenomena has been discussed in more detail in Kramer (1969, Chapter 5; 1983, Chapter 8). Some of the problems resulting from the simultaneous occurrence of both osmotic and pressure-driven water flow into roots have been discussed by Fiscus (1975) and Dalton *et al.* (1975). The amount of exudation, its composition, and the pressure developed vary widely among plants and environmental conditions (Canny and McCully, 1988).

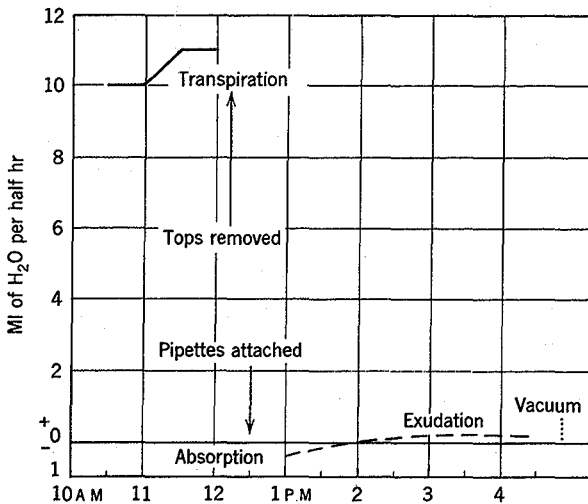


Figure 6.3 The gradual change from absorption to exudation of root systems following the removal of shoots of tomato plants growing in soil at field capacity. Because of a water deficit in the transpiring plants and possibly in the soil immediately surrounding the roots, the roots absorbed water through the stumps for over an hour after the removal of shoots. The maximum rate of exudation was much lower than the rate of transpiration and was increased by application of a vacuum of 64 cm Hg. From Kramer (1983), after Kramer (1939).

### CHARACTERISTICS OF ROOT PRESSURE EXUDATION

Although root pressure seems to play a minor role in overall plant water relations, it is so interesting physiologically and has received so much attention that we will discuss it in some detail.

#### Species Differences

It seems that any plant that can accumulate salt in the root stele should exhibit root pressure exudation. However, there are wide differences among species. Root pressure is seldom seen in woody plants, especially conifers, and the volume of exudate is much greater in plants such as maize, sugarcane, tomato, and sunflower than in legumes. Yu (1966) attributed the larger volume of exudate from corn root systems than from broad bean to the presence of more and larger vessels in corn and less ion leakage. Root pressure was rarely reported in conifers until recently, but it is now well documented. For example, White *et al.* (1958) observed exudation from roots of white pine and white and red spruce. O'Leary and Kramer (1964) observed exudation from detached roots of loblolly pine and white spruce, but not from stumps of detopped seedlings.

Lopushinsky (1980) reported exudation from stumps of detopped seedlings of eight species of conifers, and exudation persisted for many days after detopping. The total volume of exudate varied from 0.1 to 8.0 ml per root system and its osmotic potential varied from 0.024 to 0.078 MPa, which is lower than the potential usually reported for exudate from herbaceous species. Some of these seedlings had new roots, but other root systems were completely suberized. It seems possible that measurable exudation was consistently present in Lopushinsky's experiment because the seedlings were stored for 2 months at 1–2°C before detopping, and this probably favored conversion of starch to sugar and accumulation of solutes in the xylem (Clarkson, 1976). Lopushinsky's measurements of exudation were made at room temperature. Thut (1932) observed root pressure exudation from several kinds of rooted, submerged aquatic plants, and Pedersen (1993) observed guttation of tritium-labeled water from leaf tips of aquatic plants.

*Magnitude of Pressure.* Hales (1727), who made the first recorded measurements of root pressure, observed a pressure of about 0.1 MPa (0.1 MPa = 1 bar) in grape, and pressures of 0.2 to 0.3 MPa were reported in birch in New England by Merwin and Lyon (1909). Pressures ranging from 0.05 to 0.19 MPa have been reported for root systems of herbaceous species, but the highest pressure recorded, so far as the authors know, was 0.42 MPa on maize root systems growing in solution culture (Miller, 1985). White (1938) reported pressures of over 0.6 MPa on excised tomato roots in culture. Higher pressures have been reported in stems of woody plants, but they are believed to be local pressures caused by wounding or microbial activity (see section on stem pressures).

*Volume and Composition of Exudate.* The volume of exudate usually is larger from large root systems, but it often varies among root systems of similar size and past treatment for no identifiable reason. Sugarcane stools exude up to a liter of sap in a week, and maize 100 ml/day for up to 15 days. Crafts (1936) reported a daily volume of exudate from squash root systems greater than the volume of the root systems, and G. H. Yu (unpublished) estimated that exudation from apical segments of corn roots represented a turnover of xylem vessel contents of three times per hour. Minshall (1964, 1968) reported that when abundant urea or  $\text{KNO}_3$  was supplied to tomatoes, exudation was increased up to 80 ml/day per plant for tomatoes in the 16 to 18 leaf stage, a rate much greater than usually observed. Birch trees often yield 20–100 liters or more of sap in a spring (Ganns *et al.*, 1981). The chief sugar in birch sap is fructose, with lesser amounts of glucose and sucrose. Birch sap sometimes is concentrated to make syrup, and in the Ukraine, sugar and citric acid are added to make a soft drink (Sendak, 1978).



The solutes in the exudate from root systems of herbaceous plants usually are chiefly minerals, but the exudate from root systems of legumes and woody plants often contain appreciable amounts of organic substances, chiefly sugar and nitrogen compounds. Xylem sap also contains growth regulators, especially cytokinins and gibberellins, and in stressed plants, abscisic acid. Bollard (1960) reviewed considerable literature on the composition of xylem sap and its role in translocation. Its salt content is increased by fertilization, and attempts have been made to use the composition of root pressure exudate as a guide to fertilizer needs (Lowry *et al.*, 1936; Pierre and Pohlman, 1934). Stark *et al.* (1985) reported that sap extracted from conifer branches by use of a pressure chamber gave a good indication of the relative mineral composition of various trees if they were of similar age and sampled at the same time of day, season, and height. Osonubi *et al.* (1988) reported that the concentration of minerals in the xylem sap was related to the concentration in the foliage. Contrary to Stark *et al.* (1985), they found that the concentration was not sensitive to diurnal variations in rate of water movement. Canny and McCully (1988) discussed the problems encountered in collecting representative samples of xylem sap.

*Periodicity.* Over a century ago Hofmeister (1862) observed a diurnal periodicity in root pressure exudation from detopped root systems, and this has been observed by several investigators in recent decades. The maximum pressure and volume usually are observed during the day. This has been attributed to greater translocation of salt into the xylem during the day than at night. However, Parsons and Kramer (1974) found the highest salt concentration in the exudate from cotton root systems at night, possibly because the volume of exudate per hour was much lower at night. There appeared to be little difference in the total amount of salt translocated into the xylem per hour during the day and night. Raper (private communication) reported that a lower uptake of  $\text{NO}_3^-$  occurs at night than during the day.

Diurnal fluctuations in apparent root resistance or permeability also occur, with the lowest resistance at midday and the highest at night, as shown in Fig. 6.4 and in papers by Skidmore and Stone (1964), Barrs and Klepper (1968), and Parsons and Kramer (1974). The latter found that these cycles could be reset by reversing the light-dark cycle under which the plants were grown and disappeared after 8 or more days in continuous light, suggesting that they are controlled by signals from the shoots. Hagan (1949) found a similar periodicity in movement of water out of roots into dry soil when water was supplied to the stumps of detopped plants.

An intensive investigation by Fiscus (1986) indicated that diurnal fluctuations in the volume of exudate obtained from roots of *Phaseolus* under various pressures is controlled by complex interactions among several transport coeffi-

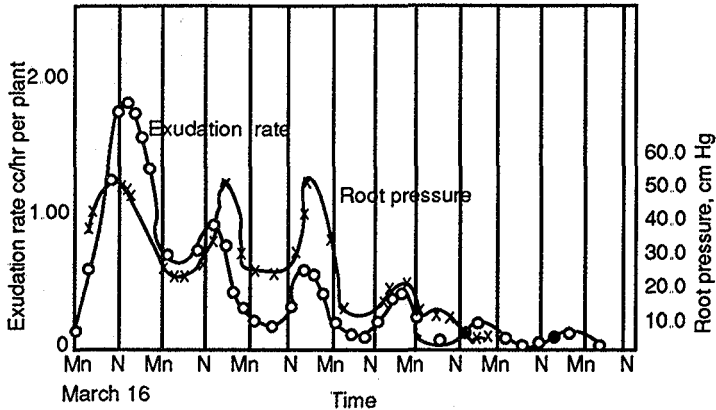


Figure 6.4 Diurnal variation in volume of exudation and root pressure of sunflower plants kept at a constant temperature in half-strength Hoagland solution. From Kramer (1969), after Vaadia (1960).

cients whose importance varies with the volume flux. These include hydraulic conductance, solute flux, reflection coefficient, and the osmotic potential of a solute compartment that lies between the exterior of the root and the xylem (Fiscus, 1977). The osmotic potential of this compartment undergoes dramatic diurnal changes and appears to be particularly important in controlling diurnal rhythms.

According to Ivanov (1980), Russian investigators suggested that the daily periodicity in root pressure exudation is related to daily periodicity in cell division and root growth. This view seems to be supported by work of Bunce (1978) who reported that an increase in apparent root resistance was correlated with decreasing root elongation. More research is needed on this topic. For example, do the completely mature suberized root systems of dormant tree seedlings show periodicity in root pressure exudation?

### Guttation

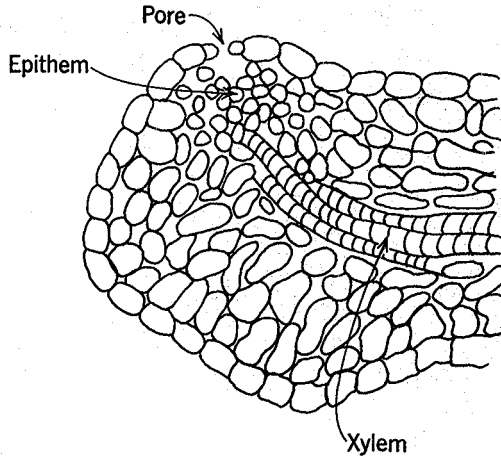
One of the most common results of root pressure is guttation, the exudation of liquid water from leaves and occasionally from leaf scars. Examples are the droplets of water on the margins of leaves in the morning, and much of the water on grass leaves in the morning is the result of guttation (see Fig. 6.5). It usually occurs from hydathodes, which are stomate-like pores in the epidermis located over intercellular spaces where small veins terminate. Figure 6.6 shows a diagram of a hydathode. When sufficient root pressure develops, water is forced out from the xylem into the intercellular spaces and flows out through the hydathodes and occasionally through stomata. Friesner (1940) reported



**Figure 6.5** Droplets of guttated water in early morning on leaves. Also note the thin layer of dew on the leaves. Photograph by J. S. Boyer.

guttation through lenticels on stump sprouts of red maple in the early spring, and Raber (1937) observed sap flow from leaf scars of deciduous trees after leaf fall in the autumn. Guttation is said to be common at night in tropical rain forests. Exudation of liquid from young roots was reported by Breazeale and McGeorge (1953), Head (1964), and Schwenke and Wagner (1992), and might be termed root guttation.

The quantity of guttation liquid exuded varies from a few drops to many milliliters, and the composition varies from almost pure water to a sufficiently concentrated solution of organic and inorganic solutes to leave a visible coating of solute on the leaves when the water evaporates (Curtis, 1944; Duell and Markus, 1977). Guttation seldom occurs during the day because transpiration



**Figure 6.6** Diagram of a hydathode showing a pore, the loose mass of parenchyma cells termed the epithem, and the termination of the xylem. Hydathodes resemble stomata with nonfunctional guard cells and usually occur along margins and at tips of leaves. From Kramer (1983).

reduces or eliminates the pressure in the xylem sap and it ceases in dry, cold, or poorly aerated soil. Guttation is said to be common in submerged aquatic plants, where it may be important in transporting mineral nutrients to growing stem tips (Pedersen, 1993).

Although it is an interesting physiological phenomenon, guttation usually is of little practical importance to plant growth. Occasionally, injury occurs by accumulation of salts on leaf margins as guttated water evaporates, and pathologists suggest that it produces conditions favorable for invasion of leaves by fungi and bacteria (Robeson *et al.*, 1989). Injection of intercellular spaces in leaves of greenhouse plants is said to occasionally cause injury. Some additional information is given in Kramer (1969, pp. 165–167).

## STEM PRESSURES

Although exudation from herbaceous plants and some woody plants such as birch and grape is caused by root pressure, exudation from sugar maple, palm, agave, and a few other plants is caused by stem pressures that are independent of root pressure.

### Maple Sap Flow

The best known example of stem exudation in North America is the flow of sap from holes bored in maple trees, chiefly *Acer saccharum* Marsh and *A. ni-*

*grum*, Michx. The sap is collected and concentrated by evaporation in pans to produce maple syrup. Because of the commercial value of maple syrup, maple sap flow has received much attention and has been discussed by W. S. Clark (1874, 1875), Jones *et al.* (1903), Wiegand (1906), Stevens and Eggert (1945), Johnson (1945), Marvin (1958), and others. It can occur from late autumn to spring, whenever freezing nights are followed by warm days with temperatures above freezing, but the largest flows are obtained in the spring. Over 60% of the flow usually occurs before noon and it often ceases during sunny afternoons because transpiration from the branches and twigs eliminates pressure in the xylem sap. The yield varies widely, usually ranging from 35 to 70 liters per tree in a season, but occasionally it is twice that amount. The sap usually contains 2–3% sucrose and certain nitrogen compounds that when heated produce the distinctive flavor of maple syrup (Pollard and Sproston, 1954).

That maple sap flow is caused by stem pressure is indicated by the fact that sap flow can be obtained from sections of tree trunks placed in tubs of water and subjected to alternating freezing and thawing (Stevens and Eggert, 1945). Maple stems are unique in absorbing water while freezing and exuding water while thawing, but this occurs only if sucrose is present in the sap (R. Johnson *et al.*, 1987). Also, simultaneous measurements of root and stem pressures indicate that in maple trees stem pressure often exceeds root pressure, whereas in birch trees root pressure always exceeds stem pressure, as shown in Fig. 6.7 from data of Kramer (1940c).

Maple sap is obtained by drilling holes into the sap wood (“tapping”) and installing spouts (“spiles”) through which sap drains by gravity into containers. The yield sometimes is increased by applying vacuum to the spouts. The sap is concentrated by boiling to produce commercial maple syrup. There is some uncertainty about the mechanism causing sap flow. According to Sauter (1971), carbon dioxide produced by respiration during the day collects in the intercellular space and forces the sap out. At night, lower temperature reduces carbon dioxide production and that present dissolves, reducing the pressure, causing upward movement of water from the roots and refilling of the xylem vessels. However, the process deserves further investigation (R. Johnson *et al.*, 1987).

### Other Stem Pressures

In India and tropical Asia, large amounts of sap are obtained from palms, chiefly coconut, date, and Palmyra. The young inflorescence is cut out, leaving a cavity in which sap collects at a rate of 6–8 or more liters per day. This flow can be maintained for months by rewounding. In some instances sap is obtained by making incisions into palm stems, but in both methods the sap comes from the phloem, and the sugar was originally mobilized for use in inflorescence and growing stem tips (Milburn and Zimmermann, 1977). The sap is used as a source of sugar or is fermented to make palm wine.

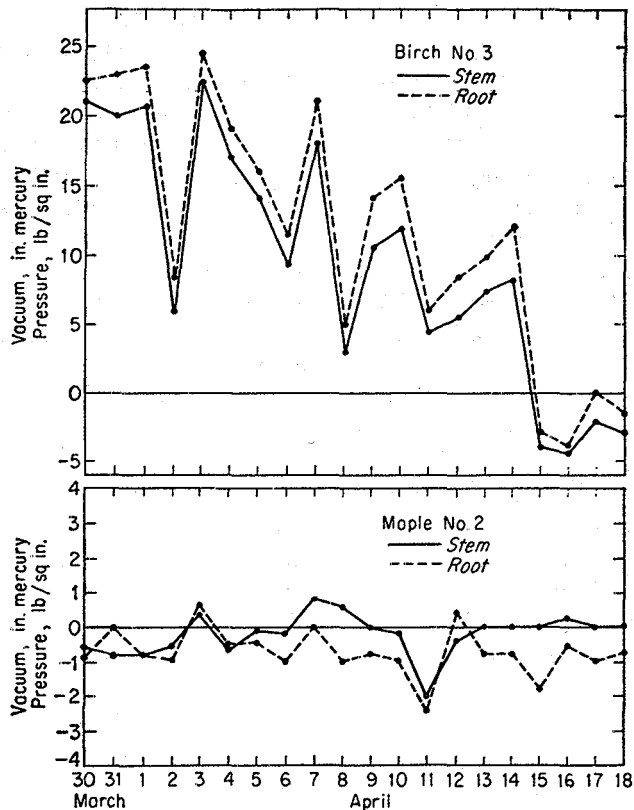


Figure 6.7 - Simultaneous measurements of root and stem pressure in river birch and red maple. In birch, root pressure always exceeded stem pressure and the two change simultaneously. In maple, root pressure was usually negative even when positive pressure existed in the stems. Measurements were made on trees in a bottomland forest. From Kramer and Kozlowski (1979).

In Mexico, large quantities of sap containing sucrose are obtained from agaves by cutting out the young inflorescence. This leaves a cavity in which sap collects at the rate of a liter or more per day for 10 to 15 days, and it is removed to be fermented into pulque. Sap flow in palms and agave originally was attributed to root pressure, but it actually is caused by local phloem pressure. Exudation from agave and palm is discussed in more detail by Van Die in Zimmermann and Milburn (1975) and by Milburn and Zimmermann (1977). The latter measured phloem sap pressures of up to 0.76 MPa in *Cocas nucifera* L.

Wounding of tree stems sometimes results in the development of local high pressure. MacDougal (1926) reported local exudation pressures in stems of *Pinus radiata*, *Juglans regia*, various oaks, and large cacti. Occasionally this sap

is fermented by bacteria or yeasts as it flows out of cracks or other wounds, causing slime flux (Carter, 1945). Pressures high enough to blow the cores out of increment borers have been observed in trees containing decaying heartwood (Abell and Hursh, 1931) and sometimes the gas contains enough methane to be flammable. The production of methane in tree trunks has been discussed by Zeikus and Ward (1974).

## LATEX AND OLEORESINS

In addition to the exudation of xylem sap, some plants exude complex organic compounds from special duct systems when wounded. The best known of these compounds are the latex from which rubber is produced, the oleoresins from which turpentine and rosin are produced, and the chicle formerly used in chewing gum. In the rubber tree, *Hevea brasiliensis*, latex accumulates in a complex system of vertically oriented ducts in the outer bark, from which it flows when wounded. Oleoresin is produced in the xylem and bark parenchyma of some coniferous trees and accumulates in resin ducts from which it flows when wounded.

These examples of exudation of complex compounds from wounded tissue are quite distinct from the exudation of xylem sap from wounded plants. However, they are related to plant water status because latex and oleoresin flow are reduced when plant water stress develops. According to Milburn *et al.* (1990), the latex pressure of banana is a good indicator of plant water potential. More details and references concerning oleoresins and latex can be found in Kramer and Kozlowski (1979, Chapter 8). Lorio (1993, pp. 91–94; 1994) discussed the rather complex relationship between tree water and resin flow in conifers.

## ABSORPTION OF DEW AND FOG THROUGH LEAVES

There is a considerable difference of opinion concerning the importance of absorption of water through leaves and stems. The early literature, reviewed by Miller (1938, pp. 188–190), indicated that significant amounts of water and solutes can enter plants through the leaves because the cuticle is moderately permeable when wet. This makes foliar fertilization possible, but also results in leaching of solutes from leaves by rain and sprinkler irrigation (Tukey *et al.*, 1965). The intake and the loss of water and solutes by twigs of trees have been discussed by Katz *et al.* (1989). According to Anderson and Bourdeau (1955), liquid water from rain, fog, and dew is the only important source of water for mosses as their lack of xylem limits conduction from the soil. This must generally be true for epiphytes, but according to Martin and Schmitt (1989), absorption of water from the humid air of its native habitat is insufficient to maintain the normal water content of Spanish moss (*Tillandsia usneoides*, L.) and occasional rain is essential for its survival.

The importance of dew and fog is somewhat controversial. Duvdevani (1953), Gindel (1973), and others in Israel claimed that absorption of dew is important for survival and growth of both herbaceous and woody plants in arid regions. Stone and Fowells (1955) showed in greenhouse experiments that dew prolonged the survival of unwatered ponderosa pine seedlings, and Went (1975) suggested that *Prosopis tamarugo* growing in the Chilean desert depends chiefly on water absorbed from fog. However, the latter was questioned by Mooney *et al.* (1980), who concluded that *Prosopis* depends on water deep in the soil.

Monteith (1963) claimed that the amount of dew deposited on leaves is too small to be important, and Slatyer (1967, pp. 231–236) pointed out that the vapor pressure deficit even in wilted leaves is so small that the inward movement of water vapor must be very slow. However, the effects of condensed fog and fog drip in reducing water loss can be important enough to affect the species composition of some forests, as in the fog belt of the Pacific Coast (Oosting, 1956, pp. 125–126) and several other areas mentioned by Chaney (1981). The importance of dew and fog probably depends on local conditions (Chaney, 1981; Rundel, 1982).

A new aspect of the fog problem has developed recently with increasing air pollution because various toxic substances become concentrated to a high degree in fog and clouds. Thus foliage at high elevations, which often is exposed to clouds and fog, is more subject to injury (Fowler *et al.*, 1989). Azevedo and Morgan (1974) stated that water and minerals deposited on foliage in the California coastal fog belt significantly affect the water and mineral nutrient balance of the vegetation. Lovett *et al.* (1982) reported that the water input to subalpine forests in the northern Appalachian mountains from fog and clouds amounted to 46% of the total precipitation. Thus, the high concentration of pollutants in a fog seems to explain the severe injury to foliage of trees sometimes observed at high elevations.

## FACTORS AFFECTING WATER ABSORPTION THROUGH ROOTS

The numerous factors affecting the absorption of water can be classified in two groups: (1) those affecting the driving force or gradient in water potential from soil to and through roots; and (2) those affecting the resistance to water movement through the soil and roots. Some, such as low temperature, may do both. They can be described by the following equation:

$$\text{Absorption} = \frac{\Psi_{\text{soil}} - \Psi_{\text{root surface}}}{r_{\text{soil}}} = \frac{\Psi_{\text{root surface}} - \Psi_{\text{root xylem}}}{r_{\text{root}}}, \quad (6.1)$$

where  $\Psi$  is the water potential,  $r$  is the resistance to water movement, and the subscripts soil, root surface, and root xylem indicate positions in the soil–root system. Nnyamah *et al.* (1978) reported that the rate of water absorption by



trees in a Douglas fir forest was linearly related to the difference between soil and root xylem water potential and that the difference remained relatively constant in drying soil. One would expect the difference in the  $\Psi_w$  required to move water through the soil to increase with decreasing soil water content, but perhaps the resistance was low in that soil.

Absorption of water by plants in moist, warm soil is controlled chiefly by the rate of transpiration, which provides most of the driving force, and by the efficiency of the root system, which depends on its extent and permeability or hydraulic conductance. Low temperature and the deficient aeration common in wet soils decrease root permeability, increasing the resistance to entry of water. As the soil dries, its water potential decreases, reducing the driving force from soil to roots, and soil resistance increases because the larger pores are emptied first (Fig. 4.7 gives an example expressed as decreasing hydraulic conductivity of the soil). Root and soil shrinkage tend to decrease root-soil contact (see Chapter 5). Increased root suberization in drying soil also decreases root permeability, increasing resistance to water absorption.

The limiting effect of low soil water potential increases as atmospheric conditions favor high potential rates of transpiration. Denmead and Shaw (1962) found that a soil water potential of only  $-0.1$  MPa limited absorption at high rates of transpiration, but  $-1.0$  MPa was not limiting at low rates. The practical significance of this is that on sunny days rapidly transpiring plants often develop water deficits in moist soil, but in cool, cloudy weather plants may show little stress in relatively dry soil.

### Efficiency of Root Systems in Absorption

The efficiency of root systems in absorption of water and minerals depends on their depth and spread, their density, often expressed as root length density in centimeters of roots per cubic centimeter of soil, and their permeability or hydraulic conductance ( $Lp$ ). Frequently the inverse of the conductance, the resistance, is used [Eq. (6.1)]. Deep, profusely branched root systems are advantageous because they occupy a larger volume of soil, containing more water. Thus, plants with deep root systems usually survive droughts with less injury than those with shallow root systems (Chapter 5; Hurd, 1974; Kramer, 1983, pp. 236–240). For example, Bremner *et al.* (1986) found that in the field sunflower extracted soil water more rapidly and to a greater depth (2m) than sorghum. Thus, it is more successful than sorghum in southern Australia when summer droughts occur.

The benefit from deep, wide spreading root systems depends on the resistance to longitudinal water movement in roots being lower than that to movement through the soil. In general, this is true despite occasional exceptions under special conditions, such as those reported for some grasses and cereals by Wind (1955) and Passioura (1972). Passioura (1972) suggested that if plants

such as wheat growing in regions with low summer rainfall mature on stored soil water, restriction of absorption early in the growing season by a limited root system may be advantageous because it conserves water that is needed later during grain filling. However, this is effective only where no other kinds of plants are competing for the stored water. Klepper has a useful discussion of root growth in relation to water absorption in Stewart and Nielsen (1990). Landsberg and Fowkes (1978) published a mathematical analysis of the effect of root system geometry and water potential in relation to water absorption.

Meyer and Ritchie (1980) reported that resistance per unit of root length decreases toward root tips in sorghum, compensating for increased distance to the shoot, and a similar situation was found in roots of red pine by Stone and Stone (1975a). Apparently, water is absorbed as readily by roots at distances of several meters from plants as from nearby (Veihmeyer and Hendrickson, 1938; Hough *et al.*, 1965). Apple trees on well-aerated loess soil absorbed water from a depth of 10 m (Wiggans, 1936), and corn grew well after the available water in the upper meter of soil was exhausted (Reimann *et al.*, 1946). McWilliam and Kramer (1968) demonstrated that plants of *Phalaris tuberosa* survived after the water potential in the upper meter of soil was reduced to  $-1.5$  MPa because some of the roots had penetrated to a deeper horizon, containing readily available water.

A root system consists of roots of various ages, ranging from young unsuberized root tips to roots that have lost their cortex during secondary growth and are enclosed in a layer of suberized tissue (bark) (Fiscus, 1977; Sands *et al.*, 1982). Obviously there are wide variations in permeability; young unsuberized roots are more permeable than those which have undergone secondary growth and suberization. Differences in the permeability of grape roots of various ages and conditions are shown in Table 6.1. Considerable water and salt must be absorbed through suberized roots because unsuberized roots often constitute less than 1% of the root surface under forests (Kramer and Bullock, 1966). Van Rees and Comerford (1990) found an uptake of water, potassium, and bromine through woody roots of slash pine and suggested that they play an important role in mineral nutrition. Sanderson (1983) reported that about 50% of the water absorbed by the main axis of barley roots entered through the suberized region. Using NMR imaging, MacFall *et al.* (1991a) showed that suberized roots of pine absorb significant amounts of water from moist sand (Fig. 5.9). Fiscus and Markhart (1979) and Fiscus (1981) studied changes in absorptive capacity of growing bean root systems. The hydraulic conductance ( $L_p$ ) of the entire root system changes in a complex manner with age and changing proportion of suberized surface, as is shown in Fig. 6.8. Slow maturation of large metaxylem vessels near the tips of some kinds of roots probably hinders absorption through root hairs (Kevekordes *et al.*, 1988; McCully and Canny, 1988; Cruz *et al.*, 1992). The development of root systems is discussed in more detail in

Table 6.1 Relative Permeabilities of Grape Roots of Various Ages to Water and <sup>32</sup>P

Zone and condition of roots	Relative permeabilities	
	Water	<sup>32</sup> P
Roots of current season (growing)		
A. Terminal 8 cm, elongating, unbranched, unsubscriberized	1	1
B. Unsubscriberized, bearing elongating branches (dormant)	155	75
C. Main axis and branches dormant and partially subscriberized before elongation is completed	545	320
D. Main axis and branches dormant and partially subscriberized	65	35
Roots of preceding seasons (segments bearing branches)		
E. Heavily subscriberized main axis with many short subscriberized branches	0.2	0.4
F. Heavily subscriberized, thick bark, and relatively small xylem cylinder		
Intact	0.2	0.02
Decorticated	290.0	140.00

Note. Measurements were taken under a pressure gradient of about 66 KPa.  
 \*From Queen (1967).

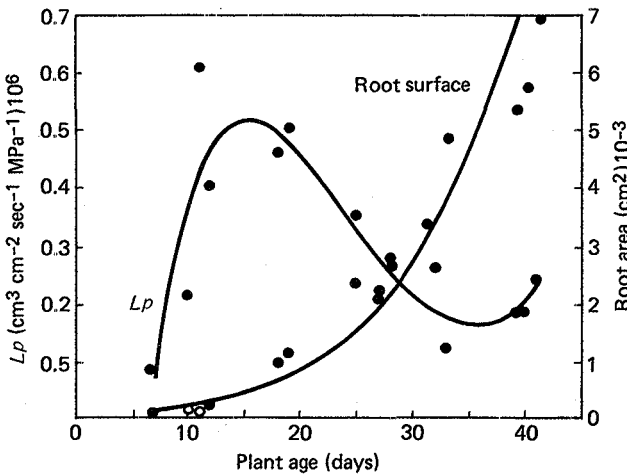


Figure 6.8 Changes in surface area and average hydraulic conductance ( $L_p$ ) of the root system of growing seedlings of bean (*Phaseolus vulgaris*). While root surface increased steadily with time, the average hydraulic conductance first increased, then decreased over time, probably because of changes in the proportion of the root system in various stages of maturation. From Kramer (1983), after Fiscus and Markhart (1979).

Chapter 5, in Wild (1988, Chapter 4), and in Gregory *et al.* (1987). Methods of studying root growth are discussed in Chapter 5, in books by Böhm (1979) and by Glinski and Lipiec (1990, Chapter 7), and in a paper by Epstein in Hashimoto *et al.* (1990).

*Radial Pathway of Water in Roots.* There has been considerable discussion concerning the relative importance of various pathways for radial water movement into roots. There are three possible pathways for water movement from the epidermis across the cortex to the xylem: (1) through the cell walls, termed the apoplastic pathway; (2) through the symplast, which consists of the cytoplasm of many cells connected through plasmodesmata; (3) from cell to cell across the cell walls, plasmalemmas, vacuoles, and tonoplasts; or a combination of these pathways (see Chapter 3 and Fig. 3.16). Pathway 2 is termed symplastic because it involves movement through protoplasm. There also may be limited movement on the outer surfaces of cell walls bordering intercellular spaces. The extensive literature on this topic has been reviewed by Boyer (1985), Davies *et al.* (1986), Drew in Gregory *et al.* (1987), Jones *et al.* (1988a), Passioura (1988b), Weatherley (1982), and others. It is difficult to reach positive conclusions concerning the most important pathway because of uncertainty concerning their relative permeabilities. Perhaps this will be resolved by the use of pressure probes, as described by Steudle in Hashimoto *et al.* (1990), Zhu and Steudle (1991), and Zimmermann *et al.* (1992). Also, as transpiration increases, the driving force changes from chiefly osmotic to pressure flow (Fiscus, 1975; Fiscus and Kramer, 1975). Boyer (1985, p. 483) concluded that the transport of water through tissue is slower than for single cells, indicating that symplastic movement is more important than apoplastic movement through cell walls. However, Radin and Matthews (1989) reported that root conductivity was about twice that of individual cells, supporting the apoplastic pathway. Zhu and Steudle (1991) also concluded that the apoplastic pathway is more important than the cell-to-cell pathway in maize roots. Hanson *et al.* (1985) found negligible apoplastic flow of a fluorescent dye in red pine roots, but Peterson *et al.* (1981) reported significant movement of apoplastic dye through the endodermis of corn and broad bean, where secondary roots passed out. It is doubtful if tracers are always reliable indicators of the path followed by water (McCully and Canny, 1988) and more research is needed on this problem.

Magnetic resonance images of root cortical parenchyma sometimes show regions resembling spokes in a wheel extending across the cortex that appear to be much higher in water content than the average of the cortex (Brown *et al.*, 1986). These patterns suggest that not all of the cortical parenchyma cells are equally involved in radial water transport. However, Zimmermann *et al.* (1992) question this interpretation. This may be related physiologically to the breakdown of cells in specific regions of poorly aerated roots (see Fig. 5.19). Accord-

ing to Drew *et al.* (1980), the strands of cortical tissue left in the aerenchyma of poorly aerated roots function effectively in water and ion transport. No satisfactory explanation of why some cortical tissue breaks down, leaving adjacent strands of healthy tissue, is available, and this problem deserves more study.

The movement of water into roots is decreased by treatments such as chilling and deficient aeration and by respiration inhibitors that decrease the permeability of protoplasmic membranes, but it is increased by killing the roots. This indicates that at some point much of the water passes through living cells, probably at the epidermis, exodermis, and endodermis, although the protoplasts of cortical parenchyma cells might also be involved. It seems probable that all possible pathways are utilized to varying degrees, depending on their relative conductances and carrying capacities. A similar problem exists with respect to the path of water movement through the mesophyll cells of leaves (Boyer, 1985). The effects of environmental factors on root resistance or conductance and water absorption are discussed later in this chapter.

### Resistances to Water Movement in the Soil-Plant System

The existence of substantial resistances to water flow through the soil-plant system is indicated by the development of significant reduction in water potential in leaves of rapidly transpiring plants growing in moist soil or dilute nutrient solution and by the lag of absorption behind transpiration (Fig. 6.1) when plants are exposed to sun. However, there has been some uncertainty concerning the location of the principal resistance which might be in the soil or soil-root interface, in the roots, or elsewhere in the plant water conducting system.

*Soil versus Root Resistance.* There has been considerable discussion concerning the relative importance of soil and root resistances with respect to water absorption. Early investigators such as Gardner (1960) and Gardner and Ehlig (1962) concluded that resistance in the soil would exceed resistance in the roots at a soil water potential of  $-0.1$  to  $-0.2$  MPa, and this view was supported by Cowan (1965) and others. However, Newman (1969) concluded that the root densities used by previous investigators were much lower than those usually found in nature, and if normal root densities were used, soil resistance in the vicinity of roots would not be limiting until the soil water content approached the permanent wilting percentage. Later, Newman (1973) reported large differences among species in root permeability (or resistance) which he regarded as supporting his view. Blizzard and Boyer (1980) found the plant resistance to water flow in soybean is greater than the soil resistance over the range of soil water potential from  $-0.025$  to  $-1.1$  MPa and other investigators observed root resistances greater than soil resistances in corn and sorghum (Reicosky and Ritchie, 1976) and in cotton (Taylor and Klepper, 1975). Passioura (1980a)

found no evidence of the large resistance at the soil-root interface reported by some investigators, but Hulugalle and Willatt (1983) claim that root resistance is important in soils with low hydraulic conductance and where root density is low. Diurnal variations in root resistance to water were discussed earlier in connection with periodicity in root pressure exudation. Harris (1971) observed strong cycling in water absorption by cotton plants growing in a constant environment, and Passioura and Tanner (1985) reported apparent oscillations in root conductivity of cotton when the rate of transpiration was changed, but this may be related to the stomatal oscillations discussed in Chapter 8.

It has been suggested that as the soil dries, water absorption is decreased by root and soil shrinkage which decreases contact at the root-soil interface (Herkelrath *et al.*, 1977; Faiz and Weatherly, 1978; Huck *et al.*, 1970). Nobel and Cui (1992) found that the roots of three species of desert succulents shrank an average of 19% during soil drying. The resulting air gap between roots and soil not only reduced absorption measurably, but also reduced loss of water from roots to soil. Loss of water from roots is discussed later in the section on efflux of water. However, Taylor and Willatt (1983) found negligible shrinkage of roots on wilting soybean plants in moist soil, and the importance of root shrinkage may have been overstated, as pointed out by Tinker (1976). The latter has a good discussion of the factors involved in water absorption, and Landsberg and Fowkes (1978) present a mathematical treatment of absorption, including consideration of soil water movement, root system geometry, and the ratio of radial to axial resistance to water flow. The evidence seems to indicate that over a considerable range of soil water content and with average root density, root resistance exceeds soil resistance to water movement. However, drying soil decreases radial root conductance by increasing lignification and suberization (North and Nobel, 1991) and axial conductance by slowing metaxylem maturation and decreasing the number and size of xylem elements (Cruz *et al.*, 1992) and Lopez and Nobel (1991) also observed decreased conductance in cactus roots in drying soil. Kramer (1950) found that wilting plants overnight decreased root permeability when they were rewatered the next day, and Xu and Bland (1993) reported that exposure of sorghum roots to drying soil decreased water uptake.

It usually is assumed that all water movement to roots occurs as liquid, but as air spaces enlarge in drying soil some movement might occur as vapor. This was proposed by Bonner (1959), but questioned by Bernstein *et al.* (1959). However, a more recent study by Dalton (1988), using deuterium as a tracer, indicates that there might be a small amount of vapor movement to roots, especially with rapidly transpiring plants.

*Resistances in Plants.* The resistance to water movement from root surfaces to root xylem was discussed in the preceding section and resistances to radial and axial or longitudinal flow are discussed in Chapter 7 in connection with the

ascent of sap. Melchior and Steudle (1993) have interesting data on changes in radial and axial conductivity of growing onion roots. It will suffice here to state that resistance to longitudinal flow in the root xylem generally is relatively low as compared to resistance to radial flow (Frensch and Hsiao, 1993; Frensch and Steudle, 1989; Sands *et al.*, 1982). In general it seems improbable that resistance to longitudinal water flow in the xylem becomes limiting unless it is blocked by injury or cavitation (see Chapter 7). The stomatal control of water movement and the importance of boundary layer resistances for transpiration are discussed in Chapters 7 and 8.

*Change in Resistance with Change in Rate of Water Flow.* It has been reported by several investigators that the rate of water flow through roots increases more rapidly than the pressure applied (Lopushinsky, 1964; Weatherley, 1982). Also, in some experiments the leaf water potential appeared to decrease with increasing transpiration, but in others it did not (see Kramer, 1983, pp. 208–210). Some of these observations suggest that the resistance to water flow through roots may decrease with an increasing rate of flow. However, the cause of this change in apparent root resistance is uncertain. Bunce (1978) suggested that in some instances it might be an artifact resulting from failure to allow enough time for equilibration in leaf water potential after a change in the rate of transpiration. In some instances it might result from the transition in driving force from predominantly osmotic to nonosmotic movement. Steudle *et al.* (1987) concluded that water movement caused by an osmotic gradient occurs primarily in the symplast, but that the much larger movement in transpiring plants, caused by hydrostatic gradients, occurs primarily in the apoplast. According to Boyer (1974) the total plant resistance may be 30 times greater at a low flux when stomata are partially closed than at a high flux when they are fully open. He established steady conditions for each measurement so that the leaf water potential reflected the measured flow. Over the entire flow range, the root resistance changed only 2.5 times, and the 30-fold change could be seen in the leaves alone without the roots. Hence he concluded that most of the change in resistance occurs in the leaves and suggested that the apparent decrease in resistance with an increase in flow was caused by an increasing proportion of water bypassing the protoplasts of cells in the leaves. Fiscus *et al.* (1983) later showed that this amount of resistance change could be predicted from a model of the flow. Boyer (1974) suggested that the bypassing water was water vapor in the intercellular spaces because the cuticle lines the intercellular spaces close to the stomata and inhibits evaporation there. Chapters 7 and 11 discuss further evidence that the cuticle inside leaves may cause sites of evaporation to be deep in the leaf.

*Root Diseases.* As mentioned in Chapter 5, the extent and efficiency of root systems for absorption often are decreased by attacks of pathogenic fungi that

kill small roots and block up the conducting system. For example, unfavorable soil conditions and damage to root systems by *Phytophthora cinnamomi* cause the littleleaf disease of shortleaf pine in the southeastern United States and damage to citrus trees in California. Damage to root systems and the lower part of stems, termed damping off, often causes the death of seedlings by reducing water absorption and transport. Root damage caused by various species of *Phytophthora* and other fungi often reduces water absorption and increases root and stem resistance, causing reduced shoot growth or death of plants (Duniway, 1977; Grose and Hainsworth, 1992). In addition to interfering with the absorption of water by decreasing root surface and increasing root resistance, a decrease in the supply of plant hormones and production of toxins may be involved (Ristaino and Duniway, 1991). Prolonged periods of irrigation and saturated soil often increase the injury from pathogens (see papers in Ayres and Boddy, 1986, and Chapter 7 in Kozlowski, 1984).

### Environmental Factors

Both root development and water and mineral absorption are strongly influenced by environmental factors, especially soil moisture, concentration and composition of the soil solution, soil aeration, and soil temperature. These factors affect the composition of natural plant communities and the success of crop plants. For instance, most species of trees cannot grow in saturated soil, but species such as cypress, white cedar, and tupelo gum are largely restricted to areas with saturated soil where competitors cannot grow. Many crop plants are injured or killed in poorly drained areas of fields during rainy springs, but some varieties of rice thrive in flooded soil. Low soil temperature also often hinders root development of seedlings of warm climate plants such as cotton.

*Availability of Soil Water.* The availability of soil water was discussed in Chapter 4, and the difference in available water content of various soils was shown in Table 4.1. The soil water potential decreases sharply as the water content decreases (Fig. 4.7) and the hydraulic conductance also decreases as water drains out of the larger pores. As pointed out earlier, the availability of soil water to plants relative to need also decreases with increasing rate of transpiration (Denmead and Shaw, 1962). The relative importance of soil versus root resistance to water movement was discussed earlier in this chapter.

There is evidence that the soil in the immediate vicinity of roots of transpiring plants often tends to become temporarily dry, increasing the soil resistance to water flow toward the root surfaces. This was demonstrated by Dunham and Nye (1973) by direct sampling of thin layers of soil in the vicinity of a root mat (Fig. 6.9) and by MacFall *et al.* (1990) using magnetic resonance imaging, as shown in Fig. 5.9. Dunham and Nye used a sandy soil and MacFall used a fine sand, both at approximate field capacity. Hasegawa (1986) used a technique somewhat similar to that of Dunham and Nye with soybean roots, except that



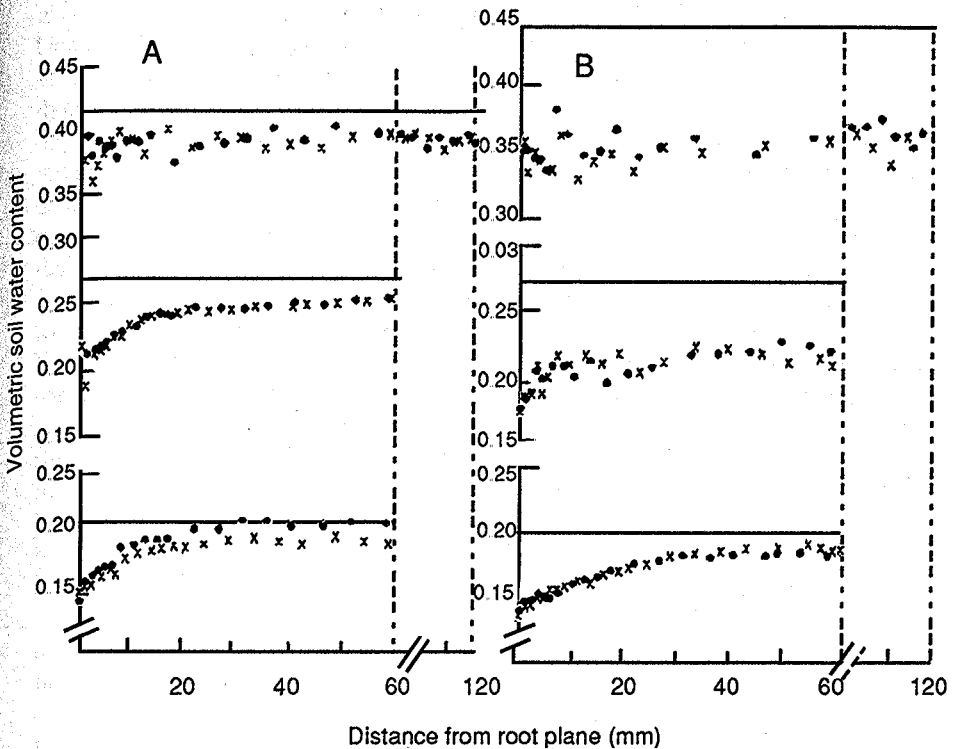


Figure 6.9 A decrease in soil water content near a mat of onion roots attached to transpiring shoots after 2.5 days (A) and 6 days (B). The roots were in sandy soil which initially contained 42–45% (upper curves), 27% (middle curves), or 20% (lower curves) water. The two curves in each part of the figure give the moisture content on opposite sides of the root mat. Readers are referred to the original paper for details. After Dunham and Nye (1973).

the change in soil water content was measured by gamma ray attenuation. He also observed progressive drying of the soil in the vicinity of the roots and absorption of water from a distance of over 10 cm from the root plane. It is possible that under some conditions this water might be at least partly replaced by upward movement through the roots from moist soil (Baker and Van Bavel, 1986; Richards and Caldwell, 1987; Corak *et al.*, 1987), in addition to movement through the soil. However, it was not entirely replaced in the experiments of Dunham and Nye (1973) or Hasegawa (1986). The drying of soil around roots emphasizes the importance of root extension into previously unoccupied soil (Kramer and Coile, 1940). Taylor (in Turner and Kramer, 1980) suggested that an increase in root depth is more important for postponing the onset of water stress in cotton and soybean than increasing root length density (cm of roots per  $\text{cm}^3$  of soil) in the surface soil.

*Concentration and Composition of Soil Solution.* A high concentration of salt in the soil inhibits the growth of most plants, and large areas of land in arid regions cannot support crop plants because of salt accumulation. Salt accumulation also is a problem on irrigated land because irrigation water often is high in salt which accumulates in the soil as water is removed by evaporation and transpiration. It seldom is a problem in humid regions because rainfall leaches salt out of the surface soil. Osmotic potentials of the soil solution of  $-0.35$  to  $-0.4$  MPa at permanent wilting seriously reduce the growth of most crop plants (Magistad and Reitemeier, 1943) and only a few halophytes survive below  $-0.4$  MPa. Excessive amounts of fertilizer sometimes produce an osmotic potential too low for good plant growth, especially in coarse-textured soils with a low cation-exchange capacity. For example, application of 1300 kg/ha of 3-9-3 fertilizer to Norfolk sandy loam temporarily decreased the osmotic potential to  $-1.4$  MPa, but a similar application to Cecil clay loam only decreased it to  $-0.3$  MPa (White and Ross, 1939). Excessively high concentrations of salt sometimes develop in greenhouse soils from overfertilization and reduce growth (Davidson, 1945; Merkle and Dunkle, 1944). This can be avoided by occasional overwatering to leach out excess salt. Rhoades and Loveday (in Stewart and Nielson, 1990) discussed the salinity problem in irrigation in more detail and Maas (1993) reviewed the effects of salinity on citrus trees.

Some of the decrease in growth seems to be caused by the osmotic effects on the driving force and root resistance rather than by toxic effects of particular ions (Eaton, 1942). Wadleigh and Ayres (1945) found similar reductions in growth at a given water potential produced by drying soil, adding salt to it, or by combining the two treatments. According to Materechera *et al.* (1992), the root elongation of dicot seedlings was reduced more than the elongation of monocot seedlings in polyethylene glycol. There usually is a considerable reduction in root permeability in concentrated soil solutions (Azaizeh *et al.*, 1992; Hayward and Spurr, 1943, 1944; O'Leary, 1969, and others). However, it is doubtful if the reduction in growth is caused solely by the reduced absorption of water because the uptake of salt by plants tends to maintain similar differences in osmotic potential between plants and substrate at various substrate concentrations, and plants maintain normal turgor over a wide range of substrate concentrations (Bernstein, 1961; Boyer, 1965; Eaton, 1942).

The reduction in growth caused by high salinity probably is related as much to metabolic effects of accumulation of salt in cells as to reduced availability of soil water. In halophytes, much of the salt accumulates in the vacuoles and the cytoplasm is not exposed directly to high concentrations (Wyn Jones, 1980). In many species the cytoplasm accumulates high concentrations of organic compounds such as proline, glycine betaine, and other amino acids and sugars that counterbalance the high salt concentrations in the vacuoles, but are compatible with enzyme and membrane functions (Wyn Jones, 1980; Hanson and Hitz, 1982). Tarczynski *et al.* (1993) reported that transgenic tobacco plants that syn-

thesize mannitol show increased tolerance of high salinity. At some point plant salt tolerance seems to be related to the concentration of salt that can be tolerated by the protoplasm (Munns and Termaat, 1986; Repp *et al.*, 1959; Slatyer, 1967, pp. 301–308).

Although general osmotic effects are emphasized, specific ion effects sometimes are important (Strogonov, 1964). For example, the growth of some kinds of plants is reduced more by sulfates than by chlorides (Hayward *et al.*, 1946), but Maas (1993) stated that citrus is more sensitive to chlorides than to sulfates. It is claimed that chlorides increase the succulence of plant tissue while sulfates decrease it. Van Eijk (1939) attributed the succulence of halophytes to an excess of chlorides and Boyce (1954) reported that ocean spray increases the succulence of vegetation near the beach.

Excesses or deficiencies of specific ions in the soil solution sometimes reduce plant growth. For example, boron is an essential element, but an excess of boron can be toxic. Radin and Boyer (1982) reported that nitrogen deficiency reduces the root permeability of sunflower roots nearly 50%, resulting in a daytime loss of turgor and a reduction in leaf growth; Radin (1983) found this to be true for several other species, although monocots were affected less than dicots. Radin and Matthews (1989) found that a phosphorus deficiency also reduces root permeability.

According to Einhellig *et al.* (in Thompson, 1985), treatment of sorghum roots with ferulic or coumaric acid or extracts from several allelopathic weeds decreases the absorption of water and increases water stress. They suggested one mechanism of allelopathic action may be through an increase in plant water stress.

**Root Aeration.** Deficient aeration of the soil not only reduces root growth but also reduces the absorption of water and minerals. The decrease in water absorption is caused chiefly by an increase in the resistance to radial movement into roots, but Everard and Drew (1989) also reported a decrease in the osmotic driving force in sunflower roots. This probably resulted from a decreased uptake of salt. The deficits that develop in flooded soil because of reduced absorption often cause serious injury to plants. For example, tobacco sometimes wilts so rapidly and severely when the sun comes out after the soil is saturated by a rain that farmers term it “flopping.” Flooding the soil sometimes causes wilting of other kinds of plants, as shown in Fig. 6.10. There are wide differences among species of plants in respect to the effect of flooding on water absorption. In one series of experiments tobacco was most seriously injured by flooding, sunflower least, and tomato was intermediate (Kramer, 1951). In experiments with woody plants, the water absorption of bald cypress, a native of swamps, was reduced very little, but absorption by flooded oaks, loblolly pine, and red cedar was reduced to less than 50% of the controls (Parker, 1950). Kramer (1940a) and Smit and Stachowiak (1988) agreed that a high concentration of



**Figure 6.10** Wilted maize in a flooded field. Water is standing between the rows which were flooded for 3 weeks. Photograph by J. S. Boyer.

$\text{CO}_2$  reduces water absorption more rapidly than a deficiency of  $\text{O}_2$ , a conclusion reached long ago by investigators cited by Kramer (1940a). However, the importance of  $\text{CO}_2$  was questioned by Willey (1970). The effects of deficient aeration on root growth were discussed in Chapter 5.

Although an important effect of deficient root aeration is a reduction in root permeability to water, not all the effects can be explained simply by the development of shoot water deficits (Kramer, 1951; Jackson, 1991; Schildwacht, 1989) because stomatal closure often results in rehydration of the shoots. The

development of adventitious roots and hypertrophy of stems near the water line of flooded plants suggest that growth regulators are involved; the occurrence of epinasty suggests the presence of ethylene (Bradford and Yang, 1980). The various roles of ethylene in flooded plants were reviewed by Jackson (1985). Interference with normal root metabolism may affect the supply of minerals, cytokinin, gibberellin, and ABA to the shoots and inhibition of downward translocation of metabolites, and growth regulators may cause some of the symptoms associated with the deficient aeration of root systems. Smit *et al.* (1989) reported that leaf expansion of flooded seedlings of a hybrid poplar was limited by decreased cell wall extensibility. In some instances, stomatal closure has been attributed to an accumulation of ABA in the leaves (Jackson and Hall, 1987), but later experiments of Jackson (1991) did not support roots as the source of ABA in flooded plants.

**Temperature.** It was observed by Hales and others in the 18th century that cold soil reduces water absorption, and in about 1860 Sachs observed that tobacco and cucurbits wilted more severely than cabbage and turnips when the soil was cooled to 3–5°C. Numerous other examples of species differences are given in Kramer (1969, Chapter 6) and differences in three species are shown in Fig. 6.11. The water stress caused by chilling roots reduces stomatal conductance and may cause both stomatal and nonstomatal reduction in photosynthesis (DeLucia, 1986). In another study it appeared that the nonstomatal inhibition of photosynthesis in loblolly pine was only important at soil temperatures

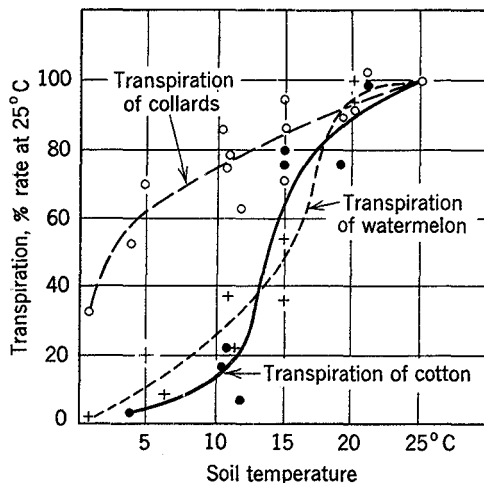
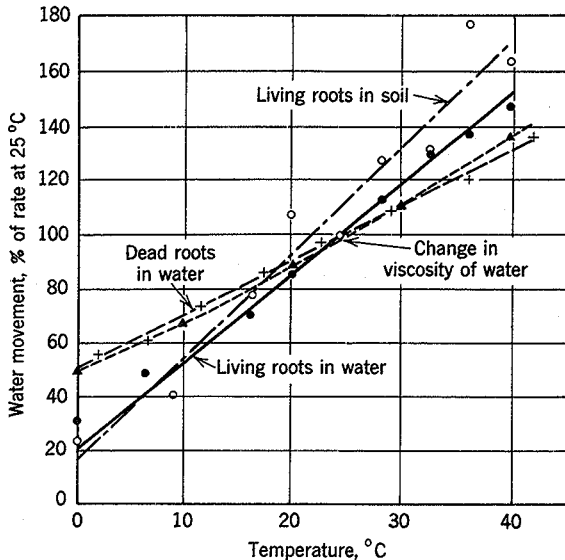


Figure 6.11 Difference in effects of low soil temperature on absorption of water by cool season (collards) and warm season plants (cotton and watermelon), as measured by rate of transpiration. From Kramer (1983), after Kramer (1942).

below 7°C (Day *et al.*, 1991). Chilling 16- or 17-day-old soybean root systems to 10°C for a week temporarily reduced stomatal conductance, CO<sub>2</sub> uptake, water potential, and leaf enlargement, but if rewarmed after a week, no permanent injury or reduction in yield occurred (Musser *et al.*, 1983).

Less is known about the effects of high temperature, although the surface soil often is subjected to fairly high temperatures near midday. BassiriRad *et al.* (1991) found that as the root temperature increased from 15 to 25°C, exudation from barley root systems increased, but then decreased sharply as temperature increased above 25°C. Exudation from detached sorghum roots increased to 35°C, but decreased nearly 50% at 40°C. There also was a large decrease in ion flux into the xylem at high temperatures, which may explain the decrease in the volume of exudation. They suggested that variations in the ion supply to shoots may constitute a messenger from the roots to shoots. Later BassiriRad and Radin (1992) found that the effect of ABA on hydraulic conductance is strongly temperature dependent for barley roots at 15 to 40°C, but for sorghum roots only at low temperatures.

The principal cause of the decrease in water absorption at low temperatures is the increase in root resistance to water movement through the roots, caused partly by the increased viscosity of water, as shown in Fig. 6.12. Much attention



**Figure 6.12** Water movement through living and dead root systems in water subjected to a vacuum of about 0.08 MPa for 1 hr. A different set of plants of identical past treatment was used for each temperature and the rates are plotted as a percentage of the rates at 25°C. The curve for the viscosity of water is the reciprocal of viscosity plotted as a percentage of the value at 25°C. Temperature affects water movement through dead roots less than movement through living roots. From Kramer (1983), after Kramer (1940b).

has been given to the effects of temperature on the permeability of cell membranes as a reason for species differences (Lyons *et al.*, 1979). For example, water absorption is reduced much less by cooling broccoli than soybean root systems and when an Arrhenius plot of water flow is made there is a discontinuity in the rate for soybean but not for the cool weather plant broccoli (see Fig. 6.13). Some investigators attribute this break to a phase separation in membrane lipids (Raison *et al.* in Turner and Kramer, 1980; Raison *et al.*, 1982) but this has been questioned by others (Lyons, 1973; Lyons *et al.*, 1979). Markhart *et al.* (1980) found a much greater increase in unsaturated fatty acids in new roots formed at low temperature on the cool weather crop broccoli than in new roots on the warm weather crop soybean, and Osmond *et al.* (1982) found a temporary increase in unsaturated fatty acids in new soybean roots grown at low temperatures. More research is needed on biochemical changes in roots of various species when cooled in order to fully explain the differences among species and cultivars in tolerance of chilling.

The reduced absorption of water through cooled roots usually is accompanied by a reduction in stomatal conductance and photosynthesis, a decrease in

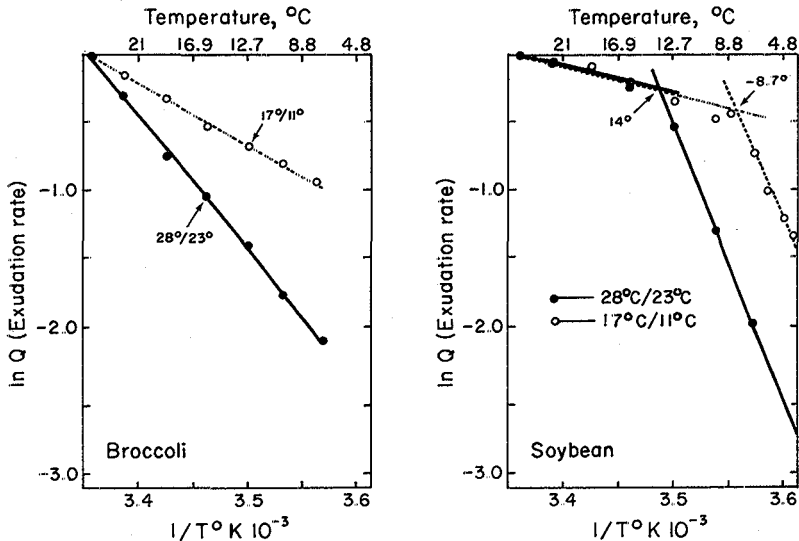


Figure 6.13 Effect of previous growth temperature on the rate of water movement through root systems of broccoli and soybean under a pressure of about 0.05 MPa. Plants were grown at day night temperatures of 28/23°C and 17/11°C, and absorption was reduced much more by cooling in roots grown at the higher temperature. The rates for individual root systems were normalized to the rate at 25°C to permit comparison. The rates are graphed as Arrhenius plots with the natural log of water flow ( $Q$ ) on the ordinate and the reciprocal of the Kelvin temperature ( $1/T$ ) on the abscissa. Celsius temperatures are given at the top for convenience. Plants of both species grown at low temperatures were less affected by cooling than those grown at higher temperatures. Also, there are sharp changes in slope for soybean. From Kramer (1983), after Markhart *et al.* (1979).

leaf water potential, and an inhibition of leaf expansion. Much relevant literature is cited by Day *et al.* (1991), Markhart *et al.* (1979), and Raper and Kramer (1987, pp. 593–597). The effects of root chilling on shoots usually are attributed to shoot water deficit. However, recent experiments with split root systems, discussed in Chapter 5 and in a review by Davies and Zhang (1991), suggest the possibility that some effects of root chilling on shoot physiology may result from chemical signals such as hormones produced in chilled roots. However, Day *et al.* (1991) found that chilling one-half of split root systems of loblolly pine seedlings had no effect on leaf water potential or net photosynthesis, leading them to doubt if nonhydraulic signals are involved in the decreased leaf water potential and photosynthesis they observed in root-chilled seedlings. The possibility that biochemical signals from chilled roots are involved in the shoot reactions probably deserves further investigation under field conditions.

#### EFFLUX OF WATER FROM ROOTS AND HYDRAULIC LIFT

Although this chapter deals primarily with the absorption of water, there are circumstances in which a measurable efflux of water occurs from roots into the surrounding soil. It was mentioned in Chapter 4 that significant amounts of water sometimes are transferred through roots from deep, moist soil to drier surface soil where it becomes available to shallow rooted plants. This is sometimes termed “hydraulic lift” and has been demonstrated by several investigators, including Baker and Van Bavel (1986), Caldwell and Richards (1989), Corak *et al.* (1987), and Xu and Bland (1993). Bormann (1957) observed water exchange between intertwined roots, Richards and Caldwell (1987) observed a significant transport of water from deep soil to grasses in drier surface soil through roots of *Artemisia tridentata*, and Corak *et al.* (1987) observed sufficient water transport through alfalfa roots to keep maize plants alive. Dawson (1993) claimed that herbaceous plants growing near deeper rooted sugar maple trees benefit from hydraulic lift.

These occurrences require reversal from normal inflow to outflow of water from roots. This probably occurs whenever the soil water potential falls below that of the donor roots, if the roots are permeable to water. However, root permeability probably decreases in dry soil (Cruz *et al.*, 1992; Lopez and Nobel, 1991). Xu and Bland (1993) reported that outflow occurred from sorghum roots when a gradient of about 0.6 MPa developed, and in their experiments, the total outflow into the soil amounted to 5 or 6% of the daily loss in transpiration. The evidence that water efflux from roots sometimes benefits neighboring plants introduces a previously unrecognized factor in plant competition.



## SUMMARY

The absorption of water is an essential part of the continuum of processes involving the soil, plant, and atmosphere. Under some circumstances small amounts of water are absorbed through leaves from rain, dew, and fog, but except for epiphytes this is negligible in amount compared to water absorbed from the soil. Two absorption mechanisms exist: osmotic absorption in slowly transpiring plants, growing in moist soil, and passive absorption by rapidly transpiring plants. The roots of slowly transpiring plants growing in moist, well-aerated soil function as osmometers, resulting in the development of root pressure, exudation from wounds, and guttation. The extent of exudation caused by root pressure varies widely among plants of different species and with environmental conditions. Most of the water absorbed by rapidly transpiring plants is "pulled" in by matric forces developed in the evaporating surfaces of cells and is transmitted to the roots through the cohesive water columns of the xylem, where the reduced water potential causes inflow from the soil. The evaporation of water from twigs and branches of leafless deciduous plants on sunny days sometimes creates tension in the xylem and causes the ascent of sap.

Exudation of sap from some plants such as maple, palms, and agave are caused by local stem pressures rather than from root pressures. Occasionally, local pressure develops as the result of microbial activity in wounds resulting in the development of gas pressure and exudation. Some plants exude complex organic compounds such as latex and oleoresin from specialized systems of ducts when wounded. These types of exudation are not directly related to root pressure, but their magnitude is often related to plant water status.

Water absorption depends on the extent and conductance or permeability of the roots and the steepness of the water potential gradient from soil to roots, which provides the driving force. Generally, the resistance to water movement from soil to root surfaces is smaller than the resistance to radial movement in roots, but as the soil dries, resistance to water movement through it increases and the driving force decreases. Water absorption also is affected by soil aeration and temperature, and by the concentration of the soil solution.

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